EFFECT OF HARVESTING METHODS ON THE PHYTOSOCIOLOGY OF A BOREAL MIXEDWOOD FOREST COMMUNITY

by

Shannon L. Robertson ©

A Graduate Thesis Submitted
In Partial Fulfillment of the Requirements
for the Degree of Master of Science in Forestry

School of Forestry
Lakehead University
May, 1994

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ABSTRACT

Robertson, S.L. 1994. Effect of harvesting methods on the phytosociology of a boreal mixedwood forest community. M.Sc.F. Thesis, Lakehead University, Thunder Bay. 334 pp.

Key Words: Boreal mixedwood, clearcutting, forest succession, harvest methods, natural regeneration, phytosociology.

A naturally regenerating boreal mixedwood site was remeasured 37 years after four harvest treatments: clearcutting (CC), deferred 'softwoods only' cutting (DC), 'softwoods only' cutting (SC), and hardwoods poisoned, followed by deferred 'softwoods only' cutting (HP). The objectives were to determine whether : 1) harvest treatments produced significantly different phytosociological communities; 2) harvest treatments altered the normal trend of hardwoods dominating early succession, and allowed *Picea* spp. to gain a competitive advantage; and 3) phytosociological trends and corresponding possible environmental influences could be identified. Median polish and/or ANOVA were used to compare: species density, dominance (basal area), frequency, cover, age, and height for the tree stratum; species density, frequency and cover for the shrub stratum; and species frequency and cover for the herb stratum. Median polish, species' diversity, resemblance measures, and canonical correspondence analysis (CCA) were employed to determine whether harvest treatments affected the overall phytosociological community. Ratios of softwood to hardwood (S:H), spruce to fir (Spr:F), and spruce to hardwood (Spr:H) were calculated for the tree stratum. Comparisons of pre-harvest data to current data were made. Correspondence analysis (CA), CCA and cluster analysis were used to search for the main phytosociological trends and to determine whether these were related to soil moisture and depth.

Some treatment differences were evident for individual species. However, species did not form groups that occurred exclusively or abundantly in only certain harvest treatments. The four harvest treatments did not produce significantly different phytosociological communities. This may be due to several factors: 1) the Initial Floristics character of boreal forests; 2) chance factors in natural regeneration, and 3) the confounding of treatment effects by complex environmental gradients. In terms of improving spruce and softwood status, the results were not conclusive as to the advantage over clearcutting of cutting only softwoods, and of poisoning hardwoods in advance of cutting. *Picea glauca* (Moench) A. Voss, *Populus tremuloides* Michx., *Populus balsamifera* L. and the Spr:H ratios, supported the expected trend of softwoods being more prominent in HP than CC, and the reverse for hardwoods. However, *Abies balsamea* (L.) Mill, *Betula papyrifera* Marsh., *Picea mariana* (Mill.) B.S.P. and the S:H ratios did not support this trend. The Spr:F was generally higher in HP than CC. Conifers were mostly of advance-growth origin in DC and HP, but of post-harvest origin in CC, matching expectations that CC caused more damage to advance growth than did partial cutting (conifer age in SC did not support this). The strongest phytosociological trend identified was the change in canopy composition from hardwood to mixedwood to softwood types. Understorey species distribution was related to either environmental gradients created by canopy composition, or to some underlying gradients that determined both canopy and understorey compositions. Soil depth and/or moisture did not appear to be the determining factors. It is suspected that the boreal mixedwood community of the RC17 site is best decribed as a continuum of species' presences and abundances, determined by a complex set of interdependent environmental factors, which would need to be clearly defined and accurately measured to determine conclusively whether harvest treatments differentially affected the community.

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ACKNOWLEDGEMENTS

As any rationale person might guess by observing the size of this thesis, this project could never have been completed without the assistance and support of many people. The first people I would like to thank are my parents, Lillian and Lyall Robertson; I thank them not only for providing me with a warm, cozy place to stay while doing my two undergraduate degrees (and all of my schooling before that!), but also for teaching me to persevere, and believe that the end of the struggle is in sight, even when it seems difficult to glimpse! I also thank my Mum for feeding me good home-cooked meals during my undergraduate degrees and during part of that final year of writing this work, my Dad for helping 'cut and paste' (literally!) to organize the vast amount of notes that I accumulated for the Literature Review of this document, and both of them for always encouraging me in the studies I chose to pursue, for even participating in some of the field-work (gull-watching!) for one of my undergraduate projects, for just believing in me and being proud of me.....and for so much more!

Dr. Jennifer Shay, formerly of the University of Manitoba Department of Biology, inspired me to enter the 'field' of plant community ecology, and provided me with much of my initial training in this area, through both courses and job experience. Thank you, Jennifer.

I thank my major advisor, Dr. Rob Farmer, for helping me locate a project that suited my goals, for providing me with sound advice when consulted, and for allowing me the freedom to develop the project according to my vision. Dr. Azim Mallik and Dr. Peter Duinker, the other members of my committee, also gave valuable inputs to the design of the project, and to editing of the final drafts. I also thank Azim for his help in deciding how to tailor the field work to fit the allotted time and budget. Dr. Roy Sutton, formerly of the Canadian Forestry Service, Sault Ste. Marie, brought to my attention the opportunity of using the RC17 experimental area as a place to examine the long-term effects of harvesting methods, and kindly located and sent me most of the original documentation of the project.

I always enjoy the field end of ecological studies more than the analyses/writing stage, and although the field part of this study was brief compared to the work that followed, it was a pleasant experience. I thank my field assistant, Paul Charrette, for contributing to this by working efficiently and enthusiastically, by offering valuable insights and suggestions, and by adding humour and good company to what would have otherwise been fairly lonely, tedious 'field weeks'.

The analysis of a data set as large as the one in this study can be intimidating to a novice graduate student. I did much reading, deliberating and nail-biting before deciding on the most appropriate methods to use for each stage of the analysis. Two people in particular provided much-appreciated advice on these analyses: Dr. Norm Kenkel (Department of Biology, University of Manitoba) on ordination methods and Dr. Ken Brown (School of Forestry, Lakehead University) on statistical design and exploratory (median polish) data analyses. In addition, several fellow forestry graduate students, including Brian Goble, Shelley Vescio, Kathy Jones and Gord Whitmore provided computer-aid, and/or let me bounce statistical ideas off them.

I am infinitely indebted to three people who contributed greatly to the final push to actually get this thesis written and onto paper in a legible, presentable form: my sister, Colleen Mernett, for typing and retyping several sections; Dave Ip, for thoroughly editing the first complete draft; and Rob Bowen, for help in typing, formatting and printing the last draft and final version of the thesis.

Fellow graduate students are really the people that provide the close-at-hand moral support that gets you through the doubts, occasional depressions, and many personal struggles inherent to pursuit of a Master's degree; and thus some of them become close friends. Although I have mentioned some of them previously, they deserve further acknowledgement: Shelley Vescio, Rob Bowen, Dave Ip, Kathy Jones, Brian

Goble, Anne Villeneuve, Glen Niznowski and John McLaughlan. In addition, Nancy Bookey and Kathleen Gazey of the School of Forestry provided friendship and support. There are also many friends in Winnipeg that have encouraged me throughout both my graduate and undergraduate degrees, especially Brenda Tazumi, Janice Lockhart, Kendra Rey, Janet Moore and Diane Kunec.

A graduate student needs a friendly home atmosphere to work and rest in, and several people provided me with this. I thank Pauline Major, my landlady in Thunder Bay, for her friendship and delightful stories; Doug Rea and Dave Ip for generously offering me free room and board during some of the unemployed, unfunded, writing stage of my thesis; my parents, as mentioned earlier; and Rob Bowen for doing more than his share of the cooking and house-work while I was occupied with the revision stages of the thesis.

I thank Doug Rea, for his love and support, for being my closest friend for so many years, for sharing with me his love of nature, especially of the forests, lakes and wildlife of northwestern Ontario, and for always believing that I could achieve my goals, and encouraging me to do that (often over a bottle of Italian wine and a meal of canneloni!).

I warmly thank my sister, Colleen, for all of the friendship and support she has given me throughout this Master's work, and the rest of my life, and I thank both her and her husband, Vern, for producing two wonderful inspirations during my graduate studies: my nephews, Kirk and Kevin.

Finally, I thank Rob Bowen, whom I likely would not have met if I hadn't endeavored to do this graduate work, and who has not only donated much of his time to helping me finish it, but has also given me much love and companionship throughout it, and opened up so many sunny possibilities in my life. Thank you, Rob.

Funding to support me during my graduate studies was provided by the Natural Sciences and Engineering Research Council of Canada, and funding to support the project was provided by the Lakehead University Centre for Northern Studies and the Canadian Forestry Service.

S. L. R.

CHAPTER 1-INTRODUCTION

1.1 STATUS OF NATURAL REGENERATION IN BOREAL FOREST MANAGEMENT

Exploitation of Canadian boreal forest resources is increasing steadily. Forestry practices require a good understanding of ecosystem responses to various human disturbances, in order to develop sound land management plans (Larsen 1980). Clearcutting and fire suppression have greatly increased in this century, and the response of vegetation to these techniques of land management is poorly understood (Brumelis and Carleton 1989). Due to fire suppression, many stands being harvested currently are uneven-aged and overmature, containing much dead timber, many stems too small to be harvested, and poorly distributed advance regeneration (Weetman 1989). Increasing *Populus tremuloides* Michx.[1] utilization from mixedwood stands has brought about a need for better protection of the conifer understorey (mainly *Picea glauca* (Moench) A. Voss), in order to minimize regeneration costs, and preserve the softwood element of these forests (Brace and Bella 1988, Brace 1991).

Most Canadian forests regenerate naturally following disturbance (Brand 1991). However, the public is increasingly concerned with the condition of Canadian forests, feeling that natural regeneration may be inadequate to keep the forests healthy, while artificial regeneration has been generally unsuccessful (Brand 1991). Intensive silviculture (planting and tending with the intent of producing stand yield equivalent to virgin conifer forests), has been unsuccessful on large portions of Canada's boreal *P. glauca* and *P. glauca*-mixedwood sites (Weetman 1989). Many of these rich sites have been converted to stands dominated by *Betula papyrifera* Marsh. and *Populus* spp., or even shrubs and grasses (Weetman 1989). Drew (1988) felt that boreal mixedwood

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[1]Common and scientific names of all species encountered in this project are given in Appendix 1.

stands would not regenerate successfully if only extensive management (i.e. seeding, modified cuts and natural regeneration) is applied, but notes that regardless of management attempts, regeneration of mixedwoods will result in some level of hardwood/softwood mixture, and this must be accepted and planned for. The public is generally dissatisfied with clearcutting, finds it aesthetically unappealing (Weetman and Vyse 1990, Brace 1991) and would like mixedwood forests to be perpetuated. This requires preservation of the *Picea* spp. component in these forests (Brace 1991).

Attempts to convert boreal mixedwoods to conifer-dominated forests have generally been unsuccessful (Johnson 1986, Armson 1988). Plantation failure is common (Brumelis and Carleton 1988, Brace 1991), as is reversion of seeded and planted cutovers to high density hardwoods and mixedwoods (Brace and Bella 1988, Navratil *et al.* 1991). Armson (1988) emphasizes that boreal mixedwood composition is a function of many factors, including chance; foresters should not feel that the regenerating forest must be identical to the original forest. However, he states that some form of site preparation, along with tending, will often be necessary for successful conifer regeneration, and that more sophisticated silvicultural systems are required, with a heavy emphasis on natural regeneration. Thus, in order to reduce regeneration costs and the length of the future rotation, protection of existing regeneration and encouragement of establishment of new regeneration by natural means is needed (Brace and Bella 1988, McInnis and Roberts 1991, Sauder and Sinclair 1991).

There is a risk that clearcutting followed by intensive management which converts natural stands to monocultures may eventually impoverish an originally productive site (Freedman 1992). Extensive forest management, including natural regeneration, promotes a more mixed forest with greater biological diversity, which benefits non-fibre uses (Navratil *et al.* 1991), provides more future management choices, and may protect against pest problems (Weetman and Vyse 1990).

1.2 THE NEED FOR A STUDY OF NATURAL POST-HARVEST REGENERATION

Knowledge of plant community development following harvesting in the boreal forest is poor (Ellis and Mattice 1974, Fraser *et al.* 1976, Weetman 1989). Forest renewal following harvesting is different from that following natural disturbances such as fire, windfall or insect infestation, due to differences in seedbed, seed supply, slash conditions, shade and vegetative competition. However, studies of long-term, naturally-regenerated secondary succession in response to harvesting in the boreal forest are scarce (Jeglum 1983). Studies of the short-term response of overstorey species to various harvesting methods are common, including response to clearcuts (Ellis and Mattice 1974, Richardson 1979, McInnis and Roberts 1991), strip clearcuts (Van Nostrand 1971, Fraser *et al.* 1976, Fleming and Crossfield 1983, Jeglum 1983), group selection cuts (Losee 1961) and shelterwood cuts (Lees 1970), as well as studies that compare several of these methods (Lees 1964, Jarvis and Cayford 1967, Weetman *et al.* 1973). Studies of the short-term response of understorey species to cutting methods in boreal forests are less abundant (Outcalt and White 1981, Walsh and Krishka 1991); most mention of understorey is related to its suitability as seedbed or its competitive effect on conifers (e.g. Van Nostrand 1971; Jarvis 1961). There is an obvious dearth of studies which examine and contrast the long-term effects of different harvesting techniques on the composition, diversity and dominance of species in either the overstorey or understorey of boreal forests (Brumelis and Carleton 1988, 1989). The study of mixedwood vegetation dynamics following harvest is important for its potential to contribute to the development of a mixedwood forest growth model which would help foresters make ecologically sound management decisions (Draper and Hamilton 1984, Morris *et al.* 1988).

1.3 ORIGIN OF THE RC17 PROJECT: THE PRESENT STUDY SITE

The cooperative research project RC17, a study that compared the effects of different harvesting and seedbed treatments on natural regeneration of boreal mixedwoods, was initiated in 1953. The goals and design of the original study were described in the Problem Appreciation (Anon. 1952) and the Plan of Work (1952). Initial 10-year results were summarized by Hughes (1967). The following background information is derived from these sources. The site and the treatments are described in more detail in Section 3.1. Additional information about pre-treatment overstorey composition, seedbed conditions, and initial (1-10 year) post-harvest results are included in Appendix 2.

In the early 1950s, the contemporary cutting method of mixedwood stands (clear-cutting of softwood species only, to an 11.5 cm dbh limit) was resulting in unsatisfactory softwood regeneration by natural means. Prior to cutting, the stands contained 45% *Picea* spp., 15% *Abies balsamea* (L.) Mill and 40% *Betula papyrifera*, *Populus balsamifera* L. and *Populus tremuloides* by volume. Five years after cutting, these stands contained only 4% *Picea* spp. by cover and 21% *A. balsamea*, while 62% of the area was covered by shrubs (mainly *Acer spicatum* Lam. and *Corylus cornuta* Marsh.) and 13% by *B. papyrifera*, *P. balsamifera* and *P. tremuloides*. Therefore, project RC17 was designed to determine methods of improving the 'natural' post-harvest regeneration of conifers, particularly *Picea* spp., to these potentially fertile, upland boreal mixedwoods.

Many factors contribute to the amount of conifer regeneration that germinates and survives in boreal mixedwood stands, including seed supply, seedbed conditions, exposure, competition with hardwoods, shrubs and herbs, smothering by hardwood leaves, climate, and damage due to animals, insects and disease. These factors vary in

their influence on three critical reproduction parameters: 1) annual seed supply, 2) percentage germination and 3) percentage survival of germinated seedlings.

Thus, to improve the three critical reproduction parameters, a combination of various overstorey (main stand) and seedbed treatments were applied. One of four main stand treatments was applied to each of the 20 approximately 7-ha plots of the experimental area, and strips of four seedbed treatments were applied within some of these plots. The four main stand treatments consisted of 1) cutting only softwoods (SC), the then contemporary harvest method and thus the control; 2) clearcutting all species (CC); 3) poisoning hardwood species, with deferral of softwood cutting (HP); and 4) deferral of softwood cutting (DC). The clearcut method was included because the project initiators foresaw that harvesting of hardwoods along with the softwoods was likely to become common practice and would quite possibly have a different effect on conifer regeneration, especially assisted by the seedbed treatments, than cutting of conifers alone. The poisoning of hardwoods along with a deferred cut was likely intended to improve all three ratios by providing time for conifers to disseminate seed before they were cut, at the same time that competition for light, nutrients and water was reduced by elimination of the hardwood component of the stand. The fourth main stand treatment, deferring the cut, was combined with the seedbed treatments, to determine whether seeding in of conifers was better on scarified and/or herbicided strips when these treatments were applied prior to the cut.

The seedbed treatments, applied to transects within the main-stand treatments, included scarification, herbicide spraying, scarification plus herbicide spraying, and a control treatment of no scarification and no herbicide. The scarification was intended to improve the percentage germination of *Picea* spp. and *A. balsamea* seeds, while herbicide spraying was intended to improve the survival of germinated seedlings by reducing hardwood, shrub and herb competition. These seedbed treatments are not described in

detail in the current work, since they did not address its main objectives, and were therefore not sampled.

1.4 OBJECTIVES OF THE PRESENT STUDY

In 1990, the RC17 study site, which had been undisturbed since the experimental harvests of 1953 to 1963, was thought to be a suitable location to examine the long-term effects of different harvesting methods on the vegetative ecology of boreal mixedwoods.

The objectives of the present study were threefold. The first was:

1. to compare the plant communities 27 to 37 years after harvest, to determine whether the harvesting treatments produced significantly different phytosociological communities.

Since the original intent of the RC17 project was to increase the quantity and quality of the softwood components, especially *Picea* spp., of post-harvest mixedwood stands, the second objective was:

2. to determine whether, in some treatments more than in others:
   a) conifers gained a competitive advantage over hardwoods early in succession, and
   b) *Picea* spp. were more important (in terms of density, dominance, frequency, cover, etc.) relative to hardwoods and to *Abies balsamea*.

It was hypothesized that the HP treatment would have provided an environment more conducive to softwood regeneration than the other treatments. In addition, since the hardwoods were essentially undisturbed in the SC and DC treatments, possibly preventing the rapid vegetative regeneration of *Populus* spp. and *Betula papyrifera*, it was suspected that these treatments may have been slightly better than the CC treatment in assisting softwood regeneration. The final objective was:

3. to search for the main phytosociological trends, and to determine possible environmental factors influencing these trends.

Soil moisture and soil depth were the principal factors examined in this regard.

CHAPTER 2 - LITERATURE REVIEW

2.1 THE BOREAL MIXEDWOOD FORESTS OF NORTHERN ONTARIO

2.1.1 Definition and Canopy Composition

The boreal mixedwood forests of Ontario lie within the Boreal Forest Region and northwestern part of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). They occupy upland sites capable of supporting good growth of five principal species: *Picea glauca* , *Picea mariana* (Mill.) B.S.P., *Populus tremuloides* , *Betula papyrifera* , and *Abies balsamea* , in either pure stands (monoculture) or various mixtures (McClain 1981, Morris *et al.* 1988). Sites incapable of supporting all of these species are excluded from the definition, e.g. *P. mariana* dominated lowlands, *Pinus banksiana* Lamb. dominated sand plains, and dry, shallow soils on rocky ridges (McClain 1981). Although this definition focuses on site potential, previous definitions of the boreal mixedwood forest encompass a compositional criterion, i.e. that neither the softwood nor the hardwood components contribute more than 75% of the stems (McClain 1981). Historically, the 'aspen-birch-spruce-fir type' of Ontario referred to forests composed of the same five species as the present day boreal mixedwood; however the compositional criterion was that no more than 80% of the volume should be either hardwoods or softwoods (MacLean 1960). Ontario's boreal mixedwood forests are not equivalent to Rowe's (1972) Boreal Mixedwood Section (B.18a), but the species composition is similar (Armson 1988). Therefore, literature referring to the latter is included here.

The canopy composition of the boreal mixedwood forest varies continuously, depending on site conditions, successional stage and disturbance history (McClain 1981, Morris *et al.* 1988). Several species excluded from the definition occur infrequently, in response to certain site types, disturbances and seed supply e.g. *P. banksiana*, *Pinus strobus* L., *Pinus resinosa* Ait., *Thuja occidentalis* L. and *Larix laricina* (Du Roi) Koch

(McClain 1981).

2.1.2 Importance and Occurrence of the Boreal Mixedwood Forests

Boreal mixedwood forests contain about 30% of the coniferous growing stock and most of the hardwood growing stock of Canada's boreal forests (Ketcheson 1981). They comprise 45% to 50% of northern Ontario's productive forest land, and about 46% of northern and central Ontario's growing stock for the five main species (McClain 1981). In Ontario, *Picea glauca* is generally associated with *Abies balsamea*, *Betula papyrifera* and *Populus tremuloides*, pure stands being uncommon (Gordon 1983). Delong (1991) stated that almost all boreal forests pass through a mixedwood stage during their development. La Roi (1967) noted that *P. glauca* and *A. balsamea* generally occur in association with each other from the Yukon Territory to Newfoundland. *Betula papyrifera* was the most common associate of these two species and *Picea mariana* was the second most common associate. *Populus tremuloides* and *Populus balsamifera* occurred in approximately two-thirds of the stands sampled west of and within the Clay Belt region south of James Bay (La Roi 1967). Carleton and Maycock (1978) noted that although most of the boreal forests in the Clay Belt region were young and monospecific, upland deciduous forests frequently contained an understorey of *A. balsamea*, and certain pairs of species frequently shared the canopy, i.e. *P. tremuloides* and *B. papyrifera*, *P. glauca* and *P. balsamifera*, and *P. mariana* and *Larix laricina*.

2.1.3 Common Soils of the Boreal Mixedwood Forests

Boreal mixedwoods are commonly located on upland tills, till over bedrock, lacustrine fine sands, silts and clays and sometimes on alluvial soils (Gordon 1983). They are generally located on soils richer than those supporting *Picea mariana*, and have low to high lime content (Gordon 1983). Ontario boreal mixedwoods of the spruce-fir-aspen type are most commonly found on fresh to moist, nutrient-rich sites, with well-drained to imperfectly drained soils that are intermediate to fine-textured, i.e. loams to

clays, and sometimes calcareous (Pierpoint 1981). The most common soil type, gray luvisol, has a grayish, leached Ae horizon above a brown, clay-enriched textural Bt horizon, underlain by a Ckg layer which may be mottled due to seasonal saturation. On these sites, organic litter decomposes and mixes with mineral soil rapidly. The overstorey on such soils ranges from almost pure hardwood to a mix with *Picea glauca* and *Abies balsamea*, or *P. mariana* or *Pinus banksiana*. Podzols and brunisols are more common on drier, less rich sites, where soils are fine sandy to loamy, with a lower pH. The podzols have a well developed organic layer, an Ae horizon, one or two Bf horizons (containing iron, aluminum and/or organic matter) and a gleyed Cg horizon underlying the C horizon. The brunisols are similar, except that they have a less-well developed B horizon and no evident Ae horizon. Productivity, litter decomposition, and nutrient cycling on these sites is lower, species richness of the herb and shrub strata is poorer, and *Acer spicatum* may dominate the shrub stratum. Litter decomposition is particularly slow under the *Picea mariana / Pleurozium schreberi* (Brid.) Mitt. association which may occur on these soil types. *Picea mariana* and *Thuja occidentalis* are common on very moist to wet soils, but various mixtures are possible (Pierpoint 1981).

2.1.4 Canopy Structure

The dynamics and structure of the boreal mixedwood forest must be included in its description: the boreal mixedwood forest has a definite post-fire successional sequence and a stratified mixture of species (Day and Bell 1988). There are often three woody-species strata (Day and Harvey 1981, Day and Bell 1988). The upper stratum is composed of intolerant, rapidly-growing species that reproduce reliably and copiously after fire by seed or vegetatively, i.e. *Populus tremuloides*, *Betula papyrifera* and *Pinus banksiana*. The middle stratum consists of moderately tolerant, slower-growing, suppressed species with less reliable, seed-dependent post-fire reproduction,

i.e. *Picea mariana* and *Picea glauca*. The lowest stratum contains very tolerant, suppressed species that have difficulty reproducing following fire, e.g. *Abies balsamea*, *Corylus cornuta* and *Acer spicatum*. These three layers are also referred to as pioneer, mid-successional and late-successional (Day and Bell 1988), although this does not necessarily refer to the time of their establishment. In fact, the upper and middle layer species are both referred to as pioneers by Day and Harvey (1981). Thus, many boreal mixedwood forests are even-aged, the component species having different growth rates and longevities, thereby producing an observable change in species dominance and productivity (Gordon 1983). In the Boreal Mixedwood Section of Saskatchewan, pioneer species, i.e. *P. tremuloides*, *Populus balsamifera*, *B. papyrifera* and *P. banksiana*, attained tree size between 20 and 60 years of age, while many saplings of *P. glauca*, *P. mariana* and *A. balsamea* were older than 60 years (Dix and Swan 1971). In naturally-regenerating boreal mixedwood stands up to 35 years old in north central Ontario, the greatest percentage of stems were seedlings, saplings, and small trees beneath the canopy (Morris *et al.* 1988). *Abies balsamea* comprised the majority of these suppressed stems (Morris *et al.* 1988). In contrast to the stratification of boreal mixedwood forests, monospecific stands of the boreal forest generally consisted of only a single tree layer and an understory herbaceous layer (Carleton and Maycock 1981).

The spatial pattern of trees in most boreal mixedwood stands was found to be highly clustered, but the hardwood component of some of these stands had an almost random distribution (Payandeh 1973). Spatial pattern indices calculated for all trees (>3.8 cm dbh) in mixedwood stands showed a more clumped distribution than those calculated for only large trees (>8.9 cm dbh). The dominant conifers in mixedwood stands all had clumped distributions (Payandeh 1973).

Conifer advance growth in the boreal mixedwood forest is mainly *A. balsamea* and *P. glauca*; *P. banksiana* is too shade intolerant to establish under a canopy, and *P. mariana*, which is moderately shade tolerant, releases seed sparingly in the absence of

disturbance (Hosie 1954). In upland forests of northern Saskatchewan, *A. balsamea* seedlings and saplings were abundant under canopies dominated by *A. balsamea*, *B. papyrifera* and *P. glauca*, although they often exhibited a patchy distribution. Numbers of *P. mariana* seedlings or saplings were often significant in stands dominated by *P. mariana*, *B. papyrifera* and *P. banksiana*. *Picea glauca* saplings and seedlings occurred, though not abundantly, under all canopy types, especially under *A. balsamea*, *B. papyrifera* and *P. balsamifera*. *Populus tremuloides* saplings were abundant in a few stands, but neither *B. papyrifera* nor *P. banksiana* seedlings and saplings were abundant under any stands (Dix and Swan 1971).

2.1.5 Understorey Composition and Structure

The understorey vegetation of aspen-birch-spruce-fir forests of Ontario is generally a herb or tall shrub-herb type, with mosses being relatively unimportant (MacLean 1960). The most common understorey association is the *Aster macrophyllus* L.-*Aralia nudicaulis* L. type, which also has *Cornus canadensis* L. as an abundant species, and *Mertensia paniculata* (Ait.) G. Don, *Acer spicatum*, *Clintonia borealis* (Ait.) Raf., *Rosa acicularis* Lindl., *Maianthemum canadense* Desf., *Mitella nuda* L., *Galium triflorum* Michx., and *Rubus pubescens* Raf. as frequent species (MacLean 1960).

Boreal mixedwood forests north of Lake Superior contained a greater variety of important understorey species than did conifer-dominated forests (Larsen 1980). This has also been reported for hardwood-dominated stands in comparison to conifer-dominated stands elsewhere in the boreal forest (MacLean and Wein 1977, Carleton 1979). La Roi (1967) reported that for the five vertical strata in his sample of boreal forest stands, species richness decreased from the lowest stratum (herb-dwarf shrub) through to the tree stratum. Larsen (1980) reported frequency values of understorey species from samples in five boreal mixedwood stands along the north shore of Lake Superior. Common species (frequency>25%) were: *Cornus canadensis, Clintonia*

borealis, Maianthemum canadense, Linnaea borealis L., *Equisetum sylvaticum* L., *Vaccinium angustifolium* Ait., *Gaultheria hispidula* (L.) Muhl., *Abies balsamea* (seedlings), and *Trientalis borealis* Raf. Species with 10% to 24% frequency included: *Vaccinium myrtilloides* Michx., *Mitella nuda* , *Rubus pubescens* , *Petasites palmatus* (Ait.) Gray, *Ledum groenlandicum* Oeder, *Lycopodium annotinum* L., *Aralia nudicaulis*, *Diervilla lonicera* Mill., and *Smilacina trifolia* (L.) Desf. Several other species were present in low abundance, including grasses, sedges, lichens and seedlings of *B. papyrifera* and *Betula lutea* Michx. Mosses were abundant, but frequencies were not reported (Larsen 1980).

Shrub species with high frequencies in *Picea glauca-Populus tremuloides* mixedwood stands of Manitoba included *Amelanchier alnifolia* Nutt., *Corylus cornuta, Lonicera dioica* L., *Prunus virginiana* L., *Ribes hirtellum* Michx., *Rosa acicularis, Rubus ideaus* L. var. *strigosus* (Michx.) Maxim., and *Viburnum edule* (Michx.) Raf. (Bailey 1968). Shrub density and height in these boreal mixedwoods were fairly high: 72,000 to 101,000 stems per ha, and 1.0 to 1.5m tall (Waldron 1959). *Acer spicatum* often exceeds these heights where it occurs (Johnson 1986).

2.2 SUCCESSION

2.2.1 Theoretical Debate

2.2.1.1 Traditional Clementsian Succession

Traditional Clementsian successional theory views the plant community as an organism, and succession as a process of development of that organism from an immature stage to a mature stage (Clements 1949). Initial seral stages are affected by soil and topography, with successive stages becoming more closely controlled by climate. The eventual climax vegetation represents the highest type of social organism possible for a particular climate (Clements 1949), its dominant species representing the highest

possible life form (Smith 1980). The climax community is self-maintaining in the absence of disturbance, and in the event of disturbance, succession will essentially repeat itself through the same stages, resulting in the same climax community (Clements 1949). Thus, succession is assumed to be linear, unidirectional and predictable (Smith 1980).

According to this interpretation of succession, only certain species are capable of invading a disturbed area, and these species alter the physical environment, making it more favourable for establishment of plant species of the next seral stage and less suitable for establishment of the colonizing species (Egler 1954, Connell and Slatyer 1977). Each species group is dominated by a particular life form, progressing through lichen-, moss-, herb-, shrub- and tree-dominated communities (Egler 1954). This mechanism of succession was referred to as Relay Floristics by Egler (1954) and the Facilitation Model by Connell and Slatyer (1977).

This traditional concept of succession assumes that regardless of the species composition and abundance of early successional communities, all communities in a particular geographical region converge to a similar climax community (Horn 1974, Finegan 1984). The climax community is assumed to be in stable equilibrium; stability in terms of resistance to disturbance or resilience (ability to recover from disturbance) is considered to be highest in the climax (Smith 1980). Also inherent in the traditional concept is that as succession progresses, resource use becomes more efficient, biological control of nutrient cycling increases (feedback mechanisms), weblike food chains develop, spatial heterogeneity increases, and niche specialization increases, i.e. the climax is a highly organized vegetational unit (Odum 1969, Connell and Slatyer 1977, Finegan 1984).

2.2.1.2 Alternative Hypotheses for Mechanisms of Succession

In the past few decades, many of the traditional concepts of succession have been

criticized. Several alternative hypotheses of the mechanisms of succession and some expansions on the original hypothesis have been developed (Gleason 1926, Egler 1954, Connell and Slatyer 1977).

Gleason's (1926) Individualistic Concept of the Plant Association provided a view of the plant community and successional development which contrasted greatly with Clements' traditional approach, challenging the notions that succession is deterministic and predictable, and that the climax community is unique, stable and highly organized. He stated that the plant association was no more than the result of migration and environmental selection acting upon individuals. Similarity between (arbitrarily delineated) vegetational units (e.g. forest stands) is due to similar available population pools (migration) and similar processes of environmental selection, due to climate, soils, etc. Thus, no two vegetation units are precisely identical in species composition and abundance. Adjacent plant associations of the same general type will have minor differences, due to the random influence of immigration and small differences in local environment. Differences will increase as the physical distance between communities increases, since both immigration from surrounding communities and geography of the sites will be different. Stability (a climax community) occurs only when migration and environmental selection remain constant for a period of time, and succession occurs whenever there is any alteration in one or both of these. Since the processes of environmental selection and migration vary stochastically, chance plays a large role in the formation of any plant community (Gleason 1926).

The distribution of individuals and species in a community is therefore determined by probability and chance (Gleason 1926) and similarly, the apparent convergence of dissimilar early successional communities to similar climax vegetation is simply a result of statistical probability and chance in a plant-by-plant replacement process (Horn 1974). Although convergence often occurs, there are many potential pathways and endpoints (equilibria) to plant succession (Gleason 1926), since many

factors, autogenic and allogenic, influence the development of vegetation on a site (Egler 1954).

Succession can be viewed as a continuum in both time and space; species exhibit gradual changes in abundance, rather than replacing each other in distinct waves or jumps (Egler 1954, Halpern 1989) and the distribution of species and plant associations over space exhibits a high degree of intergradation, resembling the succession of species in time (Gleason 1926). This results from each species responding individually, depending on its genetic, physiological and life-history characteristics, to both environmental gradients and changes in resources over time (Gleason 1926, Whittaker 1975, Halpern 1989). Rather than defining a single climax (traditional monoclimax theory), or several discrete climaxes (polyclimax theory), a climax pattern of intergrading communities can be recognized (Whittaker 1975, Smith 1980). This pattern is determined by numerous interacting ecosystem factors (Smith 1980). Thus, the pattern of intergrading climax communities corresponds to the overall pattern of environmental gradients (Whittaker 1975).

Egler (1954) hypothesized that the mechanism of Initial Floristics is more significant in old-field successions than is that of Relay Floristics. His Initial Floristics Hypothesis of succession states that most species involved in secondary succession are present as seed or vegetative propagules at or shortly after the time of disturbance, and that the apparent succession is simply a shifting of dominance due to different life forms and growth rates. He noted that in several documented old-field successions, 95% of the species present in the forest that eventually developed were present at the time of field abandonment; only 5% entered the site in a relay fashion. That Initial Floristics generally have a greater influence on community development than Relay Floristics provides an explanation for arrested succession in disturbed areas (e.g. shrublands that do not return to forests). Egler (1954) suggested that propagules for the usual climax vegetation may be absent at the time of disturbance, and since Relay Floristics is a minor

phenomenon, invasion of these species requires much more time than would their development from Initial Floristics.

In addition to their Facilitation Model for succession, Connell and Slatyer (1977) proposed the Tolerance Model and the Inhibition Model. In contrast to the Clementsian nature of the Facilitation Model, these models contain elements of Gleason's and Egler's theories. They both state that any species may colonize a site, although those with pioneer traits are more likely to. The Tolerance Model argues that the apparent relay of species during succession is primarily determined by life history characteristics--tolerance, growth rate, longevity--of the various species present. A species' influence is neutral with respect to the suitability of the site for subsequent invaders. The important emphasis in this model is that pioneer species are efficient at exploiting unlimited resources (light, water, nutrients), but incapable of surviving in dense stands where resources are limited; the reverse holds for climax species (Finegan 1984). Thus, the climax dominants will consist of species capable of growing at lower levels of resources than earlier species; the earlier, less-tolerant species will be killed in competition with them. The Inhibition Model argues that some of the early colonists will become dominant, securing the space and resources of a site, excluding other species until the dominant species begin to decline. The replacing individuals may or may not have life history traits similar to the colonizers, but they will generally be tolerant, long-lived species. Thus, the species composition gradually shifts to species with high longevity and tolerance. Local disturbance, in the form of physical extremes and natural enemies, are important agents of succession in this model. The authors noted that most examples of secondary succession in the literature fit the latter model, that only some forests with dense, light-limiting canopies and/or vegetative reproduction of climax dominants appear to support the Tolerance Model, and that the Facilitation Model applies well to some primary successions (Connell and Slatyer 1977).

Finegan (1984) argued that elements of traditional succession theory

('holistic') and of more modern theories ('reductionist') may operate simultaneously in the same community. Pioneer species may have traits that make them more successful on newly disturbed sites, but as they grow, they likely make a site more suitable (autogenic change) to species with different types of life histories. Recent research supports Finegan's (1984) observation that more than one type of mechanism is generally responsible for succession. Mechanisms of succession in temperate mixedwood forests of New Hampshire (Henry and Swan 1974, Foster 1988) and in *Pseudotsuga menziesii* (Mirb.) Franco forests of Oregon (Dyrness 1973, Halpern 1988,1989) best fit Egler's (1954) Initial Floristics Hypothesis and Gleason's (1926) Individualistic Concept of the Plant Association: most species survived or colonized shortly after disturbance (Foster 1988, Dyrness 1973, Halpern 1988,1989) and responded individually to microtopographic patterns and other environmental gradients (Henry and Swan 1974), and stochastic elements, including the timing, intensity and frequency of disturbance, as well as variations in immigration and local environment, contributed to successional development (Halpern 1988,1989). In temperate deciduous forests of Michigan (Sakai *et al.* 1984), abandoned agricultural land in Tennessee (Clebsch and Busing 1989), and conifer forests of the Cascade Range in Washington (Oliver *et al.* 1985), patterns of succession corresponded to an Initial Floristics period (survival and invasion), followed by a period where the Inhibition Model seemed to operate (species exclusion), and then by a period reflecting aspects of Relay Floristics (later establishment of several species) or the Tolerance Model (dominance by slow-growing, long-lived species). Of the reviewed literature, Relay Floristics appeared to be the dominant mechanism of succession in only eastern Texas mesic forests, but species' relative growth rates and abilities to persist in the understorey (*sensu* Tolerance Model) were also important there (Glitzenstein *et al.* 1986). In general, these studies indicate that in temperate forests, the traditional concept of succession, i.e. Relay Floristics (Facilitation Model), generally plays a minor role, while Initial Floristics, species' life

history traits (*sensu* Tolerance Model) and elements of chance (*sensu* Individualistic Concept of the Plant Association) explain most of the community changes.

2.2.1.3 Diversity and Stability in Succession

The relationship between diversity and succession in traditional theory was unclear (Odum 1969), as was that between diversity and stability (Shafi and Yarranton 1973). As succession proceeds, diversity depends on a balance between the increase in potential niches that results from increased structural diversity (stratification) and the tendency of dominant species to increase in size and longevity, tying up resources and competitively excluding other species (Odum 1969). The dominating opinion seemed to be that stability increased with the complexity of the ecosystem, and therefore with increases in species diversity. Since stability was assumed to increase throughout succession, diversity was also thought to increase (Shafi and Yarranton 1973).

Just as traditional concepts of successional mechanisms and the climax community have been reexamined, the nature of change in stability and diversity of a community during succession has also been debated. In contrast to the traditional view that diversity (complexity) of an ecosystem increases as succession proceeds (Odum 1969, Shafi and Yarranton 1973), several authors have since observed that plant species diversity is often highest early (Shafi and Yarranton 1973) or at an intermediate point in succession (Auclair and Goff 1971, Clebsch and Busing 1989, Morneau and Payette 1989). Hunter (1990) noted that according to Egler's (1954) Initial Floristics hypothesis, plant diversity should be greatest immediately after disturbance, since most mature forest species remain on the site, some open-land species invade, and dominance and competitive exclusion have not had time to operate. Horn (1974) reasoned that diversity should be highest at some intermediate stage of succession, since such a stage would encompass a mixture of early and late successional species.

Horn (1974) noted that stability increases tautologically with succession, if succession is assumed to be complete when species composition and abundance are constant. In contrast, if stability is defined as resilience (measured in speed of recovery to predisturbance state), then it evidently decreases with succession, since pioneer communities require less time to recover to a predisturbance state than do late-successional communities. He also argued that if diversity increases with succession, stability will decrease, since complex ecosystems are actually more fragile than simple ecosystems, and that they only appear more stable due to the constant external environment that accompanies them.

Connell and Slatyer (1977) noted that stability of the climax in terms of a steady state equilibrium will only occur if every individual of a climax species is replaced by another of the same species; they had not observed any such communities of sexually reproducing individuals and they assumed that succession never ceases. Indeed, they asserted that apparent stability of the climax is principally due to life-history characteristics, i.e. species composition of a site shifts to long-lived, disturbance-resistant species, because once these species invade a site and attain dominance, the long duration of their occupation simply prevents other species from usurping them. They also noted that there is no actual evidence of higher internal control (feedback mechanisms) of biological processes in mature communities.

2.2.3 Importance of Disturbance in Succession

The previous theories focus on species' characteristics and the environment as determinants of successional pathways. Recent literature emphasizes the strong dependence of forest succession and species composition upon the nature, intensity and size of the disturbance itself (Whitmore 1989, Wein and El-Bayoumi 1983, Weetman and Vyse, 1990).

Disturbance nature and intensity influence successional pathways not only by

their effect on propagule availability and distribution, but also by their long-term effects on nutrient pools, germination sites, etc. (Halpern 1989, Roberts and Dong 1991). Releasing disturbances, which kill the overstorey but preserve the understorey strata (e.g. harvest or insect attack), favour tolerant tree species that have prolific advance regeneration; severe disturbances (e.g. fire), which kill both understorey and overstorey species, favour regeneration via vegetative sprouting and unburned seed banks or wind-disseminated species (Weetman and Vyse 1990). Disturbance intensity may vary spatially, due to local topography, moisture regime, etc. (Wein and El-Bayoumi 1983).

Successional stage at the time of disturbance is important to subsequent change (Glitzenstein *et al.* 1986). In forests where conifers are succeded by tolerant, vegetatively-regenerating hardwoods, disturbance in young stands accelerates succession, while disturbance of later stages interrupts and reinitiates succession, with conifers invading first, since the remaining hardwood understorey are too few and too old to resprout (Glitzenstein *et al.* 1986).

Small disturbed areas recover more rapidly than large ones, due to the influence of surrounding undisturbed communities (Wein and El-Bayoumi 1983). A climax community can only be monospecific if the dominant species completely excludes all other species; in most climax communities, some early successional individuals will persist, since gaps usually occur among the dominant species due to mortality (Horn 1974). Such gaps maintain diversity and prevent competitive exclusion in old-growth forests that lack large-scale disturbance by allowing regeneration of species from all seral stages (Glitzenstein *et al.* 1986, Clebsch and Busing 1989). Canopy gaps may also be important in maintaining the potential, i.e. seed sources, of less shade-tolerant herb species to respond to large-scale disturbances (Moore and Vankat 1986). In some mature forests of pioneer species, these gaps are required for invasion by more shade-tolerant, climax species (Sakai *et al.* 1984, Whitmore 1989). In some cases, this

small-scale disturbance may be the most important event in forest cycling (Whitmore 1989).

The relative importance of disturbance and autogenic change varies among ecosystems; in some ecosystems which are exposed to large-scale disturbance, e.g. fire and hurricanes, disturbance is the primary or sole agent of species change (Henry and Swan 1974, Foster 1988), *sensu* Initial Floristics hypothesis. This is true for boreal forests, which are dominated by large-scale disturbance, generally in the form of fire (Wein and El-Bayoumi 1983, Heinselman 1981).

2.3 NATURAL BOREAL FOREST SUCCESSION

To understand the effect of human disturbance on forest structure and dynamics, it is essential to understand the natural structure of the forest and its response to natural disturbance (Daubenmire 1952, Brand 1991). Therefore, prior to reviewing known effects of harvesting on boreal forests, the literature pertaining to natural boreal forest succession will be reviewed.

2.3.1 Disturbance Nature of the Boreal Forest

It is now widely recognized that vegetation dynamics of the North American boreal forest do not follow the traditional Clementsian model of forest succession which suggests unidirectional, deterministic replacement of species groups, ending in a stable, self-perpetuating climax forest (Rowe 1961, Dix and Swan 1971, Carleton and Maycock 1978, Larsen 1980, Heinselman 1981, Wein and El-Bayoumi 1983, Bergeron and Dubuc 1989). In the past, closed conifer stands, such as *Picea glauca - Abies balsamea* associations and *Picea mariana* -feathermoss stands, were thought to represent the climax type of the boreal forest (La Roi 1967, Larsen 1980, Heinselman 1981, Cogbill 1985). However, it has since been recognized that the disturbance interval in boreal forests is usually too short to allow the development of late

successional vegetation phases (Dix and Swan 1971, Carleton and Maycock 1978, 1980, Day and Harvey 1981, Heinselman 1981, Cogbill 1985).

Fire is the most important natural disturbance in the boreal forest, with average fire rotations of 150 to 300 years in eastern Canada and 100 to 150 years in drier western Canada (Heinselman 1981). For Ontario boreal mixedwoods, fire rotation averages 75±50 years, rarely exceeding 125 years (Day and Harvey 1981). Other major disturbances usually ensure that succession is terminated at an early stage even in the more mesic eastern boreal forests, e.g. windfall, insect infestations, pathogens (Cogbill 1985). Disturbance maintains the boreal forest in a young, highly productive and relatively unstable state (Dix and Swan 1971, Peterson 1988, Brand 1991). It may be required to maintain the health of the boreal forest (Rowe 1961, Methven *et al.* 1975) in terms of suitable seedbeds, nutrient cycling, and arboreal structure (Cogbill 1985). For example, soil temperature, and therefore nutrient cycling rates, are increased by periodic fire in *Picea mariana* ecosystems of Alaska, simulating more productive forests for 10 to 20 years (Van Cleve *et al.* 1983).

In some areas of the boreal forest, particularly northern parts, traditional succession does not occur even in the absence of disturbance; extreme physical conditions prevent organisms from modifying their physical and chemical environment (Larsen 1980, Wein and El-Bayoumi 1983). In these areas, community continuua and ecoclines are determined mainly by physical conditions (topography, soils, climate, etc.) and fire history. Spatial pattern of the vegetation is more obvious than autogenic temporal change (Cogbill 1985). Species composition depends more on post-disturbance site conditions than on time elapsed since disturbance, i.e. in the inter-disturbance interval, there is little change in stand composition (Cogbill 1985).

2.3.2 Initial Regeneration Following Natural Disturbance

Most of the boreal tree species have evolved mechanisms of post-fire

reproduction: *Pinus banksiana* and *Picea mariana* serotinous and semi-serotinous cones are retained on the trees for several years to release seed after fire, *Populus tremuloides* root suckers respond to heat from fire and intense insolation, and *Betula papyrifera*'s abundant, light seed is readily disseminated by wind to burned areas (Day and Harvey 1981, Armson 1988, Brand 1991). *Picea glauca* and *Abies balsamea*, though most shade-tolerant of the boreal tree species, are the least-adapted to regenerate following fire, having no vegetative means of reproduction and no means for seed to survive intense fire. Thus, these two species occur more sporadically in the natural boreal forest than do other species (Dix and Swan 1971, Armson 1988).

Fires have a tendency to stabilize forest composition. Large, frequent fires which occur while stands are young, favour reestablishment of intolerant pioneer trees, dominant at the time of disturbance (Dix and Swan, 1971). Thus, catastrophic disturbance is often followed by reestablishment of dense, nearly monospecific stands, almost identical in composition to the original forest (Carleton and Maycock 1978, Heinselman 1981, Cogbill 1985, Bergeron and Dubuc 1989). Changes in composition may result, due to elimination of propagules by fire, or by immigration of propagules from surrounding unburned forest (Heinselman 1981).

Boreal understorey species have also adapted to frequent disturbance; many reproduce vegetatively from subterranean organs after fire and/or store seed in the forest floor (Carleton 1979, Heinselman 1981, Carleton and Maycock 1981). The ability to regenerate following fire may create a distinct zonation in understorey species' distributions at 47° N latitude in Ontario, north of which lightning-induced wildfire is more common (Carleton 1979).

Thus, most boreal species are not eliminated by fire and they reestablish within the first few years after fire (Rowe 1961, Heinselman 1981, Carleton and Maycock 1981). In boreal spruce-lichen woodlands, most vascular species colonized immediately after fire, with most *P. mariana* stems establishing within the first 15

years; lichen species also colonized within this period (Morneau and Payette 1989). In Ontario boreal mixedwoods, all of the common tree species except for *A. balsamea* establish almost simultaneously in the first few years following fire (Day and Harvey 1981), and the two main tree species in western mixedwoods, *P. tremuloides* and *P. glauca*, often follow the same pattern (Peterson 1988, Delong 1991). Similarly, the main tree species appeared within 50 years of stand initiation in boreal forests of northwestern Quebec (Bergeron and Dubuc 1989) and within 30 years in the Laurentian Highlands of Quebec (Cogbill 1985).

This rapid reestablishment of disturbed areas and the general fidelity of post-disturbance forest to that of the pre-disturbance forest support Egler's Initial Floristics hypothesis of succession (Heinselman 1981, Bergeron and Dubuc 1989, Morneau and Payette 1989) and Gleason's Individualistic Concept of the Plant Community.

2.3.3 Canopy Dynamics After Disturbance

Succession rarely occurs in the tree stratum of boreal forests (Dix and Swan 1971, Carleton and Maycock 1978, Cogbill 1985, Bergeron and Dubuc 1989) since most trees establish simultaneously, and there are often no replacement species available, or no time for replacement before the recurrence of disturbance (Heinselman 1981, Peterson 1988). Forests of pioneer trees (aspen, birch and jack pine) often do not appear to be developing into spruce and fir types (Cogbill 1985).

A few examples of traditional Relay Floristics have been observed in the boreal canopy (Carleton and Maycock 1978, 1980; Van Cleve and Viereck 1981; Cogbill 1985, Bergeron and Dubuc 1989, Delong 1991). In boreal mixedwoods of western Canada (Delong 1991) and Alaska (Van Cleve and Viereck 1981), if a seed source and good seed crop of *Picea glauca* is unavailable in the first few years after fire, *Populus tremuloides* stems will dominate the site, and *P. glauca* will seed in 20 to 40 years later, when aspen abundance has decreased considerably. *Abies balsamea* often seeds into boreal mixedwood

stands over several years after disturbance (MacLean 1960, Morris *et al.* 1988). However, the apparent succession of mixedwood boreal forests exhibiting a tall tree canopy and a lower tree stratum (of different species) often indicates differences in growth rates and lifespans of even-aged cohorts, rather than a relay of establishment (Rowe 1961, Carleton and Maycock 1980, Gordon 1983, Peterson 1988, Delong 1991). In boreal mixedwood forests in western Canada, aspen and spruce often establish simultaneously following fire, and *P. glauca* gradually replaces the rapidly growing *P. tremuloides* overstoreys (Rowe 1961, Peterson 1988, Delong 1991). Similarly, in northern Ontario, *P. tremuloides* and *Betula papyrifera* usually attain dominance of a site first, but spruce and fir cohorts eventually replace them (Day and Harvey 1981). In most boreal forests of the Laurentian Highlands of Quebec, all tree replacements within 110 years of stand initiation are by trees of the same cohort age as those being replaced. Some of these initial cohorts continue to dominate the canopy for 250 years (Cogbill 1985).

Thus, a large part of the apparent succession of the boreal forest canopy, including peaks of dominance and species replacements, is actually the visual expression of different life histories (growth rate, longevity) of species established at approximately the same time (Heinselman 1981, Cogbill 1985).

2.3.4 Understorey Dynamics Following Natural Disturbance

In more northerly boreal ecosystems, succession of the understorey vascular plant species is also rare (Morneau and Payette 1989). No replacement of vascular plants occurred in spruce-lichen woodland succession in northern Quebec (Morneau and Payette 1989) nor in open spruce woodland of the Northwest Territories (Black and Bliss 1978).

In moss-dominated understoreys of boreal forests of western Canada and the Laurentian highlands in Quebec, understorey composition was stable after canopy

closure, as long as canopy dominants were constant (Dix and Swan 1971, Cogbill 1985). Accumulated moss and humus inhibited seedling invasion (Cogbill 1985).

In more southerly regions of the boreal forest, the greater number of potentially dominant tree species creates a greater range of light and soil conditions, a larger number of niches, and a richer vascular understorey (Larsen 1980). This understorey therefore changes, to some extent, as the canopy changes, due to succession or disturbance. Rowe (1956) noted that dominance of the understorey in *P. glauca* - feather moss stands of Manitoba and Saskatchewan shifted, in terms of relative abundance, from tall shrubs, to medium shrubs, to herbs, to mosses, as canopy dominance shifted from *Populus* spp. to *Picea* spp. In a three-point overstorey succession (*Betula papyrifera* to mixed *B. papyrifera-Abies balsamea* to *A. balsamea*) identified in the Clay Belt south of James Bay, understorey species fell into three response groups: those favouring the deciduous canopy, those favouring the coniferous canopy, and those indifferent to canopy type. The same pattern was observed in the two-point canopy succession from *Populus tremuloides* to *A. balsamea* (Carleton and Maycock 1980).

The best example of Relay Floristics in the boreal forest occurs in the moss and lichen ground layer, where *Marchantia* spp. and other rapidly-invading mosses are replaced by *Dicranum* spp., *Sphagnum* spp. and the feathermosses, once a canopy develops (Heinselman 1981). The latter species are eliminated completely from the site by fire (Heinselman 1981), as is lichen (Morneau and Payette 1989). In northern boreal spruce-lichen woodlands of Quebec, a five-stage lichen-bryophyte succession occurred, corresponding to the Facilitation Model of succession (Morneau and Payette 1989). *Polytrichum* spp. were included in colonizing species, and were replaced by other mosses including *Pleurozium schreberi* (Brid.) Mitt. once the tree stratum had expanded. Even in this example of Relay Floristics, gradual changes in abundance, due to different growth rates and competition, were more evident than abortive replacements.

In a similar four-stage, post-fire cryptogamic sequence in open spruce woodlands of the Northwest Territories, changes in the vascular understorey were only in abundance and size (Black and Bliss 1978). In northern boreal forest of the lower Mackenzie River valley, *Marchantia polymorpha* L. was the first colonizer, with herbs, mosses and low ericaceous shrubs invading next, eventually to be dominated by a dense and vigorous *Picea mariana* stand (Strang 1973). In the absence of fire for over 150 years, a dense lichen mat developed.

Thus, fire in the boreal forest initiates cycles of species dominances: post-disturbance vegetation dynamics are principally changes in relative abundances rather than in composition, and can be attributed to differences in growth rates, longevity and shade-tolerance of boreal species (Wein and El-Bayoumi 1983, Bergeron and Dubuc 1989, Morneau and Payette 1989). The dependence of successional phases on differences in life history traits of essentially contemporaneously established species corresponds to Egler's Initial Floristics hypothesis (Heinselman 1981, Bergeron and Dubuc 1989, Morneau and Payette 1989) and Connell and Slatyer's Tolerance Model (Bergeron and Dubuc 1989). Due to the Initial Floristic character of boreal forests after fire, the first colonization of a site that occurred in response to an ancient event may be more important in determining composition and structure of the forest than even fire behaviour itself (Bergeron and Dubuc 1989)

2.3.5 No Climax and No Single Successional Pathway

Contrary to traditional notions of succession (Clements 1949), there is no single pathway in boreal forest succession, since many interdependent factors affect stand development: soil, topography, fire, propagule availability, insect and wildlife influence, etc. (Hosie 1954, Rowe 1961, Heinselman 1981, Brumelis and Carleton 1989, Bergeron and Dubuc 1989, Brand 1991). Some forests change in structure and composition, in response to disturbance or in a post-disturbance succession, while

others remain stable from generation to generation (Brand 1991). Most succession vectors derived from chronosequence studies of boreal stands are divergent, rather than convergent, indicating that there is no development towards a single climax type (Carleton and Maycock 1978). Even early studies of boreal forests concluded that the climax concept should not be applied to these disturbance-dominated ecosystems (Rowe 1961, Dix and Swan 1971). Rowe (1961) emphasized that no single climax forest community existed for upland mineral soil sites, and that the numerous community types that could develop were strongly dependent on land-type (topography, soils, etc). He noted that the endurance of certain boreal stands is due primarily to the tolerance of species (*Picea* spp. and *Abies balsamea*) and/or to the longevity of species (*Picea* spp.) that comprise these stands.

None of the boreal forest tree species have silvical characteristics that allow them to form self-perpetuating climax forests (Rowe 1961, Heinselman 1981). Even *A. balsamea*, the only one able to reproduce abundantly under all boreal canopy types, has a short lifespan, and is very susceptible to spruce budworm attacks (Heinselman 1981). In addition, the occurrence of large, frequent fires helps prevent convergence to climaxes of the shade-tolerant species (*A. balsamea*, *Picea glauca*, *Thuja occidentalis*) by persistently excluding them or preventing them from reaching seed-bearing age, thus reducing their seed sources (Carleton and Maycock 1978, Wein and El-Bayoumi 1983, Bergeron and Dubuc 1989). This may explain the common occurrence of large expanses of monospecific boreal forests (Carleton and Maycock 1978).

Some authors have suggested that in the absence of disturbance, self-perpetuating, climax boreal forests dominated by shade-tolerant conifers may develop, where these species are present in the understorey (Carleton and Maycock 1978, Bergeron and Dubuc 1989). LaRoi (1967) stated that in the absence of severe disturbance in boreal ecosystems, coniferous forests always develop, and some of these stands are uneven-aged, suggesting self-replacement. Self-replacement of old (>300

years) *Thuja occidentalis* and *Picea mariana* stands was observed on two small, fire-protected islands in northwestern Quebec (Bergeron and Dubuc 1989). However, Dix and Swan (1971) predicted that, in prolonged absence of disturbance, succession in northern Saskatchewan boreal stands would result in open 'parklands', rather than climax forests, due to poor reproduction in most stands. Carleton and Maycock (1978) predicted the same result for most eastern boreal stands.

Examples of forests that have escaped fire or other disturbance for long periods (>200 years) generally support this prediction. These forests often become open, decadent and shrub-dominated, with only scattered *Picea* spp. and *A. balsamea* canopy trees (MacLean 1960, Rowe 1961, Sutton 1964, Larsen 1980, Day and Harvey 1981), limited reproduction and poor tree growth (Cogbill 1985). Some reproduction of various species (*Betula papyrifera*, *A. balsamea*, etc.) may occur in canopy gaps, creating a physically ragged forest of mixed composition and age (Rowe 1961, Cogbill 1985). This type of development has been noted in some boreal mixedwood forests in northwestern and northcentral Ontario that have not been burned for over 200 years (MacLean 1960, Sutton 1964). Shrubs such as *Vaccinium* spp., *Kalmia* spp. and *Alnus* spp. may invade old *P. mariana* stands, and *Acer spicatum, Corylus cornuta* and ericaceous shrubs often dominate old deciduous stands, maintaining a pioneer-like community for long periods (Cogbill 1985). On wet, lowland sites, exclusion of fire results in paludification, a retrogression of forest to fens or open *P. mariana* bogs (Heinselman 1981); on more northerly boreal sites, fire exclusion allows expansion of dense lichen carpets and increased depth of permafrost, both of which impede tree regeneration and growth, and thereby lead to open, degenerating *P. mariana* stands (Strang 1973).

These forests are not self-reproducing climax-types and are actually in a state of disequilibrium with the prevailing natural conditions, which include regular disturbance by fire (Cogbill 1985). Larsen (1980) commented that the climax pattern

concept of Whittaker (1975) appears to fit the boreal forest best. The boreal forest is a mosaic of dynamic, even-aged stands which represent various phases of the community, and which correspond to positions on a continuum of combined gradients (fire severity, topography, soil type, microenvironment, etc.) (Larsen 1980, Heinselman 1981, Van Cleve *et al.* 1983).

2.3.6 Stability and Diversity

Thus, Clementsian succession does not fit the natural dynamics of the boreal forest; without disturbance, there are no stable, self-regenerating stands (Heinselman 1981, Carleton and Maycock 1978). Stability in terms of constancy of species (self-replacement) is attained on a long-term basis by the fire cycle: burned forests are often replaced by the same species that dominated the original stands (Day and Harvey 1981, Cogbill 1985, Bergeron and Dubuc 1989) and where they are not, fire creates a steady-state mosaic of boreal forest-types at the landscape level (Day and Harvey 1981, Heinselman 1981, Bergeron and Dubuc 1989).

Due to this fire-induced mosaic character of the boreal forest, diversity at a landscape scale (between-site) is large, although diversity of forest stands (within-site) is often low, with stands commonly having monotypic canopies and species-poor understories (Larsen 1980, Day and Harvey 1981, Heinselman 1981, Van Cleve *et al.* 1983, Bergeron and Dubuc 1989). The high frequency of disturbance in the boreal forests may have prevented the evolution of species adapted to stable, highly diverse ecosystems (Shafi and Yarranton 1973).

Species diversity often peaks early in the postfire succession of boreal stands (Methven *et al.* 1975, Shafi and Yarranton 1973) probably due to the shift to dense conifer canopies that occurs in later succession (Auclair and Goff 1971). These canopies tie up nutrients in live and dead organic matter, and limit understorey light and moisture, allowing only growth of mosses and some scattered vascular plants (Larsen

1980, Heinselman 1981, Van Cleve and Viereck 1981). In a study of postfire recovery of boreal *Pinus banksiana*, *Picea mariana* and mixedwood stands in northwestern Ontario, species diversity returned to pre-fire levels within 1 year (Methven *et al.* 1975). In a chronosequence study of *P. mariana* dominated lowland sites of the Ontario Clay Belt, species diversity increased in early postfire succession to 8 years, then decreased sharply from 11 to 16 years after fire, remaining fairly constant to 44 years (Shafi and Yarranton 1973). Richness and degree of intraspecific competition followed the same trends. Species diversity in a chronosequence study of lichen-spruce woodlands of the boreal forest in northern Quebec was low 4 years after fire, peaked at 25 years and then decreased to equal the earliest measurement by 100 years, remaining stable thereafter to 250 years postfire (Morneau and Payette 1989).

In deciduous forests and mixedwood boreal transition forests of the northern United States and adjacent Ontario, species diversity responded to both successional stage (time) and environmental gradients (site) (Auclair and Goff 1971). On sites at the extremes of a moisture gradient (edaphic-dominated sites that would likely support only pioneer species), diversity increased constantly over time. However, on fertile mesic sites (midpoint of moisture gradient), diversity increased to a midpoint in succession and then decreased to the climax. The increase of species diversity to late successional forests were related to increases in structural complexity and therefore in niche diversity, along with continuous immigration of species. The decrease in species diversity to the climax forests was attributed to physiological and reproductive traits of the climax species (e.g. dense conifer canopies, shade tolerance) which allowed them to competitively exclude many other species. In successional forests of short-lived species (e.g. *Populus tremuloides*), diversity of the understorey strata generally increased until pioneer overstorey species were at the median of their diameter range, then decreased with development of climax overstorey species, and finally increased in response to local disturbances (e.g. canopy gaps). In forests with relatively longer-lived species (*Betula*

papyrifera, *Pinus strobus*) understorey diversity varied inversely with tree diversity (Auclair and Goff 1971).

Therefore, stability and equilibrium exist in the boreal forest only at the ecosystem level (Larsen 1980); the prominence of disturbance in boreal forests creates low diversity and low stability in individual stands, but high diversity and stablility if the boreal forest is viewed as a mosaic of stands.

2.3.7 Importance of Disturbance Intensity and Size

Since disturbance is such an important aspect of boreal forest dynamics, its characteristics influence forest structure and species composition. A balance of several factors determines which species will predominate on a boreal forest site (Hosie 1954, Dix and Swan 1971, Brand 1991). Small scale disturbance (individual tree mortality, windfall, etc.) in older boreal forests releases suppressed tolerant pioneers (spruces, *A. balsamea*) (Day and Harvey 1981, Morris *et al.* 1988) and provides canopy gaps that allow some species to seed in (Losee 1961, Cogbill 1985), but generally, these effects are minor compared to that of fire (Heinselman 1981).

The nature of fire itself depends on characteristics of the pre-fire forest, such as site type - root systems are protected better in deep soils - and the structure and composition of the pre-fire stand, e.g. long-crowned conifers promote intense crown fire, old stands have more fuel (Day and Harvey 1981, Heinselman 1981). The nature of fire controls several factors that influence regeneration in the boreal forest (Heinselman 1981, Wein and El-Bayoumi 1983). Crown, surface and ground fires, each vary in intensity and area, which in turn influences which vegetative strata and species are killed (Heinselman 1981). The effect of fire intensity on the soil and organic layers is especially important (Heinselman 1981). The degree to which the organic layers are burned determines the extent of nutrient availability to the regenerating forest; an intense burn combusts the organic matter, releasing nutrients.

It also increases insolation, which warms the soil and therefore increases nutrient cycling (Heinselman 1981, Wein and El-Bayoumi 1983).

Species that sucker or sprout, such as *Populus tremuloides*, *Betula papyrifera*, *Corylus cornuta* and *Alnus* spp., are favoured by light disturbance, with little exposure of mineral soil (Delong 1991, Heinselman 1981). Deep burns may prevent regeneration of these species, and of understorey species that regenerate from seedbanks, e.g. *Corydalis sempervirens, Geranium bicknellii, Aralia hispida* and *Polygonum cilinode*. *Picea mariana* and *Pinus banksiana* are favoured by intense fires, which release seed from their serotinous cones and expose sufficient mineral soil for their germination (Heinselman 1981, Armson 1988). *Picea glauca* seed is destroyed by fire, and therefore this species will only be a main component of the new stand if there are adjacent seed sources, or in the case of non-fire disturbance, if advance regeneration survives (Delong 1991). If large areas of mineral soil are exposed by a disturbance, all tree species should regenerate well (Delong 1991), provided there are seed sources (Heinselman 1981).

Thus, although different site types favour different tree species (Rowe 1961, Dix and Swan 1971, Van Cleve and Viereck 1981, Peterson 1988), similar site types may support very different species mixes, due to the variability in severity and extent of disturbance (Heinselman 1981, Delong 1991).

2.3.8 Canopy Determines Understorey Composition and Succession

In forest ecosystems, canopy composition, structure and succession generally have a large influence on understorey composition and succession, since canopy is a major determinant of the seedbed and microclimate of the forest floor (MacLean and Wein 1977, Outcalt and White 1981, Alaback 1982). Canopy controls the amount of light and moisture available to the understorey (Anderson *et al.* 1969, Larsen 1980) and influences nutrient availability (Van Cleve and Viereck 1981). In a forest of mixed

overstorey composition, the canopy types differentially alter microclimatic conditions, influencing the spatial distribution of understorey species (Beatty 1984, Turner and Franz 1986). The eight tree species of boreal mixedwood forests can form numerous cover types (Rowe 1956) and the resulting canopies exert much of their influence on the understorey via light and moisture interception (Larsen 1980).

2.3.8.1 Light

The quantity and quality of light reaching the boreal understorey depends upon age and species composition of the canopy (Anderson *et al.* 1969, Ross *et al.* 1986). Boreal species in increasing order of shade rating are *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera*, *Picea mariana*, and *Abies balsamea*, with *Picea glauca* varying, but usually dominating stands with dense-moderate ratings (Dix and Swan 1971). Canopy cover in mixed hardwood stands is generally greater than in pure *P. banksiana* stands in New Brunswick (MacLean and Wein 1977). In conifer-dominated stands, the red to far red ratio (R:FR), and the percentage of photosynthetically active radiation (%PAR) that reaches the forest floor decrease continuously over the growing season, while in boreal mixedwoods and hardwood-dominated stands, they decrease rapidly in May and June, coincident with the leafing out of the deciduous species, and then increase during leaf senescence in September (Ross *et al.* 1986). Some young conifer-dominated stands do not show seasonal fluctuations in R:FR and %PAR, and at mid-season, these values were lower in old conifer stands than in young ones. These differences likely affect species composition and succession of the understorey. Old forests that have been undisturbed for long periods of time have large gaps, characterized by higher light intensites, than 'second-growth' forests, which have numerous gaps so small that their microsites differ little from those under the unbroken canopy (Clebsch and Busing 1989). The large gaps maintain the presence of intolerant overstorey and understorey species within the forest (Moore and Vankat 1986, Clebsch

and Busing 1989), increasing their ability to expand rapidly in the event of a major disturbance (Moore and Vankat 1986). Species richness is not greatly affected by gap dynamics, but overall herbaceous cover increases in a newly-formed gap, and decreases as the gap closes (Moore and Vankat 1986).

Rowe (1956) stated that understorey structure of boreal forest stands is controlled mainly by light, while the influence of the canopy on temperature, root competition, litter accumulation, etc. mainly effects understorey composition, but not structure. The relative height of understorey plants is inversely related to their shade tolerance since the lowest plants must be able to tolerate the densest shade (Rowe 1956). Thus, the understorey progression often seen during boreal 'succession', from tall shrubs, to medium shrubs and tall herbs, to low shrubs and herbs, to mosses, is essentially a progression of increasing shade tolerance. It follows the canopy succession from *Populus* spp. or *Pinus* spp. to *Picea* spp. or *Picea* spp.-*A. balsamea* forests, mainly due to the accompanying decrease of light (Rowe 1956). The highest cover of tall and medium height herbs occurs in mixedwood stands, tall shrub cover decreases steadily from *Populus* spp. to mixedwood to *Picea* spp. stands, while that of medium shrubs decreases, and moss cover increases from mixedwood to *Picea* spp. stands. Low herb cover is moderate in all stand types, but most evident in *Picea* spp. stands, since cover of tall and medium shrubs and herbs is low (Rowe 1956).

Swan and Dix (1966) also found an inverse relationship between moss cover and total number of herb and shrub species in boreal forest stands. A highly significant correlation between separate ordinations of the canopy and the sub-canopy in their study indicated that the distribution of these two were strongly allied. They concluded that the canopy exerted a strong influence on the understorey and that light was the most important vegetatively dependent factor examined; canopies that cast dense shade (*P. mariana* and *A. balsamea*) had the smallest number of understorey vascular species and low frequencies of these, but the highest percentage of moss cover, while the reverse

was true for thin-canopied stands dominated by *P. tremuloides*, *B. papyrifera*, *P. banksiana* and to some extent *P. glauca*.

2.3.8.2 Moisture

The amount of preciptitation that reaches understorey plants is partly determined by canopy density, litter layer depth, and the amount of root competition for soil moisture, all factors determined by canopy composition and structure (Anderson *et al.* 1969). In some forests, the influence of the canopy via throughfall and random drip precipitation is more important to total herbaceous cover than its influence via radiation. Variations in throughfall precipitation have a great influence on moisture content of the lower litter layers and upper soil layer, in which most northern understorey herbaceous species root. Throughfall precipitation is more closely correlated with canopy density than is illumination in some forests, due to the influence of sun-angle, skylight, and side-lighting on the latter (Anderson *et al.* 1969).

In boreal forests, some studies have found a close correlation between soil moisture and understorey species' composition and abundance (Maycock and Curtis 1960), while others have found no relationship (Swan and Dix 1966). Swan and Dix (1966) found that soil moisture had no significant effects on the composition and structure of upland boreal forest canopies and subcanopies in northern Saskatchewan. They surmised that soil moisture is rarely a limiting factor in upland forests of that area, and therefore has little influence on vegetative composition. Rowe (1956) noted that most boreal species have wide ecological amplitudes, but have preferred moisture regimes, in which they grow more vigourously and in greater abundance. He proposed that an index based on dominant structure (physiognomic type) and moisture preferences of understorey plants could aid in the classification of boreal forest stands.

Maycock and Curtis (1960) found that most of the major tree species in boreal forests of the Great Lakes region had broad tolerance of soil moisture, but optimum

development in specific portions of the linear moisture gradient: *Picea glauca*, *Populus tremuloides*, and *Betula papyrifera* on drier sites, *Abies balsamea* on wetter sites and *Picea mariana* and *Pinus banksiana* at both the wet and dry portions of the gradient. This was also true for many widespread understorey species, making them unhelpful as site moisture indicators. However, some understorey species responded to moisture as well as canopy composition, so that stands of very similar tree composition, but different moisture situations often had very different understorey composition and structure.

2.3.8.3 Canopy/Understorey Affinities Resulting from Canopy Effects on the Understorey Microclimate

The feathermosses and *Dicranum* spp. appear after canopy establishment (Heinselman 1981, Brumelis and Carleton 1989, Morneau and Payette 1989). They will not form a continuous carpet under a dense hardwood canopy, due to its heavy litterfall (Van Cleve and Viereck 1981), but they often do under dense conifer canopies (van Groenewoud 1965). Under dense conifer canopies, upper soil horizons are dry, except immediately after rain, due to high tree root concentration (van Groenewoud 1965). The mosses counteract this by retaining moisture and concentrating nutrients (Timmer 1970, Tamm 1964). Many herbaceous species cannot tolerate the dry, low light conditions beneath conifer canopies (van Groenewoud 1965), and some common ones (*Linnaea borealis, Cornus canadensis, Maianthemum canadense* Desf., *Pyrola virens* Schweigg., *Petasites palmatus, and Merternsia paniculatum*) can only survive in low abundance (Larsen 1980). Thus, aspen-dominated canopies have a well-developed shrub and herb stratum, but no moss stratum, while spruce-dominated canopies have poor herb and shrub cover, but a well-developed moss cover (Peterson 1988).

In boreal forests south of James Bay, understorey species were slightly related to the percentage of conifers in the canopy, to depth of organic matter on the forest floor and to tree basal area, but relationships between canopy-types and understorey-types

were generally poor, probably due to frequent disturbance and short lifespan of tree species (Carleton and Maycock 1980). Carleton and Maycock (1981) examined the affinity of individual boreal understorey species to monospecific canopy types. Only 121 of the 410 understorey taxa studied showed any specificity to a monospecific canopy class, or to any natural groupings of monospecific canopy classes. They attributed this lack of specificity of understorey species to canopy types partly to differences in modes of regeneration of the two strata. The understorey regenerates almost entirely from on site regeneration, in the form of persistent subterranean parts and seed banks. Some of the canopy species (conifers particularly, such as *Picea* spp. and *Abies balsamea*) seed in from surrounding areas, while others regenerate in the same manner as the understorey. Affinities that were evident were mainly due to shared substrate requirements of the understorey and overstorey species.

Populus balsamifera was the canopy species with the greatest number of understorey species definitely associated with it (Carleton and Maycock 1981). It occupied sites not suited to the other canopy types, such as low, fluvial silt terraces and rich, wet clay sites. These sites were characterized by constant nutrient input due to seasonal flooding and silt deposition, rapid decomposition of organic matter due to alkaline conditions (thus minimal accumulation of humus and peat), and absence of fires. Understorey species suited to or requiring these environmental conditions showed a fairly strong fidelity to *P. balsamifera* canopies. Few species showed a high affinity to either *Populus tremuloides* or *Betula papyrifera*, to a combined category of *Populus* spp. (*P. balsamifera* and *P. tremuloides*), or to a combined category of all three hardwood species. However, some of the species that were strongly associated with *Populus* spp. canopies had a high frequency under that type. Very few species had a strong affinity to any of the upland conifer species. Some species were associated with *A. balsamea*, due to tolerance of heavy shade; some were associated with young *Pinus banksiana* canopies, due to ability to persist after fire in full sunlight; and some were associated with old *P.*

banksiana canopies, due to high moisture and nutrient requirements, which are satisfied by retention of these resources in the organic layers of the older stands. In lowland types, larch canopies had a richer understorey with a larger number of associated species than did *Picea mariana* canopies, and this was attributed to the higher pH, aeration and nutrient content that lateral subsurface water flow gives to larch-dominated sites. Thus, more understorey species were associated with canopy types on high nutrient-import sites than with canopy types on poorer sites with tight ecosystem nutrient cycles. This was likely due to the greater variety of edaphic conditions and niches available with a more open nutrient cycle (Carleton and Maycock 1981).

In a similar study in northern Saskatchewan boreal forests, about half of the 77 understorey taxa had high frequencies in only one stand type, and none had high frequency under all canopy types (Dix and Swan 1971). *Populus tremuloides* stands had the largest number of understorey species with high and intermediate specificities for it, and *P. balsamifera* also had a large number, while no understorey species were preferentially associated with *A. balsamea* canopies, and few with *B. papyrifera* canopies or with canopies dominated by either of the *Picea* spp.. Several species had a high specificity for *P. banksiana*.

Thus, although boreal understorey species seem to exhibit a general correspondence of life forms to canopy type (hardwood vs. conifer), specificity to particular canopy species, especially conifers, is generally low.

2.3.8.4 Continuous Nature of Canopy and Understorey

Several studies have suggested that distributions of boreal understorey and canopy species cannot be described by single environmental gradients and that boreal communities cannot be classified into distinct plant associations (van Groenewoud 1965, Swan and Dix 1966, Maycock and Curtis 1960). Rather, boreal forest stands show a pattern of continuous variation in species composition and abundance in response to

several interdependent environmental gradients (van Groenewoud 1965, Swan and Dix 1966, Maycock and Curtis 1960). This continuous nature is due to the wide ecological amplitudes of many of the boreal species, and to their individual preferences for particular sections of each environmental gradient (Swan and Dix 1966). The gradients responsible for the patterns include light, moisture, organic matter depth, pH, root competition, etc. (van Groenewoud 1965, Maycock and Curtis 1960). Both the vegetation pattern and the underlying gradients are best represented in a multi-dimensional scheme such as ordination (Maycock and Curtis 1960).

2.3.9 Understorey Affects Overstorey Succession

In northern Saskatchewan, understorey species did not seem to prevent invasion of tree species in either young or old stands (Dix and Swan 1971). However, competing vegetation slows growth of conifer seedlings whether or not the conifers are overtopped; if they are, the rate of growth decreases as the degree of overtopping increases (Brand 1991).

Under declining boreal hardwood canopies, shrub and herb growth is generally rich, and constitutes serious competition to tree seedlings (Shirley 1941). These competitors can reduce light to 21% of full intensity below the tree canopy to 9% beneath the understorey, while conifer seedlings require 20% light for high survival, and 40% for optimum growth (Shirley 1941). On moist, rich sites of the boreal forest, dense, broadleaved herbs often present the most severe competition to *Picea* spp. seedlings (Rowe 1955), but on many mixedwood sites, broadleaved shrubs are their principal competitors (MacLean 1960, Johnson 1986). Grass, brush and hardwoods all contribute to seedling mortality by prolonging the period when seedlings are susceptible to snowshoe hare browsing (Drew 1988, Peterson 1988).

2.3.10 Hardwood/Softwood Interactions

There is conflicting evidence in the literature on the effect of hardwoods such as

Populus tremuloides and *Betula papyrifera* on growth of *Picea* spp. Shirley (1941) stated that *P. tremuloides* are detrimental to *Picea* spp. and *Pinus* spp. growth, unless conifer and hardwood establishment are simultaneous; conifer seedlings cannot endure the intense competition for light, moisture and nutrients of a *P. tremuloides* overstorey and its rich understorey, nor can they easily survive smothering by leaf litter. In some mixedwood stands, hardwood sprouts constitute the most serious competition to *Picea* spp. regeneration, forming a high, closed canopy (Stiell 1976) and achieving densities of up to 80,000 stems per ha in the first 5 post-disturbance years (Delong 1991). It has been shown that only very young *Picea* spp. seedlings benefit from shade (Johnson 1986), which reduces evapotranspiration and prevents lethal soil temperatures (Brix 1972). *P. tremuloides* competition has been shown to decrease growth of *Picea* spp. after the first few years (Day and Harvey 1981, Van Cleve and Viereck 1981). Growth of *Picea glauca* on naturally regenerating, rich, mixedwood sites was slower than in pure *Picea* spp. plantations on poorer sites, suggesting that *P. tremuloides* competition was severe (Day and Bell 1988). Suppressed *P. glauca* required 8.7 years to reach breast height (1.4 m), while free-growing *Picea* spp. only required 7.1 years (Cayford 1957). Waldron (1964) reported that *P. tremuloides* suckers hinder *Picea* spp. seedling growth more than overstorey *P. tremuloides*.

In contrast to these findings, *Betula* spp. are known to benefit *Picea* spp. by reducing temperature extremes, preventing insect attack, improving soil conditions and decreasing weed and grass competition (Gardiner 1968). *P. tremuloides* also protects *Picea* spp. from frost and extreme temperatures (Navratil *et al.* 1991). Mixed species stands are thought to have a greater stability, greater resistance to spread of conifer root rot, better nutrient cycling, and higher soil pH than pure conifer stands (Navratil *et al.* 1991). There is some evidence that growth of individual *P. glauca* tends to be best under *P. tremuloides* canopies, possibly because *P. tremuloides* limits its initial density (Jarvis *et al.* 1966).

2.3.11 Typical Boreal Mixedwood Succession

The preceding sections have reviewed individual components (disturbance nature, initial regeneration, canopy dynamics, understorey dynamics, etc.) of general boreal forest succession in relation to successional theory, as well as some general interactions of vegetative components of these forests (canopy/understorey, hardwood/softwood) with each other. This section will review more specifically the literature which describes actual stages of boreal mixedwood succession.

Two types of canopy succession occur commonly in upland boreal aspen-spruce mixedwoods of western Canada following disturbance. In the case of severe disturbance that produces exposed mineral soil, *Picea glauca* regenerates almost simultaneously with *Populus tremuloides* (Peterson 1988, Delong 1991). If the fire is light, or *Picea* spp. seed is unavailable, *Picea glauca* will seed in 20 to 40 years after fire, when *P. tremuloides* density has declined and low-growing, less competitive species occupy the understorey (Peterson 1988, Delong 1991). Suppressed *P. glauca* penetrates the *P. tremuloides* canopy between ages 50 and 75, while free-growing *Picea* spp. will exceed *P. tremuloides* in height between ages 40 and 65 (Johnson 1986). Spruce will eventually dominate the site if disturbance does not interrupt succession. Sites with *Betula papyrifera* as the dominant hardwood follow a similar successional path (Delong 1991).

In northern Ontario, fire originates most natural mixedwood stands (MacLean 1960). *P. tremuloides* and *B. papyrifera* vegetative regeneration is usually high following light fires which do not damage roots. Fire favours *Picea mariana* regeneration by exposing mineral soil, consuming humus, destroying competitive vegetation, but preserving *P. mariana* seed in cones on the inner branches of the trees. Since fire destroys seedlings and fallen seed, *Abies balsamea* and *P. glauca* are often scarce in burned mixedwoods. However, *P. glauca* will increase in importance if fire

occurs before a good seedfall. If mixedwoods are burned in early stages of succession, absence of mature trees to provide seed will prevent conifer reproduction, but hardwoods will regenerate well vegetatively. Succession depends partly on soil depth, with mixedwood stands on shallow sites regenerating well (commonly to *P. mariana* dominated stands following fire or harvest), as long as erosion does not occur (MacLean 1960).

Day and Harvey (1981) outlined the typical succession of a boreal mixedwood forest in northern Ontario following fire. *Populus tremuloides* and *B. papyrifera* dominate up to 25 years postfire, being two to four times taller at this stage than *P. mariana* and *P. glauca* and also taller than the scarce *Pinus banksiana*. All of these species are pioneers, establishing at about the same time, shortly after fire. Crown closure is almost complete by 25 years, and therefore few *A. balsamea* seedlings establish at this stage. By 50 years after fire, the canopy has become less dense due to self-thinning. The fast-growing pioneers (*P.tremuloides*, *B. papyrifera* and *P. banksiana*) begin to decline in vigour, releasing the slower-growing pioneers (spruces). *Acer spicatum*, *Corylus cornuta* and *A. balsamea* regeneration have become abundant in the understorey beneath the hardwood canopy, but as the dominance begins to shift to *Picea* spp., root competition increases and light intensity decreases, suppressing the understorey. At 75 years after fire, *P. mariana*, *P. glauca* and *P. banksiana* have either taken over dominance of the canopy, or share it with the fast-growing pioneers, though many of the *B. papyrifera* and *P. tremuloides* are dead or dying at this point. Canopy openings, created by the dying pioneer trees, allow growth and spread of the previously suppressed *A. balsamea* and shrub species. By 125 years postfire, *Picea* spp. dominate the upper canopy, with most pioneer hardwoods dead and only a few remaining *P. banksiana*. *Abies balsamea*, *A. spicatum* and *C. cornuta* dominate both the mid and lower understorey at this stage, preventing reproduction of other species. If no fire occurs, the *Picea* spp. may continue to dominate to 150 or 200 years postfire (Day and

Harvey 1981). The presence of *Thuja occidentalis* often increases in older boreal mixedwood forests (Hughes 1967, Janke *et al.* 1978).

Van Cleve and Viereck (1981) described a similar succession for upland sites on south facing slopes following fire in Alaska, but included more detail about the understorey strata. No live vegetation occurred for the first few days to weeks after fire. This was followed by a herb and tree seedling stage, marked by germination of light-seeded species (*Epilobium angustifolium* L. and *Salix* spp.) and of buried seed (*Geranium bicknelli, Corydalis sempervirens* (L.) Pers.), as well as sprouting of *Viburnum edule* (Michx.) Raf., *Rosa acicularis*, *Salix* spp., *P. tremuloides* and *B. papyrifera*. Mosses and liverworts, especially *Marchantia polymorpha* and *Ceratadon purpurea*, also invaded in this period, on exposed mineral soil. The next stage, a shrub and tree sapling stage, was dominated by dense shrub cover (up to 50%) and hardwood regeneration (up to 30,000 stems/ha). Spruce seedlings were also abundant, but slow-growing, and pioneer mosses and herbs declined due to the shade and dense hardwood litter. By 25 to 50 years after fire, a dense hardwood (*P. tremuloides* and *B. papyrifera*) forest had developed, shading out the *Salix* spp. and most herbs (<10% cover). *Viburnum edule* and *Rosa acicularis* prevailed, since they have a high shade tolerance, and some *Hylocomium splendens* (Hedw.) BSG. and *Pleurozium schreberi* established on mounds, although the heavy litterfall prevented development of a continuous moss carpet. The hardwoods continued to dominate for another 50 years, with *P. glauca* saplings developing in the understorey. The canopy began to open with only about 700 stems per ha of *P. tremuloides* and 300 stems per ha of *B. papyrifera*. The opening canopy allowed a much better development of the understorey, with *Rosa acicularis*, *Viburnum edule* and *Alnus crispa* (Ait.) Pursh comprising a loose shrub stratum, and lower shrubs beneath them (*Linnaea borealis, Vaccinium vitis-idaea* L. and *Ledum groenlandicum*). *Equisetum arvense* L. and *Cornus canadensis* replaced *Epilobium angustifolium* and *Calamagrostis canadensis* which characterized earlier stages. The

mosses, including *Polytrichum* spp. and *Dicranum* spp., now comprised about 5% cover. At about 100 years after fire, the canopy was either dominated by *P. glauca* alone, or shared dominance with the remaining hardwoods. Tree density at this stage was about 500 trees per ha. Hardwoods continued to fall out of the canopy as the forest aged. *Rosa acicularis* and *Viburnum edule* were still common, as were *Cornus canadensis* and *Equisetum arvense*, but feathermosses now formed a dense carpet. By 200 years post-fire, this carpet was continuous, and the *B. papyrifera* had fallen out of the canopy completely. The fate of the stand beyond this stage is unknown, but *P. glauca* does not reproduce well beneath its own canopy, so it could not continue to dominate. Most stands are destroyed by fire at this stage or before it (Van Cleve and Viereck 1981).

2.4 EFFECT OF HARVESTING ON CANOPY REGENERATION

The most common harvesting practice in the boreal forest is clearcutting conifers to a diameter limit (usually 10 cm dbh), often leaving hardwoods standing (Hosie 1954, Endean *et al.* 1971, Frisque *et al.* 1978, Chrosciewicz 1980). Prior to 1960, most boreal harvesting in eastern Canada was done by hand-felling and horse-skidding to the roadside, often by the shortwood method (Weetman and Frisque 1977, Brumelis and Carleton 1989). With the advent of mechanical logging in the early 1960s, the amount of site disturbance increased due to the greater use of wheeled skidders (Brumelis and Carleton 1989).

Natural regeneration after logging is affected by damage to advance regeneration, disturbance to the forest floor and slash remaining after harvest (Yang and Fry 1981). Hosie (1954) noted that logging practices in the boreal forest of Canada were failing to provide the two requirements for successful regeneration of desired (conifer) species: 1) the seed or living part of the tree and 2) a favourable seedbed or conditions for growth.

Various partial cutting systems in non-boreal forests have succeeded in

enhancing regeneration of desired commercial species, e.g. partial cutting of mixed conifer stands in Oregon (Seidel and Head 1983); single-tree selection, group selection, shelterwood and seed tree methods for *Pinus ponderosa* Laws. and more tolerant species in California (McDonald 1976); and patch clearcuts (Marquis 1965, Hatcher 1966), strip clearcuts (Robitaille and Roberge 1981) and shelterwood cuts with scarification (Tubbs and Metzger 1969) for *Betula alleghaniensis* Britt. in northern hardwood forests. In the past, alternatives to clearcutting were attempted to promote natural regeneration of conifers in boreal stands (Steneker 1963, Lees 1964, Hughes 1967, Jablanczy 1967, Jarvis and Cayford 1967, etc.). Recent studies focus on the different effects of whole-tree and tree-length clearcutting (e.g. McInnis and Roberts 1991). This section will review the effect of different harvesting systems and methods on the various factors that determine regeneration of tree species in the boreal forest.

2.4.1 Effect of Harvesting on Residual Stand

The harvest method determines the amount and distribution of residual trees, influencing the post-harvest growth and survival of these trees. Clearcutting of softwoods for pulpwood leaves few residual trees, mainly large hardwoods and small (<13 cm dbh) softwoods (Frisque *et al.* 1978). High mortality of residuals commonly follows some cutting methods in the boreal forest. In *Picea mariana* upland sites in Manitoba (Jarvis and Cayford 1967), mortality due to windthrow was high in all types of partial cuts (alternate strip, uniform shelterwood, group selection and patch clearcut), and exposure was the expected cause of further mortality in some intermediate and suppressed standing trees. Risk of windthrow in stripcutting increases as cut-strip width increases and residual-strip width decreases (Jablanczy 1967). However, a strip-cutting trial in *P. mariana* upland stands in northwestern Ontario indicated that mortality was only 2.4% to 4.0% higher than that following clearcut operations (Fleming and Crossfield 1983). Since windfall and mortality were greatest

within 10 m of the exposed edges of the strips, long, wide leave strips, with only one open end, were recommended. Group cutting of *P. mariana* -feather moss stands in northwestern Ontario did not affect their windfirmness, with losses of less than 1% of the uncut timber (Losee 1961).

In an Alberta mixedwood study (Lees 1964), seven softwood removal methods (from removal of 47% of *Picea* spp. volume to clearcutting), all resulted in low mortality and windfall of residual *Picea* spp. However, removal of *Populus tremuloides* in similar stands predisposes residual *Picea glauca* to windthrow, especially in dense stands or on shallow soils, where root development of *P. glauca* is poor (Johnson 1986). Early release of *P. glauca* increases windfirmness by allowing rapid root development. Therefore, to protect residual *P. glauca* from wind damage, approximately 25% of the *P. tremuloides* canopy should be left when mixedwood stands are harvested (Johnson 1986). Standing girdled or poisoned *P. tremuloides* may also protect the young *Picea* spp. from wind, as long as they do not damage the leaders by whipping (Johnson 1986). To prevent such damage, *P. tremuloides* should be removed before the *Picea* spp. reaches the overstorey (Steneker 1963).

A two-stage harvest has been proposed to protect understorey *P. glauca* in western Canada mixedwood stands (Brace and Bella 1988, Brace 1991). *Populus tremuloides* is harvested at 60 years old, when *Picea* spp. is about 40 years old; any *Picea* spp. greater than 25 cm dbh are also harvested at this time. The mature *Picea* spp. and the 60 year old sucker-origin *P. tremuloides* are then harvested 60 years after the initial cut. This should provide the young *Picea* spp. with protection from windthrow and stem weevilling, while releasing it early enough to improve its growth and minimize whipping damage.

The growth of residual *Picea* spp. in boreal stands has been examined in several studies. In Jarvis and Cayford's Manitoba study (1967), residual stand development on *P. mariana* upland sites was poorest in stands subjected to uniform shelterwood and

patch clearcuts. In Lees' Alberta study (1964), net stand volume increment, and percentage volume growth was greatest in shelterwood cutting, while individual stem increment was highest on clearcut and seed tree treatments. Recruitment to merchantable size (18 cm dbh) was good in all of the partial cutting methods and greatest on shelterwood cuts, due to a good seed supply, shelter for advance regeneration, little opportunity for invasion of competitors and accelerated growth of residual crop trees. Jarvis *et al.* (1966) noted that two-stage shelterwood cutting in Manitoba, with the first cut made at age 70 to 80 years, leaving the hardwoods and 9.2 to 13.8 m2 BA/ha of *Picea* spp., showed promise of a greater volume of *P. glauca* at rotation age than did other cutting methods. Removing *P. tremuloides* from 60-year old mixedwood stands in Manitoba improved *P. glauca* growth considerably; volume of *P. glauca* in the light release treatment (44% of stand BA removed) was double that on the control, and in the heavy release treatment (60% of stand BA removed) it was triple that on the control, while height growth on treated plots was approximately twice that on controls (Steneker 1963).

In general, *P. glauca* responds to release from *P. tremuloides* at all ages and sizes, although release at 30 to 40 years old produces the largest growth increment for a given intensity of release; the degree of the increment depends on the intensity of the release cut (Jarvis *et al.* 1966). Yang (1989) noted that the largest increase in diameter and height growth of *Picea* spp. in response to release from *P. tremuloides* occurs in young or intermediate-age stands (*Picea* spp. 15-40 years of age). However, release should not occur before the *Picea* spp. is 3.5 m tall or 25-30 years old, or new *P. tremuloides* sprouts may overtake the young *Picea* spp. (Yang 1989).

2.4.2 Effect of Harvesting on the Seedbed (Microsite)

Mineral soil, well-decomposed humus and rotten wood are generally cited as the best seedbeds for *Picea* spp., *Abies balsamea* and *Pinus* spp. reproduction in the boreal

forest (Fraser *et al.* 1976, Weetman 1980, Delong 1991). In the boreal mixedwood forests of Ontario, *Picea* spp. and *A. balsamea* seedlings survive best on mixed humus and mineral soil, and better on well-decomposed humus than on plain exposed mineral soil (MacLean 1960). In undisturbed forests, most *Picea* spp. regeneration is on rotten stumps or logs, since such seedbeds are elevated, reducing competition for light and eliminating accumulation of leaf litter (MacLean 1960). *Picea* spp. reproduction on the undisturbed forest floor is poor due to its small seed and related small root size of seedlings; *A. balsamea* has a larger seed and initial roots, and therefore fares a little better (MacLean 1960). Some media may be suitable seedbeds only under certain conditions, e.g. *Pleurozium schreberi* is generally a good seedbed when moist, but not when dessicated from exposure following harvesting (Auld 1975, Fraser *et al.* 1976). Slow-growing, compact sphagnum moss, e.g. *Sphagnum capillaceum* creates a good seedbed for *Picea mariana* (Fraser *et al.* 1976), whereas rapidly growing, loose-knit sphagnum, e.g. *Sphagnum girgensohnii* Russ. allows seed to fall among its stems and become smothered (Auld 1975).

Seedbed conditions, seedling environment, competiton, and seedbank distribution, which affect composition of regeneration, are all affected by the nature and intensity of the disturbance (Roberts and Dong 1991). In past decades, harvesting, especially clearcutting, often destroyed the seedbed required for desired commercial species (Hosie 1954). Clearcutting creates an environment very different from that under the forest stand (Endean *et al.* 1971, Freedman 1992); it encourages growth of competitive species and creates high seedbed temperatures, high light intensity, and moisture extremes, all detrimental to *Picea* spp. seedling establishment and growth (Jablanczy 1967, Endean *et al.* 1971, Marek 1975). Clearcutting leads to higher wind speeds, increased occurrence and deeper penetration of frost into soil layers, and altered precipitation effects, e.g. increased impact of rain (Endean *et al.* 1971) and deeper, denser snow accumulation (Powell 1971). Rates of oxidation and decomposition are

higher in a clearcut than in a forest stand (Endean *et al.* 1971). Therefore, if regeneration from natural seeding is expected for *Picea* spp., clearcuts must be relatively small (less than 16 ha) in order to preserve the moderating effects of the stand margins, which extend only two to three tree heights into a clearcut (Powell 1971, Freedman 1992).

Seedbed conditions following clearcutting of Ontario boreal mixedwood stands are generally unsuitable for conifers for several years after a cut, with litter and humus drying out, and understorey vegetation density increasing (MacLean 1960). Conditions for conifer regeneration do not improve until about 20 years following a cut, when a new canopy has started to develop, and residual wood on the forest floor has begun to decompose (MacLean 1960). Dried feathermosses lose their nutrient storing ability, becoming unsuitable *Picea* spp. seedbeds (Marek 1975, Chrosciewicz 1980). They decompose slowly due to slash cover, and may be eroded from shallow sites, leaving only bedrock (Marek 1975).

Unless there is some soil disturbance during harvesting, regeneration of *Picea* spp. and *A. balsamea* is very poor (Weetman *et al.* 1973). Since they regenerate mostly from post-harvest germinants, *Pinus banksiana* and *Betula papyrifera* stocking on harvested areas is closely related to the amount of exposed mineral soil and good light conditions (MacLean 1960, Van Nostrand 1971, Ellis and Mattice 1974). On many clearcut boreal sites, less than 30% of the area has any soil disturbance and less than 15% has exposed mineral soil and/or mixed mineral soil and organic matter; most of this area consists of skid roads and landings (Arnott 1968, Webber *et al.* 1968, Ellis and Mattice 1974). On average, 60% or less of the area on harvested (mostly mechanically-skidded) sites has some surface disturbance, while for horse-skidded sites this is generally less (~10-35%), with most disturbance being very light (Webber *et al.* 1968). Where soil disturbance does occur, it is often extreme and detrimental, e.g. exposure of subsoil or bare rock (Ellis and Mattice 1974). Both tree-

length, tractor-skidded and full-tree, wheel-skidded logging provide limited scarification and may cause compaction of slash and of the forest floor (Horton 1965).

In a test of several cutting methods (alternate strip, shelterwood, group selection, patch and clearcut) in *Picea mariana* upland sites of Manitoba, the most favourable seedbeds (sphagnum moss, decayed wood, mineral soil and hair-cap moss) were scarce in all harvest types, while seedbeds unfavourable for *P. mariana* regeneration (feather mosses, litter and slash) were abundant (Jarvis 1961). Strip cuts in *P. mariana* stands in northern Ontario had a higher stocking percentage and lower rate of regeneration failure than did clearcuts, partly due to the protection from dessication and high temperatures that the residual strips provide (Fraser *et al.* 1976). However, the microsite for *P. mariana* regeneration was best on moist drainageways and lower slopes; a high percentages of failure occurred on dry upland site types. Strip cuts in *P. mariana* provide three seedbeds suitable to *Picea* spp. regeneration: moist sphagnum, exposed mineral soil and moist duff (Auld 1975). Sphagnum moss and exposed mineral soil had the most *P. mariana* regeneration on stripcuts in Newfoundland, but *Picea* spp. growth was best on exposed mineral soil and humus seedbeds, and poorest on sphagnum and decayed wood, due to lack of nutrients in sphagnum and moisture deficiency in decayed wood (Van Nostrand 1971). *Betula papyrifera* seedlings grew almost exclusively on mineral soil. Although narrow cut strips (about equal to stand height) promote dense seedling establishment, seedling survival may be better on wide cut strips (more than twice the stand height), since the improved insolation speeds up decomposition and nitrification (Jablanczy 1967). However, dessication of the seedbed is greater when cut strips are wide and residual strips are narrow.

Jablanczy (1967) reported uniform shelterwood cutting to be the best method for natural regeneration of *Picea glauca*, since it prevented the microclimatic extremes created by clearcutting. In Alberta mixedwoods, shelterwood cuts, in conjunction with scarification, produced 85% milliacre stocking of *P. glauca* after 4 years; on

unscarified seedbeds, the stocking was only 30% (Lees 1970). Jablanczy (1967) stated that group cuts caused microclimatic conditions unsuitable for *P. glauca* reproduction, and were the least effective cutting method. However, seedbed conditions in group cuts in *P. mariana* stands were reported to be very suitable to *P. mariana* regeneration (Losee 1961). Large areas of feathermosses, the worst *Picea* spp. seedbeds, dried out and died following group cutting, while sphagnum mosses, the best seedbeds for germination, increased in cover from 11.1% to 24.3%.

Slash can have both beneficial and detrimental effects to germination and survival of tree seedlings (McInnis and Roberts 1991). It can impede growth of tree seedlings physically (Hall 1977) or by detrimental shading (Day 1964), but if it is uniformly and lightly distributed, it can enhance reproduction by providing shade that reduces evaporation and soil surface temperature fluctuations (Ellis and Mattice 1974, McInnis and Roberts 1991). Both tree-length and short-wood logging systems leave a large amount of slash in the form of tops and branches on cutovers (Auld 1975). Dense slash covered 5.6% of the ground immediately after clearcutting in *P. banksiana* and *P. mariana* stands of northwestern Ontario and still covered 2-4% 9 years later (Ellis and Mattice 1974). Branches and foliage contain a large proportion of the total nutrient content of trees (Weetman and Webber 1972, Mann *et al.* 1988). Thus, nutrient losses to the forest site can be 50% to over 200% greater in full-tree and whole-tree harvesting than in conventional tree-length harvesting (Timmer *et al.* 1983, Freedman and Duinker 1986, Maliondo 1988, Mann *et al.* 1988). Although these losses are usually small compared to nutrient reserves in the forest floor, they may be high for particular elements such as phosphorus, potassium and calcium (Freedman and Duinker 1986, Gordon 1983). Nutrient losses from full-tree and whole-tree harvesting may be greater for particular species and forest types, such as *A. balsamea* (Timmer *et al.* 1983) and hardwoods (Maliondo 1988), due to the high crown to stem ratio for these species. Effects of nutrient losses depend on site quality, with nutrient-poor and

shallow soil sites being much more vulnerable (Gordon 1983, Maliondo 1988).

In general, mechanical logging creates non-uniform conditions on sites, i.e. patchy distribution of slash piles, ground disturbance and surviving advance growth; this leads to variable stocking, density and size of reproduction (Weetman and Frisque 1977).

2.4.3 Site Preparation Affects Seedbed and Regeneration

Some form of site preparation is generally applied to ensure successful *Picea* spp. regeneration in boreal mixedwoods (Jarvis *et al.* 1966, Gardner 1980, Armson 1988). Without additional treatment following harvest, natural regeneration of *Picea glauca* in boreal mixedwoods of western Canada is inadequate, due to poor seed supply, poor seedbeds and rapid revegetation by competitive species (Navratil *et al.* 1991). Scarification provides receptive seedbeds for *Picea* spp. by removing slash and deep duff and exposing mineral soil and decomposed humus (Fraser *et al.* 1976), as well as by reducing shrub and hardwood competition (MacLean 1960).

In clearcut hardwood stands of New Brunswick, scarified plots had more amenable temperatures and moisture content, and therefore higher germination and lower seedling mortality than did unscarified plots (Roberts and Dong 1991). On shelterwood cuts in Alberta mixedwoods, milliacre stocking of *P. glauca* regeneration was 85% on scarified seedbeds compared to only 30% on unscarified seedbeds (Lees 1970). Scarification on *Picea mariana* stripcuts in Ontario provided a suitable seedbed for all species except *Abies balsamea*, resulting in higher stocking of *P. mariana*, *Betula papyrifera* and *Pinus banksiana* than on unscarified strips (Jeglum 1983). Scarified stripcuts in *P. mariana* stands in Newfoundland had higher stocking and much higher densities of both *P. mariana* and *B.papyrifera* regeneration than did unscarified strips (Van Nostrand 1971). Scarification in several cutting methods on *P. mariana* sites in Manitoba increased favourable seedbeds (sphagnum moss, decayed wood, mineral soil and

hair-cap moss) from 5% to 62% of the area, with intermediate seedbeds (humus, and mixes of organic matter and soil) occupying 20% of the area, and poor seedbeds (feather moss, litter and slash) only 18%; this resulted in improved seedling height growth and stocking on scarified areas (Jarvis and Cayford 1967).

If successful, scarification and planting of harvested boreal mixedwood sites truncates the 'natural' successional sequence that follows harvest disturbance on these sites, since scarification decreases and delays hardwood and shrub species' development, and destroys conifer advance growth (McNichol and Timmerman 1981), while planting increases the *Picea* spp. component of regeneration in comparison to natural stands (Morris *et al.* 1988). Scarification alone can aid *Picea* spp. regeneration by controlling shrub and herb competition and reducing the smothering effect of hardwood leaves, but it is not useful in all stand and site conditions (MacLean 1960). Exposure of mineral soil or humus is necessary, and this is only useful for sandy loams, loams and well-decomposed humus, since exposed fine-textured mineral soils are prone to crusting of surfaces, poor aeration and frost-heaving, while poorly decomposed humus rapidly becomes dessicated (MacLean 1960). Timing of scarification influences composition of natural regeneration; *P. glauca* regeneration is better if scarification is done in a good seed year, rather than the year of harvest (Navratil *et al.* 1991). Scarification a few years prior to harvest favours seeding in of spruces rather than their hardwood competitors, and reduces shrub and herb competition (MacLean 1960). In Alberta mixedwoods, scarified areas in experimental cuttings produced better density and stocking of *P. glauca* regeneration in all cutting treatments than did unscarified areas; seedling growth was better even on scarified plots in unharvested stand than on unscarified plots beneath a partially cut stand (Quaite 1956).

Prescribed burning is an efficient way to control *P. tremuloides* competition and remove *A. balsamea* advance growth (Armson 1988). However, a complete burn of the forest floor is unsuitable; alternating patches of exposed mineral soil and a thin residual

mor are best for upland sites; burning of the loose, surface moss and litter only is best for peatlands (Chrosciewiez 1980). Auld (1975) recommended slash burning immediately after *P. mariana* strip-cutting. This would release nutrients in the slash and allow immediate scarification, encouraging rapid seeding in and growth of *P. mariana* before windfall occurred in the residual stands.

Site preparation can have negative effects on conifer seedbeds, causing erosion, nutrient loss, soil drying, frost heaving, germination of competitor species' seed, and redistribution of large seeds (Jeglum 1983, Brand 1991, Roberts and Dong 1991). Mixedwood forests tend to grow on sites with highly variable soil conditions and terrain, which make mechanical site preparation difficult and not very effective (Armson 1988). Scarification can cause flooding of wet sites, decreasing survival of *P. glauca* reproduction in *P. tremuloides-P. glauca* mixedwoods (Lees 1970). Scarification can destroy advance growth of conifers, lengthening a stand's reproductive phase (McNichol and Timmerman 1981, Jeglum 1983). Prescribed burning can cause competition problems for conifer regeneration, since it stimulates the growth of large numbers of dormant shrub seeds (McDonald 1976).

2.4.4 Effect of Harvesting on Seed Supply

Clearcutting of conifers results in insufficient conifer seed for natural regeneration (Hosie 1954, Jeglum 1983, Ruel 1991). The clearcut area is often too large to allow for seeding in from adjacent stands (Webber *et al.* 1968, Harvey and Bergeron 1989). In addition, the seed supply from serotinous cones that is available following fire is unavailable after any type of harvesting (Weetman 1980).

Marek (1975) outlines several reasons for lack of seed after clearcutting versus after fire. Following fire, some live and/or dead *Picea mariana* trees are left standing; their seed is dispersed for several years over the entire burned site. By contrast, in large clearcuts, many *P. mariana* cones are crushed into the ground by machinery, and

those on the underside of felled crowns rot instead of opening. Cones on the upper side of the crowns may dry, but release seed only in the immediate vicinity of the crown. Snowfall will eventually crush the fallen crowns, rendering the remaining seed useless by 3 years post-harvest (Marek 1975). Tree-length clearcutting in Quebec *P. mariana* stands left only poorly developed and suppressed seed trees, incapable of seeding for several years, by which time seedbeds would be poor (Arnott 1968).

Several studies have shown that strip cutting in *P. mariana* stands produces higher stocking and/or density of *P. mariana* regeneration than does clearcutting, due to a lack of seed supply in the latter (Jeglum 1983, Van Nostrand 1971, Fraser et al 1976). Stripcutting provided adequate seed supply to regenerate the first cut strips satisfactorily (Auld 1975, Verry and Elling 1978), but regeneration in the leave strips was poor after the final cut (Verry and Elling 1978) and the problem of regenerating these strips naturally has not been solved (Fraser *et al.* 1976). Seed supply in strip cuts depends on the strip width and leave time of the residual strips. Narrow cut strips promote dense seedling establishment (Jablanczy 1967). Van Nostrand (1971) found that it took 5 to 10 years to attain adequate stocking (47% to 56%) of *P. mariana* on stripcuts, while Fraser *et al.* (1976) reported *Picea* spp. regeneration to be better in 4 to 6-year old strips than in either older or younger cuts. In order to obtain satisfactory conifer regeneration, clearcuts no larger than 16 ha (40 acres) and stripcuts of no greater than 200 m (10 chains) in width have been recommended (Endean et al 1971).

Limited tests of other harvest systems indicate achievement of satisfactory conifer seed supplies. Residual *Picea glauca* of shelterwood cuts in Alberta mixedwoods provided adequate seed for regeneration; 85% milliacre stocking was attained on scarified seedbeds (Lees 1970). Group cutting (in circles of 14 to 20 ft diameter) of *P. mariana*-feather moss stands in northwestern Ontario provided abundant seed to cover all parts of the clear-cut groups (Losee 1961). Thinning around the cut circles allowed crown expansion and increased seed crops. Tree-length systems of harvesting may

create a more clumped pattern of conifer regeneration than do full-tree systems, since seed-bearing cones are limited to the area around the felled crowns in the first method, while in the second, cones are distributed more evenly by some falling off of the crowns during skidding (Horton 1965).

Harvest systems may have different effects on seeding of non-conifers. Fraser *et al.* (1976) reported that species other than *P. mariana* had significantly more regeneration in clearcuts than in stripcuts. Residual hardwoods may produce a stress crop of seeds, which may germinate well, especially if scarification is applied (Jeglum 1983).

2.4.5 Effect of Harvesting on Advance Regeneration

Advance growth plays a very significant role in regenerating boreal forest cutovers (Hosie 1954, Stanek 1968, Ruel 1991). As previously noted, harvesting practices in boreal forests often destroy the seed supply and do not often provide the seedbed required for desired species such as *Picea* spp. and *Abies balsamea*; regeneration of these species is therefore often dependent on advance growth (Hosie 1954, MacLean 1960). In mature *A. balsamea-B. papyrifera-Picea* spp. forests of Quebec, advance regeneration accounted for 90% of all conifer seedlings in 3 to 8 year-old cutovers, despite heavy losses during harvest (Harvey and Bergeron 1991). In cutovers across eastern Canada, most of the post-harvest *A. balsamea* and *Picea* spp. regeneration was found to be advance growth (Weetman *et al.* 1973).

Jablanczy (1967) stated that uniform shelterwood cutting provides the best conditions for *Picea glauca* advance regeneration, preventing mortality from drought and dense slash, conditions common after clearcutting. The preparatory cut speeds up decomposition of humus and reduces moss cover, allowing increased root development of seedlings and better nutrient availability. Stripcuts can also be effective, with advance growth survival best in narrow residual strips, due to accelerated nitrification caused

by increased insolation (Jablanczy 1967). However, Fraser *et al.* (1976) found no difference in the survival of *Picea mariana* or other species' regeneration between 2-chain and 5-chain wide first-cut strips. Following stripcutting in *P. mariana* dominated stands in northern Ontario, Jeglum (1983) noted that absolute seedling stocking of *P. mariana* was constant but that for *A. balsamea* decreased greatly. This drop was likely due to high mortality of advance growth by exposure and limited seeding in (Jeglum 1983).

Several boreal forest studies have noted that horse-skidding damages and kills less conifer advance growth than does mechanical skidding (Horton 1965, Ellis and Mattice 1974, Brumelis and Carleton 1989). Horton (1965) stated that the shortwood horse-logging was the least damaging to advance regeneration while mechanized methods (tree-length system with tractor skidders, full-tree system with wheeled skidders) virtually eliminated advance growth. He also noted that full mechanization of the shortwood system would likely be as damaging as the other mechanized methods. Conversely, in Alberta subalpine forest cutovers, conifer stocking (advance growth and/or post-harvest regeneration) was higher on sites harvested by crawler tractors than by horses (Day and Duffy 1963). Although partial cutting with horse-skidding preserved more conifer advance growth than clearcutting with mechanical skidding in boreal forests of eastern Canada (Webber et al 1968), clearcutting with 16-foot horse-skidding was more damaging to advance growth than most mechanized methods (Frisque et al 1978). On *P. mariana* lowlands of northeastern Ontario, older harvested stands, likely horse-logged, generally had higher *P. mariana* and *A. balsamea* density and lower *P. tremuloides* density than younger, mechanically harvested stands (Brumelis and Carleton 1988). This may have been partly due to wheel-skidding creating a nutrient-enhanced substrate, more favourable to hardwood competitors than to conifer advance regeneration.

Thus, the onset of heavy mechanization of harvesting in boreal stands in the

1960's increased the loss of advance growth during harvesting (Ruel 1991). Tree-length wheeled-skidder logging decreased density (by 73% to 96%) and stocking (by 14% to 55%) of conifer advance growth in *P. mariana* stands in Quebec, resulting in stocking ranging between 19% and 85% (Arnott 1968). Mechanical clearcutting and whole-tree skidding in mature *A. balsamea-B. papyrifera-Picea* spp. forest of the Quebec Clay Belt reduced stocking of softwood regeneration to only 40% and density to 8% of the preharvest total (65,000 stems per hectare, 97% of this being *A. balsamea*) (Harvey and Bergeron 1991). In addition to the destruction of conifer advance growth, mechanical harvesting also greatly decreases density of hardwood advance regeneration (Harvey and Bergeron 1989).

Forwarders have been found to destroy less conifer advance growth than mechanical skidders (Frisque *et al.* 1978, Ruel 1991) but where skidders were used, Ruel (1991) found no significant difference in advance growth survival between the use of feller-bunchers and chainsaws, nor between the full-tree and tree-length methods. Although all sites were adequately stocked (≥60%) after 5 years, sites harvested with a feller-forwarder had the highest stocking (Ruel 1991). In eastern Canada cutovers, tree-length and full-tree harvesting with rubber-tired skidders, the most common systems applied, destroyed 72% and 75% of softwood advance growth stems respectively, reducing stocking by 27% and 20% (Frisque et al 1978). Tree-length and full-tree mechanized harvesting in New Brunswick mixedwood stands apparently caused similar mortality of most tree and shrub species' advance growth (McInnis and Roberts 1991). However, severe defoliation of understorey shrubs and trees, likely due to the sweeping effect of the skidders, gave the appearance of much higher mortality in the full-tree harvested sites; the resulting exposure would likely lead to further mortality. More shade and slash cover on tree-length harvested sites would likely provide better protection from dessiccation, exposure, competition and predation of the seedlings and advance growth (McInnis and Roberts 1991). In contrast, Arnott (1968)

stated that heavy slash and shading would inhibit surviving advance growth on tree-length skidded sites in *P. mariana* stands of Quebec. Advance growth destruction is generally proportional to the amount of machine travel on a site, and residual stems on most mechanically-logged sites are poorly distributed (Webber et al 1968).

Harvesting can have a beneficial effect on advance growth, releasing it earlier than would occur in an undisturbed, naturally deteriorating stand, and thereby reducing susceptibility to browsing damage, disease or weakness from prolonged suppression (MacLean 1960). Furthermore, removal of the hardwood overstorey in mixedwood stands at an early stage (conifers 25 to 35 years old) can prevent destruction of conifer leaders by whipping, producing better conifer growth (Shirley 1941, Peterson et al 1989). Therefore, boreal mixedwood crops resulting from harvesting are likely to be superior to those regenerating slowly from undisturbed stands, the latter often becoming shrublands (MacLean 1960).

2.4.6 Harvest Stimulates Vegetative Reproduction (Hardwoods)

Clearcutting creates ideal conditions for hardwood suckering (Hosie 1954, MacLean 1960, Jeglum 1983, Harvey and Bergeron 1989). As the intensity of site disturbance caused by harvesting increases, so does the development of species that are competitors of conifers (Clemmer and Atkins 1980). Hardwood presence in the initial stand does not have to be high to generate a large number of *Populus tremuloides* suckers: a volume of 26 m3 per ha and density of 25-50 trees per ha can produce over 10,000 suckers per ha (Navratil *et al.* 1991). If hardwoods are not cut in boreal mixedwood harvests, *Betula papyrifera* reproduces principally from seed; if cut, it reproduces by both seed and stump sprouting (MacLean 1960). *Populus tremuloides* regenerates on cutovers primarily by suckering, regardless of whether it is cut or not. *Betula papyrifera* is less aggressive than *P. tremuloides* in regenerating cutover sites, producing a small group of coppice stems around the root collar of each cut tree. If *B.*

papyrifera are not cut, this occurs only where root collars are exposed to direct sunlight (MacLean 1960).

Hand-felling (chain saws) of conifers only, with mechanical skidding, reduces *P. tremuloides* suckering in mixedwoods stands, in comparison to fully mechanized harvesting with *P. tremuloides* removed (Schneider 1988). Harvesting only conifers can reduce *P. tremuloides* sucker density to one-tenth of that in clearcuts, by maintaining apical dominance and keeping soil temperature and light intensity low (Navratil *et al.* 1991). However, leaving small and defective hardwood trees standing encourages suckering of *P. tremuloides* and sprouting of *Acer spicatum*, which will dominate the regeneration (Day and Harvey 1981).

2.4.7 Harvest Affects Early Regeneration Success and Species Composition

Clearcutting of a forest can cause an extreme ecological conversion, including changes in species composition (Freedman 1992), but in many cases species' frequencies and abundances, rather than actual composition, are altered (Walsh and Krishka 1991).

Eight cutting treatments (ranging through no cutting, light partial, medium partial, heavy partial, shelterwood, diameter limit, seed tree, to clearcutting) were initiated in mature *Picea glauca-Populus tremuloides* stands of Alberta in 1951 (Quaite 1956, Lees 1964). *P. tremuloides* was left standing in all treatments, and scarification was performed in a portion of each treatment replication. Ten years after harvest, *P. glauca* regeneration stocking (10-30%) and density (260-1040 stems/acre) were poor in all cutting methods without scarification (Lees 1964). Although regeneration of *P. glauca* among light, medium and heavy partial cuts showed little difference, its height growth was best in the shelterwood treatment. *Populus* spp. regeneration was most abundant in the diameter limit cut, while *Betula papyrifera* regeneration was best in the

seed tree cut and the clearcut. Although the vigour and quality of *P. glauca* regeneration were high in all harvest treatments, hardwoods averaged 10 to 12 times taller than the tallest *P. glauca* seedlings. *P. glauca* seedling stocking was much better on scarified areas (50-82%), but on these it suffered severe competition from dense grass, *P. tremuloides* and *Populus balsamifera* suckers in the clearcut and seed tree methods compared to the various partial cuts (Lees 1964).

Several cutting methods were tried to promote *P. glauca* regeneration in *P. glauca-P. tremuloides* mixedwoods in Manitoba (Waldron 1964). Scalping in strips was performed in all trials. Best regeneration stocking (~33%) and density (3400 stems per acre) occurred on compartments where hardwoods were not cut and *Picea* spp. was partially cut. The lighter cutting of these two methods had better seedling survival and height growth. Ground vegetation and *P. tremuloides* suckers, induced by cutting, caused higher *P. glauca* mortality where hardwoods were removed, indicating that *P. tremuloides* suckers were more of a competitive hindrance to the *P. glauca* seedlings than were mature *P. tremuloides*.

In a test of several cutting methods in *Picea mariana* upland sites in Manitoba, natural regeneration stocking of *P. mariana* was very poor in unscalped areas of all cutting methods (<20%), but lowest on clearcuts (9%) (Jarvis and Cayford 1967). On scalped sites, it was much higher: 53% on clearcuts and over 70% on patch and strip cuts. Height growth of *P. mariana* seedlings on unscalped sites was best where there was no residual canopy.

Boreal forests originally dominated by conifers often become mixedwood or hardwood-dominated after harvest (Wein and El-Bayoumi 1983, Clemmer and Atkins 1980, Jeglum 1983). In some areas where *Picea* spp. is the desired species, *Abies balsamea* is left unharvested; this converts large areas to uneven-aged *A. balsamea*-dominated stands (Flowers 1981). In western Canada, rich sites that support pure and mixed *P. glauca* types are the most difficult sites to successfully regenerate following

harvest; conversion to *P. tremuloides*, *B. papyrifera* or shrub and grass-dominated sites are common (Weetman 1989).

As noted previously, clearcutting without seedbed treatment favours hardwood over softwood regeneration, and *A. balsamea* over *Picea* spp. regeneration by creating ideal conditions for suckering of *P. tremuloides* and other competitive species, but poor conditions for conifer germination; thus, *Pinus banksiana* and *P. mariana*, which rely largely on seed to reproduce, are uncommon (Hosie 1954, MacLean 1960, Flowers 1981, Weetman 1980, Yang and Fry 1981). Some *P. glauca* and *A. balsamea* advance growth generally survives harvesting, but not in abundance equal to the new hardwood regeneration (Hosie 1954).

Ten-year results of a survey of (mostly) clearcut boreal stands across eastern Canada showed an increase in the ratio of hardwoods to softwoods in most stands, with mixedwoods having the poorest results (41% of quadrats had a softwood as the best specimen of reproduction, 32% had a hardwood, and 26% a shrub). *Picea* spp. reproduction on these sites was very poor due to the heavy hardwood and brush competition (Weetman and Frisque 1977).

Clearcut mixedwood sites in the Clay Belt region of Ontario had well- to fully-stocked (75%) conifer regeneration, and a density of about 4300 conifers per acre, about 75% of the total density, but the *A. balsamea:Picea* spp. ratio on these sites was 3:1 (Candy 1951). Conifer reproduction was much poorer if fire followed harvesting, due to destruction of both advance growth and post-harvest regeneration, as well as the seedbed and any remaining seed trees.

Richardson (1979) reported that in 0-20 year-old clearcut forests (mostly *A. balsamea-B. papyrifera* mixedwood) in western Newfoundland, stocking, density and height was greater for hardwoods, including shrub species, than for softwoods on most sites. *A. balsamea*, the most common softwood, was generally highly stocked, despite the hardwood dominance. *B. papyrifera* was the most common hardwood, but *Acer spicatum*

had higher stocking on some sites. These results contrast with a previous study in the same area, in which only 5% of sites supported a higher density of *B. papyrifera* regeneration than *A. balsamea*, but that study did not examine the effect of shrub hardwoods (Hall and Richardson 1973).

Harvey and Bergeron (1989) reported a large decrease in softwood regeneration, and a shift from softwood dominated to mixed regeneration (the ratio of softwood to hardwood seedlings decreased from 6.3 to 0.8) following full-tree clearcutting and mechanical skidding in the Quebec Clay Belt. Due to *A. balsamea* dominance in the surviving softwood regeneration, they predicted that *P. mariana* and *P. glauca* would become an insignificant component of these mixedwood forests in the absence of planting or natural disturbance.

The softwood to hardwood shift appears to occur in response to harvest methods other than clearcuts as well. Partial cutting is unlikely to prevent this shift without some additional treatment, since shrub and herb growth is stimulated by opening the canopy, further hindering *Picea* spp. reproduction (MacLean 1960). Following stripcutting in northern Ontario *P. mariana* stands, Jeglum (1983) noted a shift in softwood to hardwood stocking ratio from 90:10 (overstorey) before harvest to 50:50 (seedlings) following harvest, with the density ratio following harvest being even lower: 40:60. The proportion of *Pinus banksiana* and *P. mariana* showed the greatest decrease, while that for *P. tremuloides* and *B. papyrifera* showed the greatest increase. Jeglum (1983) surmised that the formerly softwood-dominated forest would become a mixedwood without further treatment, unless the hardwoods were to drop out naturally by the next rotation.

In a boreal mixedwood study, partial cutting (some hardwoods left standing) provided significantly better *A. balsamea* and *B. papyrifera* regeneration than clearcutting, while *P. tremuloides* regeneration was somewhat better after clearcutting (Yang and Fry 1981). The better *A. balsamea* regeneration under a partial canopy was

attributed to its competitive advantage in shade, while increased soil temperature and cutting of hardwoods likely stimulated *P. tremuloides* suckering in the clearcut. In the same study, tree-length cable-yarding provided significantly higher *A. balsamea* and *B. papyrifera* regeneration than did either horse-skidding or cable-yarding in bundles. Since the latter two methods are generally less damaging to advance regeneration than is tree-length skidding, the authors assumed that the increased regeneration in the tree-length method was due to better slash distribution and more soil disturbance, which promoted better seedling establishment (Yang and Fry 1981).

When horse-logging was practiced, *A. balsamea* dominated most upland boreal sites following harvest, since it comprised most of the advance growth, little of which was destroyed, while *P. banksiana*, *P. mariana* and *B. papyrifera* were largely excluded from post-harvest stands due to the lack of disturbance to the seedbed (Clemmer and Atkins 1980, Jeglum 1983). As mechanical harvesting and site preparation were introduced, advance growth survival decreased, and the hardwood component of stands increased greatly following harvest. In northwestern Ontario, shifts in composition following harvest resulted in a decrease in the *Picea* spp. and jackpine working groups (65.1% of the forest before harvest, 39.2% after), and an increase in the *A. balsamea*, mixedwood and hardwood working groups (34.9% before harvest, 60.8% after) (Clemmer and Atkins 1980). *P. tremuloides* appears to be a more common invader of *P. mariana* lowland stands that have been harvested by mechanical wheel-skidding rather than by horse-skidding (Brumelis and Carleton 1988). This is likely due to the increased rutting, disruption of the surface peat and possible conversion to a more nutrient-rich site caused by the mechanical method.

Yang and Fry (1981) conclude that if regeneration of any merchantable species, including *A. balsamea* and *P. tremuloides*, is acceptable, boreal mixedwoods can be regarded as resilient to all harvest methods.

2.4.8 Harvest Affects Tree Form and Canopy Structure

Harvest method can also influence the eventual canopy structure and form of the trees. In *Picea glauca-Populus tremuloides* mixedwoods of Manitoba, harvesting that left the *P. tremuloides* canopy intact (Waldron 1964) improved the form of the *P. glauca* regeneration, producing trees with less foliage and branches, and taller, straighter, more neatly conical boles than those of trees grown without the *P. tremuloides* protection.[1] Density of established *P. glauca* was higher on the old scarification mounds than in the troughs.[2]

High-grading of boreal mixedwood stands (i.e. removing only merchantable conifers), produces an irregular, uneven-aged canopy, with many overmature hardwoods; regeneration age and size in the understorey is also variable (Navratil *et al.* 1991).

Although response of boreal mixedwood stands may differ, canopy structure and cover varied greatly among harvest treatments, 50 years after harvesting in a mature, northern hardwood climax forest in Michigan (Metzger and Schultz 1984). Clearcut areas had dense, single layer canopies, with uniform crown structure, small, wind-firm trees and very little subcanopy. Openings were few, since dying trees were generally suppressed beneath the main canopy. Older trees, with more expansive and exposed canopies dominated both the group selection and individual tree selection treatments. Smaller trees filled in openings, created by periodic harvest, in the main canopy (Metzger and Schultz 1984).

[1,2]Personal communication, Mr. Jim Ball, Silvicultural Specialist, Manitoba District Office, Forestry Canada, Winnipeg, Manitoba, February, 1993.

2.4.9 Harvest Affects Succession

In the previous sections, harvesting has been noted to have some effect on the species composition and abundance of natural regeneration in boreal forests, with *Picea* spp. and *Pinus banksiana*, which are fairly abundant following fire, being much less common following harvest. Different harvest methods have been noted to have somewhat different effects on the species' dominances in early regeneration. Succession following clearcutting of forests has an Initial Floristics component, due to the germination of seed stored in the soil and sprouting from stumps and roots (Finegan 1984). However, like initial regeneration, post-harvest succession differs from that following natural disturbance. These findings suggest that composition and structure can be manipulated by selection of a harvest system and method (Webber *et al.* 1968, Peterson et al 1989). Information about boreal mixedwood post-harvest succession in the following paragraphs was drawn from the few existing short-term (Frisque *et al.* 1978) and chronosequence (Richardson 1979, Yang and Fry 1981, Morris *et al.* 1988) studies.

Density and stocking of shrub and hardwood species increase greatly from immediate postharvest inventories to 5 years postharvest (Frisque *et al.* 1978). Due to this rapid initial growth, hardwoods comprise over half of the dominant (in terms of canopy position) stems at age 5 (Morris *et al.* 1988). Softwood stocking increases in the first 10 years after harvest (Frisque *et al.* 1978, Yang and Fry 1981). Yang and Fry (1981) noted that hardwood stocking also increases from 5 to 10 years post-harvest, but Frisque *et al.* (1978) noted a decrease in hardwoods after 5 years, mainly due to mortality of *B. papyrifera*. From 5 to 10 years post-harvest, the rate of increase in both hardwoods and softwoods is slower than in the initial 5 years, likely due to a deterioration of seedbeds and an increase in overall competition (Yang and Fry 1981). Although *P. tremuloides* density decreases steadily after the initial influx, its basal area increases (Yang and Fry 1981).

Thus, in the early postharvest forest, *A. balsamea* comprises over 50% of stem

density, with most of the remaining stems being hardwoods, and less than 5% of the stems being *Picea* spp. (Morris *et al.* 1988). Many *Picea* spp. stems are not recruited for up to 15 years after harvest, putting them at an initial growth disadvantage (Yang and Fry 1981, Morris *et al.* 1988). By age 15, *A. balsamea* makes up almost 70% of the dominant stems (Morris *et al.* 1988). The average height of hardwoods is greater than that of softwoods for the first 20 years after harvest, but the height difference diminishes over this period (Richardson 1979). Some shrubs, e.g. *Acer spicatum* and *Sorbus decora*, are taller than *A. balsamea* in stands 0-10 years old, but this is reversed in stands 11-20 years old (Richardson 1979).

In mixedwood stands 15 to 30 years old, *P. tremuloides* has the highest basal area of all species, *A. balsamea* the highest density, and *Picea* spp. are generally minor suppressed species (Yang and Fry 1981). *A. balsamea*, which has abundant advance growth prior to harvest, generally becomes more numerous after harvest (Richardson 1979, Yang and Fry 1981). Most of its stems in young stands are seedling size, but basal area of sapling stems occupying intermediate or codominant canopy positions increases to 30 years post-harvest (Yang and Fry 1981). However, it also suffers high mortality of advance growth after harvest to about 30 years, due to increased light intensities; by age 35, it comprises only 21% of the dominant stems (Morris *et al.* 1988). *P. mariana* and *Acer spicatum* stocking increase to 20 years in Newfoundland cutovers (Richardson 1979), and *Picea* spp. density and dominance increase to 35 to 40 years postharvest (comprising about 40% of dominant stems) in Ontario cutovers (Morris *et al.* 1988). However, due to their slow growth, approximately half of the *Picea* spp. stems form the suppressed component of the vertically stratified canopy (dominant, codominant, suppressed). Many of them begin to fall out of the stand as early as 45 years postharvest. Total stand density at age 35 is about 3500 stems per hectare. Intraspecific competition causes high mortality in the dense *P. tremuloides* suckers up to age 55, at which time most of the remaining *P. tremuloides* are community dominants,

comprising about half of the canopy. Shortly after this, mature *P. tremuloides* will begin to drop out of the canopy, creating gaps that release the suppressed conifers. This causes an increase in *A. balsamea* dominance at about age 65. Because of its low height increments and therefore continuous mortality, *Picea* spp. density decreases to 200 stems per ha at age 50 and its dominance decreases to about 15% of the canopy by age 85 (Morris *et al.* 1988).

Relative height growth rate of the forest decreases steadily to age 65, and then increases slightly as mortality of overmature trees occurs (Morris *et al.* 1988). Stem volume increment increases greatly with succession, especially after age 45. *Picea* spp. volume increases by about 5 times and *P. tremuloides* volume increases by about 17 times from year 35 to 60. The hardwood component makes up the largest volume of the stand, *A. balsamea* the least, due to its poor diameter growth (Morris *et al.* 1988).

In harvested boreal mixedwood stands less than 60 years old, the *Picea* spp. to *A. balsamea* ratio for stems ≥ 1in dbh is 16:84, while in equivalent fire origin stands, the ratio is 90:10 (MacLean 1960). This increase in *A. balsamea* composition following harvest is not due primarily to cutting. It is a natural successional trend of boreal mixedwood forests that escape fire for long periods; when these forests are cut, the *A. balsamea* advance growth allows this trend to continue (MacLean 1960). Navratil *et al.* (1991) state that harvested boreal mixedwood stands in western Canada will naturally (with no additional silviculture) regenerate to all-aged *P. tremuloides*-dominated stands or *A. balsamea* and *P. tremuloides*-dominated stands, with the *Picea* spp. component greatly reduced from that in the unharvested stands; Yang and Fry (1981) predicted that *A. balsamea* and *P. tremuloides* would form the next crop on boreal mixedwood cutovers. Thus spruces are considerably less important, and *A. balsamea* and *P. tremuloides* more important, in the succession and mature stage of boreal mixedwood forests of harvest origin than they are in equivalent forests of fire origin (see section 2.3.11 for comparison).

2.5 EFFECT OF HARVESTING ON UNDERSTOREY SPECIES

2.5.1 Harvest Affects Early Survival and Regeneration

Canopy removal changes many environmental conditions simultaneously; it increases light intensity, occurrence of summer frosts, and water vapour demand (Brand 1991). This kills many understorey species, and the survivors must produce new foliage with better cuticular development and stomatal control. Removal of the canopy stimulates regeneration of understorey species from seedbanks and seed rain, and by vegetative means, especially if the forest floor is not destroyed (Brand 1991, Freedman 1992). Clearcutting increases productivity of some herbaceous plants, decreases abundance of bryophytes and lichens due to drought and exposure, and increases abundance and growth of ruderal species (Freedman 1992).

Ordination of northwestern Ontario boreal forest data indicated that vegetation composition 5 years after harvest was strongly dependent on pre-harvest stand type (Walsh and Krishka 1991). A large group of species occurred consistently on sites previously occupied by conifer (*Abies balsamea-Picea glauca*)-dominated mixedwood stands, but only a few species, mostly shrubs, had high cover/height index (an index which incorporates both species height and percentage ground cover) values on these sites. On sites previously occupied by hardwood-dominated mixedwoods, species with high frequency were mostly the same among sites. However, the upland, hardwood mixedwood types had more species with high index values than did the conifer-dominated mixedwood types, likely due to a more nutrient rich nature. *Populus tremuloides* hardwoods and mixedwoods generally had more herb species than *Betula papyrifera* hardwoods and mixedwoods, but shrub index values were about the same on these two site types. All of the mixedwoods had higher cover of *Acer spicatum* and *Corylus cornuta* than did conifer-dominated sites. These two species, along with *Populus tremuloides, Rubus idaeus, Aster macrophyllus* and some ferns had higher index values on hardwood-

dominated mixedwood sites than on any of the other site types. On lowland sites previously dominated by *P. mariana*, shrub and herb species richness was lower and species composition (consisting mainly of several ericaceous species, grasses, sedges, and *Alnus rugosa*) was quite different than the broadleaved species that dominated the upland mixedwoods.

In a comparison of full-tree clearcutting (with and without snow cover) and tree-length clearcutting (with snow-cover, and later burned) in mixedwood (*Abies balsamea-Betula papyrifera*) forests of northern Minnesota, changes in composition and density were evident in the first growing season after harvest: *Populus tremuloides, Amelanchier spp., Polygonum cilinode, Rubus idaeus,* and *Fragaria spp.* were present on harvested areas, but not on controls, and the reverse was true for *Anemone quinqefolia* and *Streptopus roseus* (Outcalt and White 1981). Densities of several low herb and fern-ally species were significantly lower on harvested sites. By the second season, 23 species found on the harvested sites were not present on controls, most of these being tall herbs, while 13 species present on the control were not found on one or more of the harvested sites. Twenty-one species present on the full-tree harvested sites were not present on the tree-length harvested sites. The tree-length harvested and burned sites lost the largest number of species,10. Compositional changes on the unburned sites were mainly due to species invasions while those on the burned site were mainly due to disappearance of species. Full-tree, winter-harvested sites had higher densities of low herbs, low shrubs and total woody vegetation than the other harvested sites, but the two full-tree harvested sites had fewer herb species than burned or control sites. Low shrubs, tall shrubs and tree reproduction were least dense on the tree-length, burned site.

Based on this study, Outcalt and White (1981) identified four understorey species response types: 1) 'invaders' that occupy niches created by disturbance (e.g. *Carex* spp., *Corydalis sempervirens, Convolvulus sepium, Epilobium angustifolium,*

Geranium bicknellii, Polygonum cilinode, Prunus spp., and *Solidago* spp.), 2) 'increasers' present on the site prior to disturbance but stimulated to reproduce and grow by disturbance (e.g. *Aster macrophyllus, Corylus cornuta, Diervilla lonicera, Fragaria* spp., *Populus tremuloides* and *Rubus idaeus*), 3) 'neutrals' that remain stable after logging (e.g. *Acer spicatum, Rubus pubescens* and *Lonicera canadensis*) and 4) 'decreasers' that decline after logging (e.g. *Abies balsamea, Clintonia borealis, Maianthemum canadense, Lycopodium clavatum* and *Lycopodium obscurum*). Some species responded similarly to different types of disturbance whereas some responses depended on the severity of disturbance. Understorey biomass increased substantially in all three treatments, but biomass of Corylus cornuta and other woody species increased only on the full-tree logged (unburned) sites. Significant changes in understorey species composition, density and biomass did not begin on any of the sites until the second season following harvest. Even then, most pre-harvest species persisted. Successional changes in the understoreys of these harvested sites were expected to continue, via gradual increases and decreases in importance of various species, in response to the gradual closing of the canopy and the accompanying microenvironmental changes.

On cutover and burned mixedwood sites in Ontario, rapid invaders included *Rubus idaeus, Prunus pensylvanica, Pteridium aquilinum* (L.) Kuhn, *Populus tremuloides* suckers, *Diervilla lonicera* and *Corylus cornuta* (Haig and Curtis 1974). In clearcut *Pinus banksiana-P. mariana* stands of northwestern Ontario, understorey species uncommon in the undisturbed stand increased substantially following harvest (Ellis and Mattice 1974). Some of these species, *Aralia hispida, Polygonum cilinode, Pteridium aquilinum* and *Rubus idaeus*, as a group, covered one-third of the ground surface 2 to 3 years after cutting, but had decreased to only 2% of cover ten years later. Several other species that increased in importance after harvest did not dissipate as rapidly, and some even increased for over ten years, e.g. *Cornus canadensis, Diervilla lonicera,* and *Prunus* spp.. It was suspected that the first group responded to changes in soil conditions

and the latter group to increased light. A third group, including *Epilobium angustifolium* and *Polytrichum* spp., was thought to respond to both changes in soil and insolation, as evidenced by their persistence on site for several years after peaking at 5-6 years postharvest. Expansion and growth of the herb layer overall peaked by 2 years after harvest, then decreased gradually as the shrub stratum developed. Exposure following harvesting caused rapid mortality of mosses. Although the changes in understorey dominances noted on these cutovers appeared to follow a relay pattern of succession, the changes were mainly shifts in abundance rather than in species composition (Ellis and Mattice 1974), supporting the Initial Floristics model.

During the first 5 years following logging of upland *P. mariana* stands in Manitoba, feather mosses, originally the dominant understorey component, decreased greatly, while shrubs herbs and grasses, which were minor prior to harvest, increased in importance (Jarvis 1961). No differences due to harvest methods were reported. Species abundance was related to moisture and topography; *Rubus* spp. formed dense patches on many moderately fresh to moderately moist sites, except for those located on south aspects, where only a few straggling shrubs remained. Dead feather mosses covered the forest floor on south aspects and beneath the numerous slash piles. Grasses, sedges and shrubs dominated moist and very moist sites. On most cutovers, lesser vegetation was dense, inhibiting *Picea* spp. regeneration.

Dyrness (1973) noted that degree and type of disturbance had a strong influence on early vegetational changes in harvested sites in the western Cascade Mountains of Oregon. Sites where the canopy was removed but the ground surface undisturbed were often fully occupied by residual species, to the exclusion of invaders. Both residual species and invader species occupied areas where the ground surface was disturbed but unburned during harvest, while burned areas were dominated by invader species. Shrubs were the principal residual component of disturbed-unburned and lightly burned areas, the herbaceous species being mainly invaders. Dry, heavily burned sites were

dominated by invader shrubs, while herbs, ferns and low shrubs dominated wetter sites exposed to the same treatment.

2.5.2 Invasion of Shrubs and Other Competitors of Conifer Seedlings

Rapid shrub growth and vegetative reproduction which occurs on many harvested boreal mixedwood sites has little effect on rapidly growing hardwood regeneration, but can seriously retard softwood advance growth, lengthening the time it is susceptible to rodent damage, and possibly causing mortality (MacLean 1960, Weetman *et al.* 1973, Johnson 1986). Following whole tree clearcutting in mixedwood (*A. balsamea-B. papyrifera-Picea* spp.) forests of northwestern Quebec, density of *Acer spicatum*, *Prunus pensylvanica*, *Salix* spp. and *Alnus* spp. together was much greater than conifer density (Harvey and Bergeron 1989). *Acer spicatum*, *Alnus rugosa* and *Corylus cornuta*, which generally occur in moderate densities under well-stocked boreal mixedwood stands, can produce a closed-canopy shrub layer in about 10 to 12 years (MacLean 1960). Growth of *Rubus idaeus* and *Calamagrostis canadensis* can also be dense and tall enough to hinder conifer seedlings (Johnson 1986). Harvesting mixedwood sites often causes a rise in the water table, which inhibits *P. tremuloides* regeneration but promotes invasion of *Alnus rugosa.*, *Salix* spp., and *Populus balsamifera* (Navratil *et al.* 1991).

Dense growth of *Corylus cornuta* is a major hindrance to *P. glauca* regeneration on mixedwood stands selectively cut for *P. glauca* in Manitoba, especially on fresh to moist sites (Johnson 1986). Harvesting only the merchantable conifers from boreal mixedwood stands can cause *Acer spicatum* and *Corylus cornuta* to invade heavily on dry, well-drained sites, while *Salix* spp. and grasses tend to invade moist sites (Navratil *et al.* 1991).

In a rich, mixedwood stand of Ontario on which softwoods only were clearcut (wheel-skidded), invasion and growth of *Populus balsamifera*, *Corylus cornuta* and *Acer*

spicatum were rapid creating severe competition for conifers, and converting the stand to a hardwood brush-dominated site (Weetman *et al.* 1973). A horse-logged mixedwood site in Quebec was similarly affected by harvest. In both stands pre-harvest *A. balsamea* advance growth stocking was high, but was overtopped by the hardwood brush (Weetman *et al.* 1973).

In north central California, abundance of shrub seedlings was highest on clearcut sites, but had high stocking and density in all of five cutting methods except single-tree selection (McDonald 1976). Shrubs grew rapidly, overtopping many of the conifer seedlings. Broadcast burning in the clearcut sites stimulated thousands of shrub seeds dormant in the soil. Clearcutting with broadcast-burning of slash produced a much denser and diverse shrub layer than did partial cuttings (selection, seedtree and shelterwood) in cedar-hemlock forests of Idaho (Irwin and Peek 1979). Differences in shrub biomass were largely due to overstorey species composition, but also to the intensity of canopy removal (e.g. low-growing shrubs were more common under seed tree and shelterwood canopies). Shrub composition did not depend on time since harvest, but sampling was not conducted until 5 years after harvesting, so shrub species were either present at logging or established shortly after.

2.5.3 Successional development after initial stages

In post-logged (0-56 years old) *P. mariana* lowland stands of Quebec, species capable of rapid regeneration following canopy removal showed peak abundance in logged as compared to unlogged stands (Brumelis and Carleton 1989). Several rhizomatous, perennial herbs and shrubs, known to resprout and rapidly recolonize following fire were widespread, but showed peak abundance on horse-skidded as compared to wheel-skidded sites. Most of these species produce small, thick, deeply-pigmented 'sun' leaves following canopy removal. Only *Epilobium angustifolium* and *Carex trisperma* Dewey were listed as having peak abundance on wheel-skidded stands. The feathermosses and

Sphagnum girgensohnii, common to unlogged and old logged stands, were less common in recently harvested stands.

Successional pathways of understorey development in these logged *P. mariana* lowlands were found to be related to the degree of disturbance caused by logging, and to the nutrient regime of the site (Brumelis and Carleton 1989). Where nutrient regime was rich, horse-logged sites were regenerated principally by 'facultative stress tolerators', species that grow rapidly when released, but endure deep shade, including several common rhizomatous perennial herb and shrub species. Nutrient rich, machine-logged sites seemed to follow the Inhibition Model of succession, with competitive broad-leaved shrubs and some herb species invading and dominating for many years. Nutrient-poor, horse-logged sites showed little shift in their moss-dominated understorey composition, since the original canopy was not continuous, but those that were mechanically logged had two new microsites created by rutting: exposed bare peat, which was colonized very slowly by stress-tolerant bryophytes, and wet depressions which filled in with weedy emergent aquatics.

In a mature, northern hardwood climax forest in Michigan, the amount and structure of the crown canopy created by harvesting was largely responsible for understorey response, especially immediately after harvest (Metzger and Schultz 1984). Partially harvested stands (group and single-tree selection cuts) developed patchy canopies; this and the periodic disturbance which accompanied partial harvesting promoted high herb diversity, and maintained a weed and disturbed species component in the stand.

Early post-harvest dynamics on all sites showed immigration of weed and disturbed-forest species, but continued dominance by the pre-harvest species (Metzger and Schultz 1984). Plant density increased by an average of 50% on harvested sites in the first year, and by 600% in the first 5 years. Herbaceous species typical to the undisturbed forest always accounted for over two-thirds of the total importance values

for each harvest treatment during the first 5 years, with partially harvested stands maintaining the highest proportion of these species, and clearcuts the least. Sedges and grasses showed the greatest increase after harvest, most evident on the clearcuts; *Galium* spp. and *Aster* spp. also increased. Violets, dominant in the undisturbed forest, decreased on all sites, but especially the clearcuts. Weed and disturbed forest species, e.g. *Epilobium angustifolium, Taraxacum* spp. and *Cirsium* spp., had greatest importance on clearcuts, peaking at 4 to 5 years, along with the grasses and sedges. *Acer saccharum* Marsh. maintained its pre-harvest dominance in all harvest types, with density and frequency of its larger stems increasing. *Rubus idaeus* invaded all harvest types, but was most important on clearcuts.

Species composition of 50th year understory communities was very similar to early postharvest communities and the undisturbed site, with typical forest species continuing to dominate the understorey of all sites (Metzger and Schultz 1984). Variation in species composition, diversity and structure among the different harvest types did not exceed that which occurred before harvest. Violets had regained dominance of the herbaceous layer on all sites, including the clearcuts. The single tree selection cut and the 3-group cut had several important differences in herb species' abundances from the clearcuts and the 8-group cut, but overall herbaceous layer composition was similar among all treatments. Greatest similarity occurred between the two clearcuts, and between the 3-group cut and the single-tree selection cut. Similarity was also high between each 50th-year community and either the reserve or early postharvest communities.

Due to the continuing dominance of *Acer saccharum* in all harvested sites, similarity among harvest types was even greater in the woody vegetation layer than the herbaceous layer (Metzger and Schultz 1984). The 50th year woody vegetation layers of all treatments were highly similar to the reserve, the 1-year post-harvest 3-group selection, and their own earliest post-harvest communities. The 5th year postharvest

communities were most dissimilar to the 50th year communities, especially for the clearcuts. The differences which did exist were likely caused by different light regimes, determined by the canopy. Canopy changes in the selection cuts resembled changes that occurred naturally due to small disturbances e.g. windthrow. The selection harvests were characterized by patchy canopies and more frequent disturbances, which affected the herb and woody understorey layers in several ways: diversity originally increased due to some invasion by weed and disturbed-forest species, but development of a dense subcanopy layer reduced the ephemeral population.

Metzger and Schultz (1984) noted that such studies show that as harvest disturbance intensity increases, the proportion of 'forest species' in the early postharvest understory decreases, with partial harvests maintaining a proportion over 80%, clearcuts about 50% and disturbances that include clearcutting followed by burning or other disturbance becoming dominated by seed-regenerated and disturbed-forest species. The authors surmised that recent changes in harvesting practices (increase in size and power of harvesting equipment and more complete utilization of wood) had led to greater site disturbance, including uprooting or destruction of perennating organs of many herbs, as well as reduced slash. Slash can be beneficial in providing a less harsh microsite than exposed areas and protection from browsing, but can also smother established plants. Its removal may decrease nutrient availability and therefore slow plant responses. However, they judged that since the different harvesting methods used in their study did not cause major changes in composition, or continued dominance by disturbance species, the recent changes in harvesting practices were also unlikely to alter the communities greatly. The understorey in their study showed high resilience to different harvesting intensities and frequencies, with a high resemblance of pre-harvest and late post-harvest communities in terms of species composition and diversity.

2.6 HARVEST AFFECTS DIVERSITY

It has been hypothesized that plant communities subjected to intermediate levels of disturbance (such as partial cutting) will be more diverse than those undergoing intense or widespread disturbance, since disturbed patches will undergo gap or microsuccession, each at different stages of recovery, and therefore along with undisturbed patches will encompass a greater diversity of species than undisturbed or large disturbed areas (Fox 1981). Place (1974) noted that small harvested areas create a diversity of ecotones and of patches of different age classes in the forest; this landscape-level diversity promotes wildlife diversity.

Navratil *et al.* (1991) stated that extensive as opposed to intensive silviculture practices in boreal mixedwood forests will promote biological diversity, yet Freedman (1992) stated that clearcutting can lead to an impoverishment of diversity in forest communities. In their study of the effects of different harvest systems on northern hardwood forests, Metzger and Schultz (1984) found that plant species diversity increased immediately after harvest, peaked by 4 to 5 years postharvest, and had almost returned to preharvest levels by the 50th year. At 50 years postharvest, undisturbed (control) stands had the lowest diversity, clearcuts almost as low as preharvest levels, and a single tree selection cut and a 3-group selection cut had slightly higher diversity than did an 8-group selection cut.

In another northern hardwood forest, plant species diversity was higher in a watershed harvested by progressive stripcuts than in one harvested as a 12-ha block clearcut, at both 1 year and 10 years after treatment (Gove *et al.* 1992). On both treatments, the diversity was lowest immediately after treatment, and peaked in the stripcut at 10 years. In the clearcut it appeared to increase after the first year, but was declining by 10 years postharvest. In the same area as this study, successional trends in diversity were examined after experimental deforestation and 3 years of herbicide

application (Reiners 1992). Species richness increased in the first 20 years after disturbance, but evenness decreased to 5 years postharvest, and then remained level, while diversity followed the same trend as evenness until age 20, when it began to increase. The decreases in evenness and diversity were attributed to changes in dominance structure of the forest, with increased concentrations of biomass in a small number of large tree and shrub stratum species, and in a large number of very small, rare species. The latter was likely brought about by decreases in shrub and herb competition resulting from the increase in tree-stratum dominance. In fact this secondary succession had both Initial Floristics and Relay Floristic components, with most of the biomass concentrated in the latter but most of the species richness in the former. In an oak-pine mixedwood of Georgia, 10-year post-harvest diversity and evenness of woody species were higher in a 10-cm diameter limit cut than in a 2.5-cm diameter limit cut, for stands harvested in the dormant season (McMinn 1992).

CHAPTER 3-METHODS

3.1 SITE DESCRIPTION AND HISTORY OF RC17

The RC17 experimental area is a 150 ha site located on former limits of the Ontario Paper Company Limited approximately 70 km northeast of Heron Bay (49° 00' N, 85° 49' W) (Figure 3.1.1). This site is part of Rowe's Forest Section B.8 (MacLean 1956).

3.1.1 Soils

The site has a rolling topography, incorporating a series of parallel rock-cored ridges and depressions (Hughes 1967). The bedrock which underlies the soils of the mixedwood forest is composed of granite, gneiss, quartz, feldspar and small amounts of horneblende and biotite (Burger 1955). The soils of the area are made of stony, moderately limey till resulting from the last glaciation. The texture ranges from sand and sandy loam to loam and silt loam, and soil depth ranges from < 5 cm to 2 m: the shallow soil tends to be coarser and the deep soil tends to be finer (Hughes 1967).

Figure 3.1.2 shows the soil depth and moisture classes that occur on the site. These classes were determined and described by Hills (1954) on aerial photographs and mapped by the RC17 project supervisor. The till was referred to as Lindsley and the bedrock as Barehead by Hills in the classification, but the classes are abbreviated by dropping those names. Four moisture classes and four depth classes were recognized on the upland sites; the lowland sites were referred to collectively as 'mucky peat' (Hughes 1967). Only nine combinations of soil depth and soil moisture classes existed on the site, the approximate area covered by each of these is presented in Table 3.1.1.

The seedbed treatment transects were located only on fresh and moist soil types. Soil profiles of representative fresh and moist deep soils are in Appendix 3. The highest concentration of organic matter occurred in the B2 horizon of the fresh soils

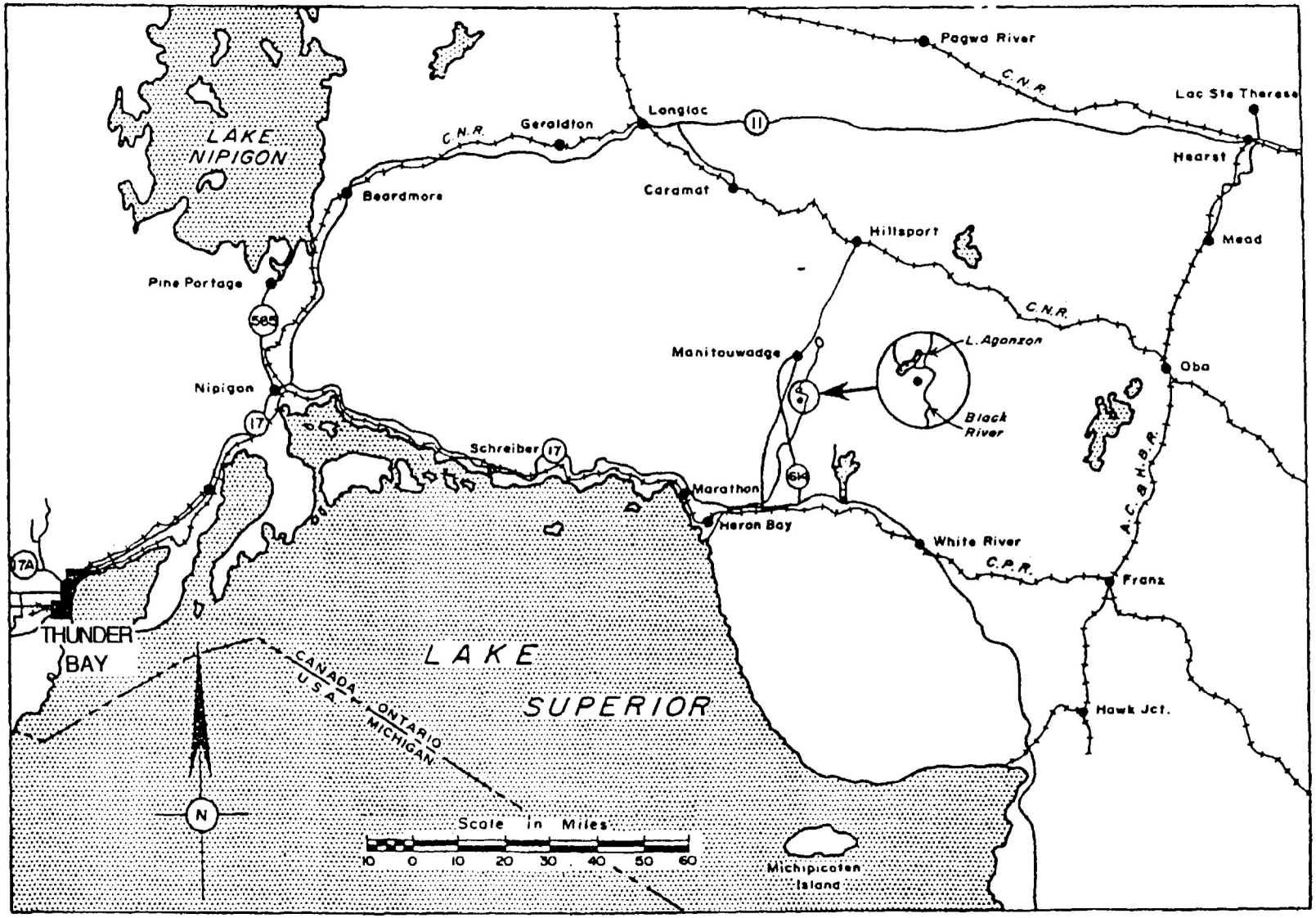


Figure 3.1.1. Location of the RC17 project (Sutton 1964).

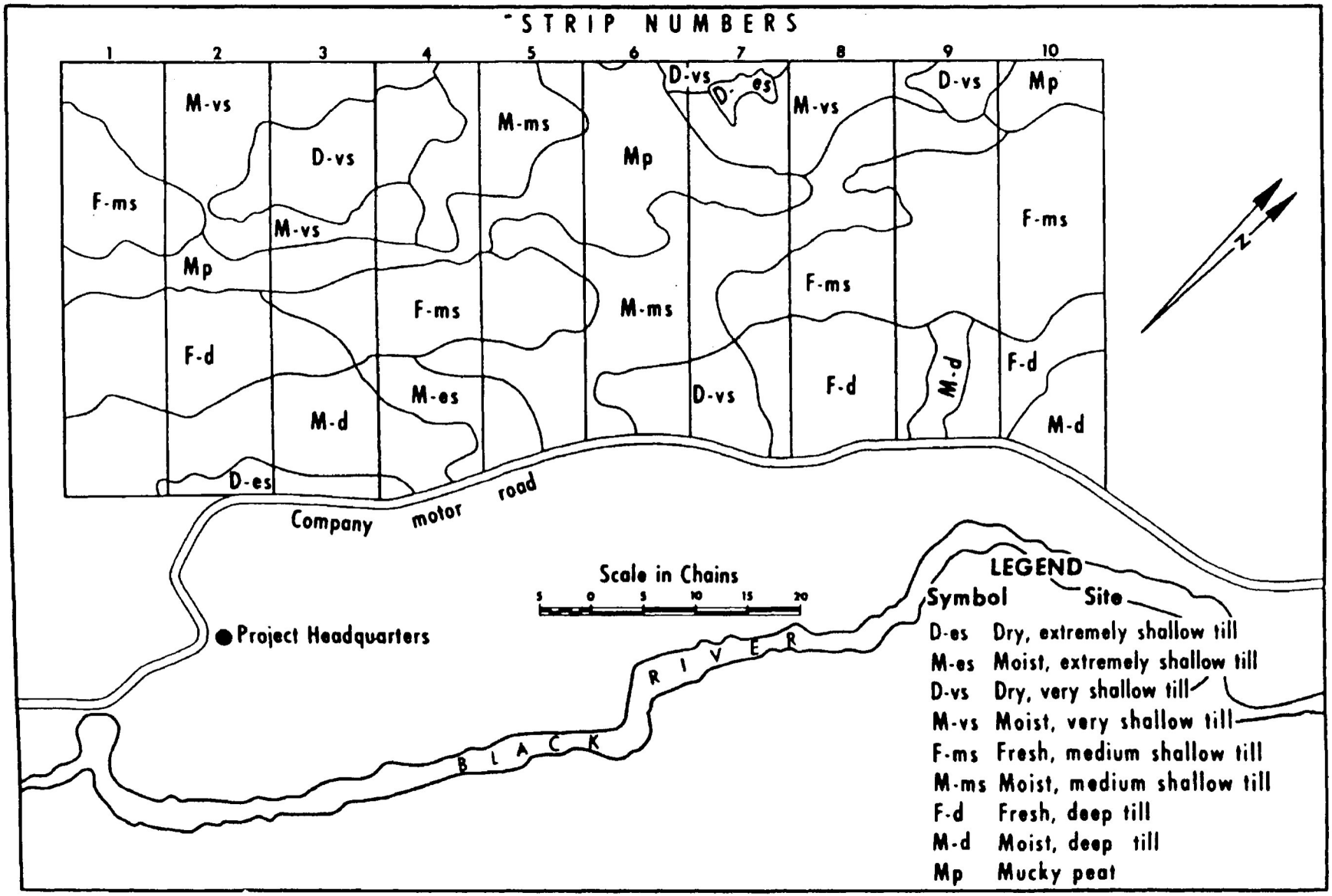


Figure 3.1.2. Soil depth and soil moisture classes of the RC17 project (Hughes 1967).

Table 3.1.1. Distribution of soil moisture and depth class combinations on the RC17 experimental area.

Soil Moisture* and Depth Classes	Hectares	Abbreviation
Dry, Barehead extremely shallow	4.5	D-es
Dry, very shallow Lindsley over Barehead	13.8	D-vs
Fresh, medium shallow Lindsley over Barehead	32.0	F-ms
Fresh, deep Lindsley	19.4	F-d
Moist, Barehead extremely shallow	4.5	M-es
Moist, very shallow Lindsley over Barehead	19.4	M-vs
Moist, medium shallow Lindsley over Barehead	24.7	M-ms
Moist, deep Lindsley	13.8	M-d
Mucky peat (wet)	16.6	Mp

*The moisture classes were each composed of three of Hills' moisture regimes: Dry=θ,0,1; Fresh=1,2,3; Moist=3,4,5; Wet=6,7,8.
(Hughes 1967)

and the B2g horizon of the moist soils (Hughes 1967).

3.1.2 Disturbance History Prior to Harvest

Prior to harvest, the area had not been burned by a major fire since 1761, except for less than 1 ha in the southeast corner of the project site that burned in 1850. Three disturbances, thought to be wind storms, occurred in about 1880, 1895 and 1922, and a heavy windstorm in 1949 caused a blowdown of more than 20% of the existing merchantable volume (MacLean 1954).

3.1.3 Overstorey Composition Prior to Harvest

After the 1761 fire, various mixtures of the typical boreal tree species (*Picea mariana*, *Picea glauca*, *Abies balsamea*, *Pinus banksiana*, *Thuja occidentalis*, *Betula papyrifera*, *Populus tremuloides* and *Abies balsamea*) became established. By the initiation of the RC17 experiment in 1953, most of the *P. tremuloides*, *P. banksiana* and *P. balsamifera* had been replaced to a large extent by *Acer spicatum* and *Corylus cornuta*, and to a lesser extent by *A. balsamea* (MacLean 1954). At that time, the overall merchantable volume of the stand was approximately 94 m^3 to 160 m^3 per ha (Hughes 1967) with an average basal area of 19 m^2 per ha for trees greater than or equal to 1.3 cm dbh (MacLean 1954). The area was described as an open and decadent, overmature mixedwood forest (Sutton 1964), severely understocked due to the blowdowns mentioned above (MacLean 1954). *Picea* spp. and *B. papyrifera* still comprised a large portion of the volume of the area. *Abies balsamea* content of the stand had increased since the 1761 fire (MacLean 1954). On fresh, deep sites, *A. balsamea* and *Picea* spp. accounted for 60% of total stand volume, with *P. glauca*, although scattered, being more frequent and dominant than *P. mariana* (Sutton 1964). The densities of all species on each site (soil depth and moisture) type at the initiation of the experiment are reported in Table 4.5.1 of this report, in comparison with 1990 densities. Unfortunately, the document (Berry 1953) reporting 1953 density and volume estimates by treatment plots could not be

relocated. However, Hughes (1967) reported that volume estimates calculated from that initial inventory showed no significant differences at the 5% level for the plots, although the estimates were significantly different at the 1% level for site types.

3.1.4 Reproduction

A survey of tree species reproduction by treatment plots was conducted prior to harvesting (Anon. 1954), but could not be located for this study. Thus, pre-harvest density and percentage stocking of tree seedlings by site type, rather than by treatment plots (Hughes 1967) are included later in this report, in comparison to present day values (Table 4.5.2). In general, *Abies balsamea* seedlings had the highest percentage stocking and density of the softwood species (Hughes 1967). However, these seedlings were mostly less than 0.5 m tall and were suspected to be mostly first-year seedlings with a high susceptibility to mortality. *Betula papyrifera* seedlings were very common on exposed mineral soil of windthrown trees, and sprouts were common from root collars. *Thuja occidentalis* seedlings were common on extremely shallow soils, and on moist, medium shallow and moist, deep soils (Hughes 1967). Hughes (1967) noted that *T. occidentalis* trees were only common on the extremely shallow sites.

3.1.5 Understorey Composition

Along with the tree species reproduction survey conducted in 1953, pre-treatment frequency of subordinate vegetation was also recorded by treatment and site (Anon., 1954). Since this report was unavailable, descriptions of characteristic understorey species on each site type (Listed in Table 4.5.3, later in this report) have been adapted from Hughes (1967). In general, the understorey of fresh and moist sites with medium shallow and deep soils were dominated by *Acer spicatum* and/or *Corylus cornuta* with other abundant species including *Aster macrophyllus, Aralia nudicaulis* and *Cornus canadensis*. Very shallow sites had large components of *C. canadensis* and *Vaccinium myrtilloides* (dry site) or *A. spicatum* (moist site), and extremely shallow

sites were dominated by *C. canadensis* and *Alnus crispa* (dry site) or *Pleurozium schreberi* (moist sites) (Hughes 1967). Understorey conditions on mucky peat sites were not reported, since the experiment was focused on changes in species composition and abundance of upland mixedwoods in response to overstorey and seedbed treatments. The composition and frequency of understorey species in the transects that were undisturbed in 1957 (deferred cut, no seedbed treatments, Sutton 1964) are compared later in this report to the present day results (Table 4.5.3). The most abundant and most frequent (>95%) understorey species on these undisturbed transects were *Abies balsamea, A. spicatum, A. macrophyllus, Clintonia borealis, Cornus canadensis, Streptopus roseus* Michx. and *Viola renifolia* Gray; *A. nudicaulis, Anemone quinquefolia* and *Lycopodium obscurum* were also common (Sutton 1964).

3.1.6 Harvest Methods

The main experiment consisted of main stand (overstorey) treatments and seedbed treatments. The study area was divided into 20 plots, each approximately 200 m (10 chains) wide by 340 to 400 m (17 to 20 chains) long (Figure 3.1.3). Four overstorey treatments were applied to the plots: clearcut (CC), softwoods only cut (SC), hardwoods poisoned (HP) and a deferred cut (DC). Although the application of the treatments to the plots was not random, it is assumed to be for the purposes of this follow-up study, since complete blocks (i.e. with one replication of each harvest treatment) are not available. The seedbed treatments were done as strips through several of the overstorey treatment plots (Hughes 1967).

For the CC treatment, trees of all species with a diameter at breast height (dbh) greater than 11.4 cm were cut. Only merchantable trees of *Picea* spp., *Abies balsamea* and *Pinus banksiana*, greater than 11.4 cm dbh were cut in the SC treatment. The CC treatment and the SC treatment were applied in the late summer and fall of 1953. Blocks 1A, 1B, 5A, 5B, and 7A were clearcut. The SC treatment was applied to plots 3A,

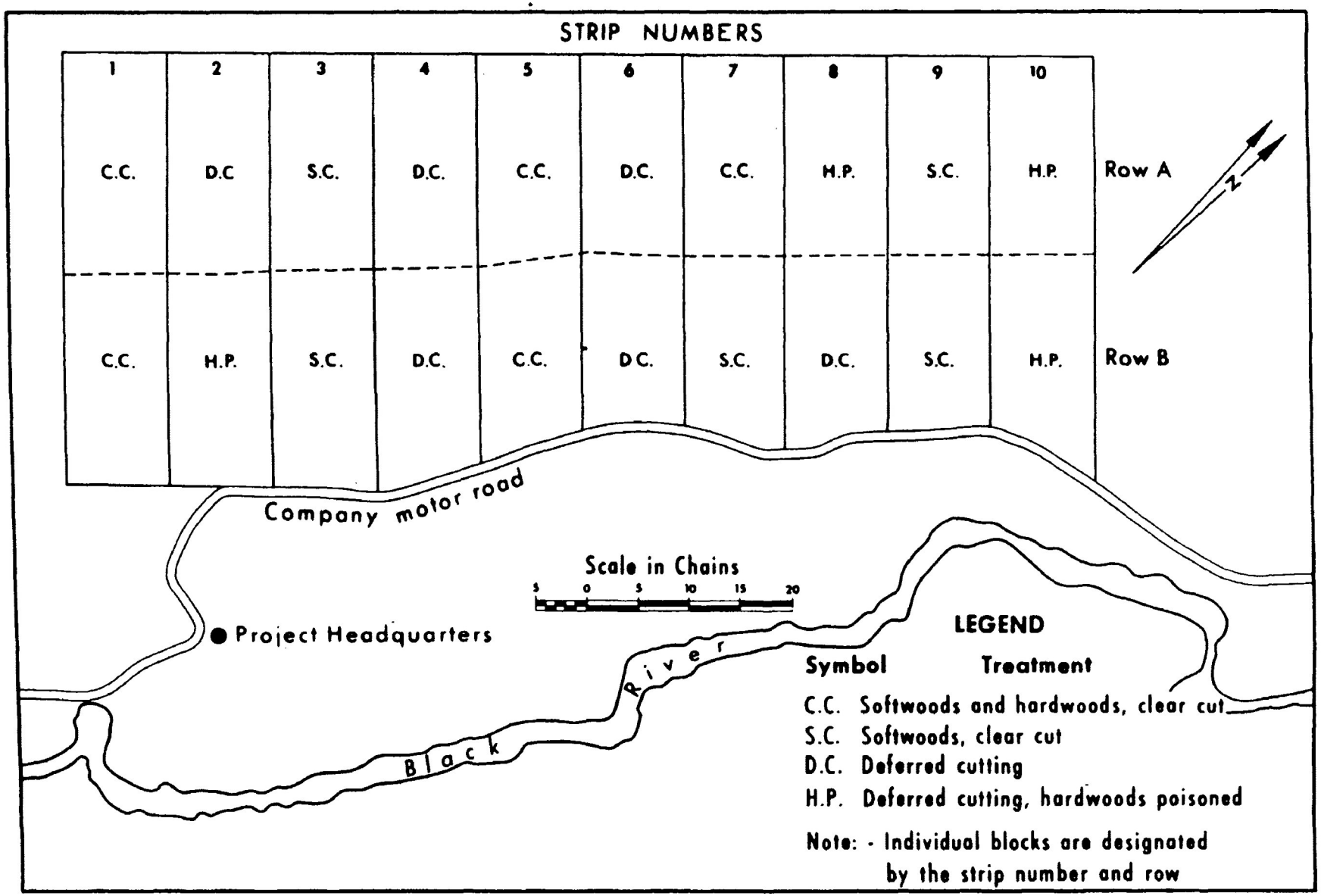


Figure 3.1.3. Assignment of harvest treatments to the plots of the RC17 project (Hughes 1967).

3B, 7B, 9A, and 9B (Figure 3.1.3).

For the HP treatment, hardwoods were frill-girdled to 2.5-4.0 cm deep at about 1.07 m above ground level, and 2,4,5-T was applied to the frills. The HP treatment was applied to plots 2B, 6B, and 8B in August 1954, and to plot 8A in August 1955 (Hughes 1967). Block 6A was originally intended to be included in the HP treatment, but since hardwoods were scarce within it, the deferred cut was applied instead (MacLean 1959).

For both the HP and DC treatments, cutting was done between 1961 and 1963, eight to ten years after the cutting of the CC and SC treatments, and seven to nine years after the poisoning of the hardwoods in the HP treatment. Blocks 2A, 4A, 4B, 6A, 6B and 8B had the DC treatment applied to them (Working Plan, 1964-65). In both DC and HP, only merchantable softwoods were cut, as in the SC treatment (Racey 1962).

During the harvest of CC and SC plots, trees were limbed and topped where felled, and the logs were skidded with horses to one of the two strip roads within each plot, where they were cut into 1.2 m (4 ft) bolts. Strip roads approximately twenty feet wide were made by bulldozer. On the strip roads, there was some exposure of mineral soil and humus, but no exposure occurred in the rest of the stands. The slash created by the harvest was about 0.46 m deep, and was loosely distributed over the stands, covering approximately one-half of the ground in the plots that were clearcut and one-third of the ground in the plots in which only softwoods were cut (Hughes 1967). The DC and HP plots were also horse-skidded (Racey 1962), and therefore harvest of these plots was likely similar to that for CC and SC. Thus, the SC and DC harvest treatments were essentially the same, with the latter performed 10 years later than the former.

The following canopy densities (density of growth of all vegetation greater than 1.83 m in height), were determined in 1957 from 100 random 'moosehorn' readings in each treatment, after cutting of the CC and SC treatments and poisoning in the HP treatment: DC, 89%; HP, 80%; SC, 26%; CC, 12.5% (Sutton, 1964). These values were obtained from the strips used as controls in the seedbed treatments.

3.2 REMEASUREMENT OF THE EXPERIMENTAL AREA IN 1990

3.2.1 Field Procedures

Due to time and financial constraints, only 15 of the original 20 plots were sampled. For all treatments, except the HP treatment, four of the five (or six) plots were sampled. Only three of the four HP plots were sampled, since a supplementary experiment involving strip clearcutting was overlain on a large portion of plots 10A and 10B (Hughes 1967). Records were unclear as to the exact extent of this experiment, and since only 3 HP plots remained, a decision was made to sample the lower part of 10B, despite the possible confounding of treatment effects.

Prior to sampling, the boundaries between adjacent pairs of plots were chained and distances along them, beginning at the northwest baseline, were remarked. For sampling purposes, it was only necessary to remark five of the boundaries, those between plots one (A and B) and two (A and B), between plots three (A and B) and four (A and B), etc. (Figure 3.1.3). Blocks were scheduled for sampling by selecting random numbers between one and five (the number of plot boundaries); plots on the same boundary were sampled sequentially due to time constraints. During the remarking of the plot boundaries, the location of the seedbed treatments was recorded and these areas were excluded from sampling.

Vegetation was sampled at 15 to 20 points in each of the 15 plots. Point coordinates were chosen randomly, with points located by finding the marked distance along the appropriate plot boundary and then chaining to distances (in metres) perpendicularly from the plot boundary. At each selected distance along a boundary, two points were sampled.

Tree, shrub and herb strata were measured separately. Woody-stemmed plants with dbh>5 cm were considered to be trees, since the canopy was composed largely of trees with small diameters. A larger dbh criterion would have poorly represented the

community structure. Woody plants greater than 50 cm tall and less than 5 cm dbh were considered to be in the shrub stratum. All plants less than 50 cm in height were included in the herb stratum. Therefore, a single species could be measured in more than one strata.

At each point, the dbh (cm) and distance (m) from the point were measured for each of four trees, using the point-centred quarter method (Smith 1980). The quadrant to the upper right of the direction of travel was always numbered as the first quadrant. For each of the four trees, the T-square sampling method for determining spatial pattern (Ludwig and Reynolds,1988) was used to select the nearest neighbouring tree, and the nearest neighbouring tree of the same species (if these were not the same). Distances (m) from the original point-quarter trees to these nearest neighbors were recorded. In determining the nearest neighbor to a tree, stems growing from the same stump were considered to be separate trees if their point of attachment could not be seen above ground. At five of the points within each plot, the age (years) and height (metres) of the four 'point-quarter' trees were measured, using an increment borer and a clinometer, respectively. Percentage canopy cover, of only plants which fit the tree criterion, was ocularly estimated for each species within a 50-m^2 circular quadrat surrounding each sample point.

Within the 50-m^2 circular quadrat at each point, percentage cover of each shrub species was estimated. In order to estimate shrub density, the point-centred quarter method was also applied to the shrub stratum. For each of the four shrubs at a point, distance (m) was measured to the centre of the shrub clump.

In the first quadrant of the point-centred quarter layout, a 1-m^2 quadrat was placed approximately 2m from the point. If the first quadrant was obstructed by dense shrubbery or tree stems, the fourth quadrant was generally used as a substitute location. Percentage cover was estimated for all vascular plant species and identifiable bryophyte species within the quadrat. Cover estimates were made for generalized categories of

unidentifiable grasses, sedges, mosses and lichens. The percentage of the quadrat covered with litter alone was also recorded. A count of tree seedlings was made, by species, within the quadrat. Seedlings were plants less than 50 cm tall, of species with the potential to reach tree size.

Twenty complete (all strata) points were sampled in plots 3A and 3B, the first sampled points. The number of points per plot was reduced to 15 for plots 1B, 2B, 5A, 5B, 6A, 7A, 7B, 8A, 9B, and 10B. In the transition of determining a sufficient number of sample points, 17 points were sampled in plot 6B. In addition, at 5 of the 20 points sampled in plots 4A and 4B, only tree data were collected, using the point-centred quarter method. Due to an oversight, tree data only were collected in one point of plot 5B as well. All points were included in data summarization and analyses, since mean values were calculated for each plot.

3.2.2 Distribution of Soil Types on the Experimental Area and within the Samples

Table 3.2.1 shows the approximate percentage of area that was covered by each of Hills' (1954) soil depth and moisture classifications in each harvest treatment and the percentage of the sample units (SUs) that fell in each soil classification. The approximate percentages of Hills' soil types in each treatment were estimated from an overlay of the soils map provided in Hughes (1967) on the treatment plot map in the same publication (Figure 3.2.1). The location of individual SUs is shown on enlarged copies of each of the sampled plots (Appendix 4).

Fresh medium-shallow (F-ms) and moist medium-shallow (M-ms) were the two most common soil types, covering 20% of the area each (Figure 3.2.1, Table 3.2.1). Due to the exclusion of certain plots from sampling because of time constraints, the avoidance of certain areas because of cultural (seedbed) treatments and other experiments, and the sampling method (random) within the plots, the distribution of the

Table 3.2.1. Distribution of soil types within harvest treatment plots of the RC17 experimental area, and percentage of sample units in each soil type for each harvest treatment.

Soil type†	Approximate % of area in each harvest treatment belonging to each soil type.* All	CC	DC	HP	SC	% of sample units in each soil type for each harvest treatment. All	CC	DC	HP	SC
D-es	5	4	0	4	4	6	2	0	9	14
D-vs	5	4	13	tr	20	13	5	27	0	21
F-ms	20	20	13	31	27	6	0	8	7	10
F-d	10	10	11	19	13	17	14	0	27	27
M-es	5	5	6	0	0	3	5	5	0	1
M-vs	10	7	13	8	7	11	14	8	11	11
M-ms	20	25	25	13	7	20	39	24	16	1
M-d	10	10	4	19	13	12	10	13	22	4
Mp	10	10	17	6	4	8	12	15	0	7
SUM	95	95	102	100	95	98	100	100	92	99

†D=dry, F=fresh, M=moist, Mp=mucky peat, es=extremely shallow, vs=very shallow, ms=medium shallow, d=deep.

*Percentages for 'All' are derived from estimated acreages in Hughes (1967, p.3), percentages for each harvest treatment are estimated from Figure 3.2.1.

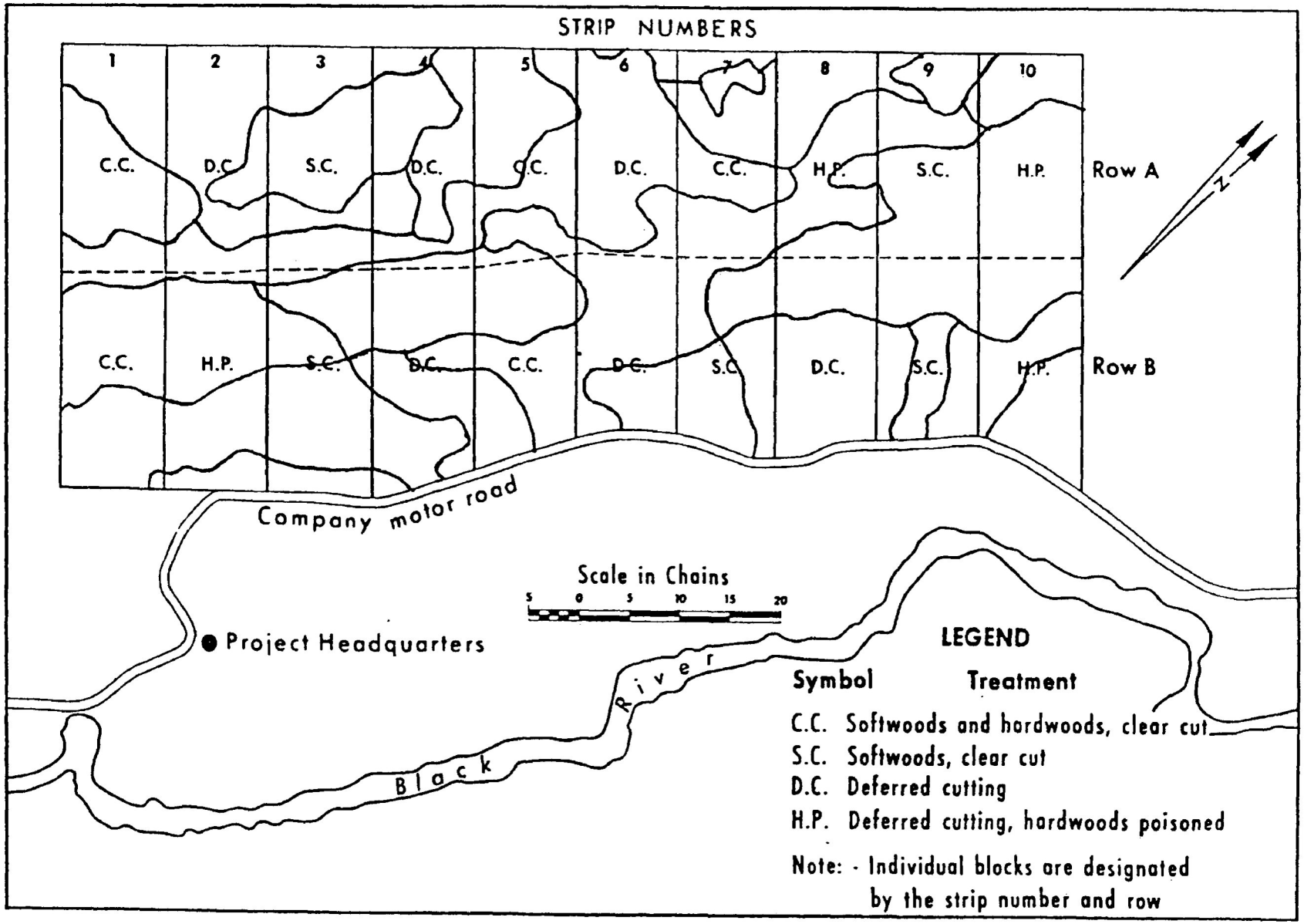


Figure 3.2.1. Overlay of soil depth and moisture classes on the treatment plots of the RC17 project (after Hughes 1967).

SUs among soil types was not proportional to the percentage of area which each soil type occupied on the entire experimental area (Table 3.2.1). Some of the important differences should be noted. Samples of all treatments except DC had a much smaller percentage of SUs on F-ms sites than the percentage of these site types in those areas. This is especially true for CC in which no F-ms sites were sampled. Similarly, no F-d sites were sampled in the DC treatment. In HP and SC, the percentage of SUs located on F-d sites was considerably greater than the percentage of area that these site types occurred on. This was also true for M-ms sites in CC and for moist-deep (M-d) soils in DC. However, in SC, the proportion of SUs on M-d sites was less than the proportion of the area they occupied.

Thus, in the present study, data for the CC and DC treatments were obtained mostly from moist soils, the majority of these being medium shallow (Table 3.2.1). A fair percentage of the DC SUs were on dry-very shallow (D-vs) soils. HP data were derived mostly from moist soils, these being mostly deep, although a fair percentage were medium-shallow. For the SC treatment, most of the data were obtained from SUs located on dry or fresh soils, these being a mixture of depths from extremely shallow to deep.

3.2.3 Data Summarization

In each plot, density (trees per hectare), dominance (m^2 of basal area per hectare) and percentage frequency were calculated for each tree species using the point-centred quarter data. Relative values of these three measures were calculated and summed to give an importance value (IV) for each species in the tree stratum. Total density of all tree species combined was also calculated.

The mean dbh of each tree species in each plot was also determined from the point-centred quarter data. Percentage canopy cover of each tree species, as estimated in the 50-m^2 circular quadrats, was averaged for the 15 to 20 sample points in each

plot.

T-square distances were summed for each plot. At each point, only the shortest nearest neighbour distance (of the four measured for point-quarter calculations) was used for the calculation of overall spatial pattern (all species together). In addition, to calculate spatial pattern for each species, the distances between nearest neighbors of a particular species were summed over a treatment. In cases where two or more nearest neighbour pairs of the same species occurred at a single point, only the shortest distance was used.

Point-centred quarter calculations were performed on the shrub stratum to determine each species' density (shrubs per hectare) for each plot. Percentage cover values of shrub species, as obtained in the 50-m^2 circular quadrat, were averaged for each plot. Frequency was calculated as the number of quadrats in which a shrub species occurred; this was expressed as a percentage. Importance values were calculated for species in the shrub stratum by summing relative cover and relative frequency.

Plot values of percentage frequency and mean percentage cover for each species in the herb stratum were calculated (using data from the 1-m^2 quadrats) in the same manner as in the shrub stratum. Relative cover and relative frequency were summed to yield herb importance values. Seedling counts for each tree species were averaged for each plot, and seedling density per hectare was calculated for each plot by multiplying the average seedling count per 1-m^2 quadrat by 10,000 m^2 per hectare. Seedling stocking (percentage frequency) in each plot was tallied for each species.

3.2.4 Forest Ecosystem Classification Type Identification and Distribution

Forest Ecosystem Classification (FEC) types (Sims *et al.* 1989) were identified after data collection, in order to facilitate interpretation of the classification and ordination results. Several differences exist between the FEC sampling strategy and the

strategy employed for this study. The FEC vegetation classification is intended for application to mature (>50 years of age), undisturbed stands (Sims *et al.* 1989), while the stands on the RC-17 project were 27 to 37 years old, naturally regenerated from a harvest. Sites 'typical' of a stand are generally selected for placement of FEC sample plots; SUs were randomly selected in the current study. The basic sample plot for FEC is a 10m x 10m square plot; in this study tree and shrub cover were estimated in a 50-m^2 circular plot, and herb cover estimated in a single 1-m^2 plot within that. For FEC, woody plants do not belong to the tree stratum (for classification purposes) unless they are greater than 10m tall or have a dbh of greater than or equal to 10 cm; in this study, any stem with a dbh greater than 5 cm was considered to be a tree.

Despite these differences, most of the SUs were classified fairly easily from the FEC vegetation key using the cover values as originally assigned to the three strata. For borderline or difficult classifications, the point-centered quarter data for trees (and shrubs) and the FEC vegetation fact-sheets (Sims *et al.* 1989) were used to aid in decision-making. In a few cases, they were used to override obvious misclassifications from using the vegetation key. The resulting classification of SUs to FEC vegetation types (V-types) is summarized in Figure 3.2.2.

3.3 ANALYSES OF 1990 DATA FROM THE RC17 EXPERIMENTAL AREA

To determine whether the four canopy treatments applied between 1953 and 1963 produced significantly different phytosociological communities, 37 years after harvest, species composition and abundance of the tree, shrub and herb strata were analyzed separately using Median Polish and ANOVA. For the tree stratum, age, height and spatial pattern of trees were compared among treatments as well. Diversity indices and resemblance measures, calculated for all three strata combined, were also compared among treatments. To determine whether conifers gained a competitive advantage over hardwoods early in succession in some treatments more than in others, softwood to

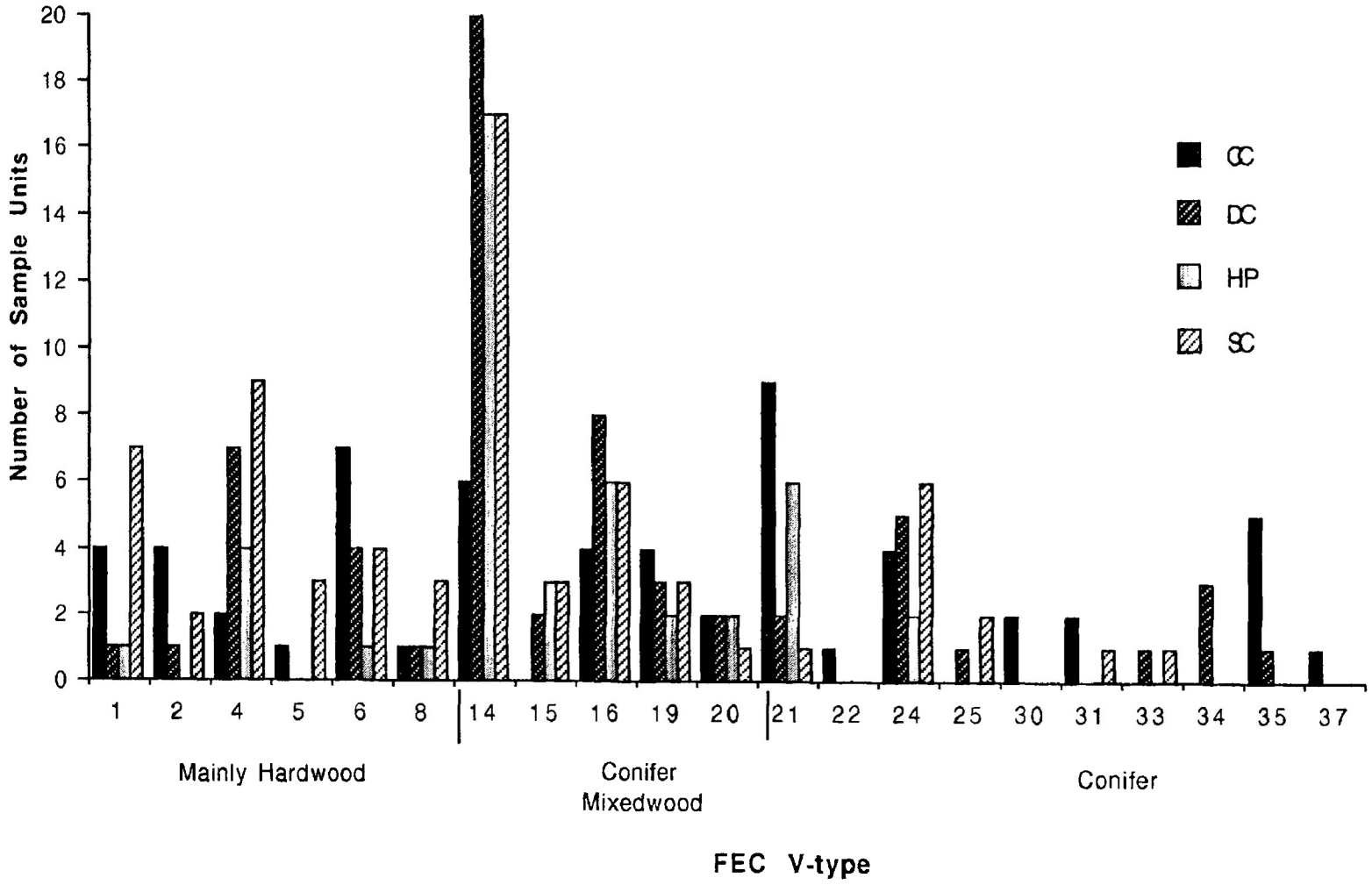


Figure 3.2.2. Distribution of sample units in FEC vegetation types for the harvest treatments of the RC17 study area.

hardwood ratios (S:H) were calculated for tree dominance, density, frequency and I.V., and these as well as their age and height were compared among the four treatments. To determine whether *Picea* spp., relative to hardwoods and to *Abies balsamea*, had an advantage in some treatments compared to others, *Picea* spp.:*Abies balsamea* ratios (Spr:F) and *Picea* spp. to hardwood ratios (Spr:H) were also calculated for the tree stratum. Ordination and classification methods were done on data for the three strata separately, and all combined, to search for multidimensional treatment differences (all species combined) as well as to search for the main phytosociological trends in the data, and to determine possible environmental factors influencing these trends. The soil moisture and soil depth classes outlined above were the principal factors examined with regard to the latter objective.

3.3.1 Comparison of Overstory Characteristics

3.3.1.1 Median Polish

Median polish was performed on data sets of harvest treatment means for density, dominance, frequency, canopy cover, dbh and height of tree stratum species, in order to detect joint reponses of species to harvest treatments. The main objective of the present study is to determine whether any differences in community structure and composition exist due to the four initial harvest methods twenty-seven to thirty-seven years after treatment. Since each attribute (cover, frequency, etc.) is measured over many variables (species) in a particular stratum, a multivariate test would be ideal to determine whether an overall difference exists among treatments. However, the number of species plus the number of treatment levels exceeds the number of replications per treatment level in all strata and therefore traditional multivariate tests of centroid equality, such as discriminant function analysis, are not possible (Ter Braak, 1987). In addition, formal multivariate statistical methods assume that the data structure

adhere to a multivariate normal distribution, which is unlikely in a natural plant community, and difficult to test.

Tests of means in univariate data, such as analysis of variance (ANOVA) have very poor resistance to outliers, with one or two anomalies in a data set having a large impact on the fitted model, and therefore on the test of equality of means (Emerson and Hoaglin, 1983). This therefore extends to the multivariate case, since multivariate analysis of variance (MANOVA) and discriminant analysis test the equality of multivariate centroids among different factors (treatment levels) (Green, 1978). In order to counter this sensitivity to outliers, robust exploratory techniques have been developed, one such technique being median polish (Emerson and Hoaglin, 1983). This technique is typically used on a two-way table composed of two factors and one response variable, in the fashion of a two-way ANOVA (Emerson and Hoaglin, 1983). In such a case, each row represents a level of one factor, and each column a level of the other factor. The cells represent the value of the response variable for that treatment combination. The data matrix for a plant community study comparing the effects of four levels of a treatment (harvesting) has the form of a two-way table, with each row representing a species and each column a treatment level. The response variables are the values of each species for each treatment level. Thus, median polish seems an appropriate method to detect any overall differences in community composition (in terms of abundance measured by density, frequency, cover, etc.) among the four levels of the harvest treatment.

The additive model for a median polish is equivalent to that of a two-way factorial ANOVA, without the interaction effect: $y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$, where μ= the common value or overall effect (also referred to as the grand median), α_i= a row effect, β_j= a column effect, and ε_{ij}= the residuals, i.e. the departure of y_{ij} from the purely additive model. The median polish procedure is computationally simple. Row medians and column medians are subtracted from cells of the data matrix iteratively until all values

of both sets of medians are approximately zero (Emerson and Hoaglin, 1983). The data matrix resulting from the last iteration contains the residuals of the analysis (Tukey, 1977). These values are subtracted from the values in their corresponding cells in the original data matrix to obtain the fit. The effects are then obtained as follows. Row medians and column medians are determined for the matrix of fits. The overall effect is the grand median of this data matrix. Row effects are calculated by subtracting the grand median from the row medians of the fits, and column effects are calculated as the difference between the column medians and the grand median of the fits.

In the case of the species x treatment level matrix of the present study, the effects of interest will be the column effects; these will indicate whether there are any systematic differences in overall species composition among the four harvest treatment levels (i.e. whether there are joint responses of species to harvest treatments). The row effects will simply reflect relative species importance over all four treatments, which has already been determined by relative values for cover, frequency, etc. The overall effect simply represents the grand median of all values (all species, all treatments) for the parameter being measured. The residuals may also be informative; extreme negative or positive residuals may simply represent random error, or may in this case indicate that although the species composition did not respond in concert to the different harvest levels, individual species did respond to harvest treatment.

The main advantage of median polish is its resistance to outliers. An analysis of means tends to produce residuals of moderate size, with fewer residuals of large magnitude and fewer residuals near zero than does median polish. Median polish tends to recognize extreme values in a small number of cells as residuals rather than as part of the additive model. The fit of the model, i.e. the overall effect, the row effect and the column effect are not affected much by such outliers (Emerson and Hoaglin, 1983).

3.3.1.2 Analysis of Variance (ANOVA)

Density, dominance, frequency, and canopy cover for each species with a frequency greater than 5% were compared among treatments using individual ANOVAs. Overall tree density was also compared among treatments by ANOVA. Bartlett's test of homogeneity was done on plot values of the four measures prior to conducting ANOVAs. For percentage frequency and percentage cover, which theoretically follow a binomial distribution (Anderson and McLean 1974), an arcsine transformation (i.e. arcsine$\sqrt{p}$; p=the percentage expressed as a proportion) was done for those species for which Bartlett's test was significant at α=0.01. There is no reason to assume that the statistical distributions of density and dominance are nonnormal, and therefore square-root transformations were done for these two measures only on those species for which Bartlett's test was significant at α=0.001 (Anderson and MacLean 1974).

To allow for the typically noisy data obtained in studies of plant communities, a liberal p-value of 0.10 was used to test for significant differences among species in the ANOVAs, and species that produced p-values less than 0.20 were also reported. Fisher's protected least significant difference, a multiple means test, was done for species with p-values less than 0.10, to determine which treatments were significantly different from each other; for species with p-values greater than 0.10 but less than 0.20, this calculation was also done, but is considered to be 'unprotected', i.e. its results are less reliable, since the accompanying ANOVA F-value was non-significant (Steel and Torrie 1980).

3.3.1.3 Spatial Pattern

Spatial pattern of trees was determined for each plot using the T-square distance method and the Johnson and Zimmer distance index of dispersion (Ludwig and Reynolds, 1988]. For the T-square method, an index of clumping, C, is calculated:

$$C = \frac{\sum_{i=1}^{N} \left[x_i^2 / \left(x_i^2 + \frac{1}{2} y_i^2 \right) \right]}{N}$$

where: x_i = distance from point to individual
y_i = distance from individual to nearest neighbor
N = total number of sample points.

This index is tested for significance using the statistic:

$$z = \frac{C - \frac{1}{2}}{\sqrt{\frac{1}{12N}}}$$

If the overall distribution of trees (or a particular species of tree) is random, C will be approximately 0.50. Significant negative deviations of C from 0.50 indicate uniform patterns, while significant positive deviations of C from 0.50 indicate clumped patterns.

The Johnson and Zimmer index of dispersion, I, which requires only distances from point to individual, was calculated for comparison to the T-square index:

$$I = (N+1) * \frac{\sum_{i=1}^{N} (x_i^2)^2}{\left[\sum_{i=1}^{N} (x_i^2) \right]^2}$$

I is tested for significance by the statistic:

$$z = \frac{I - 2}{\sqrt{\frac{4(N-1)}{(N+2)(N+3)}}}$$

I converges to normality only at moderate sample sizes; it is quite close at N=100. I is approximately 2 when the distribution of individuals is random, with significant negative deviations indicating a uniform pattern and significant positive deviations indicating a clumped pattern. Both of these indices, I and C, are based on the logic that if the pattern of individuals across a continuous area is completely random, $E(x^2) = \frac{1}{2} E(y^2)$, where E= expected. Therefore if the pattern is clumped, $E(x^2) > \frac{1}{2} E(y^2)$, and if

it is uniform, $E(x^2) < \frac{1}{2} E(y^2)$.

For each plot, the overall pattern of tree distribution was determined using both C and I. An overall C and I were also determined for each treatment by calculating C and I using all points within a treatment. In addition, where the number of x-y pairs of species was a reasonable size (greater than ten) in all four treatments (combining plots in a treatment), the T-square index, C, was calculated for the individual species, in order to make a rough comparison among treatments.

3.3.1.4 Age and Height

Mean and median tree height were determined for each plot using the five points (20 trees) at which age and height were measured. Due to the small sample sizes, a median polish analysis was used to search for differences among treatments in the median heights of tree species. An ANOVA was done to compare average tree height (all species combined) among the treatments.

Mean and median ages for trees (all species combined) were determined for plots and compared among treatments.

3.3.2 Comparison of Understory Characteristics

Median polish analyses and individual ANOVAs were used to compare differences in density, percentage cover and percentage frequency among treatments for the most frequent shrub species, and to compare treatment differences in cover and frequency among frequent herb species. Prior to testing by ANOVA, Bartlett's test for homogeneity was conducted on percentage cover and percentage frequency values. As for the tree data, arcsine transformations were done if Bartlett's test was significant at α=0.01.

Due to the low stocking of seedlings in most plots, tree seedling density and stocking per plot were simply tabulated for comparison.

3.3.3 Comparison of Combined Strata

3.3.3.1 Diversity

For comparisons of treatment effects on all three strata combined, overall importance values were calculated for each plot by summing IVs across the three vegetation strata (trees, shrubs and herbs). In order to do this the tree IVs had to be scaled down since they were summed across three measures, as opposed to two measures for the other two strata. This was achieved by multiplying tree IVs by two-thirds. IVs for each treatment were calculated by averaging the plot IVs.

Species richness, of all three strata combined, was tallied for each plot and compared by ANOVA. Using the overall IV values for each plot, four diversity indices and an evenness index were computed.

The diversity indices used were Shannon's index (H'), Simpson's index (λ) and two of Hill's diversity numbers derived from these: N1 and N2. N1 is the natural anti-logarithm of Shannon's index, and N2 is the reciprocal of Simpson's index (Ludwig and Reynolds 1988). These indices are estimated from samples of infinite populations as follows:

$$H' = -\sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right]$$

$$N1 = e^{H'}$$

$$\lambda = \sum_{i=1}^{S}\left[\frac{n_i(n_i-1)}{n(n-1)}\right]$$

$$N2 = \frac{1}{\lambda}$$

where: n_i = the number of individuals of the i^{th} species in a sample, or in this case, the IV of the i^{th} species
n = the total number of individuals in the sample or in this case, the sum of all species' IVs,
ln = the natural logarithm
e = base of the natural logarithm,
S = the number of species in the sample.

H', which describes the degree of uncertainty in a population in terms of which species a randomly selected individual belongs to, increases as the number of species in a sample increases and as the evenness of the distribution of individuals among species increases. Thus its upper limit is infinity. H' is zero (its lower limit) only if the sample contains only one species, and it attains its maximum for a given number of species when each species has the same number of individuals (or equal abundances, IVs, etc.). λ expresses the probability that any two individuals drawn at random from any of the treatment populations would belong to the same species. Its possible range is therefore zero to one, and the higher is its value, the lower is the diversity of the population (Ludwig and Reynolds,1988).

Both of the diversity numbers, N1 and N2, represent the effective number of species present in a sample, according to proportional abundances, i.e. they represent the number of species that would produce the same H' or λ if each species were equally abundant (or in this case, if each species had equivalent IVs). The two measures differ in the degree to which they emphasize abundance: N1 is essentially the number of abundant species, while N2 is essentially the number of *very* abundant species in the sample (Ludwig and Reynolds,1988).

The evenness index employed is the 'modified Hill's ratio', computed by: $E = \frac{N2-1}{N1-1}$, where N1 and N2 are defined as in the diversity measures. Thus it is essentially a ratio of the number of very abundant species to the number of abundant species. This evenness index approaches zero as a single species becomes more dominant, and is relatively unaffected by species richness and sample size (Ludwig and Reynolds,1988).

Since importance values, which are weighted by species abundances, were used rather than straight counts for the diversity measures, ANOVA cannot be used for comparison (Ludwig and Reynolds,1988).

3.3.3.2 Plot Resemblance

In order to take into account the different emphases of different measures, four resemblance measures were calculated for plot pairs to determine whether plots within a treatment were more similar in species composition and abundance than were plots of different treatments. The measures used were: euclidean distance (ED), Mean absolute distance (MAD), Bray and Curtis' percentage dissimilarity (PD) and the chord distance (CRD). These are calculated as follows:

$$ED_{jk}=\sqrt{\sum_{i=1}^{s}(x_{ij}-x_{ik})^2}\quad , \text{ where:}$$

s=the number of species, and
x_{ij}=the abundance (or IV) of the i^{th} species in the j^{th} plot,
x_{ik}=the abundance (or IV) of the i^{th} species in the k^{th} plot,

$$MAD_{jk}=\frac{\sum_{i=1}^{S}\left|x_{ij}-x_{ik}\right|}{S}$$

$$PD=1-PS, \text{ where: } PS=\frac{2W}{A+B}, \text{ and } W=\sum_{i=1}^{S}\min(x_{ij},x_{ik})), \quad A=\sum_{i=1}^{S}x_{ij}, \quad B=\sum_{i=1}^{S}x_{ik}$$

$$CRD_{jk}=\sqrt{2(1-cosq_{jk})}, \text{ where: } \quad cosq_{jk}=\frac{\sum_{i=1}^{S}x_{ij}x_{ik}}{\sqrt{\sum_{i=1}^{S}x_{ij}^2\sum_{i=1}^{S}x_{ik}^2}}$$

The first two measures emphasize differences in abundances of species between plot pairs; this is especially true for ED, in which these differences are squared. PD also focuses on actual abundances, equalling zero if the abundances of species in the two plots are identical. CRD on the other hand places more importance on the relative proportion of species than on their absolute quantities.

Calculated MADs for the plot pairs were almost 10 times greater than the PDs; thus only the latter measure is reported because it is thought to be more reliable

(Ludwig and Reynolds 1988) and has an upper limit of one, rather than infinity (as does MAD), making it intuitively easier to interpret.

For each of PD, CRD and ED, the actual range of values and the 20th and 80th percentiles of these ranges were calculated, in order to compare high and low plot resemblances. This revealed some differences in resemblance as calculated by PD in comparison to CRD and ED. The latter two had very similar results in terms of plot pair resemblances falling below the 20th percentile or above the 80th percentile. Thus, only CRD is presented, since it is considered to be less prone to spurious results than is ED (Ludwig and Reynolds 1988), and its upper limit of $\sqrt{2}$=1.414 is intuitively easier to understand than is that of ED (infinity).

3.3.4 Comparisons to Pre-Harvest Observations

Density and frequency of tree species in 1990 were summarized for the soil moisture and soil depth classes in order to make comparisons to 1953 tree density and frequency as well as to 1953 advance growth stocking and density; the 1953 measurements were made prior to harvest treatments (reported in Hughes 1967). Comparisons were also made of the post-harvest (1990) tree density and frequency for each treatment, to pre-harvest data (1953) for the soil site types most prominent in samples of that treatment (Table 3.2.1), as follows: 1990 CC vs. 1953 M-ms, F-d and M-vs; 1990 DC vs. 1953 D-vs, M-ms and M-d; 1990 SC vs. 1953 F-d, D-vs and D-es; and 1990 HP vs 1953 F-d, M-d and M-ms. The same procedure was used to compare pre-harvest advance growth density and stocking to post-harvest tree density and stocking and to post-harvest shrub and herb densities and frequencies for tree species. This provided some information about harvest-induced changes in overstorey structure and composition and in regeneration characteristics, as well as about the influence of pre-harvest advance growth on post-harvest tree composition. Understorey species composition and cover in 1990 were compared to available lists and data of the

pre-harvest (Hughes 1967) and immediate post-harvest (Sutton 1964) understorey community.

3.3.5 Ordination of the RC17 Data

Indirect ordinations were performed on the 1990 data to reveal underlying ecological gradients on the study site and to determine whether these gradients are related to harvest method and/or soil moisture and depth. Direct ordinations were performed to quantify the extent of any such relationships. All ordinations were performed using the program CANOCO, Version 3.11 (Ter Braak, 1990). Four data sets were used for the ordinations: 1) tree stratum percentage cover, 2) shrub stratum percentage cover, 3) herb stratum percentage cover, and 4) percentage cover of all three strata (1, 2 and 3 combined). Rare species (those with frequency <3%), except for a few thought to be ecologically significant, were removed from these data sets in order to minimize spurious correlations and covariances in ordination calculations.

3.3.5.1 Ordination Theory

Principal component analysis (PCA) and correspondence analysis (CA) are related indirect ordination methods (Pielou 1984) which both operate directly on species data, but their operations differ in a way that makes them appropriate for detecting different types of data structure (Ter Braak 1987). PCA is based on a linear response model, assuming that the main patterns of species variation are monotonic, i.e. that each species' abundance either continuously increases or continuously decreases with changes in the value of each underlying (environmental) variable (Ter Braak 1987). In contrast, CA is more closely related to a unimodal response model; a species is assumed to occur within a limited range of values of an underlying variable, its abundance rising and falling over this range, with a single peak or plateau (the mode) in abundance at the species' optimum value(s) of this variable (Ter Braak 1987). This

latter model is closer to the Gaussian (bell-shaped) curves of species' responses to environmental gradients (Ter Braak 1987) that have been detected in studies of direct gradient analysis on known coenoclines (Whittaker 1978).

PCA is the simplest ordination method, involving projection of the data swarm, as is, onto a differently oriented species-space (s-space) so that the first principal axis of the new coordinate frame accounts for the largest possible percentage of the actual variance among the n sample units being ordinated, the second axis accounts for as much of the remaining variation as possible, etc. (Pielou 1984). Essentially, PCA creates a theoretical variable that determines the fit of straight lines for the species' abundance data that will minimize the total residual sum of squares for that data after the fit (Ter Braak 1987). The theoretical variable is constructed by an eigenanalysis that determines the site scores that will accomplish this fit (Ter Braak 1987).

CA also creates a theoretical variable (the first ordination axis) that accounts for the greatest amount of variation in the species data, by choosing site scores that maximize the dispersion of the species scores. The second and further CA axes maximize the residual variation in the species data; i.e. they are uncorrelated (orthogonal) with the first and any previous axes (Ter Braak 1987). This is accomplished by either an eigenanalysis (Pielou 1984) or by reciprocal averaging (Ter Braak 1987). CA produces as many eigenvalues (λ) as there are species in the data set. Each eigenvalue corresponds to an ordination axis. Eigenvalues are produced in descending order of importance. They represent the dispersion of the species scores on their corresponding ordination axes. All eigenvalues fall between 0 and 1, and values greater than 0.5 tend to indicate good separation of species along an axis (Ter Braak 1987).

Site scores and species scores of CA can be standardized by Hill's scaling, which expresses them in multiples of one standard deviation (s.d.)(Ter Braak 1987). Species distributions represented by Gaussian curves typically rise and fall over 4 s.d., sample units separated by 4 s.d. or more can be expected to have few coincident common species

(Ter Braak 1987). Hill's scaling also requires that site scores be weighted averages of species scores, placing sites (sample units, SU) in the ordination at the centroid of the species that they contain. Since the CA method is based on Gaussian response curves (or multidimensional surfaces) that are typical of species data, the species points should lie close to the optima of the surfaces. Therefore, SUs that are located near a species point in a joint plot of species and sites are likely to have a high abundance of that species, and as distance from a species point increases, its probability of occurrence and expected abundance decrease (Ter Braak 1987).

Canonical correspondence analysis (CCA) is a direct gradient analysis variant of correspondence analysis, which extracts patterns of variation in a data set that are (most likely) due to measured environmental variables (Ter Braak 1986). CCA determines the linear combination of these variables that maximizes the spread of species scores along the first axis, i.e. it determines the weights for the environmental variables that best explain variability in the species data (Ter Braak 1987). As in CA, the eigenvalue of each axis in CCA represents the dispersion of species scores along that axis. However, since the axis is restricted to variation explained by selected environmental variables, the eigenvalue also measures the degree of association between the species and the environmental variable. The species-environment correlation, R, i.e. the multiple correlation coefficient between the site scores that are weighted averages of the species scores and site scores that are a linear combination of environmental variables, also measures the association between species and environment, but may be misleadingly high in analyses that produce small eigenvalues (Ter Braak 1987).

The relative importance of each environmental variable in determining each canonical axis is measured by the canonical coefficients and the intraset correlations. The canonical coefficients define the ordination axes as linear combinations of the environmental variables, while the intraset correlations are the correlation coefficients

of the environmental variables with the ordination axes. Both are a measure of the rate of change in species composition by changing the corresponding environmental variable. If the environmental variables are totally uncorrelated with each other, these provide the same information. However, if the variables are correlated, the intraset correlations are more stable (Ter Braak 1987).

3.3.5.2 Application of Ordination

CA and PCA were initially run on the data set containing percentage cover of all three strata and on that containing only percentage cover of species in the tree stratum. PCA accounted for higher percentages of the species' variance on the first two axes than did CA, but its ordination diagrams of species made less 'ecological sense' than those of the corresponding CAs. For the CAs, the most typical mixedwood tree species fell near the centre of the ordination diagrams, while less common species with narrower niches were located near the ends of axes. PCA pulled *Abies balsamea* (tree) far out on axis 2, and *Acer spicatum* (shrub) far out on axis one, with these common species clearly separated from many others that they usually occurred with, e.g. *Picea glauca, Betula papyrifera*. Clumping of SUs by FEC types was also more pronounced in the CAs than in the PCAs. Since the CAs produced ordination axes with lengths greater than 4 standard deviations (s.d.), it was likely that the ecological gradients contained in the species data are too broad to be handled by PCA (ter Braak 1987). Detrended correspondence analysis (DCA), using detrending by polynomials, was attempted on the same data sets, but showed almost no difference from the CA in the eigenvalues of axis two and in the ordination diagrams. From the output of these runs, CA was chosen as a superior ordination method for the RC17 data and all further runs were based upon it.

A CA was done on the combined strata data set with all SUs located on wet (mucky peat) sites removed, in order to determine whether clearer distinctions (by harvest treatment, by soil parameters) would be evident among the upland SUs. The resulting

ordination diagram was almost identical to the original CA, but for a reduction in the length of axis 1 at the positive end. Thus, no further analyses were performed with these SUs removed.

Two CCAs were performed on each data set. The first used harvest treatment as a nominal canonical variable, by assigning 'dummy variables' (each gets a score of 0 or 1 on each level), to each type (level) of harvest treatment. Thus the four levels of harvest treatment are represented on the ordination diagrams as points, located at the centroid of sample units belonging to each class, close to species points that are highly represented in the sample units of that class (Ter Braak 1986). Since there is only one true variable, only one canonical axis was extracted. The second CCA was done using soil depth and soil moisture as canonical variables. The levels of these variables provided by the original study (Hughes 1967) were ordinal, but not quantitative, so they were simply entered as finite integers from 1 (dry) to 4 (wet=mucky peat) on the moisture scale and from 1 (extremely shallow) to 4 (deep) and then 5 for mucky peat on the depth scale. Each of these two variables is represented on the ordination plots as environmental arrows, the direction of each arrow representing the direction in the ordination diagram along which the values of the environmental variable increase, and the relative length of one arrow to another representing their relative influence on species' variation, and their relative degree of correlation with the species axes (Ter Braak 1987). The coordinates of the harvest treatment centroids and of the soil moisture and depth arrow heads were scaled up by appropriate multiples to match the sample unit and species coordinates, as suggested by Ter Braak (1987). The multiplying factor for this upscaling is given in each CCA ordination diagram.

All CA and CCA were done with Hill's scaling and with downweighting of rare species. The program CANOCO (Ter Braak, 1990) has a CA option that downweights species according to their frequency. This option was used in all CA and CCA runs and the resulting weights of each species included in the ordinations are given in Table 3.2.2.

Table 3.2.2. Downweights applied to rare species in the correspondence analyses and canonical correspondence analyses of the vegetation cover data sets collected on the RC17 project, 1990.

Species	Downweight*	Species	Downweight	Species	Downweight
Abies balsamea		*Lycopodium obscurum*	0.490	*SH C. stolonifera*	
Acer spicatum		*Maianthemum canadense*		*SH C. cornuta*	
Alnus rugosa	0.346	*Mertensia paniculata*	0.747	*SH D. lonicera*	0.589
Anemone quinquefolia		*Mitella nuda*		*SH F. nigra*	0.232
Aralia nudicaulis		*Mnium spp.*	0.690	*SH K. polifolia*	0.031
Aster ciliolatus	0.452	*Moneses uniflora*	0.584	*SH L. laricina*	0.116
Aster macrophyllus		Moss spp.		*SH L. groenlandicum*	0.536
Athyrium filix-femina	0.355	*Petasites palmatus*	0.884	*SH L. canadensis*	
Betula papyrifera	0.419	*Pleurozium schreberi*		*SH L. involucrata*	0.469
Brachythecium sp.		*Polytrichum juniperinum*	0.404	*SH L. oblongifolia*	0.095
Carex spp.		*Prunus pensylvanica*	0.123	*SH L. villosa*	0.107
Carex trisperma	0.140	*Ptilium crista-castrensis*	0.495	*SH P. glauca*	
Circaea alpina	0.180	*Rhamnus alnifolia*	0.072	*SH P. mariana*	
Cladonia spp.	0.747	*Rhytidiadelphus triquestrus*	0.340	*SH P. balsamifera*	0.320
Cladina rangiferina	0.374	*Ribes lacustre*	0.141	*SH P. pensylvanica*	0.429
Climacium dendroides	0.078	*Ribes triste*	0.546	*SH P. virginiana*	0.330
Clintonia borealis		*Rosa acicularis*	0.715	*SH S. decora*	
Coptis trifolia	0.749	*Rubus idaeus var. strigosus*	0.331	*SH R. alnifolia*	0.220
Cornus canadensis		*Rubus pubescens*		*SH R. hispidus*	0.297
Cornus stolonifera	0.209	*Sorbus decora*	0.739	*SH R. lacustre*	0.884
Corylus cornuta	0.364	*Sphagnum capillifolium*	0.286	*SH R. acicularis*	
Dicranum spp.		*Sphagnum magellanicum*	0.161	*SH R. idaeus*	0.855
Diervilla lonicera	0.693	*Streptopus roseus*		*SH Salix spp.*	0.705
Epilobium angustifolium	0.078	*Thelypteris phegopteris*	0.276	*SH T. occidentalis*	0.563
Equisetum arvense	0.384	*Thuja occidentalis*	0.157	*SH V. edule*	
Equisetum pratense	0.896	*Trientalis borealis*		†*TR A. balsamea*	
Fragaria virginiana	0.246	*Vaccinium angustifolium*	0.492	*TR A. rugosa*	0.675
Galium triflorum		*Vaccinium myrtilloides*	0.443	*TR B. papyrifera*	
Gaultheria hispidula	0.707	*Vaccinium oxycoccos*	0.058	*TR F. nigra*	0.172
Geocaulon lividum	0.050	*Viburnum edule*	0.532	*TR P. balsamifera*	
Grass spp.		*Viola renifolia*		*TR P. glauca*	
Gymnocarpium dryopteris		†*SH A. balsamea*		*TR P. mariana*	0.395
Hylocomium splendens	0.491	*SH A. spicatum*		*TR P. pensylvanica*	0.887
Ledum groenlandicum	0.507	*SH A. crispa*	0.714	*TR P. tremuloides*	0.210
Lichen spp.	0.496	*SH A. rugosa*		*TR S. decora*	0.395
Linnaea borealis		*SH A. bartramiana*	0.680	*TR Salix spp*	0.456
Lonicera canadensis	0.165	*SH. A. humilis*	0.471	*TR T. occidentalis*	0.715
Lycopodium annotinum		*SH B. papyrifera*			

*Downweights are applied automatically by an option in CANOCO (ter Braak 1990), based on species' frequency in sample units.
†SH indicates shrub stratum species, TR indicates tree stratum species, unlabelled species belong to the herb stratum.

Species with no weight adjacent to them were given full weight (1.0) in the ordination. The attempted PCA's were done with species centering and euclidean distance plotting with covariance-based scores (Ter Braak 1990, 1987).

3.3.5.3 Tabular Comparison of CA-Ordered Cover Data

As noted by Pielou (1984), one of the advantages of correspondence analysis is that it allows the user to order the original data set, both species and sample units, by any chosen axis of the ordination, thus allowing a tabular comparison of species trends in abundance across the ordered SU's. Species scores and sample unit scores on the first axis of the CA performed on cover values of all three strata were used to order the species and the sample units in the table of cover values. A tabular comparison was then made on this table of cover data.

3.3.6 Cluster Analysis

Cluster analyses were performed on the four data sets (tree cover, shrub cover, herb cover and the combined data of all three strata) using the CLUSTER algorithms of SPSS-X (Anon. 1988). All species observed (including rare species) and all SUs sampled were included. Three methods of clustering, centroid (an unweighted average linkage method), median (a weighted average linkage method) and Ward's method were attempted, all with the squared euclidean distance option (which is required in SPSS-X for Ward's method) used as the distance coefficient. Ward's method actually uses the euclidean distance between each SU of a cluster and the centroid of a cluster, but since within cluster variance is being calculated, these distances are squared (Pielou 1984). This is the reason that SPSS-X requires squared euclidean distances. The actual equation for within-cluster variance that is calculated at each step for each cluster and each potential cluster that would result from possible fusions is:

$$Q_{[1...n]} = \sum_{j=1}^{n} d_{jc}, \quad \text{where:}$$

d=the distance coefficient, in this case euclidean distance,
j = an SU, n = total number of SUs, c = centroid of a cluster.

This variance is usually calculated by a simplified equation:

$$Q_{[1...n]} = \frac{1}{n}\sum_{j<k} d^2_{jk}, \quad \text{where k=another SU (Pielou 1984).}$$

Both of the group average algorithms, the centroid method and the median method, showed very indistinct clusters, with many reversals and a large degree of chaining. Ward's method produced dendrograms with much more distinct clusters, especially at higher levels of the dendrogram. Although the lower internodes were quite small, and the length of many of them were indistinguishable on the SPSS-X dendrogram output, later fusions had much longer internodes, suggesting that the clusters represented by these internodes were non-arbitrary with possible ecological significance. Thus, only the dendrograms produced by Ward's method were reported. For Ward's method of clustering, the height of the nodes on the dendrogram represents Q, the within-cluster dispersion (sum of squares) of the newly formed clusters. (Pielou 1984).

Sample units on the dendrogram were labeled by their harvest treatment, soil moisture and soil depth classifications and FEC V-types as well as by their plot and point number. Since most clusters, at both low and high levels, contained a mixture of harvest treatments and of soil classifications, the highest (or most distinct) 5 or 6 clusters were identified for each of the four analyses. For the cluster analysis of herb cover, one fusion within cluster 4 that occurred at a higher level than the fusion between cluster 3 with cluster 1 and 2 was ignored, since it produced one very small cluster (3 SUs). Similarly, another fusion within cluster 4 and another within cluster 5 that were at higher levels than the fusion between cluster 1 and cluster 2 were ignored because they produced small clusters with similar soil types and FEC V-types. For each of the 5 or 6 clusters of each classification, summaries of the number of SUs belonging to each harvest treatment, to each soil classification and to each FEC type were made.

CHAPTER 4 - RESULTS

4.1 TREE STRATUM

Seventeen woody species had attained tree size on the RC17 study area (Table 4.1.1). Two of these species (*Amelanchier humilis* Wieg. and *Pinus banksiana*) did not occur as trees in the point-centered quarter data, but were included in cover data from the 50-m2 quadrats. *Abies balsamea* and *Betula papyrifera* were the only species present in all of the sampled plots (Appendix 5). *Picea glauca* and *Picea mariana* each occurred in all but one plot. Most tree species occurred in the tree stratum of some plots in all four treatments (Table 4.1.1). Six tree species did not occur in the tree stratum in all treatments: *Acer spicatum*, *Amelanchier humilis*, *Pinus banksiana, Larix laricina, Prunus virginiana*, and *Prunus pensylvanica*. Species' treatment means for density, dominance, frequency, cover and dbh are summarized in Table 4.1.1. Plot values are given in Appendix 5.

Total tree densities (treatment means, Table 4.1.1; plot values, Appendix 6) were based on all species attaining tree size. Only commercial species (*A. balsamea, P. glauca, P. mariana, B. papyrifera, Populus balsamifera* and *Populus tremuloides*) were included in the hardwood and conifer classifications. The mean densities were approximately the same for all four treatments: 2000 trees per ha for all species, 1000 trees per ha for commercial conifers and 500 trees per ha for commercial hardwoods. There was no evident trend by treatments. Conifer density was greater than hardwood density in all plots except SC9B. ANOVAs (α=0.10) of each of these density categories showed no significant treatment differences: total ($F_{3,11}$=0.321, p=0.8104), conifers ($F_{3,11}$=0.82, p=0.5093) and hardwoods ($F_{3,11}$=1.263, p=0.3348).

Table 4.1.1. Harvest treatment averages for tree parameters on the RC-17 project, 1990 (species ordered by overall importance values in Table 4.1.2).

	DENSITY (trees/ha)				DOMINANCE (m2/ha)				FREQUENCY (%)				COVER (%)				DBH (cm)			
TREATMENT:	CC*	SC*	DC*	HP*	CC	SC	DC	HP	CC	SC	DC	HP	CC	SC	DC	HP	CC	SC	DC	HP
Abies balsamea	652	803	946	666	7.06	9.66	7.11	4.88	77	73	79	78	21.2	22.5	28.1	25.0	10.7	11.8	9.3	8.9
Betula papyrifera	268	429	371	382	2.32	4.31	3.26	2.85	47	59	50	53	11.8	20.3	21.3	18.1	9.7	12.7	9.6	9.2
Picea glauca	57	176	168	253	0.54	5.24	4.27	6.58	7	28	27	38	2.7	9.5	9.6	13.4	9.2	18.6	15.1	15.7
Picea mariana	274	126	248	108	2.21	1.93	3.29	1.93	33	15	33	13	10.7	7.3	10.7	7.7	9.7	10.4	11.8	14.1
Thuja occidentalis	207	30	61	120	2.45	0.85	2.88	1.75	20	4	5	13	8.5	1.4	2.8	6.7	5.6	3.3	4.2	6.6
Populus tremuloides	142	159	54	20	2.15	4.31	0.40	0.55	13	17	7	5	11.8	8.7	2.7	0.9	7.0	18.6	7.9	10.5
Alnus rugosa	37	103	88	35	0.09	0.25	0.24	0.09	8	13	10	5	1.1	2.0	3.6	1.7	4.1	5.9	2.9	3.9
Populus balsamifera	70	48	37	18	0.47	0.96	0.67	0.19	10	6	4	4	1.5	2.6	1.5	0.6	4.9	5.1	8.5	3.8
Salix	14	48	10	70	0.05	0.24	0.06	0.28	3	8	2	13	0.3	1.0	0.7	1.4	3.5	5.1	2.2	7.0
Sorbus decora	29	42	19	37	0.08	0.19	0.08	0.15	7	8	4	4	0.9	1.7	0.4	0.4	4.2	6.7	3.5	2.4
Fraxinus nigra	41	22	11	7	0.49	0.54	0.06	0.04	2	3	3	2	2.9	0.6	0.4	0.1	2.9	3.6	4.2	2.7
Prunus pensylvanica	9	22	-	7	0.03	0.07	-	0.05	2	4	-	2	0.3	0.4	-	0.6	1.6	3.3	-	3.1
Prunus virginiana	15	-		-	0.04	-	-	-	2	-		-	0.2	-		-	nm**	nm	nm	nm
Larix laricina	6	-	-	-	0.02	-	-		5	-		-	0.1	-	-		nm	nm	nm	nm
Acer spicatum	-	6	8	-	-	0.01	0.02		-	2			0.1	0.1	0.2		nm	nm	nm	nm
Pinus banksiana	-	-	-	-		-	-		-	-	-		-	0.4	-		nm	nm	nm	nm
Amelanchier humilis	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0	-	-	nm	nm	nm	nm
Total spruces	330	301	417	362	2.8	7.2	7.6	8.5					13.4	16.8	20.3	21.1				
Total softwoods†	983	1104	1363	1027	9.8	16.8	14.7	13.4					34.6	39.3	48.4	46.1				
Total hardwoods†	480	636	461	420	4.9	9.6	4.3	3.6					25.1	31.6	25.5	19.6				
Total (all species)	1821	2013	2020	1722	18.0	28.6	22.3	19.3					74.1	78.5	82.0	76.6				
Softwood : Hardwood													1.4	1.2	1.9	2.4				
Spruce : Fir													0.6	0.7	0.7	0.8				
Spruce : Hardwood													0.5	0.5	0.8	1.1				

*CC=clearcut, SC=softwoods only cut, DC=deferred cut, HP=hardwoods poisoned (deferred cut).

**nm=no individuals measured

† Total softwoods = *A. balsamea* + *P. glauca* + *P. mariana*. Total hardwoods= *B. papyrifera* + *P. balsamifera* + *P. tremuloides*.

Relative values and summed importance values (IVs) for the point-centred quarter measures (density, dominance and frequency) are presented in Table 4.1.2. *A. balsamea* had the highest overall IV and the highest IV in each harvest treatment. IVs of several species varied among treatments: *P. glauca* had a low IV (9.0) in treatment CC compared to treatment HP (65.1). *P. mariana* had high IVs in CC and DC (~41) versus those in SC and HP (~20). SC had a very low IV (6.1) for *Thuja occidentalis* in comparison to the other three treatments. *Populus tremuloides* had a much higher IV in CC and SC than in DC and HP. *Populus balsamifera* was most important in CC (10.7), and *Salix* spp. in HP (11.3).

Analyses of the main tree measures, by median polish and by analysis of variance (ANOVA), indicated that, in general, the composition and dominance of the tree stratum did not appear to be influenced greatly by harvest treatments. However, some individual species did seem to be affected by harvest treatments, as outlined in sections 4.1.1 and 4.1.2.

4.1.1 Median Polish Analysis of Tree Density, Dominance, Frequency, Cover and DBH

Median polish is an exploratory analysis, used to highlight variations in complex or noisy data sets. It lacks the power of distinguishing significant differences, but the 'fit' that it creates is very resistant to outliers, i.e. it recognizes extreme values as residuals (Emerson and Hoaglin 1983). It is used here, and in following sections, to uncover any evidence of joint responses of species to harvest treatments, and to highlight variation of individual species' responses among treatments. In the present study, the median polish results should be interpreted as follows: column (treatment) effects indicate whether there are any systematic differences in overall species composition among the four harvest treatments (i.e. whether there are joint responses of species to harvest treatments), row (species) effects reflect relative species

Table 4.1.2. Relative values and importance values for tree parameters in the four harvest treatments of the RC-17 project, 1990 (species ordered by overall importance values).

	RELATIVE DENSITY				RELATIVE DOMINANCE				RELATIVE FREQUENCY				IMPORTANCE VALUES				OVERALL SUM
TREATMENT:	CC*	SC*	DC*	HP*	CC	SC	DC	HP	CC	SC	DC	HP	CC	SC	DC	HP	
SPECIES:																	
Abies balsamea	35.8	39.9	46.8	38.6	39.2	33.8	31.8	25.2	32.6	30.7	35.4	33.7	107.7	104.4	114.0	97.6	423.7
Betula papyrifera	14.7	21.3	18.3	22.2	12.9	15.1	14.6	14.7	19.8	25.0	22.2	23.1	47.4	61.3	55.2	60.0	224.0
Picea glauca	3.1	8.7	8.3	14.7	3.0	18.4	19.1	34.1	2.8	11.6	12.1	16.4	9.0	38.7	39.6	65.1	152.4
Picea mariana	15.0	6.3	12.3	6.3	12.3	6.8	14.7	10.0	14.2	6.2	14.5	5.8	41.5	19.2	41.6	22.0	124.2
Thuja occidentalis	11.4	1.5	3.0	6.9	13.6	3.0	12.9	9.1	8.5	1.6	2.2	5.8	33.5	6.1	18.2	21.8	79.5
Populus tremuloides	7.8	7.9	2.7	1.1	11.9	15.1	1.8	2.8	5.7	7.2	2.9	1.9	25.4	30.2	7.3	5.9	68.9
Alnus rugosa	2.0	5.1	4.3	2.0	0.5	0.9	1.1	0.4	3.5	5.4	4.5	1.9	6.1	11.4	9.9	4.4	31.8
Populus balsamifera	3.9	2.4	1.8	1.1	2.6	3.4	3.0	1.0	4.3	2.4	1.9	1.9	10.7	5.7	6.7	4.0	27.1
Salix	0.8	2.4	0.5	4.0	0.3	0.8	0.3	1.5	1.4	3.2	0.7	5.8	2.5	6.4	1.4	11.3	21.6
Sorbus decora	1.6	2.1	0.9	2.1	0.4	0.7	0.4	0.8	2.8	3.2	1.7	1.9	4.9	5.9	3.0	4.8	18.6
Fraxinus nigra	2.2	1.1	0.5	0.4	2.7	1.9	0.3	0.2	0.7	1.1	1.3	1.0	5.7	4.0	2.1	1.6	13.4
Prunus pensylvanica	0.5	1.1	-	0.4	0.2	0.2	-	0.3	0.7	1.8	-	1.0	1.4	3.1	-	1.6	6.1
Prunus virginiana	0.8	-	-	-	0.2	-	-	-	0.7	-	-	-	1.7	2.4	-	-	4.2
Larix laricina	0.3	-	-	-	0.1	-	-	-	2.1	-	-	-	2.5	-	-	-	2.5
Acer spicatum	-	0.3	0.4	-	-	0.0	0.1	-	-	0.7	0.6	-	-	1.1	1.0	-	2.1
Total spruces	18.1	15.0	20.6	21.0	15.3	25.1	33.9	44.0	17.0	17.7	26.6	22.1	50.5	57.8	81.1	87.1	
Total softwoods†	54.0	54.8	67.5	59.6	54.6	58.9	65.7	69.3	49.6	48.5	62.0	55.8	158.2	162.3	195.2	184.7	700.3
Total hardwoods†	26.4	31.6	22.8	24.4	27.5	33.5	19.4	18.6	29.7	34.6	27.0	26.9	83.6	97.3	69.2	69.9	320.0
Softwoods : Hardwoods	2.05	1.74	2.96	2.44	1.99	1.76	3.39	3.73	1.67	1.40	2.29	2.07	1.89	1.67	2.82	2.64	2.19
Spruce : Fir	0.51	0.38	0.44	0.54	0.39	0.74	1.06	1.74	0.52	0.58	0.75	0.66	0.47	0.55	0.71	0.89	
Spruce : Hardwood	0.69	0.47	0.90	0.86	0.56	0.75	1.75	2.37	0.57	0.51	0.99	0.82	0.60	0.59	1.17	1.25	

*CC = clearcut, SC = softwoods only cut, DC = deferred cut, HP = hardwoods poisoned (deferred cut).

† Total softwoods = *A. balsamea* + *P. glauca* + *P. mariana*. Total hardwoods = *B. papyrifera* + *P. balsamifera* + *P. tremuloides*.

importance over all four treatments, the overall effect represents the grand median of all values (all species, all treatments) for the parameter being measured, and extreme negative (low) or positive (high) residuals suggest that although the species composition did not respond in concert to the different harvest levels, individual species did respond to harvest treatment. An extremely low residual for a species in a treatment suggests that it has a lower value of that measure in that treatment, compared to one or more of the other treatments; extremely high residuals indicate the reverse.

Median polish analyses of density, dominance, frequency, cover and dbh of tree species revealed very little evidence of a joint response of tree species to harvest treatments (Table 4.1.3). Treatment (column) effects were low (<2.0) for all treatments and all measures, except for tree density in SC; even this treatment effect (9.5 trees/ha) was small compared to the corresponding species (row) effects (Table 4.1.3a). For all five measures, SC had a slightly higher treatment effect than did the other treatments, suggesting that species generally had high density, dominance, etc. in SC. However, non-polished treatment means showed that only a few species had highest values in SC for all measures except dbh (Table 4.1.1). In fact, species tended to have moderate values in SC, and only *Thuja occidentalis* and *Picea mariana* had low values. However, several species, including *Abies balsamea*, *Betula papyrifera*, *Picea glauca*, *Populus tremuloides*, *Alnus rugosa* and *Sorbus decora*, did have a higher mean dbh in SC than in the other treatments.

The species (row) effects. of the five median polishes indicated the order of importance of the tree species in each measure over all four harvest treatments (Table 4.1.3). The dominant species in each of density, dominance, frequency and cover were the same as indicated by the overall sum of IVs across treatments (Table 4.1.2): *A. balsamea, B. papyrifera, P. glauca, P. mariana, T. occidentalis* and *P. tremuloides*. The order of importance was slightly different for each measure (Table 4.1.3) and for harvest treatments in each measure (Table 4.1.2).

Table 4.1.3. Median polish results for density, dominance, frequency and cover of the tree stratum on the RC-17 project, 1990 (species ordered by overall importance values of Table 1.2).

a) Fits and effects for density (trees/ha).

TREATMENT:	CC	SC	DC	HP	Species effects
Abies balsamea	731	740	728	729	691
Betula papyrifera	379	387	376	377	339
Picea glauca	170	178	166	167	130
Picea mariana	185	193	182	182	145
Thuja occidentalis	93	101	90	90	53
Populus tremuloides	99	107	96	96	59
Alnus rugosa	64	72	61	61	24
Populus balsamifera	40	48	37	37	0
Salix spp.	27	35	24	24	-13
Sorbus decora	31	39	28	28	-9
Fraxinus nigra	14	22	11	11	-26
Prunus pensylvanica	9	17	6	6	-31
Prunus virginiana	3	11	0	-	-37
Larix laricina	3	11	0	-	-37
Acer spicatum	1	9	-2	-2	-39
				Overall	effect
Treatment effects:	1	10	-2	-1	39

b) Residuals for density (trees/ha).

CC	SC	DC	HP
-79	63	**218**	-63
-112	41	-6	6
-113	-2	2	**87**
89	-67	67	-74
114	-71	-29	29
43	52	-42	**-77**
-27	31	27	-27
30	0	-	**-19**
-13	13	-14	**46**
-2	2	-9	8
27	-	0	-4
-	5	-6	1
12	-11	0	-
3	-11	0	-
-1	-3	10	2

c) Fits and effects for dominance (m2/ha).

TREATMENT:	CC	SC	DC	HP	Species effects
Abies balsamea	7.08	7.19	7.09	7.03	6.82
Betula papyrifera	3.07	3.19	3.08	3.03	2.82
Picea glauca	4.70	4.81	4.71	4.65	4.44
Picea mariana	2.10	2.21	2.10	2.05	1.84
Thuja occidentalis	2.12	2.24	2.13	2.08	1.87
Populus tremuloides	1.37	1.48	1.38	1.32	1.11
Alnus rugosa	0.14	0.25	0.14	0.09	-0.12
Populus balsamifera	0.57	0.68	0.57	0.52	0.31
Salix spp.	0.09	0.20	0.10	0.04	-0.17
Sorbus decora	0.08	0.19	0.08	0.03	-0.18
Fraxinus nigra	0.26	0.37	0.26	0.21	0.00
Prunus pensylvanica	0.01	0.12	0.02	-0.04	-0.25
Prunus virginiana	0.02	0.13	0.02	-0.03	-0.24
Larix laricina	0.01	0.12	0.01	-0.04	-0.25
Acer spicatum	0.01	0.12	0.01	-0.04	-0.25
				Overall	effect
Treatment effects:	0.00	0.11	0.00	-0.05	0.26

d) Residuals for dominance (m2/ha).

CC	SC	DC	HP
-0.02	**2.46**	0.02	**-2.15**
-0.75	**1.13**	0.17	-0.18
-4.16	0.43	-0.43	**1.93**
0.12	**-0.27**	**1.19**	-0.12
0.32	**-1.39**	**0.75**	-0.32
0.77	**2.82**	-0.98	-0.78
-0.05	0.00	0.09	-
-0.10	0.28	0.10	-0.33
-0.04	0.04	-0.04	**0.24**
-	-	-	0.12
0.23	0.17	-0.20	-0.17
0.02	-0.05	-0.02	0.09
0.02	-0.13	-0.02	0.03
0.01	-0.12	-0.01	0.04
-0.01	-0.10	0.01	0.04

(continued)

Table 4.1.3 (cont.)

e) Fits and effects for frequency (%).

TREATMENT:	OC	SC	DC	HP	Species effects
Abies balsamea	77.3	79.0	77.0	77.3	72.2
Betula papyrifera	51.6	53.3	51.4	51.6	46.5
Picea glauca	26.5	28.2	26.3	26.5	21.4
Picea mariana	23.0	24.7	22.8	23.0	17.9
Thuja occidentalis	9.3	11.0	9.1	9.3	4.2
Populus tremuloides	10.0	11.7	9.8	10.0	4.9
Alnus rugosa	9.3	11.0	9.1	9.3	4.2
Populus balsamifera	4.4	6.1	4.2	4.4	-0.7
Salix spp.	4.6	6.3	4.4	4.6	-0.5
Sorbus decora	5.1	6.8	4.9	5.1	0.0
Fraxinus nigra	2.0	3.7	1.7	2.0	-3.2
Prunus pensylvanica	2.0	3.7	1.7	2.0	-3.2
Prunus virginiana	1.0	2.7	0.8	1.0	-4.1
Larix laricina	0.1	1.8	-0.1	0.1	-5.0
Acer spicatum	-	1.7	-0.2	-	-5.1
					Overall effect
Treatment effects	0.0	1.7	-0.2	0.0	5.1

f) Residuals for frequency (%).

OC	SC	DC	HP
-0.6	**-6.1**	2.0	0.6
-5.0	**5.9**	-1.7	1.7
-19.8	-0.7	0.7	**11.3**
10.3	**-10.1**	**9.7**	**-9.7**
10.7	**-7.2**	-4.1	4.0
3.3	**5.4**	-3.3	**-5.5**
-1.0	1.9	1.0	**-4.8**
5.6	-0.3	-	0.0
-1.2	1.2	-2.9	**8.7**
1.6	0.7	-1.1	-0.7
-0.3	-1.2	1.2	0.3
-0.3	0.6	-1.7	0.3
0.7	-2.7	-0.8	-1.0
4.9	-1.8	0.1	-0.1
-	-	1.5	-

g) Fits and effects for cover (%).

TREATMENT:	OC	SC	DC	HP	Species effects
Abies balsamea	23.9	24.0	23.8	23.7	22.3
Betula papyrifera	19.0	19.1	18.9	18.8	17.4
Picea glauca	9.5	9.6	9.4	9.4	7.9
Picea mariana	9.3	9.4	9.2	9.2	7.7
Thuja occidentalis	4.9	5.0	4.8	4.8	3.3
Populus tremuloides	5.8	6.0	5.7	5.7	4.3
Alnus rugosa	1.9	2.0	1.8	1.7	0.3
Populus balsamifera	1.6	1.7	1.5	1.4	0.0
Salix spp.	0.8	1.0	0.7	0.7	-0.7
Sorbus decora	0.7	0.8	0.6	0.6	-0.8
Fraxinus nigra	0.5	0.6	0.4	0.4	-1.1
Prunus pensylvanica	0.3	0.4	0.2	0.2	-1.3
Prunus virginiana	0.1	0.2	0.0	-	-1.4
Larix laricina	0.1	0.2	-	0.0	-1.5
Acer spicatum	0.1	0.2	0.0	-	-1.4
					Overall effect
Treatment effects	0.1	0.2	-0.1	-0.1	1.5

h) Residuals for cover (%).

OC	SC	DC	HP
-2.7	-1.3	**4.4**	1.3
-7.2	1.0	**2.5**	-1.0
-6.8	0.2	-0.2	**4.0**
1.4	**-2.5**	**1.8**	-1.5
3.6	**-3.6**	-2.0	2.0
6.0	3.1	-3.0	**-4.6**
-0.8	0.0	1.9	0.0
-0.1	0.9	0.1	-0.7
-0.5	0.1	0.0	0.7
0.2	0.9	-0.2	-0.2
2.4	-	0.0	-0.3
0.0	-	-0.2	0.4
0.1	-0.2	0.0	-
-	-0.2	-	0.0
0.0	-0.1	0.2	-

i) Fits and effects for dbh (cm).

TREATMENT:	OC	SC	DC	HP	Species effects
Abies balsamea	10.1	11.8	9.3	9.9	5.2
Betula papyrifera	10.0	11.7	9.3	9.8	5.1
Picea glauca	15.8	17.5	15.1	15.7	11.0
Picea mariana	11.1	12.8	10.4	10.9	6.2
Thuja occidentalis	5.3	7.0	4.6	5.1	0.4
Populus tremuloides	9.6	11.3	8.9	9.5	4.8
Alnus rugosa	4.0	5.7	3.3	3.9	-0.8
Populus balsamifera	4.4	6.1	3.7	4.3	-0.4
Salix spp.	3.5	5.2	2.7	3.3	-1.4
Sorbus decora	4.3	6.0	3.5	4.1	-0.6
Fraxinus nigra	2.9	4.6	2.1	2.7	-2.0
Prunus pensylvanica	1.6	3.3	0.8	1.4	-3.3
					Overall effect
Treatment effects	0.1	1.8	-0.7	-0.1	4.8

j) Residuals for dbh (cm).

OC	SC	DC	HP
0.6	0.0	0.0	-1.0
-0.3	1.0	0.3	-0.6
-6.6	1.1	0.0	0.0
-1.4	**-2.4**	1.4	**3.1**
0.3	**-3.7**	-0.3	1.5
-2.6	**7.3**	-1.0	1.0
0.0	0.1	-0.4	0.0
0.4	-1.0	**4.8**	-0.4
0.0	-0.1	-0.5	**3.7**
0.0	0.8	0.0	-1.7
0.1	-1.0	**2.1**	0.0
0.0	0.0	-0.8	1.7

Despite the lack of joint response of tree species to harvest treatments (according to treatment effects), the residuals of the median polishes indicated that there may be some individual responses of tree species to harvest treatments (Table 4.1.3). A few species (*B. papyrifera, P. glauca, P. mariana , P. tremuloides, Salix* spp. and *T. occidentalis*) showed evidence of the same treatment differences in three or four of the measures. *P. glauca* had contrasting high and low residuals in HP and CC for all measures except dbh, for which the HP residual was not high. *B. papyrifera* had low residuals in CC for all measures except dbh, with high residuals in SC for dominance and frequency and a high residual in DC for cover. *P. tremuloides* had low residuals in HP for density, frequency and cover, with corresponding high residuals in SC (and CC, to some extent) for frequency and cover. *P. tremuloides* also had a high residual in SC for dominance and for dbh. *T. occidentalis* had low residuals in SC for all measures, accompanied by a high residual in DC for dominance, and high residuals in CC for frequency and cover. In the latter two measures, *T. occidentalis* also showed some contrast between the residuals for HP (high) and DC (low). *P. mariana* had low residuals in SC and high residuals in DC for dominance, frequency and cover. For frequency, this was accompanied by a low residual in HP and a high residual in CC. However, for dbh, *P. mariana* residuals were low in SC and high in HP. *Salix* spp. had high residuals in HP in density, dominance, frequency and dbh.

The median polish residuals showed the same treatment differences for some species in two measures (*A. balsamea, Fraxinus nigra*, and *Populus balsamifera*) (Table 4.1.3). *A. balsamea* had a high residual in DC and *F. nigra* Marsh. had a high residual in CC for both density and cover. For cover of *A. balsamea*, this was accompanied by a low residual in CC. *A. balsamea* showed different trends for frequency (a low residual in SC) and for dominance (contrasting high and low residuals in SC and HP). *P. balsamifera* had a high residual in CC for frequency and density; this was accompanied by a low residual in HP for the latter measure. It also had a high residual in DC for dbh.

Two species showed notably high or low residuals in only one of the measures. *A. rugosa* had a low residual in HP, and *L. laricina* had a high residual in CC, both for frequency (Table 4.1.3f). However, *L. laricina* occurred in the tree stratum only in CC.

4.1.2 ANOVA of Tree Density, Dominance, Frequency and Cover

Only a few of the apparent treatment differences indicated by the exploratory median polish analyses were confirmed by ANOVA (α=0.10) and Fisher's protected least significant difference (PLSD), a multiple means test (Table 4.1.4a). There were no significant treatment differences for dominance, but several species showed significant or nearly significant differences for the other measures. *Betula papyrifera* had a nearly significant treatment difference for density, and a significant difference for percentage cover. These differences were due to low density in CC compared to SC and HP (as indicated by the 'unprotected' least significant difference, i.e. LSD), and low cover in CC compared to all other treatments (as indicated by PLSD). *Picea glauca* frequency and cover had nearly significant treatment differences due to high means in HP and low means in CC. Treatment differences of *Salix* spp. frequency were significant, and treatment differences of its density were nearly significant, with HP treatment means significantly higher than those of CC and DC for both measures.

Differences on upland sites were tested by ANOVA excluding data from mucky peat-dominated sites (plots 5A and 6A) (Table 4.1.4b). Significance of treatment differences for *B. papyrifera* in frequency and cover were essentially the same as before, although for cover, the DC mean became significantly higher than the HP mean. *P. glauca* no longer exhibited treatment differences for any measures. *Salix spp.* had the same significant treatment difference for frequency, but the F-test on treatment means of density was not significant. *Abies balsamea* cover was significantly higher in DC than in other treatments, and treatment differences for *Alnus rugosa* cover became nearly significant, also with the DC mean higher than those of the other treatments. DBH was

Table 4.1.4. Results of significant (p≤0.10) or nearly significant (p≤0.20) ANOVAs, testing harvest treatment differences for tree species on the RC-17 project, 1990.

a) all plots included

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD, LSD†
DENSITY	*Betula papyrifera*	2.62	0.103	CC-SC	-161	106
				CC-HP	-114	114
	Salix spp.	2.08	0.161	CC-HP	-56	51
				DC-HP	-60	51
FREQUENCY	*Picea glauca*	1.85	0.196	CC-HP	-31.1	25.1
	Salix spp.	2.96	0.080	CC-HP	-10.0	7.7
				DC-HP	-11.8	7.7
COVER	*Betula papyrifera*	6.19	0.010	CC-SC	-8.3	4.3
				CC-DC	-9.5	4.3
				CC-HP	-6.0	4.6
	Picea glauca	2.05	0.165	CC-HP	-10.8	8.2
	Sorbus decora	2.15	0.152	SC-DC	1.4	1.1
				SC-HP	1.3	1.2

b) plots 5A and 6A (mostly wet sites) excluded.

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD, LSD†
FREQUENCY	*Betula papyrifera*	2.53	0.123	CC-SC	-12.5	11.2
				SC-DC	15.1	11.2
	Salix spp	2.37	0.139	CC-HP	-11.1	9.0
				DC-HP	-11.3	9.0
COVER	*Abies balsamea*	3.89	0.049	CC-DC	-11.7	7.5
				SC-DC	-11.9	7.0
				DC-HP	9.5	7.5
	Alnus rugosa	2.68	0.110	CC-DC	-4.1	2.8
				SC-DC	-2.8	2.6
				DC-HP	3.1	2.8
	Betula papyrifera	6.63	0.012	CC-SC	-7.4	4.2
				CC-DC	-10.4	4.5
				CC-HP	-5.2	4.5
				DC-HP	5.3	4.5

†PLSD= Fisher's protected least significant difference, for mean differences with significant F-values at a 0.10 (i.e. p-value ≤ 0.10); LSD='unprotected' least significant difference, for p-values >0.10, but ≤0.20.

not tested by ANOVA due to the few individuals encountered in some plots for some species (often ≤ 2.0 individuals; Appendix 5).

Several species that did not have significant differences according to ANOVA had highly variable treatment means (e.g. *P. glauca, Picea mariana, Thuja occidentalis*; Table 4.1.1, Table 4.1.2), corresponding to the median polish residuals (Table 4.1.3). The lack of significance in the formal ANOVA tests was due to the high variance among plots within treatments (Appendix 5).

In general, the composition and dominance of the tree stratum did not appear to be influenced greatly by harvest treatments. Fisher's PLSD and LSD indicated that, for the few species for which treatment differences were significant or nearly significant, low values generally occurred in CC, in contrast to high values in either HP or DC. However, for the many differences suggested by the median polish residuals, several species had high values in CC, and there was no consistent trend of treatment differences among species, as emphasized by the low median polish treatment effects.

4.1.3 Comparison of Importance of Softwoods and Hardwoods

In order to compare the relative importance of softwoods and hardwoods in the four harvest treatments of the RC17 project, relative values of density, dominance and frequency, as well as overall IVs, were summed over the commercial softwood species (*Abies balsamea, Picea glauca* and *P. mariana*) and over the principal hardwood species (*Betula papyrifera, Populus balsamifera* and *P. tremuloides*), and the ratio of softwoods to hardwoods (S:H) for each of these values was determined for each treatment (Table 4.1.2). This was also done for non-relativized percentage cover (Table 4.1.1).

Despite the absence of many significant differences in these measures for individual species (Table 4.1.4), there was an evident and consistent treatment pattern in S:H ratios (Tables 4.1.1, 4.1.2). They indicated that, following harvesting of this boreal mixedwood, abundance and growth of softwoods in comparison to hardwoods was

better in the DC and HP treatments than in the CC and SC treatments. In terms of density, frequency and overall IV, the S:H was largest for DC, descending through HP, CC and SC. For dominance and cover, the S:H was higher for HP than for DC, but the order of the other two treatments was the same.

The S:H was about the same for density as it was for dominance for treatments CC (~2.00) and SC (~1.75), but was higher for dominance in DC (by 0.42) and especially in HP (by 1.31). The higher S:H in terms of dominance for HP and DC was mainly due to high relative dominances for *P. glauca* and low relative dominances for *B. papyrifera*, in comparison to their relative densities. The S:H was about 0.35 lower for frequency than for density in all treatments except DC, for which it was 0.66 lower. The difference was mainly due to a higher relative density than relative frequency for *A. balsamea*, and the reverse for *B. papyrifera*.

In both treatments DC and HP, the relative importance of *A. balsamea* was lower for dominance than for density, although the S:H was higher for dominance (Table 4.1.2). In general, a comparison of the relative values indicated that *A. balsamea* stems were more frequent and more numerous in DC and HP than in CC and SC, but that the size of individual trees (indicated by dominance) in DC and HP was smaller than in CC and SC. Relative dominance of *P. glauca* was higher than its relative density and frequency in all treatments except CC, suggesting that *P. glauca* was generally larger in diameter than *A. balsamea*. This was also indicated by dbh treatment means (Table 4.1.1). Relative dominance of *B. papyrifera* was smaller than its relative density and frequency, in all treatments, the reverse being true for *P. tremuloides*, except for in DC. Thus *B. papyrifera* was represented by smaller, more numerous individuals than was *P. tremuloides*.

4.1.4 Comparison of Importance of Spruce to Balsam Fir and Hardwoods

Harvest treatments appeared to affect the proportion of *Picea* spp. in comparison

to *Abies balsamea* and the hardwoods (Table 4.1.2). *Picea* spp. abundance and growth were generally best in HP and DC, in comparison to abundance and growth of *A. balsamea* and hardwoods. With two exceptions, the ratio of *Picea* spp. to *A. balsamea* (Spr:F) and the ratio of *Picea* spp. to hardwoods (Spr:H) were higher in HP and DC than in SC and CC, as they were for the S:H. Spr:F was highest in HP for all measures except frequency. *Picea* spp. was actually more dominant (basal area) than *A. balsamea* in HP. CC had the lowest Spr:F in all measures except density. Spr:H was highest in either HP or DC for all measures, and generally similar in these two treatments. For dominance and IV, Spr:H was greater than 1.0 in these two treatments.

4.1.5 Tree Age and Height

Age and height means and medians for plots were calculated from samples of 20 trees per plot, except when age could not be determined (Table 4.1.5); individual measurements are presented by plot in Appendix 7. Due to the point-centred quarter sampling method, samples for individual species and for softwood and hardwood groups within a plot were often small. Therefore, the median, a more robust measure, was used for analyses involving these measures.

CC and SC differed from HP and DC in terms of conifer species' ages and tree height over all species. The trend of early applied treatments (CC and SC) differing from later ones (HP and DC), first noted in the S:H, Spr:F and Spr:H ratios, was also evident in tree age and height: CC and SC were mostly post-harvest, HP and DC were mostly pre-harvest, while CC and SC were generally taller than HP and DC.

Since the site was harvested between 1953 and 1963, the expected age of most trees would be 27 to 37 years. All mean plot and median plot ages fell into this range except for two DC plots (40 and 50 years). Most mean and median ages were within 3 years of each other. Minimum tree age per plot ranged from 15 to 31 years and was generally approximately 20 years. Maximum age per plot ranged from 36 to 92 years

Table 4.1.5. Summary of tree height and age measurements on the RC-17 project, 1990.

TREATMENT	PLOT	MEAN HGT(m)	MEAN AGE(yrs)	MEDIAN AGE	MIN. AGE	Species*	MAX. AGE	Species*	SOFTWOOD AGE (years) Mean	SOFTWOOD AGE (years) Median	HARDWOOD AGE (years) Mean	HARDWOOD AGE (years) Median
CC	1B	10.3	35	35	21	*Bp/Pt*	68	*Ab*	39	36	28	25
CC	5A	8.7	33	31	20	*Pm*	52	*Fn*	32	31	34	31
CC	5B	7.4	34	35	20	*Salix*	49	*Pg*	35	34	28	28
CC	7A	8.3	37	36	20	*Bp*	59	*Pm*	40	38	28	26
DC	4A	8.5	40	37	20	*Al rug*	79	*Pm*	43	38	36	26
DC	4B	8.2	30	28	18	*Al rug*	44	*Ab*	36	34	24	22
DC	6A	8.2	50	42	31	*Bp/Pm*	92	*Pm*	52	39	44	43
DC	6B	6.0	25	25	17	*Ab/Salix*	37	*Ab*	26	25	21	23
HP	10B	7.8	34	32	23	*Ab/Al rug*	68	*Pg*	39	35	29	28
HP	8A	7.3	30	29	17	*Bp*	56	*Ab*	40	39	28	27
HP	2B	8.2	36	36	24	*Salix*	56	*To*	34	35	24	25
SC	3A	10.2	35	34	15	*Al rug*	73	*Pg*	40	35	27	25
SC	3B	7.5	32	33	20	*Ab*	46	*Ab*	33	33	29	29
SC	7B	10.4	30	28	18	*Al rug/Bp*	55	*Ab*	39	27	25	26
SC	9B	14.5	30	29	22	*Pt*	36	*Bp/Pt*	33	33	30	29

Species	CC		DC		HP		SC	
	RANGE	MEDIAN	RANGE	MEDIAN	RANGE	MEDIAN	RANGE	MEDIAN
Ab	28-68	36	17-45	31	23-56	35	20-55	34
Pg	39-49	45	25-42	36	26-68	36	30-73	34
Pm	20-59	34	31-92	72			32-55	50
Bp	20-37	30	20-56	31	17-44	27	18-39	29
Pt	21-39	32	26	-	25-28	-	22-39	30
Pb	22	-					24	-

**Ab=Abies balsmea, Al rug= Alnus rugosa, Bp=Betula papyrifera, Pb=Populus balsamifera, Pg=Picea glauca, Pm=Picea mariana, Pt=Populus tremuloides, To=Thuja occidentalis.*

and was generally about 50 years. These figures indicate that many trees in 1990 were of pre-harvest origin, and some of the older ones were likely saplings, <4 cm dbh, at the time of harvest. In addition, some trees established several years after the cuts. There were no obvious treatment differences in these age parameters and ANOVAs (at α=0.10) confirmed this (none significant).

In CC and SC, which were cut 37 years prior to resampling, *Abies balsamea* stems were a mixture of pre and post-cut reproduction, but the majority of stems appeared to have seeded in after harvest. *Picea glauca* and *P. mariana* were also mixed in regeneration origin. *P. glauca* was mostly of post-harvest origin in SC, but the few stems measured in CC were of advance growth origin. The situation was reversed for *P. mariana*, with most stems in SC being advance growth, but most in CC being of post-cut origin.

In HP and DC, where harvesting was done 27 years prior to resampling, *A. balsamea* and *P. glauca* stems were of mixed origin, but originated primarily before the harvest of these plots, at about the time of the CC and SC harvest. All *P. mariana* sampled in DC were of advance growth origin; none were sampled for age in HP.

In all treatments, hardwoods were almost entirely of post-harvest origin. In SC and CC, those that were of post-harvest origin had established within 19 years of the cut, most within 7 years. In HP and DC, all hardwoods of post-harvest origin had established within 10 years of the cut, but several in HP had established just prior to the cut, and in DC6A, *Betula papyrifera* stems sampled for age were all of pre-harvest origin.

A median polish was done on the median heights of those species that had values for at least three treatments (Table 4.1.6). The results should be cautiously interpreted for *Populus tremuloides*, *Salix* spp, *Sorbus decora* and *Thuja occidentalis*, since some of the treatment sample sizes were one or two trees (Appendix 7). The species' effects indicated that *P. tremuloides* had the greatest median height over the four

Table 4.1.6. Tree height medians and median polish of selected species on the RC-17 project, 1990.

a) Medians of tree height for all measured species.

Treatments:	CC	DC	HP	SC
Abies balsamea	8.4	6.1	6.8	7.6
Alnus rugosa		7.1	6.5	7.4
Betula papyrifera	10.8	8.7	9.2	10.2
Fraxinus nigra	11.0	9.5		
Larix laricina	5.0			
Picea glauca	9.2	7.0	11.2	7.6
Picea mariana	8.6	10.4		13.2
Populus balsamifera	8.7			11.9
Populus tremuloides	14.1	7.8	13.3	19.2
Prunus pensylvanica			7.8	6.7
Prunus virginiana	6.1			
Salix spp.	7.2	6.0	6.9	8.2
Sorbus decora	7.4	7.5	7.6	7.9
Thuja occidentalis	4.9		5.4	4.8

b) Median polish fits for selected species

Treatment:	CC	DC	HP	SC	Species effects
Abies balsamea	7.5	6.1	6.9	7.6	-0.9
Alnus rugosa		5.7	6.5	7.2	-1.6
Betula papyrifera	10.1	8.7	9.5	10.2	1.7
Picea glauca	8.8	7.4	8.2	8.9	3.7
Picea mariana	11.8	10.4		11.9	0.4
Populus tremuloides	14.0	12.6	13.4	14.1	5.6
Salix spp.	7.4	6.0	6.8	7.5	-3.2
Sorbus decora	8.5	7.2	7.9	8.6	-1.0
Thuja occidentalis	4.9		4.3	5.0	0.1
				Overall	effect
Treatment effects	0.5	-0.9	-0.7	0.5	8.1

c) Median polish residuals.

CC	DC	HP	SC
0.9	0.0	-0.1	0.0
	1.3	0.0	0.2
0.7	0.0	-0.3	0.0
0.4	-0.4	3.0	-1.3
-3.2	0.0		1.3
0.1	-4.8	-0.1	5.1
-0.2	0.0	0.1	0.7
-1.1	0.3	-0.3	-0.7
0.0		1.1	-0.2

treatments followed by *P. glauca* and *B. papyrifera*. Treatment effects were very low, showing little evidence of a joint response of species' height to harvest treatments, although treatment effects. for DC and HP were slightly lower than for CC and SC. This corresponded to results of the least significant difference test (LSD), which indicated significant differences in tree height (α=0.10) between SC and DC (mean diff.=-2.925, LSD=2.228), and between SC and HP (mean diff.=-2.883, LSD=2.406), although the overall ANOVA did not indicate differences ($F_{3,11}$=2.335, p=0.13). The absolute values of median polish residuals were generally low, but high absolute values occurred for *P. tremuloides* in DC and SC, for *P. mariana* in CC and for *P. glauca* in HP.

Therefore, formal statistical testing (ANOVA) showed no significant differences in age and height of trees among the treatments, but examination of individual tree species' ages, and median polish and LSD on tree height over all species, indicated that differences existed. These tended to be mainly between treatments applied at different times, i.e., CC and SC were different from DC and HP.

4.1.6 Spatial Pattern of Trees

The data sets used to analyze the spatial pattern of trees via the T-square and the Johnson and Zimmer indices are included in Appendix 8. For CC, DC and HP, the square of the mean point-to-individual distance, x_i, was greater than one-half times the square of the mean individual-to-nearest neighbour distance, y_i (Table 4.1.7), suggesting that spatial pattern of trees was clumped. This was also true for several individual plots, including all HP plots. For the others, and for SC, x_i^2 was less than 1/2 y_i^2, suggesting a uniform pattern. The T-square index of clumping, C, and the Johnson and Zimmer index of dispersion, I, were calculated to test the significance of clumping and uniformity (Table 4.1.7).

According to the indices, trees in most individual plots had a random distribution (all species combined), and there was no indication of uniform distributions of trees on

Table 4.1.7. Distance statistics and spatial pattern indices by treatment and individual plot for trees (all species combined) on the RC-17 project, 1990.

Treatment/plot	CC	1B	5A	5B	7A	SC	3A	3B	7B	9B
Statistics and indices†:										
n	60	15	15	15	15	70	20	20	15	15
Mean x (m)	1.10	1.03	1.13	0.99	1.25	1.12	1.18	0.93	1.12	1.30
Mean y (m)	1.31	1.35	1.69	1.01	1.19	1.67	1.33	1.78	1.64	2.00
C	0.58	0.55	0.45	0.66	0.66	0.49	0.59	0.41	0.48	0.46
z	2.17*	0.68	-0.64	2.17*	2.14*	-0.41	1.37	-1.42	-0.22	-0.60
significance (p-value)	0.03	0.50	0.52	0.03	0.03	0.69	0.17	0.16	0.83	0.55
I	4.23	1.81	6.93	2.34	1.93	2.15	2.53	2.22	1.74	1.93
z	9.08*	-0.44	11.52*	0.79	-0.17	0.68	1.37	0.57	-0.62	-0.17
significance (p-value)	<0.01	0.66	<0.01	0.43	0.87	0.50	0.17	0.57	0.54	0.87

Treatment/plot	DC	4A	4B	6A	6B	HP	10B	2B	8A
Statistics and indices:									
n	72	20	20	15	17	45	15	15	15
Mean x (m)	1.15	1.09	0.99	1.59	1.03	1.40	1.33	1.16	1.71
Mean y (m)	1.61	1.60	1.53	1.58	1.72	1.62	1.86	1.35	1.67
C	0.51	0.53	0.45	0.64	0.44	0.58	0.49	0.58	0.67
z	0.33	0.50	-0.73	1.86*	-0.82	1.86*	-0.07	1.04	2.26*
significance (p-value)	0.74	0.62	0.47	0.06	0.41	0.06	0.94	0.30	0.02
I	2.40	2.33	2.25	2.11	1.65	3.16	1.73	2.24	3.29
z	1.76*	0.84	0.63	0.26	-0.86	4.17*	-0.64	0.55	3.03*
significance (p-value)	0.08	0.40	0.53	0.79	0.39	<0.01	0.52	0.58	<0.01

† x=point-to-nearest individual distance, y=individual-to-nearest neighbor distance, C=T-square index of clumping, I=Johnson & Zimmer Index of Dispersion. *Significant at $\alpha = 0.10$.

the study site. However, the lack of significant clumping for individual plots may have been due to small sample sizes, since indices calculated for each treatment, using combined plot data, indicated that CC, HP and possibly DC had significantly clumped distributions of trees.

Tree distribution in CC and HP was significantly clumped according to C and I. According to C, trees in treatments SC and DC were randomly distributed. However, I indicated significant clumping of trees in treatment DC. Plots CC5B, CC7A, DC6A and HP8A were the only individual plots with significantly clumped tree distributions according to C. I confirmed this for only HP8A. I also indicated significant clumping in plot CC5A. Trees of all other plots were assumed to have random spatial patterns, since neither I nor C values were significant. The significance of tree clumping calculated for HP seemed to be mainly due to plot 8A. However, indices for the individual plots should be interpreted cautiously, due to the small sample sizes ($n \leq 20$).

Since plot samples were very small for individual tree species, spatial pattern indices were only calculated for treatments (Table 4.1.8). N varied greatly among species and among treatments due to the sampling (see Methods). *Abies balsamea* was significantly clumped in CC, DC and HP according to I, but only in HP according to C. I indicated significant clumping of *Betula papyrifera* in CC, SC and DC, but according to C, *B. papyrifera* was randomly distributed in all treatments. C indicated significant clumping of *Picea mariana* in CC, but according to I, *P. mariana* was not clumped in either of the two treatments for which spatial indices were calculated. Both C and I indicated random distributions for *Picea glauca* and *Thuja occidentalis* in the treatments for which indices were calculated.

4.1.7 Summary of Tree Results

Although treatment differences in tree density, dominance, frequency, cover and dbh were observed for several species in the residuals of the exploratory median polish

Table 4.1.8. Distance statistics and spatial pattern indices for individual tree species in each treatment, on the RC-17 project, 1990.

Species	*Abies balsamea*				*Betula papyrifera*				*Picea mariana*		*Picea glauca*		*Thuja occidentalis*
Treatment	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	DC	HP	CC
Statistics and indices†:													
n	46	58	35	52	28	35	24	41	21	21	19	18	12
Mean x (m)	1.95	1.65	2.25	1.55	2.12	1.87	2.16	2.24	2.04	2.00	2.32	1.79	1.72
Mean y (m)	2.41	2.19	2.26	2.40	3.11	3.29	3.27	2.59	2.16	3.48	4.18	3.22	2.16
C	0.56	0.54	0.60	0.50	0.54	0.47	0.51	0.57	0.63	0.52	0.47	0.44	0.62
z	1.29	1.00	2.09*	0.01	0.79	-0.59	0.09	1.44	2.12*	0.31	-0.50	-0.83	1.47
significance (p-value)	0.20	0.32	0.04	0.99	0.43	0.56	0.93	0.15	0.03	0.76	0.62	0.41	0.14
I	3.92	3.09	3.09	2.06	3.18	3.53	2.09	2.85	2.58	2.35	1.96	1.95	2.61
z	6.95*	4.37*	3.50*	0.24	3.46*	4.91*	0.24	2.92*	1.53	0.93	-0.10	-0.13	1.34
significance (p-value)	<0.01	<0.01	<0.01	0.81	<0.01	<0.01	0.81	<0.01	0.13	0.35	0.92	0.90	0.18

†x=point-to-nearest individual distance, y=individual-to-nearest neighbor distance, C=T-square index of clumping, I=Johnson & Zimmer Index of Dispersion. *Significant at $\alpha = 0.10$.

analyses, only a few species (*Betula papyrifera, Picea glauca, Salix* spp., *Sorbus decora*) exhibited significant or nearly significant differences in the formal ANOVA tests. Furthermore, although Fisher's PLSD and the LSD suggested that these differences were principally between low CC values and high HP or DC values, the treatment effects of the median polishes indicated that there were no consistent trends of treatment differences among the tree species. This was confirmed by the various treatment contrasts exhibited in the median polish residuals.

The S:H ratio suggested that, in comparison to hardwoods, softwoods fared better in DC and HP than in SC and CC, and the Spr:F and Spr:H indicated that spruce growth in comparison to both hardwoods and to *Abies balsamea* was also better in DC and HP than in SC and CC. Analysis of tree age and height also highlighted treatment differences of DC and HP versus SC and CC.

Spatial pattern indices indicated that neither all trees combined, nor individual species, were uniformly distributed in any of the RC17 treatments. Most individual plots seemed to have a random distribution of trees (all species combined), but this may have been due to small sample sizes, since combined plot samples indicated that CC, HP and possibly DC had clumped distributions of trees. In addition, according to the Johnson and Zimmer index, *A. balsamea* and *B. papyrifera*, the two most common tree species, may have been clumped in CC and DC, as well as in HP for the former species and in SC for the latter.

4.2 SHRUB STRATUM

4.2.1 Shrub Cover and Frequency

Means for shrub cover and frequency along with their relative values and importance values (IVs), are presented in Table 4.2.1. In each treatment, only five species had IVs greater than 10. *Acer spicatum, Abies balsamea* and *Alnus rugosa* were

Table 4.2.1. Harvest treatment averages, relative values and importance values for shrub parameters measured in 50-m2 circular plots on the RC-17, 1990 (values in order of overall shrub importance).

	COVER(%)				FREQUENCY(%)				RELATIVE COVER				RELATIVE FREQUENCY				IMPORTANCE VALUE				OVERALL IV
HARVEST TREATMENT:	CC*	DC*	HP*	SC*	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	SUM
SHRUB SPECIES																					
Acer spicatum	17.0	33.3	27.6	33.8	70.0	81.7	95.6	94.2	23.9	33.3	29.4	47.1	10.5	12.0	11.7	17.0	34.3	45.3	41.1	64.1	184.8
Abies balsamea	5.8	15.3	13.1	7.5	68.4	88.3	86.6	68.8	8.1	15.3	13.9	10.5	10.2	12.9	10.6	12.4	18.4	28.2	24.6	22.8	94.0
Alnus rugosa	11.9	11.8	14.7	4.9	40.0	56.1	53.3	22.5	16.7	11.8	15.6	6.8	6.0	8.2	6.5	4.0	22.7	20.0	22.2	10.9	75.8
Corylus cornuta	2.5	6.2	5.6	8.1	20.0	34.1	40.0	51.3	3.5	6.2	6.0	11.3	3.0	5.0	4.9	9.2	6.5	11.2	10.9	20.5	49.1
Betula papyrifera	3.3	6.9	3.1	3.1	43.3	52.8	40.0	43.8	4.6	6.9	3.3	4.3	6.5	7.7	4.9	7.9	11.1	14.6	8.2	12.2	46.2
Sorbus decora	1.5	2.0	1.6	1.3	31.7	46.9	46.7	39.6	2.1	2.0	1.7	1.8	4.7	6.9	5.7	7.1	6.8	8.9	7.4	8.9	32.1
Cornus stolonifera	2.7	1.8	4.7	1.1	36.7	26.9	51.1	22.5	3.8	1.8	5.0	1.5	5.5	3.9	6.3	4.0	9.3	5.7	11.3	5.6	31.9
Lonicera canadensis	1.0	1.6	2.1	1.3	25.0	34.5	44.4	25.8	1.4	1.6	2.2	1.8	3.7	5.1	5.4	4.6	5.1	6.7	7.7	6.5	25.9
Picea mariana	2.7	3.5	1.4	0.5	31.7	40.9	24.5	11.7	3.8	3.5	1.5	0.7	4.7	6.0	3.0	2.1	8.5	9.5	4.5	2.8	25.3
Thuja occidentalis	4.4	1.0	5.8	0.7	20.0	8.1	17.8	5.0	6.2	1.0	6.2	1.0	3.0	1.2	2.2	0.9	9.2	2.2	8.4	1.9	21.6
Alnus crispa	2.5	3.6	-	2.9	20.0	23.3	-	14.6	3.5	3.6	-	4.0	3.0	3.4	-	2.6	6.5	7.0	-	6.7	20.2
Viburnum edule	0.8	0.5	1.2	0.8	26.7	17.0	40.0	26.3	1.1	0.5	1.3	1.1	4.0	2.5	4.9	4.7	5.1	3.0	6.2	5.8	20.1
Ledum groenlandicum	5.4	3.8	0.6	-	33.3	15.0	6.7	-	7.6	3.8	0.6	-	5.0	2.2	0.8	-	12.6	6.0	1.5	-	20.0
Rosa acicularis	0.8	0.8	1.6	0.3	25.0	24.0	31.1	12.5	1.1	0.8	1.7	0.4	3.7	3.5	3.8	2.2	4.9	4.3	5.5	2.7	17.4
Diervilla lonicera	0.8	1.2	1.8	1.2	18.4	9.4	20.0	22.5	1.1	1.2	1.9	1.7	2.8	1.4	2.5	4.0	3.9	2.6	4.4	5.7	16.5
Picea glauca	0.3	1.3	1.6	0.8	8.3	19.4	33.3	20.8	0.4	1.3	1.7	1.1	1.2	2.8	4.1	3.7	1.7	4.1	5.8	4.9	16.4
Amelanchier bartramiana	2.3	0.8	0.7	0.1	35.0	21.5	13.3	2.5	3.2	0.8	0.7	0.1	5.2	3.1	1.6	0.4	8.5	3.9	2.4	0.6	15.4
Salix spp.	0.5	0.8	1.4	0.4	10.0	10.7	24.4	10.9	0.7	0.8	1.5	0.6	1.5	1.6	3.0	2.0	2.2	2.4	4.5	2.5	11.6
Rubus idaeus var. strigosus	0.5	0.3	0.9	0.2	20.0	8.1	24.4	5.9	0.7	0.3	1.0	0.3	3.0	1.2	3.0	1.1	3.7	1.5	3.9	1.3	10.5
Ribes lacustre	0.3	0.4	0.8	0.1	10.0	13.6	26.7	4.6	0.4	0.4	0.9	0.1	1.5	2.0	3.3	0.8	1.9	2.4	4.1	1.0	9.4
Prunus pensylvanica	1.1	0.3	0.1	0.4	16.7	6.5	2.2	7.9	1.5	0.3	0.1	0.6	2.5	0.9	0.3	1.4	4.0	1.2	0.4	2.0	7.6
Amelanchier humilis	0.3	0.3	0.6	0.3	5.0	4.8	20.0	6.7	0.4	0.3	0.6	0.4	0.7	0.7	2.5	1.2	1.2	1.0	3.1	1.6	6.9
Lonicera involucrata	0.4	0.2	0.6	0.1	10.0	4.4	15.6	2.9	0.6	0.2	0.6	0.1	1.5	0.6	1.9	0.5	2.1	0.8	2.6	0.7	6.1
Prunus virginiana	0.2	0.2	0.6	0.6	1.7	4.4	15.5	6.3	0.3	0.2	0.6	0.8	0.3	0.6	1.9	1.1	0.5	0.8	2.5	2.0	5.9
Populus balsamifera	0.4	0.2	0.1	0.2	11.7	1.5	2.2	6.7	0.6	0.2	0.1	0.3	1.7	0.2	0.3	1.2	2.3	0.4	0.4	1.5	4.6
Rhamnus alnifolia	0.4	-	0.6	0.2	6.7	-	8.9	1.7	0.6	-	0.6	0.3	1.0	-	1.1	0.3	1.6	-	1.7	0.6	3.9
Fraxinus nigra	0.1	0.3	0.2	0.4	1.7	5.0	2.2	5.0	0.1	0.3	0.2	0.6	0.3	0.7	0.3	0.9	0.4	1.0	0.5	1.5	3.4
Ribes hirtellum	-	0.1	0.4	-	-	3.1	17.8	-	-	0.1	0.4	-	-	0.5	2.2	-	-	0.6	2.6	-	3.2
Lonicera villosa	0.5	0.7	-	-	5.0	3.3	-	-	0.7	0.7	-	-	0.7	0.5	-	-	1.4	1.2	-	-	2.6
Lonicera hirsuta	-	0.2	0.2	-	-	6.3	4.5	-	-	0.2	0.2	-	-	0.9	0.6	-	-	1.1	0.8	-	1.9
Sambucus pubens	0.1	-	-	0.1	5.0	-	-	3.3	0.1	-	-	0.1	0.7	-	-	0.6	0.9	-	-	0.7	1.6
Lonicera oblongifolia	0.2	0.1	0.1	-	3.4	1.7	2.2	-	0.3	0.1	0.1	-	0.5	0.2	0.3		0.8	0.3	0.4		1.5
Larix laricina	0.1	0.2	-	-	1.7	5.0	-	-	0.1	0.2	-	-	0.3	0.7	-	-	0.4	0.9	-	-	1.3
Ribes triste	-	0.1	0.1	-	-	2.9	2.2	1.3	-	0.1	0.1	-	-	0.4	0.3	0.2	-	0.5	0.4	0.2	1.1
Ribes oxycanthoides	0.1	-	-	0.1	1.7	-	-	1.7	0.1	-	-	0.1	0.3	-	-	0.3	0.4	-	-	0.4	0.8
Populus tremuloides	-	-	-	0.1	-	-	-	3.4	-	-	-	0.1	-	-	-	0.6	-	-	-	0.8	0.8
Vaccinium angustifolium	-	0.1	0.1	-	-	1.7	2.2	-	-	0.1	0.1	-	-	0.2	0.3	-	-	0.3	0.4	-	0.7
Ribes glandulosum	-	-	-	0.1	-	-	-	2.9	-	-	-	0.1	-	-	-	0.5	-	-	-	0.7	0.7
Kalmia polifolia	0.1			-	1.7			-	0.1			-	0.3			-	0.4			-	0.4
Myrica gale	0.1			-	1.7			-	0.1			-	0.3			-	0.4			-	0.4
Ribes hudsonianum	0.1	-		-	1.7		-	-	0.1		-	-	0.3	-	-	-	0.4	-	-	-	0.4

*CC=clearcut, SC=softwoods only cut, DC=deferred cut, HP=hardwoods poisoned (deferred cut).

included in the top five species of each treatment, with the other two comprising pairs of the following species: *Betula papyrifera, Cornus stolonifera* Michx., *Corylus cornuta* and *Ledum groenlandicum.*

Most of the 41 shrub species occurred in all four treatments, although only eight species were recorded in all 15 plots (Appendix 9): *A. balsamea, A. spicatum, A. rugosa, B. papyrifera, C. stolonifera, Lonicera canadensis, Sorbus decora, and Viburnum edule.* Several species did not occur in all four treatments, e.g. *Ribes glandulosum* Grauer and *Populus tremuloides* only occurred in SC, and *Myrica gale* L. and *Kalmia polifolia* Wang. only occurred in CC. However, most of these are rare species, with small IVs, that only occurred in one or two plots per treatment (Appendix 9). Thus, there did not seem to be any treatment pattern of species coincidences and absences (fidelity).

The number of shrub species per treatment ranged from 31 to 35, with CC having the highest number (Table 4.2.1). *A. spicatum* had the highest percentage cover in all four treatments, with high values in both DC and SC (33% and 34%) and its lowest value in CC (17%). *A. balsamea* was the only other shrub layer species to have greater than 5% cover in all four treatments. Its values in CC(6%) and SC(8%) were considerably lower than in DC(15%) and HP(13%). *A. rugosa* had greater than 5% cover in treatments CC, DC and HP; *C. cornuta* exceeded 5% cover in DC, HP and SC; and *B. papyrifera* and *Thuja occidentalis* had mean cover values greater than 5% in DC and HP respectively. All other species were below 5% cover in all treatments.

Percentage frequency was considerably higher than percentage cover for most shrub layer species. *A. spicatum* and *A. balsamea* were the most frequently occurring species in all treatments. Frequency of *A. spicatum* was somewhat higher in HP (96%) and SC (94%) than in CC (70%) and DC (82%). *A. balsamea* was more frequent in DC (88%) and HP (87%) than in CC and SC (both 69%). All other species had mean frequencies less than 60% in all treatments.

4.2.2 Shrub Density

Only 31 shrub species were recorded in the measurement of shrub density via the point-centred quarter method (Table 4.2.2; plot values in Appendix 9). The ten species not encountered by this method that were encountered within the 50-m2 quadrats were *Kalmia polifolia, Larix laricina, Lonicera oblongifolia* (Goldie) Hook., *Myrica gale, Populus tremuloides, Vaccinium angustifolium*, and four *Ribes* spp. These species were all rare in the 50-m2 quadrats, and absent from at least one of the treatments (Table 4.2.1).

Acer spicatum had the highest density in the shrub layer for all four treatments, although the range was large, with its density in CC and SC (2100-3000 stems/ha) being about half of that in HP and DC (5200-6000 stems/ha). *Abies balsamea* had the second highest shrub density for HP and DC (2800-3000 stems/ha), *Alnus rugosa* in CC (1000 stems/ha), and *Corylus cornuta* in SC (1000 stems/ha).

4.2.3 Median Polish Analysis

The median polishes of shrub cover and frequency indicated that there was almost no joint species response to the harvest treatments; the treatment (column) effects were all close to zero (Table 4.2.3a,b). Although the treatment effects for density appeared to be larger than those for cover and frequency, they were small relative to the fits and species (row) effects for density (Table 4.2.3c). The treatment effects suggested, however, that shrub densities were slightly higher in DC and HP than in CC and SC.

Due to the low treatment effects, 'fits' for shrub cover and frequency were almost equivalent to the species effects plus the overall effect, and thus are not shown. The species effects of the three analyses indicated that in terms of cover and density, the four most important species in the shrub layer were *Acer spicatum, Abies balsamea, Alnus rugosa* and *Corylus cornuta*, but that *Betula papyrifera* was more important than *C.*

Table 4.2.2. Harvest treatment values for shrub density and shrub relative density, measured by the point-centred quarter method on the RC-17 project, 1990 (species ordered by sums of relative density over the four harvest treatments).

	DENSITY (shrubs/ha)				RELATIVE DENSITY				
HARVEST TREATMENT:	CC*	DC*	HP*	SC*	CC	DC	HP	SC	OVERALL SUM
SHRUB and TREE SPP.									
Acer spicatum	2140	6008	5221	3647	26.1	34.5	33.1	48.6	142.4
Abies balsamea	692	3012	2793	952	8.4	17.3	17.7	12.7	56.2
Alnus rugosa	1010	1939	2274	176	12.3	11.1	14.4	2.4	40.2
Corylus cornuta	331	1029	708	998	4.0	5.9	4.5	13.3	27.7
Thuja occidentalis	619	244	1200	49	7.6	1.4	7.6	0.7	17.2
Ledum groenlandicum	782	1150	-	-	9.5	6.6	-	-	16.2
Betula papyrifera	433	636	298	265	5.3	3.7	1.9	3.5	14.4
Cornus stolonifera	238	338	954	60	2.9	1.9	6.1	0.8	11.7
Viburnum edule	154	131	289	449	1.9	0.8	1.8	6.0	10.5
Picea mariana	107	794	171	34	1.3	4.6	1.1	0.5	7.4
Alnus crispa	228	364	-	131	2.8	2.1	-	1.7	6.6
Amelanchier bartramiana	230	434	-	34	2.8	2.5	-	0.5	5.8
Diervilla lonicera	135	-	319	113	1.6	-	2.0	1.5	5.2
Lonicera canadensis	284	180	86	-	3.5	1.0	0.5	-	5.0
Rosa acicularis	96	28	470	30	1.2	0.2	3.0	0.4	4.7
Picea glauca	82	124	86	115	1.0	0.7	0.5	1.5	3.8
Sorbus decora	110	172	-	76	1.3	1.0	-	1.0	3.4
Prunus virginiana	43	49	177	68	0.5	0.3	1.1	0.9	2.8
Lonicera involucrata	41	248	-	60	0.5	1.4	-	0.8	2.7
Lonicera villosa	67	288		-	0.8	1.7	-	-	2.5
Prunus pensylvanica	120	98	-	34	1.5	0.6	-	0.5	2.5
Salix spp.	40	49	142	51	0.5	0.3	0.9	0.7	2.3
Rubus idaeus var. strigosus	75	-	112	-	0.9	-	0.7	-	1.6
Amelanchier humilis	-	-	168	30	-		1.1	0.4	1.5
Rhamnus alnifolia	-	-	121	30	-		0.8	0.4	1.2
Fraxinus nigra	34	-	-	50	0.4	-	-	0.7	1.1
Lonicera hirsuta	-	83	56	-	-	0.5	0.4	-	0.8
Ribes hudsonianum	67	-	-	-	0.8	-	-	-	0.8
Populus balsamifera	-	-	121	-	-		0.8	-	0.8
Sambucus pubens	-		-	51	-		-	0.7	0.7
Ribes lacustre	41	-	-	-	0.5	-	-	-	0.5

*CC=clearcut, SC=softwoods only cut, DC=deferred cut, HP=hardwoods poisoned (deferred cut).

Table 4.2.3. Effects and residuals for median polishes of treatment means for shrub cover, frequency and density on the RC-17 project, 1990 (species in order of IV sums of Table 4.2.1).

a) Residuals and effects for shrub percentage cover.

Treatment	Residuals CC*	DC*	HP*	SC*	Species effects
Acer spicatum	-13.4	2.9	-2.9	3.5	30.0
Abies balsamea	-4.5	5.0	2.8	-2.7	9.9
Alnus rugosa	0.1	-0.1	2.8	-6.9	11.5
Corylus cornuta	-3.4	0.3	-0.3	2.3	5.5
Betula papyrifera	0.1	3.6	-0.2	-0.1	2.9
Sorbus decora	0.0	0.5	0.0	-0.2	1.2
Cornus stolonifera	0.5	-0.5	2.4	-1.1	1.9
Lonicera canadensis	-0.5	0.1	0.6	-0.1	1.1
Picea mariana	0.7	1.5	-0.7	-1.5	1.7
Thuja occidentalis	1.7	-1.7	3.1	-1.9	2.3
Alnus crispa	-0.3	0.8	-2.8	0.2	2.4
Viburnum edule	-0.1	-0.4	0.3	0.0	0.5
Ledum groenlandicum	3.2	1.6	-1.6	-2.1	1.8
Rosa acicularis	-	0.0	0.8	-0.4	0.4
Diervilla lonicera	-0.4	-0.1	0.5	0.1	0.9
Picea glauca	-0.8	0.2	0.5	-0.2	0.7
Amelanchier bartramiana	1.6	0.1	-0.1	-0.5	0.3
Salix spp.	-0.2	0.1	0.7	-0.2	0.3
Rubus idaeus var. strigosus	0.1	-0.1	0.5	-0.1	0.0
Ribes lacustre	-0.1	0.0	0.4	-0.2	0.0
Prunus pensylvanica	0.7	-0.1	-0.3	0.1	0.0
Amelanchier humilis	-0.1	-0.1	0.2	0.0	0.0
Lonicera involucrata	0.1	-0.1	0.3	-0.1	-0.1
Prunus virginiana	-0.2	-0.2	0.2	0.3	0.0
Populus balsamifera	0.2	-0.1	-0.2	0.1	-0.2
Rhamnus alnifolia	0.1	-0.4	0.2	-0.1	0.0
Fraxinus nigra	-0.1	0.1	-0.1	0.3	-0.2
Ribes hirtellum	-0.1	-	0.3	-	-0.3
Lonicera villosa	0.2	0.4	-0.3	-0.2	-0.1
Lonicera hirsuta	-0.1	0.1	0.1	0.0	-0.3
Sambucus pubens	0.1	-0.1	-0.1	0.1	-0.3
Lonicera oblongifolia	0.1	-	0.0	-	-0.3
Larix laricina	-	0.1	-0.1	0.0	-0.3
Ribes triste	-0.1	0.0	-	0.0	-0.3
Ribes oxycanthoides	0.1	-0.1	-0.1	0.1	-0.3
Populus tremuloides	-	0.0	0.0	0.2	-0.4
Vaccinium angustifolium	-0.1	0.0	-	0.0	-0.3
Ribes glandulosum	-	0.0	0.0	0.2	-0.4
Kalmia polifolia	0.1	-0.1	-0.1	0.1	-0.4
Myrica gale	0.1	-0.1	-0.1	0.1	-0.4
Ribes hudsonianum	0.1	-0.1	-0.1	0.1	-0.4
				Overall	effect
Treatment effects	0.0	0.0	0.0	-0.1	0.4

b) Residuals and effects for shrub percentage frequency.

Residuals CC	DC	HP	SC	Species effects
-18.2	-6.6	6.6	7.5	81.0
-9.7	10.2	7.8	-7.7	70.8
-6.3	9.8	6.3	-22.2	39.0
-16.6	-2.6	2.6	16.2	29.4
-1.1	8.4	-5.1	1.0	37.1
-4.8	10.4	9.5	4.7	29.2
4.9	-4.9	18.5	-7.7	24.6
-5.9	3.6	12.7	-3.6	23.7
4.0	13.1	-4.0	-14.5	20.5
1.5	-10.5	-1.5	-12.0	11.3
1.9	5.2	-18.9	-1.9	10.9
-0.6	-10.4	11.9	0.6	20.1
22.9	4.5	-4.5	-8.9	3.2
5.5	4.4	10.8	-5.5	12.3
-0.4	-9.5	0.4	5.2	11.6
-12.6	-1.5	11.7	1.5	13.6
18.0	4.5	-4.5	-12.9	9.7
-1.3	-0.6	12.4	1.2	4.0
2.0	-10.0	5.6	-10.6	10.8
1.6	5.1	17.5	-2.2	1.2
10.4	0.1	-4.9	3.2	-0.9
-1.7	-1.9	12.6	1.6	-0.6
2.8	-2.9	7.6	-2.8	0.0
-4.9	-2.3	8.1	1.3	-0.6
6.9	-3.4	-3.4	3.4	-2.4
1.7	-5.0	3.1	-1.7	-2.3
-1.7	1.6	-1.9	3.2	-3.9
-1.6	1.5	15.5	-	-5.7
2.6	0.9	-3.2	-0.9	-4.8
-2.6	3.6	1.1	-1.1	-4.6
0.1	-5.0	-5.7	-0.1	-2.3
1.8	0.1	-0.2	-0.1	-5.6
0.1	3.3	-2.4	-0.1	-5.6
-1.4	1.4	-	1.4	-5.8
-0.8	-2.5	-3.3	0.8	-4.8
-0.4	-0.4	-1.1	4.6	-6.9
-1.5	0.2	-0.1	0.1	-5.8
-	0.0	-0.8	4.5	-7.3
0.9	-0.8	-1.5	0.8	-6.5
0.9	-0.8	-1.5	0.8	-6.5
0.1	-1.6	-2.3	-	-5.7
			Overall	effect
0.0	0.0	0.7	-1.6	7.3

(continued)

Table 4.2.3 (cont.).

c) Effects and fits for shrub density (trees/ha).

Treatment	CC*	DC*	HP*	SC*	Species effects
Acer spicatum	4431	4473	4462	4406	4349
Abies balsamea	1869	1911	1901	1845	1788
Alnus rugosa	1454	1496	1485	1429	1372
Corylus cornuta	832	874	863	807	750
Thuja occidentalis	411	453	442	386	329
Ledum groenlandicum	404	446	435	379	322
Betula papyrifera	361	403	392	337	280
Cornus stolonifera	267	309	298	242	185
Viburnum edule	206	248	237	181	125
Picea mariana	124	166	155	99	42
Alnus crispa	192	234	223	167	110
Amelanchier bartramiana	144	186	176	120	63
Diervilla lonicera	136	179	168	112	55
Lonicera canadensis	96	139	128	72	15
Rosa acicularis	76	118	107	51	-6
Picea glauca	82	124	113	57	0
Sorbus decora	106	148	137	81	24
Prunus virginiana	68	110	99	43	-14
Lonicera involucrata	63	105	94	38	-19
Lonicera villosa	46	88	77	21	-35
Prunus pensylvanica	57	99	88	32	-24
Salix	58	100	89	33	-24
Rubus idaeus var. strigosus	50	92	81	25	-32
Amelanchier humilis	27	69	58	3	-54
Rhamnus alnifolia	27	69	58	3	-54
Fraxinus nigra	1	43	32	-24	-80
Lonicera hirsuta	25	67	56	0	-57
Ribes hudsonianum	-3	39	28	-28	-85
Populus balsamifera	12	55	44	-12	-69
Sambucus pubens	-16	27	16	-40	-97
Ribes lacustre	-3	39	28	-28	-85
				Overall	effect
Treatment effects	-16	27	16	-40	97

d) Residuals for shrub density.

CC	DC	HP	SC
-2291	1535	759	-759
-1177	1100	893	-893
-444	444	789	-1252
-500	155	-155	191
209	-209	758	-337
379	704	-435	-379
72	233	-94	-72
-29	29	656	-183
-52	-117	52	268
-16	629	16	-65
36	130	-223	-36
86	248	-175	-86
-2	-179	151	2
187	42	-42	-72
21	-90	363	-21
0	0	-27	59
5	25	-137	-5
-25	-61	78	25
-22	143	-94	22
21	199	-77	-21
62	-1	-88	1
-18	-51	53	18
25	-92	31	-25
-27	-69	109	27
-27	-69	63	27
32	-43	-32	74
-25	16	0	0
71	-39	-28	28
-12	-54	78	12
16	-27	-16	91
45	-39	-28	28

*CC=clearcut, SC=softwoods only cut, DC=deferred cut, HP=hardwoods poisoned (deferred cut).

cornuta in terms of frequency over the whole study area.

Despite the lack of joint response of shrub species to the harvest treatments, the median polish residuals of the three measures revealed that many individual species appeared to have responded to the harvest treatments, with contrasting high and low residuals between some treatments.

4.2.4 Analysis of Variance

Only 13 shrub species had significant or nearly significant treatment differences, as tested by ANOVA and Fisher's protected least significant difference (PLSD) or the 'unprotected' least significant difference (LSD) (α=0.10, Table 4.2.4a). The following ANOVA results were supported by median polish residuals (Table 4.2.3). *Abies balsamea* and *Amelanchier bartramiana* (Tausch) Roem. had significant treatment differences for cover and density and nearly significant differences for frequency. Cover and density of *A. balsamea*, were significantly lower in CC and SC than in DC and HP, while for *A. bartramiana*, they were significantly higher in CC than in SC. LSD showed significant frequency differences among the same treatments, although the ANOVA did not. For *Cornus stolonifera*, frequency in HP was significantly higher than in DC and SC, and differences in cover and density for the same treatments were nearly significant. *Ledum groenlandicum* frequency in CC was significantly higher than in the other treatments. Although the difference in *L. groenlandicum* cover between CC and SC was not significant according to the ANOVA of all treatments, it was significant according to LSD. Significantly high values were obtained for *Betula papyrifera* cover in DC, and for *Rosa acicularis* density in HP.

The following treatment differences were not obvious in median polish residuals, but produced significant or nearly significant ANOVA results. *Prunus pensylvanica* frequency was significantly high in CC, and its cover produced a nearly significant F-test. *Rubus idaeus* L. cover was significantly high in HP, and its frequency in CC and HP

Table 4.2.4. Results of significant ($p \leq 0.10$) or nearly significant ($p \leq 0.20$) ANOVAs, testing harvest treatment differences for shrub species on the RC-17 project, 1990.

a) all plots included.

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD, LSD†
COVER	*Abies balsamea*	5.39	0.016	CC-DC	-9.5	4.8
				CC-HP	-7.3	5.2
				DC-SC	7.8	4.8
				HP-SC	5.7	5.2
	*Amelanchier bartramiana**	3.07	0.073	CC-SC	7.1	4.2
	Betula papyrifera	2.95	0.080	CC-DC	-3.6	2.7
				DC-HP	3.7	2.9
				DC-SC	3.8	2.7
	Cornus stolonifera	2.05	0.166	DC-HP	-2.9	2.8
				HP-SC	3.7	2.8
	*Ledum groenlandicum**	2.40	0.124	CC-SC	12.5	8.5
	Prunus pensylvanica	2.15	0.152	CC-DC	0.8	0.7
				CC-HP	1.0	0.8
	Rubus idaeus	5.59	0.014	CC-HP	-0.4	0.4
				DC-HP	-0.7	0.4
				HP-SC	0.8	0.4
FREQUENCY	*Abies balsamea*	2.61	0.104	CC-DC	-20.0	16.7
				CC-HP	-18.3	18.1
				DC-SC	19.6	16.7
	*Alnus crispa**	2.02	0.170	CC-HP	23.2	20.1
				DC-HP	25.3	20.1
	Amelanchier bartramiana	2.19	0.146	CC-SC	32.5	23.4
	Amelanchier humilis	2.19	0.147	CC-HP	-15.0	12.1
				DC-HP	-15.2	12.1
				HP-SC	13.3	12.1
	Cornus stolonifera	3.19	0.067	DC-HP	-24.2	17.9
				HP-SC	28.6	17.9
	*Ledum groenlandicum**	4.12	0.035	CC-DC	22.1	18.0
				CC-HP	19.7	19.4
				CC-SC	34.7	18.0
	Lonicera involucrata	2.06	0.164	DC-HP	-11.2	10.2
				HP-SC	12.6	10.2
	Prunus pensylvanica	3.21	0.066	CC-DC	10.2	8.2
				CC-HP	14.4	8.9
				CC-SC	8.8	8.2
	*Rhamnus alnifolia**	2.45	0.118	CC-DC	12.8	10.6
				DC-HP	-13.9	11.5
	Rubus idaeus	4.63	0.025	CC-DC	11.8	10.1
				CC-SC	14.1	10.1
				DC-HP	-16.3	10.9
				HP-SC	18.6	10.9
DENSITY	*Abies balsamea*	5.45	0.015	CC-DC	-2320	1281
				CC-HP	-2101	1384
				DC-SC	2060	1281
				HP-SC	1841	1384
	*Amelanchier bartramiana**	6.22	0.010	CC-HP	12	10
				CC-SC	9	9
				DC-HP	20	10
				DC-SC	17	9
	Cornus stolonifera	1.84	0.199	CC-HP	-717	711
				HP-SC	895	711
	*Diervilla lonicera**	3.94	0.039	CC-HP	-12	9
				DC-HP	-18	9
				DC-SC	-9	9

(continued)

Table 4.2.4 (cont.).

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD, LSD†
	Rosa acicularis	8.13	0.004	CC-HP	-373	183
				DC-HP	-442	183
				HP-SC	440	183
b) plots 5A and 6A (mostly wet sites) excluded.						
COVER	*Abies balsamea*	4.40	0.036	CC-DC	-10.4	6.1
				CC-HP	-7.4	6.1
				DC-SC	8.7	5.7
	Acer spicatum	5.48	0.020	CC-DC	-26.0	12.2
				CC-SC	-17.3	11.4
				DC-HP	14.9	12.2
	*Amelanchier bartramiana**	3.06	0.084	CC-SC	5.0	3.1
	Betula papyrifera	3.80	0.052	CC-DC	-3.7	3.0
				DC-HP	4.6	3.0
				DC-SC	4.7	2.8
	*Ledum groenlandicum**	9.84	0.003	CC-DC	12.4	5.0
				CC-HP	8.1	5.0
				CC-SC	12.4	4.6
	Prunus pensylvanica	3.48	0.064	CC-DC	1.0	0.8
				CC-HP	1.3	0.8
				CC-SC	1.0	0.7
	Rubus idaeus	11.88	0.002	CC-HP	-0.5	0.3
				DC-HP	-0.8	0.3
				HP-SC	0.8	0.3
FREQUENCY	*Cornus stolonifera*	3.09	0.083	CC-HP	-20.0	18.9
				DC-HP	-21.8	18.9
				HP-SC	28.6	17.7
	*Ledum groenlandicum**	28.62	0.000	CC-DC	34.6	8.2
				CC-HP	19.6	8.2
				CC-SC	34.6	7.6
				DC-HP	-15.0	8.2
				HP-SC	15.0	7.6
	Prunus pensylvanica	4.82	0.029	CC-DC	13.6	9.0
				CC-HP	17.8	9.0
				CC-SC	12.1	8.4
	Rubus idaeus	9.37	0.004	CC-DC	11.3	8.2
				CC-HP	-8.9	8.2
				CC-SC	9.7	7.6
				DC-HP	-20.2	8.2
				HP-SC	18.6	7.6
DENSITY	*Abies balsamea*	5.18	0.024	CC-DC	-2626	1542
				CC-HP	-2042	1542
				DC-SC	2424	1442
				HP-SC	1841	1442
	Acer spicatum	2.25	0.152	CC-DC	-4690	3594
				DC-SC	3725	3362
	*Amelanchier bartramiana**	4.22	0.040	CC-HP	13	11
				DC-HP	18	11
				DC-SC	15	10
	*Diervilla lonicera**	2.98	0.089	DC-HP	-18	11
	*Ledum groenlandicum**	4.58	0.033	CC-DC	22	13
				CC-HP	22	13
				CC-SC	22	12
	Rosa acicularis	6.35	0.013	CC-HP	-370	220
				DC-HP	-433	220
				HP-SC	440	205

*For these species, ANOVAs were performed on arcsine values of percentage cover and percentage frequency, and on square roots of density.

†PLSD= Fisher's protected least significant difference, for mean differences with significant F-values at a=0.10 (i.e. p-value ≤ 0.10); LSD= 'unprotected' least significant difference, for p-values >0.10, but ≤0.20.

was significantly higher than in DC and SC. *Diervilla lonicera* density was significantly higher in HP than in CC and DC, and in SC than DC.

A total of 57 treatment pairs were significantly different according to Fisher's PLSD and the LSD; 35 included HP, 29 included CC, 27 included DC and 23 included CC. There were no consistent treatment pairings, and therefore no indication that certain treatments were consistently unlike other ones in terms of shrub species' composition and abundances.

Several species that did not exhibit significant treatment differences had evidently disparate treatment values for cover, frequency and/or density (Tables 4.2.1, 4.2.2) and did show contrasting median polish residuals (Table 4.2.3), e.g. *Acer spicatum*, *Thuja occidentalis* and *Alnus rugosa*. High variance of these measures among plots within treatments (Appendix 9) was responsible for the lack of significance in these differences.

4.2.5 ANOVA with Mucky Peat-dominated Plots Excluded

ANOVAs were repeated excluding data from the mostly wet plots, 5A and 6A (Table 4.2.4b). The significance of most of the species' treatment differences remained the same. However, the significance of some treatment differences increased considerably: *Rubus idaeus* cover and frequency, and *Ledum groenlandicum* frequency. Treatment differences for *Prunus pensylvanica* cover, previously nearly significant, became significant; *L. groenlandicum* density differences became significant; and *Acer spicatum*, previously without significant treatment differences, showed significantly higher cover in DC than in CC and SC, and in HP than in CC, and almost significant density differences.

4.2.6 Reproduction of Softwood and Hardwood Species

Of the six 'commercial' species, *Abies balsamea, Betula papyrifera, Picea mariana* and *Picea glauca* were the only ones that were important in the shrub stratum (Tables 4.2.1, 4.2.2). Of these, only *A. balsamea* and *B. papyrifera* occurred in over

40% of the sample units, had mean percentage cover greater than 3% (Table 4.2.1) and had densities exceeding 300 shrubs per ha (Table 4.2.2) in all treatments. As noted previously, these two were also the only commercial species to have significant treatment differences in cover, density and/or frequency (Table 4.2.4). However, median polish residuals indicated that frequency and density of *P. mariana* were noticeably higher in DC than in the other treatments, especially SC (Table 4.2.3 b,d). Median polish residuals also showed some evidence of a difference between treatments CC and HP in *P. glauca* frequency (Table 4.2.3).

Since *Populus balsamifera* and *P. tremuloides* were extremely minor elements in the shrub stratum, softwood regeneration in this stratum exceeded that of hardwoods in all measures for all treatments (Tables 4.1.1, 4.1.2). However, with the exception of high density and frequency for *P. mariana* in DC, the spruces were relatively unimportant compared to the main shrub species, with *A. balsamea* clearly dominating the softwood advance reproduction.

4.2.7 Summary of Shrub Stratum Results

Acer spicatum, Abies balsamea, Alnus rugosa, Corylus cornuta and *Betula papyrifera* were the most important species in terms of cover, frequency and density in the shrub stratum. Median polishes of these measures yielded very small treatment effects, indicating essentially no joint species responses to harvest treatments, although for density, treatment effects of DC and HP were slightly higher than CC and SC. Several species had significant or nearly significant differences (ANOVA) among treatments for one or more measures, and median polish residuals suggested several more differences, but Fisher's PLSD tests, LSD tests and median polish residuals did not show consistent treatment pairings. In terms of commercial softwoods and principal hardwoods, only *A. balsamea, B. papyrifera* and the two spruces were important in the shrub stratum, and only the first two of these had any significant treatment differences in cover, density

and/or frequency. For *A. balsamea*, these differences followed the pattern noted in earlier sections, with values in DC and HP being higher than those in CC and SC, while for *B. papyrifera*, its cover was significantly higher in DC than in all other treatments. *A. balsamea* was much more prevalent than the spruces in this stratum.

4.3 HERB COVER AND FREQUENCY

Table 4.3.1 contains harvest treatment averages for herb species: percentage cover and percentage frequency, their corresponding relative values and importance values (=relative cover plus relative frequency). Percentage frequency and plot means for percentage cover of plant species in the herb stratum are presented in Appendix 10.

A total of 113 'species' (including groups such as the grass species and *Viola* spp.) were encountered. Ninety-three occurred in treatment CC, 85 in DC, 80 in HP and 79 in SC. The 22 'species' appearing first in Table 4.3.1 had IVs greater than 3.0, and are common boreal forest species, appearing in a variety of habitats. Most of these species occurred in all 15 plots (Appendix 10). The most dominant species over the whole site, in terms of IV, were *Pleurozium schreberi, Clintonia borealis, Rubus pubescens* and *Cornus canadensis*. These species had the highest IVs in treatments CC and DC, while in treatment HP, *Aster macrophyllus* and *Streptopus roseus* were more important than *C. canadensis* and *R. pubescens*, and in SC, *Acer spicatum* was more important than *C. canadensis* .

Plot means for percentage cover were all lower than 20% (Appendix 10) and therefore the treatment means for cover were low for all species; the highest value occurred in DC for *Pleurozium schreberi* (11%). This species had the highest percentage cover for herb layer species in all four treatments. Cover values were generally less than 2% for species with mean IVs less than 3% (Table 4.3.1).

The highest mean frequency for a treatment was that of *S. roseus* (71%) in treatment HP (Table 4.3.1). All herbaceous layer species with importance values less

Table 4.3.1. Harvest treatment averages, relative values and importance values for herb parameters measured on the RC-17 project, near Manitouwadge, Ontario, in1990.

TREATMENT	COVER (%)				FREQUENCY (%)				RELATIVE COVER				RELATIVE FREQUENCY				IMPORTANCE VALUE				MEAN I.V.
	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	
Species with mean I.V. ≥3.0																					
Abies balsamea	1.8	1.4	1.5	0.7	40.7	26.6	37.8	25.4	1.6	1.2	1.2	0.8	3.1	2.0	2.4	2.2	4.7	3.3	3.6	3.0	3.6
Acer spicatum	1.7	2.6	3.4	3.4	27.0	34.7	42.2	52.1	1.5	2.3	2.7	3.7	2.1	2.7	2.7	4.5	3.6	4.9	5.4	8.2	5.5
Anemone quinquefolia	1.0	1.1	1.2	1.2	31.0	18.8	42.2	25.0	0.9	1.0	1.0	1.3	2.4	1.4	2.7	2.2	3.3	2.4	3.6	3.5	3.2
Aralia nudicaulis	4.4	3.8	5.1	3.1	42.6	40.8	46.6	30.4	3.9	3.3	4.1	3.4	3.3	3.1	3.0	2.6	7.1	6.4	7.0	6.0	6.7
Aster macrophyllus	6.2	5.1	9.2	3.0	30.6	25.1	46.7	27.9	5.5	4.4	7.4	3.3	2.3	1.9	3.0	2.4	7.8	6.4	10.3	5.7	7.6
Brachythecium sp.	1.6	0.5	3.5	1.3	23.6	7.7	42.2	18.3	1.4	0.4	2.8	1.4	1.8	0.6	2.7	1.6	3.2	1.0	5.5	3.0	3.2
Carex spp.	3.0	4.7	5.3	3.5	41.1	43.7	57.8	38.4	2.6	4.1	4.2	3.9	3.2	3.4	3.7	3.3	5.8	7.4	7.9	7.2	7.1
Clintonia borealis	6.6	5.0	7.3	8.2	53.8	58.5	57.8	63.3	5.8	4.4	5.8	9.0	4.1	4.5	3.7	5.5	9.9	8.8	9.5	14.5	10.7
Cornus canadensis	5.8	6.3	3.5	3.3	51.0	62.7	53.3	46.3	5.1	5.5	2.8	3.6	3.9	4.8	3.4	4.0	9.0	10.3	6.2	7.6	8.3
Dicranum spp.	2.3	3.8	2.9	3.3	37.6	31.8	26.7	33.8	2.0	3.3	2.3	3.6	2.9	2.4	1.7	2.9	4.9	5.7	4.0	6.6	5.3
Grass spp.	1.6	1.8	1.1	0.8	32.4	25.7	26.7	18.8	1.4	1.6	0.9	0.9	2.5	2.0	1.7	1.6	3.9	3.5	2.6	2.5	3.1
Gymnocarpium dryopteris	0.9	1.9	2.2	2.6	13.4	31.1	31.1	32.1	0.8	1.7	1.8	2.9	1.0	2.4	2.0	2.8	1.8	4.0	3.7	5.6	3.8
Linnaea borealis	2.7	2.2	1.9	2.0	34.2	38.2	28.9	30.4	2.4	1.9	1.5	2.2	2.6	2.9	1.8	2.6	5.0	4.8	3.4	4.8	4.5
Lycopodium annotinum	4.9	4.1	3.2	4.4	33.5	27.7	28.9	35.4	4.3	3.6	2.6	4.8	2.6	2.1	1.8	3.1	6.9	5.7	4.4	7.9	6.2
Maianthemum canadense	3.6	3.8	2.4	3.1	54.5	51.2	48.9	52.1	3.2	3.3	1.9	3.4	4.2	3.9	3.1	4.5	7.3	7.2	5.0	7.9	6.9
Mitella nuda	3.1	3.3	4.1	3.9	39.3	41.8	55.5	35.8	2.7	2.9	3.3	4.3	3.0	3.2	3.5	3.1	5.7	6.1	6.8	7.4	6.5
Moss spp.	0.8	2.0	2.7	1.2	12.0	30.5	31.1	17.9	0.7	1.7	2.2	1.3	0.9	2.3	2.0	1.5	1.6	4.1	4.1	2.9	3.2
Pleurozium schreberi	7.7	10.7	9.7	8.7	44.1	54.7	57.8	43.8	6.8	9.3	7.8	9.6	3.4	4.2	3.7	3.8	10.2	13.5	11.4	13.4	12.1
Rubus pubescens	7.0	6.8	5.2	4.8	54.2	54.7	51.1	44.6	6.2	5.9	4.2	5.3	4.2	4.2	3.2	3.9	10.3	10.1	7.4	9.1	9.2
Streptopus roseus	2.2	3.7	4.9	2.6	33.7	41.6	71.1	40.0	1.9	3.2	3.9	2.9	2.6	3.2	4.5	3.5	4.5	6.4	8.4	6.3	6.4
Trientalis borealis	0.9	1.7	0.9	1.2	25.8	42.0	31.1	34.2	0.8	1.5	0.7	1.3	2.0	3.2	2.0	3.0	2.8	4.7	2.7	4.3	3.6
Viola renifolia	1.9	2.1	3.0	2.4	42.5	37.4	57.8	43.8	1.7	1.8	2.4	2.6	3.3	2.9	3.7	3.8	4.9	4.7	6.1	6.4	5.5
Species with mean I.V. < 3.0																					
Alnus rugosa	0.5	0.3	0.8	0.1	7.0	6.7	11.1	2.5	0.4	0.3	0.6	0.1	0.5	0.5	0.7	0.2	1.0	0.8	1.3	0.3	0.9
Amelanchier bartramiana	0.2	0.1	0.2	0.1	5.0	3.3	4.5	1.7	0.2	0.1	0.2	0.1	0.4	0.3	0.3	0.1	0.6	0.3	0.4	0.3	0.4
Amelanchier humilis	-	-	0.1	-	-	-	4.4	-	-	-	0.1	-	-	-	0.3	-	-	-	0.4	-	0.1
Anaphalis margaritaceae	-	-	-	-	-	1.5	-	-	-	-	-	-	-	0.1	-	-	-	0.1	-	-	0.0
Anemone canadensis	0.2	-	0.1	-	1.8	1.5	2.2	-	0.2	-	0.1	-	0.1	0.1	0.1	-	0.3	0.1	0.2	-	0.2
Aquilegia canadensis	0.2	-	-	-	1.7	-	-	-	0.2	-	-	-	0.1	-	-	-	0.3	-	-	-	0.1
Aralia hispida	-	0.1	-	0.2	-	1.7	-	1.7	-	0.1	-	0.2	-	0.1	-	0.1	-	0.2	-	0.4	0.1
Aster ciliolatus	0.3	0.4	0.9	0.2	8.6	9.4	13.3	6.7	0.3	0.3	0.7	0.2	0.7	0.7	0.8	0.6	0.9	1.1	1.6	0.8	1.1
Aster spp.	0.1	-	0.1	0.1	1.8	-	2.2	3.8	0.1	-	0.1	0.1	0.1	-	0.1	0.3	0.2	-	0.2	0.4	0.2
Athyrium filix-femina	0.6	2.7	1.3	1.6	5.1	14.8	8.9	7.5	0.5	2.3	1.0	1.8	0.4	1.1	0.6	0.6	0.9	3.5	1.6	2.4	2.1
Betula papyrifera	0.2	0.3	0.1	0.1	6.9	7.8	4.5	5.0	0.2	0.3	0.1	0.1	0.5	0.6	0.3	0.4	0.7	0.9	0.4	0.5	0.6
Botrychium virginianum	0.2	0.2	-	-	5.4	4.6	-	-	0.2	0.2	-	-	0.4	0.4	-	-	0.6	0.5	-	-	0.3
Caltha palustris	0.4	-	-	0.2	1.7	-	-	1.7	0.4	-	-	0.2	0.1	-	-	0.1	0.5	-	-	0.4	0.2
Carex disperma	0.2	-	-	-	1.7	-	-	-	0.2	-	-	-	0.1	-	-	-	0.3	-	-	-	0.1
Carex trisperma	0.4	0.5	-	-	3.4	5.0	-	-	0.4	0.4	-	-	0.3	0.4	-	-	0.6	0.8	-	-	0.4
Circaea alpina	0.4	-	-	0.4	5.0	-	-	5.4	0.4	-	-	0.4	0.4	-	-	0.5	0.7	-	-	0.9	0.4

(continued)

Table 4.3.1 (cont.).

TREATMENT	COVER (%)				FREQUENCY (%)				RELATIVE COVER				RELATIVE FREQUENCY				IMPORTANCE VALUE				MEAN I.V.
	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	
Cladina mitis	0.6	0.2	-	0.1	6.8	1.7	-	1.3	0.5	0.2	-	0.1	0.5	0.1	-	0.1	1.0	0.3	-	0.2	0.4
Cladina rangiferina	0.8	0.4	0.4	-	12.2	12.4	11.1	-	0.7	0.3	0.3	-	0.9	1.0	0.7	-	1.6	1.3	1.0	-	1.0
Cladina stellaris	0.1	-	0.4	-	1.7	-	2.2	-	0.1	-	0.3	-	0.1	-	0.1	-	0.2	-	0.5	-	0.2
Cladonia sp	0.7	0.5	0.4	0.2	15.5	16.1	13.4	6.3	0.6	0.4	0.3	0.2	1.2	1.2	0.9	0.5	1.8	1.7	1.2	0.8	1.4
Climacium dendroides	0.3	-	-	0.1	3.3	-	-	2.9	0.3	-	-	0.1	0.3	-	-	0.3	0.5	-	-	0.4	0.2
Coptis trifolia	1.9	1.9	1.2	0.6	18.7	23.0	22.2	15.0	1.7	1.7	1.0	0.7	1.4	1.8	1.4	1.3	3.1	3.4	2.4	2.0	2.7
Corallorhiza trifida	-	-	-	0.1	-	-	-	1.7	-	-	-	0.1	-	-	-	0.1	-	-	-	0.3	0.1
Cornus stolonifera	0.5	0.3	0.2	0.1	8.4	3.3	4.4	1.7	0.4	0.3	0.2	0.1	0.6	0.3	0.3	0.1	1.1	0.5	0.4	0.3	0.6
Corylus cornuta	0.1	0.2	0.3	0.7	3.5	4.8	4.5	12.5	0.1	0.2	0.2	0.8	0.3	0.4	0.3	1.1	0.4	0.5	0.5	1.9	0.8
Diervilla lonicera	1.4	1.4	3.4	1.7	11.9	11.3	20.0	7.5	1.2	1.2	2.7	1.9	0.9	0.9	1.3	0.6	2.1	2.1	4.0	2.5	2.7
Dryopteris austriaca	0.3	-	0.2	0.1	3.3	-	2.2	1.3	0.3	-	0.2	0.1	0.3	-	0.1	0.1	0.5	-	0.3	0.2	0.3
Epilobium angustifolium	0.2	-	0.2	0.1	1.8	-	2.2	1.7	0.2	-	0.2	0.1	0.1	-	0.1	0.1	0.3	-	0.3	0.3	0.2
Equisetum arvense	1.0	0.3	0.3	0.1	14.2	6.7	8.9	1.7	0.9	0.3	0.2	0.1	1.1	0.5	0.6	0.1	2.0	0.8	0.8	0.3	1.0
Equisetum pratense	0.5	0.5	1.1	0.2	12.3	12.5	33.3	6.7	0.4	0.4	0.9	0.2	0.9	1.0	2.1	0.6	1.4	1.4	3.0	0.8	1.6
Equisetum scirpoides	-	-	0.3	-	-	-	11.1	-	-	-	0.2	-	-	-	0.7	-	-	-	0.9	-	0.2
Equisetum sylvaticum	0.3	0.4	-	0.1	5.0	6.7	-	3.8	0.3	0.3	-	0.1	0.4	0.5	-	0.3	0.6	0.9	-	0.4	0.5
Fragaria vesca	0.1	0.1	-	0.3	1.8	3.2	-	4.2	0.1	0.1	-	0.3	0.1	0.2	-	0.4	0.2	0.3	-	0.7	0.3
Fragaria virginiana	0.2	0.3	0.7	0.1	1.8	6.5	8.9	2.5	0.2	0.3	0.6	0.1	0.1	0.5	0.6	0.2	0.3	0.8	1.1	0.3	0.6
Fraxinus nigra	-	0.1	-	-	-	1.7	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	-	0.1
Galium triflorum	0.9	0.8	1.6	0.9	22.3	23.8	35.6	25.9	0.8	0.7	1.3	1.0	1.7	1.8	2.3	2.2	2.5	2.5	3.5	3.2	2.9
Gaultheria hispidula	1.7	1.3	1.1	0.4	18.7	18.0	24.4	7.1	1.5	1.1	0.9	0.4	1.4	1.4	1.6	0.6	2.9	2.5	2.4	1.1	2.2
Geocaulon lividum	0.1	0.4	-	-	1.7	3.3	-	-	0.1	0.3	-	-	0.1	0.3	-	-	0.2	0.6	-	-	0.2
Geranium bicknelli	0.2	-	-	-	1.7	-	-	-	0.2	-	-	-	0.1	-	-	-	0.3	-	-	-	0.1
Goodyera repens	0.1	0.1	0.1	0.1	1.7	1.7	2.2	2.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.3	0.2
Halenia deflexa	-	-	0.1	-	-	-	2.2	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	0.1
Hylocomium splendens	0.7	0.6	4.0	1.4	12.4	10.9	31.1	10.0	0.6	0.5	3.2	1.5	1.0	0.8	2.0	0.9	1.6	1.4	5.2	2.4	2.6
Larix laricina	0.1	0.1	-	-	1.7	1.7	-	-	0.1	0.1	-	-	0.1	0.1	-	-	0.2	0.2	-	-	0.1
Ledum groenlandicum	2.1	2.3	0.9	-	16.9	15.0	6.7	-	1.8	2.0	0.7	-	1.3	1.2	0.4	-	3.1	3.2	1.1	-	1.9
Lichen spp.	0.2	0.3	0.7	0.2	5.4	9.2	15.6	4.2	0.2	0.3	0.6	0.2	0.4	0.7	1.0	0.4	0.6	1.0	1.6	0.6	0.9
Lonicera canadensis	0.1	0.1	0.4	0.2	1.7	3.0	4.5	4.2	0.1	0.1	0.3	0.2	0.1	0.2	0.3	0.4	0.2	0.3	0.6	0.6	0.4
Lonicera involucrata	-	0.2	0.1	-	-	4.6	2.2	-	-	0.2	0.1	-	-	0.4	0.1	-	-	0.5	0.2	-	0.2
Lonicera villosa	0.2	0.1	-	-	5.1	1.7	-	-	0.2	0.1	-	-	0.4	0.1	-	-	0.6	0.2	-	-	0.2
Lycopodium clavatum	0.3	0.2	-	-	5.0	1.7	-	1.3	0.3	0.2	-	-	0.4	0.1	-	0.1	0.6	0.3	-	0.1	0.3
Lycopodium complanatum	-	0.1	0.1	0.1	-	1.7	2.2	2.5	-	0.1	0.1	0.1	-	0.1	0.1	0.2	-	0.2	0.2	0.3	0.2
Lycopodium obscurum	0.2	0.3	0.8	1.1	6.7	5.0	11.1	13.8	0.2	0.3	0.6	1.2	0.5	0.4	0.7	1.2	0.7	0.6	1.3	2.4	1.3
Menyanthes trifoliata	0.1	-	-	-	1.7	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	-	-	0.1
Mertensia paniculata	1.1	2.0	1.7	0.7	15.1	10.9	20.0	8.3	1.0	1.7	1.4	0.8	1.2	0.8	1.3	0.7	2.1	2.6	2.6	1.5	2.2
Mnium spp.	2.6	1.1	2.7	1.0	13.6	14.0	26.7	14.6	2.3	1.0	2.2	1.1	1.0	1.1	1.7	1.3	3.3	2.0	3.9	2.4	2.9
Moneses uniflora	0.1	0.3	0.2	0.2	5.4	12.5	8.9	6.7	0.1	0.3	0.2	0.2	0.4	1.0	0.6	0.6	0.5	1.2	0.7	0.8	0.8
Peltigera spp.	-	0.2	0.3	0.4	-	3.2	6.7	2.9	-	0.2	0.2	0.4	-	0.2	0.4	0.3	-	0.4	0.7	0.7	0.4
Petasites palmatus	1.0	1.5	2.3	1.0	18.9	17.5	28.9	9.2	0.9	1.3	1.8	1.1	1.4	1.3	1.8	0.8	2.3	2.6	3.7	1.9	2.6

(continued)

Table 4.3.1 (cont.).

TREATMENT	COVER (%)				FREQUENCY (%)				RELATIVE COVER				RELATIVE FREQUENCY				IMPORTANCE VALUE				MEAN I.V.
	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	CC	DC	HP	SC	
Picea glauca	-	0.1	-	0.1	-	1.7	-	1.7	-	0.1	-	0.1	-	0.1	-	0.1	-	0.2	-	0.3	0.1
Picea mariana	0.1	0.1	0.1	-	3.6	3.3	4.5	-	0.1	0.1	0.1	-	0.3	0.3	0.3	-	0.4	0.3	0.4	-	0.3
Pinus banksiana	-	0.1	-	-	-	1.7	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	-	0.1
Polygonum scandens	-	-	0.4	-	-	-	2.2	-	-	-	0.3	-	-	-	0.1	-	-	1.1	-	-	0.3
Polytrichum juniperinum	0.2	0.3	0.1	0.3	6.9	8.2	4.4	6.7	0.2	0.3	0.1	0.3	0.5	0.6	0.3	0.6	0.7	0.9	0.4	0.9	0.7
Populus balsamifera	0.2	-	-	-	3.5	-	-	-	0.2	-	-	-	0.3	-	-	-	0.4	-	-	-	0.1
Populus tremuloides	-	-	-	0.1	-	-	-	4.6	-	-	-	0.1	-	-	-	0.4	-	-	-	0.5	0.1
Prunus pensylvanica	0.1	0.1	-	-	3.4	3.2	-	-	0.1	0.1	-	-	0.3	0.2	-	-	0.3	0.3	-	-	0.2
Prunus virginiana	-	-	0.1	0.2	-	-	2.2	2.9	-	-	0.1	0.2	-	-	0.1	0.3	-	-	0.2	0.5	0.2
Ptilium crista-castrensis	0.7	0.2	0.7	0.9	10.1	6.5	8.9	15.0	0.6	0.2	0.6	1.0	0.8	0.5	0.6	1.3	1.4	0.7	1.1	2.3	1.4
Pyrola rotundifolia	-	-	0.1	-	-	-	2.2	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	0.1
Rhamnus alnifolia	-	-	0.3	0.3	-	-	4.5	1.7	-	-	0.2	0.3	-	-	0.3	0.1	-	-	0.5	0.5	0.3
Rhytidiadelphus triquestrus	0.9	0.8	1.3	0.2	8.8	9.8	24.4	3.3	0.8	0.7	1.0	0.2	0.7	0.8	1.6	0.3	1.5	1.4	2.6	0.5	1.5
Ribes glandulosum	-	-	0.1	0.2	-	-	2.2	2.5	-	-	0.1	0.2	-	-	0.1	0.2	-	-	0.2	0.4	0.2
Ribes hirtellum	-	-	0.2	-	-	-	6.7	-	-	-	0.2	-	-	-	0.4	-	-	-	0.6	-	0.1
Ribes lacustre	0.1	0.1	0.3	0.2	1.8	1.7	4.5	2.9	0.1	0.1	0.2	0.2	0.1	0.1	0.3	0.3	0.2	0.2	0.5	0.5	0.4
Ribes triste	0.3	0.4	0.7	0.6	8.5	6.1	15.6	10.4	0.3	0.3	0.6	0.7	0.7	0.5	1.0	0.9	0.9	0.8	1.6	1.6	1.2
Rosa acicularis	1.6	1.5	1.9	0.1	15.6	15.5	26.7	1.7	1.4	1.3	1.5	0.1	1.2	1.2	1.7	0.1	2.6	2.5	3.2	0.3	2.1
Rubus hispidus	-	-	-	0.2	-	-	-	1.3	-	-	-	0.2	-	-	-	0.1	-	-	-	0.3	0.1
Rubus idaeus var. strigosus	0.5	0.7	0.4	0.3	3.4	11.3	4.4	4.2	0.4	0.6	0.3	0.3	0.3	0.9	0.3	0.4	0.7	1.5	0.6	0.7	0.9
Salix spp.	0.2	0.1	-	-	1.8	1.7	-	-	0.2	0.1	-	-	0.1	0.1	-	-	0.3	0.2	-	-	0.1
Smilacina trifolia	0.3	0.2	-	-	1.7	1.7	-	-	0.3	0.2	-	-	0.1	0.1	-	-	0.4	0.3	-	-	0.2
Sorbus decora	0.4	0.1	0.1	0.6	13.6	3.3	2.2	19.2	0.4	0.1	0.1	0.7	1.0	0.3	0.1	1.7	1.4	0.3	0.2	2.3	1.1
Sphagnum capillifolium	2.9	3.6	0.3	-	11.8	10.0	4.4	-	2.6	3.1	-	-	0.9	0.8	-	-	3.5	3.9	-	-	1.8
Sphagnum magellanicum	2.0	1.1	-	-	6.7	5.0	-	-	1.8	1.0	-	-	0.5	0.4	-	-	2.3	1.3	-	-	0.9
Sphagnum spp.	0.1	-	-	-	1.7	-	-	-	0.1	-	0.2	-	0.1	0.1	0.3	-	0.2	0.1	0.5	-	0.2
Thelypteris phegopteris	0.3	0.6	1.7	0.6	3.3	3.4	11.1	6.7	0.3	0.5	1.4	0.7	0.3	0.3	0.7	0.6	0.5	0.8	2.1	1.2	1.2
Thuja occidentalis	0.4	-	0.3	-	5.3	-	13.3	-	0.4	-	0.2	-	0.4	-	0.8	-	0.8	-	1.1	-	0.5
Trillium cernuum	0.1	-	-	-	1.7	-	-	-	0.1	-	-	-	0.1	-	-	-	0.2	-	-	-	0.1
Vaccinium angustifolium	3.9	2.3	0.7	0.5	30.3	21.7	8.9	7.9	3.4	2.0	0.6	0.6	2.3	1.7	0.6	0.7	5.8	3.7	1.1	1.2	2.9
Vaccinium myrtilloides	0.8	0.5	0.5	0.1	15.3	8.4	8.9	1.7	0.7	0.4	0.4	0.1	1.2	0.6	0.6	0.1	1.9	1.1	1.0	0.3	1.0
Vaccinium oxycoccos	0.1	-	-	-	3.4	-	-	-	0.1	-	-	-	0.3	-	-	-	0.3	-	-	-	0.1
Viburnum edule	1.0	0.3	0.6	1.2	8.4	8.1	13.3	18.3	0.9	0.3	0.5	1.3	0.6	0.6	0.8	1.6	1.5	0.9	1.3	2.9	1.7
Viola spp.	0.1	0.1	-	0.1	1.8	1.7	-	5.8	0.1	0.1	-	0.1	0.1	0.1	-	0.5	0.2	0.2	-	0.6	0.3
Total number of species					93	85	80	79													
Litter	39.4	41.5	36.0	47.9	100.0	98.3	100.0	97.5													

than 3.0 had less than 36% frequency in each treatment.

4.3.1 Median Polish Analysis

The treatment effects for the median polish of herb cover were all zero, and those for frequency were very small, indicating no joint responses of species to harvest treatments (Table 4.3.2). For cover, the species effects indicated that the dominant species were *Pleurozium schreberi*, *Clintonia borealis*, *Rubus pubescens* and *Aster macrophyllus*. For frequency, the highest species effects were for *C. borealis*, *R. pubescens*, *P. schreberi*, *Cornus canadensis* and *Maianthemum canadense*.

4.3.2 ANOVA of Herb Frequency and Cover

Five species in the herb stratum had significant (α=0.10) or nearly significant treatment differences for both cover and frequency (Table 4.3.3a). Cover and frequency of *Diervilla lonicera* were significantly greater in HP than in the other three treatments. Moss species' cover and frequency in treatment CC were significantly less than those of treatment DC and HP. *Rosa acicularis* had significant treatment differences in cover and frequency; for frequency, the only significant difference was between HP and SC, but cover in SC was significantly lower than in the other three treatments. Cover and frequency means of *Sorbus decora* in SC were significantly greater than those in DC and HP. *Trientalis borealis* had nearly significant treatment differences for both cover and frequency, due to high means in DC and low means in CC and HP.

Corylus cornuta had significant treatment differences only in cover, with the mean for SC being significantly greater than those of the other treatments. Several other species had nearly significant treatment differences for cover: *Abies balsamea, Brachythecium* spp., *Cornus canadensis, Equisetum pratense* Ehrh., *Hylocomium splendens* and *Vaccinium angustifolium*. *Gymnocarpium dryopteris* (L.) Newm., *Petasites palmatus, Rhytidiadelphus triquestrus* (Hedw.) Warnst. and *Streptopus roseus* had nearly significant differences for frequency.

Table 4.3.2. Effects and residuals for median polishes of treatment means for herb cover and herb frequency on the RC-17 project, 1990.

a) Residuals and effects for herb percentage cover.

b) Residuals and effects for herb percentage frequency.

Treatment	Residuals CC*	DC*	HP*	SC*	Species effects	Residuals CC	DC	HP	SC	Species effects
Species with mean I.V. ≥3.0										
Abies balsamea	0.4	-0.1	0.1	-0.8	1.3	8.6	-5.4	5.3	-6.2	27.7
Acer spicatum	-1.3	-0.4	0.4	0.4	2.8	-11.3	-3.5	3.5	14.3	34.0
Anemone quinquefolia	-0.2	-0.1	0.1	0.1	1.0	2.8	-9.3	13.6	-2.8	23.9
Aralia nudicaulis	0.3	-0.3	1.0	-1.0	3.9	0.8	-0.9	4.4	-10.9	37.4
Aster macrophyllus	0.6	-0.6	3.6	-2.7	5.5	1.1	-4.3	16.8	-1.1	25.2
Brachythecium sp.	0.2	-1.0	2.1	-0.2	1.3	2.4	-13.4	20.6	-2.4	16.9
Carex spp.	-1.1	0.6	1.2	-0.6	3.9	-1.4	1.4	14.9	-3.6	38.1
Clintonia borealis	-0.4	-2.0	0.4	1.3	6.8	-4.2	0.6	-0.6	5.8	53.7
Cornus canadensis	1.2	1.7	-1.2	-1.4	4.5	-1.0	10.9	1.0	-5.2	47.6
Dicranum spp.	-0.8	0.7	-0.2	0.2	2.9	4.5	-1.2	-6.8	1.2	28.8
Grass spp.	0.3	0.5	-0.3	-0.6	1.2	6.3	-0.3	0.2	-6.8	21.7
Gymnocarpium dryopteris	-1.2	-0.2	0.2	0.6	1.9	-17.6	0.3	-0.3	1.6	26.6
Linnaea borealis	0.6	0.1	-0.2	-0.1	1.9	1.7	5.8	-4.0	-1.7	28.2
Lycopodium annotinum	0.7	-0.2	-1.1	0.2	4.1	2.5	-3.2	-2.5	4.9	26.7
Maianthemum canadense	0.3	0.5	-1.0	-0.3	3.2	2.6	-0.6	-3.4	0.6	47.6
Mitella nuda	-0.5	-0.3	0.5	0.3	3.4	-1.3	1.3	14.5	-4.3	36.3
Moss spp.	-0.8	0.4	1.1	-0.4	1.4	-12.5	6.1	6.2	-6.1	20.2
Pleurozium schreberi	-1.5	1.5	0.5	-0.5	9.0	-5.4	5.3	7.9	-5.3	45.2
Rubus pubescens	1.0	0.8	-0.8	-1.2	5.8	1.8	2.4	-1.8	-7.4	48.1
Streptopus roseus	-1.0	0.6	1.8	-0.6	3.0	-7.4	0.6	29.6	-0.6	36.8
Trientalis borealis	-0.2	0.7	-0.2	0.2	0.9	-6.9	9.4	-2.0	2.0	28.4
Viola renifolia	-0.4	-0.2	0.8	0.2	2.1	-0.9	-5.9	14.0	0.9	39.1
Species with mean I.V. ≤3.0										
Alnus rugosa	0.1	-0.1	0.4	-0.3	0.2	0.1	-0.1	3.8	-3.9	2.6
Amelanchier bartramiana	0.1	-0.1	0.1	-0.1	-0.1	1.2	-0.4	0.3	-1.6	-0.6
Amelanchier humilis	-	-	0.1	-	-0.2	-0.3	-0.2	3.7	0.2	-4.0
Anaphalis margaritaceae	-	-	-	-	-0.2	-0.2	1.4	-0.6	0.3	-4.1
Anemone canadensis	0.2	-0.1	0.1	-0.1	-0.2	0.1	-0.1	0.1	-1.2	-2.6
Aquilegia canadensis	0.2	-	-	-	-0.2	1.4	-0.2	-0.7	0.2	-4.0
Aralia hispida	-0.1	0.1	-0.1	0.2	-0.2	-0.9	0.9	-1.3	1.3	-3.4
Aster ciliolatus	-0.1	0.1	0.6	-0.2	0.2	-0.5	0.5	3.8	-1.9	4.7
Aster spp.	-	-0.1	-	-	-0.1	-	-1.7	-	2.5	-2.5
Athyrium filix-femina	-0.9	1.3	-0.2	0.2	1.3	-3.1	6.7	0.3	-0.3	3.9
Betula papyrifera	0.1	0.2	-0.1	-0.1	-0.1	0.7	1.7	-2.1	-0.7	1.9
Botrychium virginianum	0.1	0.1	-0.1	-0.1	-0.1	2.8	2.1	-3.0	-2.1	-1.7
Caltha palustris	0.3	-0.1	-0.1	0.1	-0.1	0.8	-0.8	-1.3	1.3	-3.4
Carex disperma	0.2	-	-	-	-0.2	1.4	-0.2	-0.7	0.2	-4.0
Carex trisperma	0.2	0.3	-0.2	-0.2	-	1.5	3.2	-2.3	-1.5	-2.4
Circaea alpina	0.2	-0.2	-0.2	0.2	-	2.4	-2.5	-3.0	3.3	-1.8
Cladina mitis	0.5	0.1	-0.2	-0.1	-0.1	5.0	0.0	-2.2	0.0	-2.5
Cladina rangiferina	0.4	-	-	-0.4	0.2	0.8	1.1	-0.8	-11.0	7.1
Cladina stellaris	0.1	-0.1	0.4	-0.1	-0.2	0.6	-1.0	0.7	-0.6	-3.3
Cladonia sp.	0.3	0.1	-0.1	-0.3	0.3	1.3	2.0	-1.3	-7.5	9.9
Climacium dendroides	0.3	-0.1	-0.1	0.1	-0.2	1.6	-1.8	-2.1	1.7	-2.6
Coptis trifolia	0.4	0.4	-0.4	-1.0	1.4	-1.6	2.9	1.6	-4.8	15.9
Corallorhiza trifida	-	-	-	0.1	-0.2	-0.1	0.1	-0.5	2.1	-4.3
Cornus stolonifera	0.3	0.1	-0.1	-0.2	0.1	4.7	-0.3	0.3	-1.5	-0.6
Corylus cornuta	-0.2	-0.1	0.1	0.5	0.1	-1.0	0.4	-0.4	8.5	0.2
Diervilla lonicera	-0.2	-0.2	1.9	0.2	1.4	0.2	-0.3	7.9	-3.7	7.3
Dryopteris austriaca	0.2	-0.2	0.1	-0.1	-0.1	1.5	-1.7	0.0	-	-2.6
Epilobium angustifolium	0.1	-0.2	0.1	-0.1	-0.1	-	-1.7	-	0.4	-2.5
Equisetum arvense	0.7	-	-	-0.2	0.1	6.5	-0.9	0.8	-5.5	3.3
Equisetum pratense	-	-	0.6	-0.3	0.3	-0.2	0.2	20.4	-5.3	8.1
Equisetum scirpoides	-	-	0.3	-	-0.2	-0.3	-0.2	10.4	0.2	-4.0
Equisetum sylvaticum	0.1	0.2	-0.2	-0.1	-	0.4	2.2	-5.0	-0.4	0.3
Fragaria vesca	-	-	-0.1	0.2	-0.1	-0.8	0.8	-3.0	2.1	-1.8

(continued)

Table 4.3.2 (cont.).

a) Residuals and effects for herb percentage cover (cont.).

Treatment	Residuals CC	DC	HP	SC	Species effects
Fragaria virginiana	-0.1	0.1	0.5	-0.2	0.1
Fraxinus nigra	-	0.1	-	-	-0.2
Galium triflorum	-	-0.1	0.7	-	0.7
Gaultheria hispidula	0.5	0.1	-0.1	-0.8	1.0
Geocaulon lividum	0.1	0.4	-0.1	-0.1	-0.2
Geranium bicknelli	0.2	-	-	-	-0.2
Goodyera repens	-		-	-	-0.1
Halenia deflexa	-	-	0.1	-	-0.2
Hylocomium splendens	-0.4	-0.5	3.0	0.4	0.9
Larix laricina	0.1	0.1	-0.1	-0.1	-0.2
Ledum groenlandicum	0.6	0.8	-0.6	-1.5	1.3
Lichen spp.	-0.1	0.1	0.5	-0.1	0.1
Lonicera canadensis	-0.1	-0.1	0.3	0.1	-0.1
Lonicera involucrata	-0.1	0.2	0.1	-0.1	-0.2
Lonicera villosa	0.2	0.1	-0.1	-0.1	-0.2
Lycopodium clavatum	0.2	0.1	-0.1	-0.1	-0.1
Lycopodium complanatum	-0.1	-	-	-	-0.1
Lycopodium obscurum	-0.4	-0.3	0.3	0.6	0.4
Menyanthes trifoliata	0.1	-	-	-	-0.2
Mertensia paniculata	-0.3	0.6	0.3	-0.7	1.2
Mnium spp.	0.8	-0.8	0.9	-0.9	1.7
Moneses uniflora	-0.1	0.1	-	-	-
Peltigera spp.	-0.3	-0.1	0.1	0.2	0.1
Petasites palmatus	-0.3	0.3	1.1	-0.3	1.1
Picea glauca	-0.1	0.1	-0.1	0.1	-0.2
Picea mariana	-	-	-	-0.1	-0.1
Pinus banksiana	-	0.1	-	-	-0.2
Polygonum scandens	-0.1	-0.1	0.4	0.1	-0.2
Polytrichum juniperinum	-0.1	0.1	-0.2	0.1	0.1
Populus balsamifera	0.2	-	-	-	-0.2
Populus tremuloides	-	-	-	0.1	-0.2
Prunus pensylvanica	0.1	0.1	-0.1	-0.1	-0.2
Prunus virginiana	-0.1	-0.1	0.1	0.2	-0.2
Ptilium crista-castrensis	-	-0.5	-	0.2	0.5
Pyrola rotundifolia	-	-	0.1	-	-0.2
Rhamnus alnifolia	-0.2	-0.2	0.2	0.2	-0.1
Rhytidiadelphus triquestrus	0.1	-0.1	0.5	-0.7	0.7
Ribes glandulosum	-0.1	-0.1	0.1	0.2	-0.2
Ribes hirtellum	-	-	0.2	-	-0.2
Ribes lacustre	-0.1	-0.1	0.2	0.1	-0.1
Ribes triste	-0.2	-0.1	0.2	0.1	0.3
Rosa acicularis	0.1	-0.1	0.4	-1.5	1.4
Rubus hispidus	-	-	-	0.2	-0.2
Rubus idaeus var. strigosus	0.1	0.3	-0.1	-0.2	0.3
Salix spp.	0.2	0.1	-0.1	-0.1	-0.2
Smilacina trifolia	0.2	0.1	-0.1	-0.1	-0.1
Sorbus decora	0.2	-0.2	-0.2	0.4	0.1
Sphagnum spp.	0.1	0.0	0.0	0.0	-0.2
Sphagnum capillifolium	1.5	2.2	-1.5	-1.5	1.3
Sphagnum magellanicum	1.5	0.6	-0.6	-0.6	0.4
Thelypteris phegopteris	-0.3	-	1.1	-	0.4
Thuja occidentalis	0.3	-0.2	0.2	-0.2	-0.1
Trillium cernuum	0.1	-	-	-	-0.2
Vaccinium angustifolium	2.4	0.8	-0.8	-1.0	1.3
Vaccinium myrtilloides	0.3	-	-	-0.4	0.3
Vaccinium oxycoccos	0.1	-	-	-	-0.2
Viburnum edule	0.2	-0.5	-0.2	0.4	0.6
Viola spp.	-	-	-0.1	-	-0.1
				Overall	effect
Treatment effects	0.0	0.0	0.0	0.0	0.2

b) Residuals and effects for herb percentage frequency (cont.).

Residuals CC	DC	HP	SC	Species effects
-3.0	1.8	3.7	-1.8	0.5
-0.2	1.6	-0.6	0.3	-4.1
-2.8	-1.2	10.1	1.2	20.8
0.3	-0.3	5.6	-10.8	14.1
0.6	2.3	-1.5	-0.6	-3.3
1.4	-0.2	-0.7	0.2	-4.0
-0.1	-	0.0	1.2	-2.5
-0.3	-0.2	1.5	0.2	-4.0
0.7	-0.7	19.0	-1.2	7.4
0.6	0.7	-1.5	-0.6	-3.3
6.2	4.4	-4.4	-10.2	6.4
-2.0	2.0	7.8	-2.7	3.0
-1.9	-0.5	0.5	1.1	-0.7
-1.1	3.6	0.7	-0.7	-3.2
4.0	0.7	-1.5	-0.7	-3.2
3.2	0.0	-2.2	0.0	-2.5
-1.8	-	0.0	1.2	-2.5
-2.0	-3.6	2.0	5.6	4.4
1.4	-0.2	-0.7	0.2	-4.0
2.0	-2.1	6.5	-4.3	8.7
-1.0	-0.5	11.7	0.5	10.3
-2.4	4.8	0.7	-0.7	3.5
-3.3	0.0	3.0	0.0	-1.0
0.6	-0.7	10.2	-8.6	13.9
-0.9	0.9	-1.3	1.3	-3.4
0.1	-0.1	0.6	-3.0	-0.8
-0.2	1.6	-0.6	0.3	-4.1
-0.3	-0.2	1.5	0.2	-4.0
-0.1	1.3	-3.0	0.2	2.7
3.2	-0.2	-0.7	0.2	-4.0
-0.1	0.1	-0.5	5.0	-4.3
1.5	1.4	-2.3	-1.4	-2.4
-1.0	-0.9	0.8	2.4	-3.4
0.8	-2.7	-0.8	6.2	5.0
-0.3	-0.2	1.5	0.2	-4.0
-1.1	-1.0	3.0	1.0	-3.2
-0.6	0.6	14.6	-5.6	5.0
-1.0	-0.9	0.8	2.0	-3.4
-0.3	-0.2	6.0	0.2	-4.0
-0.8	-0.8	1.5	0.8	-1.7
-1.2	-3.5	5.5	1.2	5.4
0.0	-	10.7	-13.4	11.3
-0.1	0.1	-0.5	1.7	-4.3
-0.9	7.1	-0.3	0.4	0.0
0.7	0.7	-1.5	-0.7	-3.2
0.6	0.7	-1.5	-0.6	-3.3
5.1	-5.1	-6.7	11.2	4.2
-0.1	0.1	2.2	-1.3	-2.6
6.5	4.8	-5.7	-4.8	1.0
3.9	2.3	-3.2	-2.3	-1.5
-2.0	-1.8	5.4	1.8	1.0
2.4	-2.8	10.0	-2.4	-1.5
1.4	-0.2	-0.7	0.2	-4.0
15.1	6.7	-6.7	-6.8	10.8
6.8	-	0.0	-6.3	4.2
3.1	-0.2	-0.7	0.2	-4.0
-2.3	-2.4	2.3	8.1	6.3
0.0	-	-2.2	4.5	-2.5
			Overall	effects
0.1	-0.1	0.5	-0.4	4.3

*CC=clearcut, SC=softwoods only cut, DC=deferred cut, HP=hardwoods poisoned (deferred cut).

Table 4.3.3. Results of significant ($p \leq 0.10$) or nearly significant ($p \leq 0.20$) ANOVAs, testing harvest treatment differences for herb species on the RC-17 project, 1990.

a) all plots included.

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD. LSD†
COVER	*Abies balsamea*	2.6	0.106	CC-SC	1.1	0.8
				HP-SC	0.9	0.8
	Brachythecium spp.	2.4	0.125	DC-HP	-3.0	2.1
				HP-SC	2.2	2.1
	Cornus canadensis	2.7	0.100	CC-SC	2.5	2.3
				DC-HP	2.7	2.5
				DC-SC	3.0	2.3
	Corylus cornuta	2.9	0.085	CC-SC	-0.6	0.4
				DC-SC	-0.5	0.4
	Diervilla lonicera	3.0	0.077	CC-HP	-2.0	1.4
				DC-HP	-2.1	1.4
				HP-SC	1.7	1.4
	Equisetum pratense	1.9	0.181	HP-SC	0.9	0.7
	Hylocomium splendens	2.2	0.150	CC-HP	-3.3	2.7
				DC-HP	-3.4	2.7
	Moss spp.	3.5	0.053	CC-DC	-1.2	1.1
				CC-HP	-1.9	1.1
				HP-SC	1.5	1.1
	*Rosa acicularis**	2.8	0.092	CC-SC	5.3	4.6
				DC-SC	5.2	4.6
				HP-SC	7.2	4.9
	Sorbus decora	3.0	0.074	DC-SC	-0.4	0.3
				HP-SC	-0.5	0.3
	Trientalis borealis	2.4	0.124	CC-DC	-0.8	0.6
				DC-HP	0.8	0.6
	Vaccinium angustifolium	1.8	0.199	CC-HP	3.2	3.1
				CC-SC	3.4	2.9
FREQUENCY	*Diervilla lonicera*	3.5	0.055	CC-HP	-8.1	7.1
				DC-HP	-8.7	7.1
				HP-SC	12.5	7.1
	Gymnocarpium dryopteris	2.1	0.159	CC-DC	-17.6	15.6
				CC-HP	-17.6	16.9
				CC-SC	-18.7	15.6
	Moss spp.	3.2	0.065	CC-DC	-18.5	12.9
				CC-HP	-19.1	13.9
	Petasites palmatus	2.3	0.138	HP-SC	19.7	13.6
	Rosa acicularis	2.7	0.098	HP-SC	25.0	16.1
	Rhytidiadelphus triquestrus	2.1	0.155	CC-HP	-15.6	15.4
				HP-SC	21.1	15.4
	Sorbus decora	3.2	0.067	DC-SC	-15.8	11.2
				HP-SC	-16.9	12.1
	Streptopus roseus	2.7	0.100	CC-HP	-37.4	25.2
				DC-HP	-29.6	25.2
				HP-SC	31.1	25.2
	Trientalis borealis	2.0	0.178	CC-DC	-16.2	12.2

(continued)

Table 4.3.3 (cont.)

b) plots 5A and 6A (mostly wet sites) excluded.

Measure	Species	F-value at df=3,11	Significance (p-value)	Treatment pairs signif. at 90%	Mean diff. between pairs	PLSD. LSD†
COVER	*Diervilla lonicera*	2.2	0.161	CC-HP	-1.8	1.6
				DC-HP	-1.9	1.6
				HP-SC	1.7	1.5
	Gaultheria hispidula	2.4	0.134	CC-DC	1.2	1.0
				CC-SC	1.3	1.0
	Ledum groenlandicum	5.8	0.017	CC-DC	1.8	1.0
				CC-SC	1.8	0.9
				HP-SC	0.9	0.9
	Sorbus decora	7.6	0.008	CC-DC	0.5	0.3
				CC-HP	0.4	0.3
				DC-SC	-0.6	0.3
				HP-SC	-0.5	0.3
	Streptopus roseus	5.4	0.021	CC-DC	-3.2	1.9
				CC-HP	-3.4	1.9
				DC-SC	2.1	1.7
				HP-SC	2.3	1.7
FREQUENCY	*Gaultheria hispidula*	3.3	0.071	CC-SC	11.2	10.9
				DC-HP	-13.8	11.7
				HP-SC	17.4	10.9

*For indicated species, ANOVAs were performed on arcsin values of percentage cover and percentage frequency.
†PLSD= Fisher's protected least significant difference, for mean differences with significant F-values at a=0.10 (i.e. p-value ≤ 0.10); LSD= 'unprotected' least significant difference, for p-values >0.10, but ≤0.20.

Of the 45 significantly different (according to Fisher's PLSD and the LSD) treatment pairs for the species' ANOVAs of herb cover and frequency, 29 contained HP, 24 contained SC, 20 contained CC and 17 contained DC. HP had 13 significantly different treatment pairs with SC, 9 with CC and 7 with DC. Thus, although there seemed to be slightly more significant differences between HP and SC than between other treatment pairs, there was no evidence that certain treatments were consistently dissimilar in herb species' abundances.

For the 'top' 22 herb species, there were several statistically non-significant differences among cover and frequency that showed up in the median polish residuals (Table 4.3.2). For cover, contrasting high and low residuals were evident for *Aster macrophyllus* in HP and SC, *Clintonia borealis* in DC and SC, *Pleurozium schreberi* in DC and CC and *S. roseus* in HP and CC. For frequency, contrasting high and low residuals occurred for *Brachythecium* spp. in HP and DC, *C. canadensis* in DC and SC, and *Acer spicatum* in SC and CC. Several species had high residuals in HP for frequency: *Anemone quinquefolia, A. macrophyllus, Carex* spp., *Mitella nuda, and Viola renifolia. Anemone quinquefolia* and *A. macrophyllus* also had low residuals in DC for frequency.

Several species with mean IV less than 3.0 also showed high or low median polish residuals for non-significant treatment differences (Table 4.3.2). For cover, *D. lonicera* and *Sphagnum capillifolium* (Ehrh.) Hedw. had high residuals in HP and DC, respectively. For frequency, *H. splendens* and *V. angustifolium* had high residuals in HP and CC, respectively. As in the top 22 species, several minor species had high frequency residuals in HP: *E. pratense, Galium triflorum, Mnium* spp. and *Thuja occidentalis.* For SC, *Cladina rangiferina* (L.) Harm., *Galtheria hispidula* and *Ledum groenlandicum* had low frequency residuals (Table 4.3.2b). As it was for the tree and shrub strata, the lack of statistical significance for these differences was due to a high degree of variance among plots within treatments (Appendix 10).

With the data from the mainly mucky peat sites excluded, the significance of

treatment differences for herb species was greatly altered (Table 4.3.3b). The treatment difference for *G. hispidula* frequency became significant and that for cover nearly significant. Treatment differences for *L. groenlandicum* and *S. roseus* cover also became significant. Treatment differences for *S. decora* became more significant, while all other previously significant differences became non-significant, and p-values of those that had been nearly significant decreased.

4.3.3 Tree Seedling Density and Frequency

Treatment means for tree seedling (<50cm high) frequency in the 1-m^2 herb quadrats were very low (≤13%) for all species except *Abies balsamea*, which had a mean frequency of 25% for treatment DC, and of approximately 40% for the other three treatments (Table 4.3.4). Thus, density of seedlings was also generally low, with plot values less than or equal to 4000 seedlings per ha and treatment means less than 2000 seedlings per ha for all species except *A. balsamea*. *A. balsamea* seedling density in plots ranged from 1300 to 21300 seedlings/ha, and treatment means from 4500 seedlings/ha in DC to 13,600 seedling/ha in CC. *Betula papyrifera* had the highest hardwood seedling density and frequency in all four treatments. Relatively high *Thuja occidentalis* seedling frequencies and densities occurred in three plots, and high *Picea mariana* densities occurred in two plots (Table 4.3.4).

4.3.4 Summary of Herb Stratum Results

The dominant species in this stratum, in terms of cover and frequency, were *Pleurozium schreberi, Clintonia borealis, Rubus pubescens, Aster macrophyllus, Cornus canadensis*, and *Maianthemum canadense*. Only 22 species had IVs greater than 3.0, with cover and frequency treatment means generally low for most species. Median polish of herb stratum cover and frequency produced small treatment effects, indicating no joint species responses. ANOVA indicated that several species had significant or nearly significant individual treatment differences, but Fisher's PLSD and

Table 4.3.4. Summary of tree seedling (<50 cm high) density and frequency on the RC17 project, 1990, as measured in the 1-m2 herb stratum quadrats.

Treatment:	CC				DC				HP			SC				Treatment Means			
Plot:	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B	CC	DC	HP	SC
Seedling density (no. per ha)																			
Abies balsamea	9300	18700	5000	21300	2700	5300	4000	5900	10700	21300	6000	7000	19000	8700	1300	13575	4475	12667	9000
Betula papyrifera	-	2000	1400	-	-	700	1300	1800	700	-	700	-	-	3300	-	850	950	467	825
Fraxinus nigra	-	-	-	-	1300	-	-	-	-		-	500		-	-	-	325	-	125
Larix laricina	-	-	-	700	-	-	700	-	-		-	-		-	-	175	175	-	-
Picea glauca	-	-	-	-	-	700	-	-	700	-	-			700	-	-	175	233	175
Picea mariana	-	-	700	-		-	3300	-	700	-	1300			-	-	175	825	667	-
Populus balsamifera	1300	-	1400	-		-	-	-	-	-	-			-	-	675	-	-	-
Populus tremuloides	-	-	-	-				-	-	-	-		-	700	700	-		-	350
Thuja occidentalis	700	-	2100	-				-	1300	4000	-		3000	-	-	700		1767	750
Percentage frequency in 1m2 plots																			
Abies balsamea	33.3	33.3	42.9	53.3	13.3	26.7	13.3	47.1	33.3	53.3	33.3	45.0	45.0	53.3	13.3	40.7	25.1	40.0	39.2
Betula papyrifera	-	13.3	14.3	-	-	6.7	13.3	17.6	6.7	-	6.7	-	-	20.0	-	6.9	9.4	4.4	5.0
Fraxinus nigra	-	-	-	-	13.3	-	-	-	-		-	5.0		-	-	-	3.3	-	1.3
Larix laricina		-	-	6.7	-	-	6.7	-	-		-	-		-	-	1.7	1.7	-	-
Picea glauca	-		-	-	-	6.7	-	-	13.3		-			6.7	-	-	1.7	4.4	1.7
Picea mariana	-		7.1	-		-	13.3	-	-		6.7			-	-	1.8	3.3	2.2	-
Populus balsamifera	6.7	-	7.1	-		-	-	-	-	-	-			-	-	3.5	-	-	-
Populus tremuloides	-	-	-	-		-	-	-	-	-	-		-	6.7	6.7	-		-	3.3
Thuja occidentalis	6.7	-	14.3	-	-	-	-	-	6.7	33.3	-		5.0	-	-	5.2		13.3	1.3
Sample size (no. quadrats):	15	15	14	15	20	20	15	17	15	15	15	20	20	15	15				

the LSD showed that these did not occur consistently among the same treatment pairs. However, when median polish residuals were examined in addition to the PLSD and LSD, it was evident that a large number of species had high values in HP compared to the other treatments. Exclusion of plots dominated by mucky peat sites altered many of the ANOVA results, cancelling the significance of most previously identified treatment differences, and creating a few new significant differences. Tree seedling frequency and density were low for most species. *Abies balsamea* was the only species with generally high seedling density, and *Betula papyrifera* had the highest hardwood seedling density. *A. balsamea* was also the only one of the main tree species to have a nearly significant difference among treatments in the herb stratum: cover of its seedlings was less in SC than in HP and CC.

4.4 SPECIES DIVERSITY AND PLOT RESEMBLANCES

Diversity and resemblance of treatment plots were calculated from the total importance values (all strata included) for each plot (Appendix 11). Neither one of these measures revealed trends corresponding to harvest treatments.

4.4.1 Species Diversity Among Treatments

Richness, diversity and evenness are presented for treatments and individual plots in Table 4.4.1. Species' richness for treatments ranged from 88 species in HP to 107 species in CC. Species richness was lower for plots than for treatments, ranging from 60 to 79 species. ANOVA for species richness showed no significant differences among treatments ($F_{3,11}$=.792, p=.5232).

Based on Simpson's index (λ) and Shannon's index (H'), diversity was highest in CC (lowest λ, highest H'), descending through HP, DC and SC (λ was identical for the latter two). However, variation among treatments was very small. Plot values of λ ranged from 0.048 to 0.080. DC values tended to be a little higher than those for the

Table 4.4.1. Species richness, evenness and diversity measures, calculated with species' importance values for each plot of the RC-17 project, 1990.

TREATMENT	CC	DC	HP	SC
sample size (n)	60	72	45	70
RICHNESS				
Number of species	107	95	88	91
DIVERSITY				
Lambda*	0.048	0.059	0.053	0.059
H'*	3.69	3.51	3.57	3.48
N1*	39.95	33.48	35.59	32.42
N2*	20.93	16.90	19.04	16.97
EVENNESS				
E*	0.512	0.490	0.522	0.508

PLOT	1B	5A	5B	7A	4A	4B	6A	6B
TREATMENT	CC	CC	CC	CC	DC	DC	DC	DC
sample size (n)	15	15	15	15	20	20	15	17
RICHNESS								
Number of species	61	79	77	62	60	72	62	72
DIVERSITY								
Lambda*	0.065	0.048	0.066	0.075	0.074	0.059	0.078	0.080
H'*	3.34	3.61	3.44	3.19	3.22	3.42	3.20	3.29
N1*	28	37	31	24	25	31	25	27
N2*	15	21	15	13	13	17	13	13
EVENNESS								
E*	0.525	0.551	0.471	0.534	0.522	0.538	0.504	0.450

PLOT	10B	2B	8A	3A	3B	7B	9B
TREATMENT	HP	HP	HP	SC	SC	SC	SC
sample size (n)	15	15	15	20	20	15	15
RICHNESS							
Number of species	73	66	72	64	66	66	60
DIVERSITY							
Lambda	0.054	0.069	0.062	0.067	0.070	0.064	0.059
H'	3.51	3.33	3.44	3.32	3.34	3.33	3.29
N1	33	28	31	28	28	28	27
N2	18	14	16	15	14	16	17
EVENNESS							
E	0.537	0.500	0.508	0.524	0.489	0.543	0.620

*Lambda=Simpson's index; H'=Shannon's index; N1 and N2=Hill's diversity numbers; E=Hill's modified ratio.

other treatments. All treatments and plots showed a fairly high diversity (low λ), with the probability of any two individuals drawn at random from any of the treatment populations belonging to the same species being less than 10% ($\lambda < 0.10$). H' was fairly uniform throughout the plots, with a total range of 3.19 to 3.61; this was also the greatest range within a treatment (CC).

Hill's diversity numbers indicated that for all treatments, the number of abundant species (N1) was a little over one-third of the total number, and for plots it was a little less than one-half. For treatments and plots in general, the number of very abundant species (N2) was about one-quarter to one-fifth of the total number. Since they are derived from the diversity indices, N1 and N2 followed the same trends across treatments; N1 ranged from 32 in SC to 40 in CC, and N2 ranged from 17 in SC and DC to 21 in CC. Plot values of N1 and N2 were more variable, with N1 ranging from 24 to 37 and N2 ranging from 13 to 21. As with their derivatives, H' and λ, Hill's numbers showed little evidence of treatment differences. Treatment SC had the most consistent values of N1 across plots (27 to 28). For the other treatments, N1 varied as greatly within treatments as it did among treatments, and the variations were closely related to the small variations in total species richness. Similarly, variation of N2 was almost as great among plots within treatments as it was among all plots. Groups of plots that appeared most similar in diversity, as judged by all four of these diversity measures were not exclusively within treatments:

1) SC3A, SC3B, SC7B, HP2B and CC1B

2) HP8A and CC5B

3) CC7A, DC4A, DC6B and DC6A.

Evenness (Hill's modified ratio) was also very similar among treatments. It was highest in HP, and descended through CC, SC and DC. For plots evenness ranged from 0.45 to 0.62, with the largest within treatment range being from 0.49 to 0.62 (SC) and the smallest from 0.50 to 0.54 (HP). All of the values were close to 0.50, indicating

that there were about twice as many abundant species as there were very abundant species in each plot. There were no evident treatment differences, and treatments CC and DC even had the same range in evenness (0.08). Thus, richness, diversity and evenness were not affected by harvest treatment.

4.4.2 Plot Resemblance

The resemblance functions were calculated to determine whether plots belonging to the same treatment were more similar to each other in terms of species composition and species' abundance than they were to plots of other treatments. In addition, these measures should reveal any similarities between specific pairs of treatments.

In terms of Percentage Dissimilarity (PD), all plot pairs fell between 0.20 and 0.59 (Table 4.4.2a). Since most plot pairs had PD<0.50, all plots were fairly similar in species composition and species' abundances. For plot pairs within treatments, only seven fell at or below the 20th percentile (0.28) of the actual values of PD, indicating that they had a strong resemblance: DC4A, DC4B and DC6B; HP2B and HP8A; and SC3A, SC3B and SC7B. None of the CC plot pairs had PD≤0.28, indicating that they were not greatly similar in species composition and abundance. Several 'between-treatment' plot pairs had high resemblance (PD≤0.28), most of these involved the same plots that had high 'within-treatment' resemblances with other plots. Each of the CC plots also had a strong resemblance to at least one of those plots. Only seven plot pairs had PDs greater than or equal to 0.50 (the 80th percentile of the actual range of PDs), indicating strong dissimilarity; only one of these was a within treatment (DC) pair.

The range of chord distances (CRD) for the plot pairs was 0.26 to 1.09 (20th percentile=0.43, 80th=0.92) (Table 4.4.2b). Since the possible range for CRD is 0 to 1.14, CRD indicated less resemblance among plots than did PD, i.e. there were 55 pairs with CRD≥0.57 (middle of the possible range), while with PD, there were only 7 pairs with PD≥0.50. This means that the plots had lower resemblance in terms of

Table 4.4.2. Measures of resemblance between plot pairs of the RC17 project, calculated using species' importance values, as measured in 1990.

a) Bray and Curtis percent dissimilarity (PD) between plots.

	CC 1B	CC 5A	CC 5B	CC 7A	DC 4A	DC 4B	DC 6A	DC 6B	HP 10B	HP 2B	HP 8A	SC 3A	SC 3B	SC 7B
CC 5A	0.35													
CC 5B	0.43	0.40												
CC 7A	0.49	0.35	0.49											
DC 4A	0.33	0.29	0.42	0.37										
DC 4B	0.27	0.32	0.29	0.45	***0.22***									
DC 6A	**0.55**	0.34	0.46	***0.21***	0.40	0.47								
DC 6B	***0.28***	0.41	0.37	0.49	***0.27***	***0.26***	**0.52**							
HP 10B	0.38	0.39	0.34	**0.52**	0.34	0.31	0.49	0.31						
HP 2B	0.31	0.39	***0.28***	0.49	0.30	***0.24***	**0.53**	***0.21***	0.36					
HP 8A	***0.27***	***0.28***	0.38	0.38	***0.20***	***0.25***	0.40	***0.27***	0.33	***0.28***				
SC 3A	0.29	0.30	0.44	0.35	***0.20***	***0.26***	0.41	0.29	0.41	0.34	***0.23***			
SC 3B	0.29	0.33	0.37	0.44	***0.23***	***0.21***	0.47	***0.25***	0.35	***0.25***	***0.25***	***0.23***		
SC 7B	***0.28***	0.36	0.38	0.38	***0.24***	***0.24***	0.45	***0.21***	0.31	***0.28***	***0.24***	***0.23***	***0.24***	
SC 9B	0.30	0.45	**0.50**	**0.58**	0.36	0.34	**0.59**	0.32	0.38	0.38	0.35	0.37	0.37	0.31

Possible range = 0.00 to 1.00
Actual range = 0.20 to 0.59
Midrange = 0.40

20th percentile = ***0.28***
80th percentile = **0.50**

b) Chord distances (CRD) between plots.

	CC 1B	CC 5A	CC 5B	CC 7A	DC 4A	DC 4B	DC 6A	DC 6B	HP 10B	HP 2B	HP 8A	SC 3A	SC 3B	SC 7B
CC 5A	0.49													
CC 5B	0.87	0.87												
CC 7A	0.82	0.53	**0.96**											
DC 4A	0.47	***0.37***	0.85	0.63										
DC 4B	0.44	0.52	0.59	0.78	***0.37***									
DC 6A	**0.98**	0.68	1.01	***0.31***	0.78	0.91								
DC 6B	0.44	0.55	0.88	0.78	***0.36***	0.44	**0.94**							
HP 10B	0.80	0.78	**0.93**	**0.92**	0.62	0.64	**0.96**	0.61						
HP 2B	0.55	0.62	0.52	0.81	0.53	***0.32***	**0.95**	0.45	0.75					
HP 8A	0.46	***0.36***	0.84	0.60	***0.26***	***0.42***	0.75	***0.39***	0.68	0.51				
SC 3A	***0.42***	***0.39***	0.88	0.62	***0.26***	***0.42***	0.78	***0.40***	0.74	0.54	***0.29***			
SC 3B	***0.38***	***0.43***	0.74	0.71	***0.29***	***0.28***	0.88	***0.32***	0.70	***0.36***	***0.31***	***0.30***		
SC 7B	0.48	0.55	0.87	0.77	***0.32***	***0.41***	0.90	***0.32***	0.54	0.54	***0.36***	***0.35***	***0.36***	
SC 9B	0.55	0.74	**1.02**	**1.01**	0.67	0.63	**1.09**	0.62	0.75	0.73	0.65	0.62	0.64	0.52

Possible range = 0.00 to 1.14
Actual range = 0.26 to 1.09
Midrange = 0.68

20th percentile = ***0.43***
80th percentile = **0.92**

proportional abundances of species than in actual abundance. Most of the resemblance patterns indicated by PD were also evident with CRD, with some differences, especially in the pairing of CC and DC plots with plots of other treatments.

The main pattern evident from the two distance measures was that plots SC3A, SC3B, SC7B, DC4A, DC4B, DC6B and HP8A all closely resembled each other. DC6A tended to be (relatively) highly dissimilar to several plots: CC1B, CC5B, DC6B, HP2B, HP10B, and SC9B. Although three SC plots (3A, 3B and 7B) had similar diversity and high resemblance to each other, they also shared these similarities with plots from different treatments. Therefore, species diversity and plot resemblance measures, separatley or together, revealed no trends corresponding to harvest treatment.

4.5 PRE-TREATMENT VS. POST-TREATMENT COMMUNITIES

4.5.1 Canopy and Regeneration in 1953 and 1990

The pre-treatment inventory of tree seedling stocking and tree density by treatment plots (Berry 1953) could not be located. Therefore, the corresponding data organized by soil site types in Hughes (1967) was substituted (Tables 4.5.1, 4.5.2). Current (1990) tree density and frequency from the point quarter data were therefore recalculated, with points sorted by soil site types (Tables 4.5.1, 4.5.2). Some information about the changes due to harvesting can be inferred from comparing the pre- and post-harvest data in each soil site type, and comparing the pre-harvest data for a soil site type to the post-harvest data for the treatment(s) in which that soil site type was most prominent.

4.5.1.1 Tree Density in 1953 and 1990

Abies balsamea, Betula papyrifera, Picea glauca and *Picea mariana* were the most dominant tree species in 1953 in terms of density on six site types: Dry-very shallow (D-vs), fresh-medium shallow (F-ms), fresh-deep (F-d), moist-very shallow (M-

Table 4.5.1. Comparison of tree density (trees/ha) on the RC-17 project before harvest treatments were applied (1953) to tree density 27 to 37 years after treatment (1990).

(Density reported by soil depth and moisture classifications, numbers to the right of densities indicate relative importance rank).

Species	Dry-extremely shallow				Dry-very shallow				Fresh-medium shallow				Fresh-deep			
	1953*		1990**		1953		1990		1953		1990		1953		1990	
Abies balsamea	279.7	2	1255.0	1	208.3	1	1093.1	1	206.1	1	896.5	1	297.3	1	682.4	1
Larix laricina	2.7		0.0		0.0		0.0		0.0		0.0		0.0		0.0	
Picea glauca	51.9	4	582.7	2	44.2	4	128.6	4	77.3	3	241.4	4	88.7	3	213.9	4
Picea mariana	206.1	3	493.0	3	142.3	3	321.5	3	67.5	4	34.5		39.3	4	30.6	
Pinus banksiana	0.0		0.0		2.5		0.0		0.7		0.0		0.0		0.0	
Thuja occidentalis	527.3	1	358.6		9.4		0.0		5.2		275.8	3	3.7		20.4	
Total Softwoods	1067.7		2689.3		406.7		1543.2		356.8		1448.2		429.0		947.2	
Betula papyrifera	51.9	4	448.2	4	157.7	2	610.9	2	129.0	2	379.3	2	104.8	2	407.4	2
Populus balsamifera	2.7		44.8		0.0		48.2		6.7		0.0		7.4		40.7	
Populus tremuloides	0.0		0.0		6.2		112.5		8.2		137.9		3.7		234.3	3
Total Hardwoods	54.6		493.0		163.8		771.6		143.8		517.2		115.9		682.4	
Ratio Softwoods:Hardwood	19.6		5.5		2.5		2.0		2.5		2.8		3.7		1.4	

Species	Moist-extremely shallow				Moist-very shallow				Moist-medium shallow				Moist-deep				Mucky peat†
	1953		1990		1953		1990		1953		1990		1953		1990		1990
Abies balsamea	345.9	1	661.4	1	93.4	3	606.2	1	225.4	1	831.4	1	308.4	1	754.0	1	235.57 2
Larix laricina	0.0		0.0		0.0		0.0		0.0		0.0		0.0		0.0		12.40 4
Picea glauca	54.4		147.0	3	20.5	4	73.9	4	73.4	4	105.0	4	119.8	3	414.7	2	12.40 4
Picea mariana	113.7	3	73.5	4	444.3	1	443.6	2	220.7	2	105.0	4	58.8	4	113.1		347.15 1
Pinus banksiana	0.0		0.0		3.0		0.0		0.5		0.0		0.0		0.0		0.00
Thuja occidentalis	281.7	2	440.9	2	0.0		0.0		36.1		166.3	3	5.9		75.4		0.00
Total Softwoods	795.7		1322.7		561.2		1123.7		556.0		1207.7		493.0		1357.2		607.52
Betula papyrifera	64.3	4	661.4	1	262.7	2	266.2	3	183.8	3	280.1	2	136.6	2	358.2	3	148.78 3
Populus balsamifera	0.0		0.0		1.5		14.8		4.9		17.5		17.3		132.0		12.40 4
Populus tremuloides	0.0		73.5	4	0.0		14.8		3.2		61.3		13.6		188.5	4	0.00
Total Hardwoods	64.3		734.8		264.2		295.7		192.0		358.8		167.5		678.6		161.18
Ratio Softwoods:Hardwood	12.4		1.8		2.1		3.8		2.9		3.4		2.9		2.0		3.8

*Source of 1953 data is Hughes' (1967) Appendix III-Stand and Stock Tables. This data originates from eight to sixteen 0.1 acre plots randomly distributed in each treatment block. In order to compare this data to 1990 data, stems < 2 in. (5.08 cm) dbh were excluded.

**The 1990 data was collected at fifteen to twenty points per treatment block. Points were sorted by soil and site type and point-centred quarter calculations were then applied. The number of points per site type is therefore variable: D-es 15, D-vs 38, F-ms 16, F-d 44, M-es 8, M-vs 26, M-ms 49, M-d 30, Mp 21.

†No data were collected for mucky peat sites in 1953.

Table 4.5.2. Advance growth density (stems/ha) and percentage stocking by milliacres on the RC-17 project before harvest treatments were applied (1953).

Soil classification:	Dry-extremely shallow		Dry-very shallow		Fresh-medium shallow		Fresh-deep	
Species	density*	stocking**	density	stocking	density	stocking	density	stocking
Abies balsamea	11786.5	94	19916.0	96	10501.6	93	15987.2	93
Picea glauca	0.0	0	741.3	15	518.9	11	1062.5	28
Picea mariana	4398.3	34	1532.0	31	840.1	19	815.4	11
Thuja occidentalis†	5189.0	34	98.8	0	222.4	8	296.5	11
Total Softwoods	21373.9	NA	22288.1	NA	12083.0	NA	18161.6	NA
Betula papyrifera	41635.8	NA	18902.9	NA	4843.1	NA	18260.4	NA
Populus balsamifera	0.0	NA	0.0	NA	24.7	NA	0.0	NA
Populus tremuloides	0.0	NA	24.7	NA	98.8	NA	0.0	NA
Total Hardwoods	41635.8	34	18927.6	82	4966.6	87	18260.4	85
Ratio Softwood:Hardwoo	0.5		1.2		2.4		1.0	

Soil classification:	Moist-extremely shallo		Moist-very shallow		Moist-medium shallow		Moist-deep	
Species	density	stocking	density	stocking	density	stocking	density	stocking
Abies balsamea	16086.0	96	14306.9	95	14652.8	96	15394.1	96
Picea glauca	0.0	0	197.7	8	420.1	11	1655.5	31
Picea mariana	2174.5	31	2668.6	40	2050.9	28	1803.8	28
Thuja occidentalis†	2026.2	31	173.0	2	1705.0	22	2495.7	25
Total Softwoods	20286.6	NA	17346.2	NA	18828.8	NA	21349.1	NA
Betula papyrifera	5386.7	NA	20212.5	NA	24610.8	NA	9612.1	NA
Populus balsamifera	0.0	NA	0.0	NA	74.1	NA	24.7	NA
Populus tremuloides	321.2	NA	0.0	NA	0.0	NA	24.7	NA
Total Hardwoods	5707.9	61	20212.5	73	24685.0	79	9661.5	72
Ratio Softwood:Hardwoo	3.6		0.9		0.8		2.2	

*Source of 1953 advance growth density is Table 2, p. 9 in Hughes (1967). This data originates from 0.25 milliacre quadrats spaced 1-chain apart along nine survey lines separated by 1 chain in each treatment block. All advance growth, including saplings to 4.5in dbh, was included, but the majority of stems were < 0.5in (1.27cm) dbh.

**Source of 1953 advance growth stocking is Table 1, p. 8 in Hughes (1967). This data originates from the same survey that provided the 1953 advance growth density.

†For stocking of advance growth, this row also includes L. laricina and P. banksiana classified with T. occidentalis as "other softwoods" in Hughes' Table 1 (1967).

vs), moist-medium shallow (M-ms) and moist-deep (M-d) (Table 4.5.1). *A. balsamea* had the highest density, ranging from 200 to 300 trees/ha, in all of these types except for M-vs, and *B. papyrifera* was generally second most important. However, *P. mariana* was important on M-vs and M-ms soils. In these six site types, all of the other species were of minor importance. In the extremely shallow (-es) site types, *Thuja occidentalis* had high density, although *A. balsamea* had the highest on moist-extremely shallow (M-es) soils.

The relative order of importance of these four main species in 1990 was the same as in 1953 on only the D-vs soil type. However, the principal two or three dominant (density) species on each site type in 1953 generally maintained this dominance to 1990, with some internal shifts of importance. In 1990, *A. balsamea* had the highest density on all soil types; *B. papyrifera* shared this position on M-es. From 1953 to 1990, *T. occidentalis* dropped from highest to fifth highest density, and *P. glauca* rose from fourth to second on dry-extremely shallow (D-es) soils. On F-ms soils, *T. occidentalis* rose to third highest density, and on F-d soils, *Populus tremuloides* rose from a very low density in 1953 to third highest. On M-es soils, *T. occidentalis* maintained second highest density, but *B. papyrifera* increased to share the highest density with *A. balsamea*, while *P. glauca* and *P. mariana* exchanged relative importance. On M-ms, *T. occidentalis* increased to third highest density and *P. mariana* dropped in importance. *P. glauca* and *P. tremuloides* increased in importance on M-d soils.

Densities of *A. balsamea, B. papyrifera, P. glauca* and *P. tremuloides* increased on all soil site types, except for *P. tremuloides* on D-es. *A. balsamea* density increased to about 2 to 6 times its 1953 density by 1990, depending on soil type. *P. glauca* density increased by 3 to 11 times its 1953 values. The increase in *B. papyrifera* ranged from only 1% to 10 times its 1953 density. On sites where it occurred in 1953, *P. tremuloides* had increased its density by 14 to 60 times by 1990, and it appeared on two types from which it was previously absent. *P. tremuloides* had low densities on all sites

in 1953.

The species which did not increase consistently across soil types were *P. mariana, T. occidentalis, Populus balsamifera, Larix laricina* and *Pinus banksiana*. The latter two species occurred on only a few site types, with low densities where they did occur. *P. mariana* decreased on F-ms, F-d, M-es and M-ms soils. Its 1990 density on M-vs soils was almost identical to that in 1953, while on D-es, D-vs and M-d soils its 1990 density was about twice that in 1953. *T. occidentalis*, which was absent or had low density on all site types except -es soils in 1953, had increased on most site types by 1990.

Softwood density was higher than hardwood density on all site types in 1953 and was still higher in 1990. The ratio of total softwoods to hardwoods (S:H) decreased from 1953 to 1990 on all soil types except F-ms, M-vs and M-ms. Of these three soil types, only M-vs had a substantial increase (1.7) in the ratio. The decreases in S:H were small on D-vs (0.5) and on M-d (0.9) soils, larger on F-d soils (2.3), and very large for D-es (14.1) and for M-es (10.6) soils. The forests on the latter two soil types were essentially converted from softwood to mixedwood forests by harvesting. The stands with the highest S:H in 1990 were on D-es (5.5), M-vs (3.8) mucky peat (3.8) and M-ms (3.4) soils.

Increases in tree density by treatment were estimated by comparing 1990 treatment densities (Table 4.1.1) to 1953 densities on the soil types most prominent in the 1990 samples of those treatments (Table 3.2.1) as follows: 1990 CC vs. 1953 M-ms, F-d and M-vs; 1990 DC vs. 1953 D-vs, M-ms and M-d; 1990 SC vs. 1953 F-d, D-vs and D-es; and 1990 HP vs 1953 F-d, M-d and M-ms. These comparisons revealed that *A. balsamea, B. papyrifera* and both poplar species increased in all treatments. For *A. balsamea*, this increase was by about 2 to 3 times its 1953 density in CC and HP, and by 3 to 5 times its 1953 density in SC and DC. *B. papyrifera* increased by 2 to 3 times its 1953 density on CC, DC and HP, and about 4 times on SC.

Poplar densities were very low on all sites in 1953. *P. tremuloides* increased most on CC and SC to about 150 trees/ha from less than 10 trees/ha. Its increase in HP was negligible, as was that of *P. balsamifera*. Moderate increases of *P. balsamifera* occurred on the other three treatments. *P. glauca* appears to have increased by 2 to 3 times its 1953 density in all treatments except CC where it has decreased slightly. *T. occidentalis* increased in all treatments except when its density in SC is compared to that in D-es; in this comparison it has decreased to about 6% of the 1953 value. *P. mariana* appears to have maintained its density or increased slightly in all treatments, except for when CC, SC and HP are compared to their less important component soil types, i.e. M-vs, D-es and M-ms respectively. In these cases, *P. mariana* density is about 50% of its 1953 value.

4.5.1.2 Advance Growth Density in 1953 vs. Tree Density in 1990

Advance growth (all stems ≤11.4cm dbh, mostly stems <1.3cm) on each soil type prior to the harvest treatments (Table 4.5.2) was compared to tree density 27 to 37 years after the treatments (Table 4.5.1). Before harvesting, the S:H of advance growth density was less than 1.0 on D-es, M-vs and M-ms soil types and 1.0 on F-d soils. On the other soil types S:H ranged from 1.2 in D-vs to 3.6 in M-es. As noted previously, softwood tree density in 1990 was greater than hardwood density on all soil types, the S:H ranging from 1.4 on F-d soils to 5.5 on D-es soils. Softwood advance growth density in 1953 was greatest on D-vs soils and lowest on F-ms. Hardwood advance growth density in 1953 was greatest on D-es soils and lowest on M-es soils. After treatment (1990), total softwood tree density was greatest on D-es soils and lowest on M-vs soils, disregarding mucky peat (Mp) soils. Total hardwood tree density in 1990 was greatest on D-vs soils and lowest on M-vs soils, excluding Mp soils. Thus, 27 to 37 years after harvest, neither softwood nor hardwood tree density appeared to be related to advance growth density before harvest.

Abies balsamea had the highest softwood advance growth density (10000 and 20000 stems/ha) on all soil types in 1953. Of all softwood species, it had decreased the most, its 1990 tree density being about 5% of its 1953 advance growth density on most soil types (Tables 4.5.1, 4.5.2). *Picea glauca* decreased, its 1990 tree density ranging from 17% (on D-vs soils) to 50% (on F-ms soils) of its 1953 advance growth density (200 to 1700 trees/ha), except on soil types from which it was absent in 1953, i.e. D-es and M-es (Tables 4.5.1, 4.5.2). *Picea mariana*, which had a fairly high advance growth density in 1953 (800 to 2600 stems/ha), also decreased, its tree density in 199 ranging from 3% (M-es) to 20% (D-vs) of its 1953 advance growth density. Similarly, *Thuja occidentalis*' 1990 tree density decreased 3% (M-d) to 50% (F-d) of its 1953 advance growth density. In contrast to these trends, *T. occidentalis* had a higher tree density in 1990 on F-ms (280 trees/ha; Table 4.5.2) soils than its advance growth density in 1953 (220 trees/ha; Table 4.5.1). *Betula papyrifera* decreased the most of all species, its 1990 tree density ranging from 1% to 3% of its 1953 advance growth density, on all sites except F-ms, M-es and M-d, for which 1953 densities were low (<10,000 stems/ha).

4.5.1.3 Advance Regeneration in 1953 and 1990

Betula papyrifera dominated the hardwood reproduction in both the shrub and herb strata in 1990 (Tables 4.2.1, 4.2.2, 4.3.1), as it was in 1953 (Table 4.5.2). Using the same treatment/soil type comparisons as in section 4.5.1.1, *B. papyrifera* density decreased greatly (to less than 10% of 1953 values) in both the shrub and herb strata, in all treatments. However, due to the variability among site types in 1953, treatment patterns could not be easily discerned; decreases in *B. papyrifera* density to 1990 appeared to be greatest in HP for the herb stratum, and in both HP and SC for the shrub stratum. *Betula papyrifera* frequency in both strata in 1990 was also lower than 1953 advance growth stocking: approximately 50% of 1953 stocking in the shrub

stratum, and less than 15% of 1953 advance growth stocking in the herb stratum. *Betula papyrifera* density was higher in the herb stratum than in the shrub stratum in 1990, and the reverse was true for its frequency. However, this may be an artifact of the different sampling methods for these strata. *Populus balsamifera* and *Populus tremuloides* were generally minor elements in both strata, at both dates, but 1990 *P. balsamifera* density in the herb stratum of CC was fairly high (675 stems/ha), as was that of *P. tremuloides* in SC (350 stems/ha), compared to their 1953 densities (<100 stems/ha) in corresponding site types.

Frequencies and densities of conifer species in 1990 were generally lower than in 1953 in all treatments (Tables 4.2.1, 4.2.2, 4.3.1, 4.5.2). As with *B. papyrifera*, 1990 frequency of *Abies balsamea* in the shrub stratum was higher than in the herb stratum, while the reverse was true for its density. Its advance growth density in 1990 was lower than in 1953 in all treatments, but especially in CC and SC for the shrub stratum (~5% of 1953 density) and in DC and SC for the herb stratum (as low as 20-45% of 1953 density). Its density decreased only slightly (by ≤20%) in CC and HP for the herb stratum. Shrub frequencies of *Picea glauca* and *Picea mariana* in 1990 were about the same as 1953 advance growth stocking, while herb frequencies were considerably lower. *Picea mariana* density decreased to 1990 in both strata, with this decrease being greatest in SC (to 0 stems/ha for the herb stratum). *Picea glauca* also decreased in both strata except for an increase when comparing its 1990 shrub and herb densities in SC to 1953 advance growth density in D-es (0 stem/ha). The largest decrease is likely its density in the herb stratum in CC (to 0 stems/ha). The trends of *Thuja occidentalis* advance growth from 1953 to 1990 are difficult to interpret, due to the high variability of 1953 density and stocking among site types.

4.5.2 Understorey in 1953 and 1990

Hughes (1967) listed 52 woody and non-woody species encountered during pre-

treatment sampling of the understorey, including seven mosses and six grass and sedge species. Sutton (1964) encountered 106 species, including 29 mosses and several grass and sedge species, during the 1957 sampling of understorey vegetation in response to overstorey and seedbed treatments after the CC and SC harvest, but prior to the HP and DC harvest. On unscarified strips of the DC plots (i.e. untreated area), Sutton (1964) encountered only 29 species, including *Carex* spp. and mosses as general categories. In 1990, 95 species were encountered in the herb stratum (less than 0.5 m high), with 67 to 75 species in each harvest treatment (excluding lichens and counting mosses, sedges and grasses as only one species each) (Table 4.5.3). These numbers were comparable to the general list compiled by Sutton (1964) but higher than the counts of the 1957 untreated transects (Sutton 1964) and the pre-treatment list (Hughes 1967). The 1990 total was higher than all of the previous tallies, considering that it included mosses, grasses and sedges as only single species.

Most of the species named as dominant, abundant and frequent in one or more of the plant communities identified by Hughes (1967), and most of the species with high frequencies in the 1957 untreated DC transects (Sutton 1964), were also included in the list of species with mean IV≥3.0 in the 1990 herb layer survey (Table 4.5.3). However, several species that were abundant or frequent in some community types prior to harvesting (Hughes 1967) had mean IVs less than 3.0 in the 1990 herb stratum. These include *Alnus crispa, Coptis trifolia* (L.) Salisb., *Corylus cornuta, Diervilla lonicera, Equisetum arvense, Equisetum sylvaticum, Galium triflorum, Gaultheria hispidula, Lycopodium clavatum., Lycopodium obscurum, Mertensia paniculata, Petasites palmatus, Sorbus decora, Vaccinium angustifolium* and *Vaccinium myrtilloides*. Also in contrast to the 1990 results, *C. cornuta*, *D. lonicera*, and *L. obscurum* had high frequencies in the herb stratum in the untreated DC strips in 1957. Five of these species (*A. crispa, C. cornuta, D. lonicera, S. decora* and *V. angustifolium*) were, however, common in the shrub stratum in 1990 (Table 4.2.1), four of them having

Table 4.5.3. Comparison of tree seedling percentage stocking (by milliacres) on the RC-17 project before harvest treatments were applied (1953) to tree percentage frequency (estimated by point-centred quarter method) approximately 35 years after treatment (1990).

Soil classification:	Dry-extremely shallow		Dry-very shallow		Fresh-medium shallow		Fresh-deep	
	1953*	1990**	1953	1990	1953	1990	1953	1990
Species	advance growth	tree	advance growth	tree	advance growth	tree	advance growth	tree
Abies balsamea	94.00	86.67	96.00	86.64	93.00	75.00	93.00	88.64
Picea glauca	0.00	13.33	15.00	13.16	11.00	31.25	28.00	31.82
Picea mariana	34.00	33.33	31.00	34.21	19.00	6.25	11.00	4.55
OTHER SOFTWOODS†:								
Larix laricina	NA	0.00	NA	0.00	NA	0.00	NA	0.00
Pinus banksiana	NA	0.00	NA	0.00	NA	0.00	NA	0.00
Thuja occidentalis	NA	33.33	NA	0.00	NA	25.00	NA	4.55
TOTAL OTHER	34.00	33.33	0.00	0.00	8.00	25.00	11.00	14.89
Betula papyrifera	NA	53.33	NA	73.68	NA	31.25	NA	61.36
Populus balsamifera	NA	6.67	NA	5.26	NA	0.00	NA	4.55
Populus tremuloides	NA	0.00	NA	13.16	NA	12.50	NA	25.00
Total Hardwoods†	34.00	NA	82.00	NA	87.00		85.00	NA

Soil classification:	Moist-extremely shallow		Moist-very shallow		Moist-medium shallow		Moist-deep		Mucky peat††
	1953	1990	1953	1990	1953	1990	1953	1990	1990
Species	advance growth	tree	advance growth	tree	advance growth	tree	advance growth	tree	tree
Abies balsamea	96.00	62.50	95.00	80.77	96.00	81.63	96.00	76.67	57.14
Picea glauca	0.00	25.00	8.00	11.54	11.00	18.37	31.00	46.67	4.76
Picea mariana	31.00	12.50	40.00	57.69	28.00	18.37	28.00	16.67	52.38
OTHER SOFTWOODS*:									
Larix laricina	NA	0.00	NA	0.00	NA	0.00	NA	0.00	4.76
Pinus banksiana	NA	0.00	NA	0.00	NA	0.00	NA	0.00	0.00
Thuja occidentalis	NA	37.50	NA	0.00	NA	18.37	NA	6.67	0.00
TOTAL OTHER	31.00	37.50	2.00	0.00	22.00	18.37	25.00	6.67	4.76
Betula papyrifera	NA	62.50	NA	50.00	NA	38.73	NA	46.67	42.85
Populus balsamifera	NA	0.00	NA	3.85	NA	4.08	NA	16.67	4.76
Populus tremuloides	NA	12.50	NA	3.85	NA	8.16	NA	13.33	0.00
Total Hardwoods	61.00	NA	73.00	NA	79.00	NA	72.00	NA	NA

*Source of 1953 data is Table 1, p. 8 in Hughes (1967). This data originates from 0.25 milliacre quadrats spaced 1-chain apart along nine survey lines seperated by 1 chain in each treatment block. All advance growth, including saplings to 4.5 in dbh, was included, but the majority were < 4.5 in (11.43cm) dbh.

**The 1990 data was collected at fifteen to twenty points per treatment block. Points were sorted by soil and site type, point-centred quarter calculations were then applied. The number of points per site type is therefore variable: D-es15, D-vs 38, F-ms16, F-d 44, M-es 8, M-vs 26, M-ms 49, M-d 30, Mp 21.

†Only 'total other softwoods' and 'total hardwoods' seedling stocking available from 1953; only individual tree species' frequencies available from 1990.

††No data were collected for mucky peat sites in 1953.

mean IV>3.0.

All dominant herb layer species observed in 1990 were frequent, abundant or dominant in at least one of the understorey communities listed by Hughes (1967) and/or were frequent in the untreated DC samples in 1957 (Sutton 1964), except for the general categories of Grass species and *Carex* spp. *Gymnocarpium dryopteris* and *Mitella nuda* were absent from the untreated DC strips in 1957, and *Abies balsamea* and *Anemone quinquefolia* were not listed as frequent, abundant or dominant in the 1953 survey. However, all of the species with IVs greater than 3.0 in 1990 were present in at least one of the four treatments on the strips sampled in 1957.

The frequency of 'Moss spp.' appeared to be much lower in 1990 than it was in 1957. This was deceptive, since in 1957 the category included all moss species, while in 1990 it included only mosses that could not be identified. Frequencies of the dominant herb stratum species in 1990 were generally ≤50% of their 1957 frequencies on the DC strips. The exceptions were *Linnaea borealis* and *Rubus pubescens* which had increased to 1990, and *Lycopodium annotinum* and *Maianthemum canadense* which were about as frequent in 1990 as in 1957 (Table 4.5.3). Direct comparison of frequency was inappropriate since the sampling strategies and area covered in the present study were very different than in Sutton's (1964) study.

Several species, mostly rare, were absent at either one or the other period; 17 were only present in the 1953-57 samples, and 29 were only present in 1990.

4.5.3 Summary of Pre-treatment vs. Post-treatment Comparisons

In general, comparison of the post-harvest communities to the pre-harvest communities indicates that species' occurrences and abundances are similar, and do not show obvious, consistent patterns related to harvest treatment. However, abundance of tree species in the canopy was generally higher in 1990 than it was in 1953, and the reverse is true for abundance of tree species in the understorey (advance growth).

In terms of density, *Abies balsamea, Betula papyrifera, Picea glauca* and *Picea mariana* were the most important canopy species prior to treatment. Density of the first three had increased greatly on all soil site types by 37 years after harvest, as had that of *Populus tremuloides*. *Picea mariana* density decreased on 4 site types, but was about twofold greater in 1990 than it was in 1953 on 3 site types. *Thuja occidentalis* was important in the canopy only on extremely shallow sites prior to treatment, but had increased in importance on most site types by 1990. The S:H for tree density was >1.0 on all soil types at both periods, but had decreased on most types, especially on the extremely shallow types, which had essentially been converted from softwood to mixedwood. Only the moist-very shallow site type had a notable increase in S:H.

In 1953, S:H of advance growth density was >1.0 on all except 4 site types; by 1990, S:H of tree density was >1.0 on all site types. Neither softwood nor hardwood post-harvest tree density appeared to be directly related to pre-harvest advance growth density. Decreases from 1953 advance growth density to 1990 tree values were greatest for *B. papyrifera* and *A. balsamea*, occurring on all site types. Density of *P. mariana* decreased on all site types, as did that of *P. glauca* on all except extremely shallow types, and that of *T. occidentalis* on all except the fresh-medium shallow type.

Comparisons of 1990 treatment values to 1953 values in their correspondingly predominant site types gave some indication of canopy and regeneration changes by harvest treatment. Density of *A. balsamea, B. papyrifera* and both poplar species in the tree stratum had increased in all treatments by 1990. This increase was greatest for *A. balsamea* in SC and DC, for *B. papyrifera* in SC and for *P. tremuloides* in CC and SC. *P. glauca* increased in all treatments except CC, where it decreased slightly, and *T. occidentalis* and *P. mariana* also generally showed increases in tree density. Frequency and density of conifer advance growth in 1990 was generally lower than 1953 advance growth stocking and density. This was true in all treatments for *A. balsamea*, especially in CC and SC for the shrub stratum and in DC and SC for the herb stratum. Advance

growth density decreased in both strata for the spruces, especially in SC for *P. mariana* (both strata), and in CC for *P. glauca* (herb stratum). For these two species, 1990 shrub stratum frequencies in all treatments were about the same as 1953 advance growth stocking, but 1990 herb stratum frequencies were much lower. Hardwood advance regeneration was mainly *B. papyrifera* in both periods, with its 1990 density and frequency in both the herb and shrub stratum being lower than its 1953 density and stocking in all treatments. Decreases in *B. papyrifera* advance growth appeared to be greatest in HP for the herb stratum and in HP and SC for the shrub stratum. *Populus balsamifera* and *P. tremuloides* advance growth values were generally low at both times, except for high 1990 values in CC for *P. balsamifera* and in SC for *P. tremuloides*.

Species richness was higher for understorey plants in 1990 than in the pre-treatment tally and the 1957 tally of untreated strips (DC). Most species with high importance prior to harvest were also important in 1990, and vice versa, though most species dominant in 1990 appeared to have much lower frequencies than they did prior to harvest (i.e. in the 1957 DC strips).

4.6 ORDINATION

4.6.1 Correspondence Analyses

The first two axes of each correspondence analysis (CA) accounted for low proportions of the total variance for the data sets of species' cover (Table 4.6.1). Only one of the eigenvalues of these indirect ordinations was greater than 0.50 (tree data axis 1), suggesting that there were no strong underlying variables that controlled these species distributions.

The highest and lowest percentages of species variation accounted for by the first two axes occurred in the CA on tree cover alone (36.3%), and that for herb cover alone (15.2%), respectively. This is partly due to the smaller number of variables (species)

Table 4.6.1. Summary of ordinations performed on the data sets of species' percentage cover in individual sample units, as recorded on the RC17 study area, 1990.

Strata ordinated	'Environmental' variables used	Correlation of variables with each other	Intraset correlations axis 1	axis 2	No. of canonical axes	Eigenvalues and cumulative % variance of species data accounted for axis 1	axis 2	axis 3	axis 4	Total inertia in species data (eigenvalues sum)	Multiple correl. coeff. (R) & % of total R axis 1	axis 2
Correspondence analyses (CAs)												
combined						0.379	0.265	0.235	0.174	3.586		
						10.6%	18.0%	24.5%	29.3%			
tree						0.508	0.401	0.361	0.316	2.503		
						20.3%	36.3%	50.8%	63.4%			
shrub						0.478	0.36	0.324	0.275	2.924		
						16.3%	28.6%	39.7%	49.1%			
herb						0.476	0.329	0.308	0.236	5.306		
						9.0%	15.2%	21.0%	25.4%			
all						0.331	0.271	0.201	0.145	3.164		
						10.5%	19.0%	25.4%	30.0%			
Canonical correspondence analyses (CCA) with harvest treatment as 'environmental variable', dummy variables for each of the levels (CC, DC, HP, SC).												
all	CC*		0.93	0.00		0.054	0.371	0.264	0.234	3.586	0.56	0.00
	DC		-0.15	0.00		1.5%	11.8%	19.2%	25.7%		48.8%	0.0%
	HP		-0.07	0.00								
	SC		-0.66	0.00								
tree	CC		0.96	0.00		0.073	0.491	0.400	0.351	2.503	0.44	0.00
	DC		-0.42	0.00		2.9%	22.5%	38.5%	52.6%		70.8%	0.0%
	HP		-0.44	0.00								
	SC		-0.08	0.00								
shrub	CC		0.73	0.00		0.084	0.432	0.356	0.309	2.924	0.46	0.00
	DC		-0.15	0.00		2.9%	17.6%	29.8%	40.4%		62.7%	0.0%
	HP		0.27	0.00								
	SC		-0.79	0.00								
herb	CC		-0.67	0.00		0.060	0.470	0.328	0.289	5.306	0.50	0.00
	DC		-0.42	0.00		1.1%	10.0%	16.2%	21.6%		52.7%	0.0%
	HP		0.38	0.00								
	SC		0.75	0.00								
Canonical correspondence analyses (CCA) with soil depth and soil moisture as 'environmental variables'.												
all	1 moisture	0.52	0.98	0.22	2	0.079	0.049	0.357	0.26	3.586	0.62	0.44
	2 depth		0.70	-0.72		2.2%	3.6%	13.5%	20.8%		61.6%	100.0%
tree	1 moisture	0.48	0.15	0.99	2	0.071	0.018	0.457	0.400	2.503	0.39	0.25
	2 depth		-0.79	0.61		2.9%	3.6%	21.8%	37.8%		79.9%	100.0%
shrub	1 moisture	0.54	1.00	0.10	2	0.104	0.045	0.438	0.356	2.924	0.54	0.38
	2 depth		0.62	-0.79		3.6%	5.1%	20.1%	32.3%		69.6%	100.0%
herb	1 moisture	0.54	0.99	0.12	2	0.104	0.036	0.463	0.317	5.306	0.61	0.37
	2 depth		0.64	-0.77		2.0%	2.6%	11.4%	17.3%		74.1%	100.0%

*CC=clearcut, DC=deferred cut, HP=hardwoods poisoned, SC=softwoods only cut.

in the tree stratum compared to the herb stratum (contributing to a lower overall variance, i.e. total inertia, for trees=2.503, as compared to for herbs=5.306), which therefore require a lesser degree of reduction by ordination. However, the data set containing all three strata (tree, shrub and herb) had a lower overall variance (total inertia=3.586), and the first two axes of its CA accounted for more of this (18.0%), than did those for herb cover alone, despite the larger number of variables in all strata. Therefore, the differences noted between the tree and herb CAs, in terms of variance accounted for by the CA axes, may have another explanation. This may be simply that the trees generally had higher cover values than the herbs and shrubs, giving them more weight in the ordinations, but could also indicate that the tree stratum was dominant in determining vegetation pattern or in responding to ecological pattern.

The negative extreme for the first axis of the CA on combined strata is represented by *Populus tremuloides, Fraxinua nigra, Prunus pensylvanica*, and *Populus balsamifera* in the tree stratum, *Corylus cornuta* and *Prunus virginiana* in the shrub stratum, and *Climacium dendroides* (Hedw.) Web. & Mohr, *C. cornuta, P. pensylvanica, Circaea alpina* L. and *Mertensia paniculata* in the herb stratum (Figure 4.6.1). The positive end of the axis is composed of typical bog species such as *Kalmia polifolia, Ledum groenlandicum, Picea mariana* and *Larix laricina*, in the shrub stratum, while the herb stratum is represented by *Vaccinium oxycoccus* L., *Geocaulon lividium* (Richards.) Fern., the sphagnum mosses (*Sphagnum magellanicum* Brid. and *Sphagnum capillifolium*), *Vaccinium angustifolium, Cladina rangiferina, Gaultheria hispidula* and *Vaccinium myrtilloides*. The only tree species strongly positive on this axis is *P. mariana*. The most common tree species, *Abies balsamea, Betula papyrifera* and *Picea glauca* fall near the centre of axis 1 and the centre of the ordination.

The second axis is dominated by *Thuja occidentalis* in all three strata at the positive end, with several mosses, lichens, and other herb stratum species occurring at a high but less extreme position: *Equisetum arvense, Hylocomium splendens,*

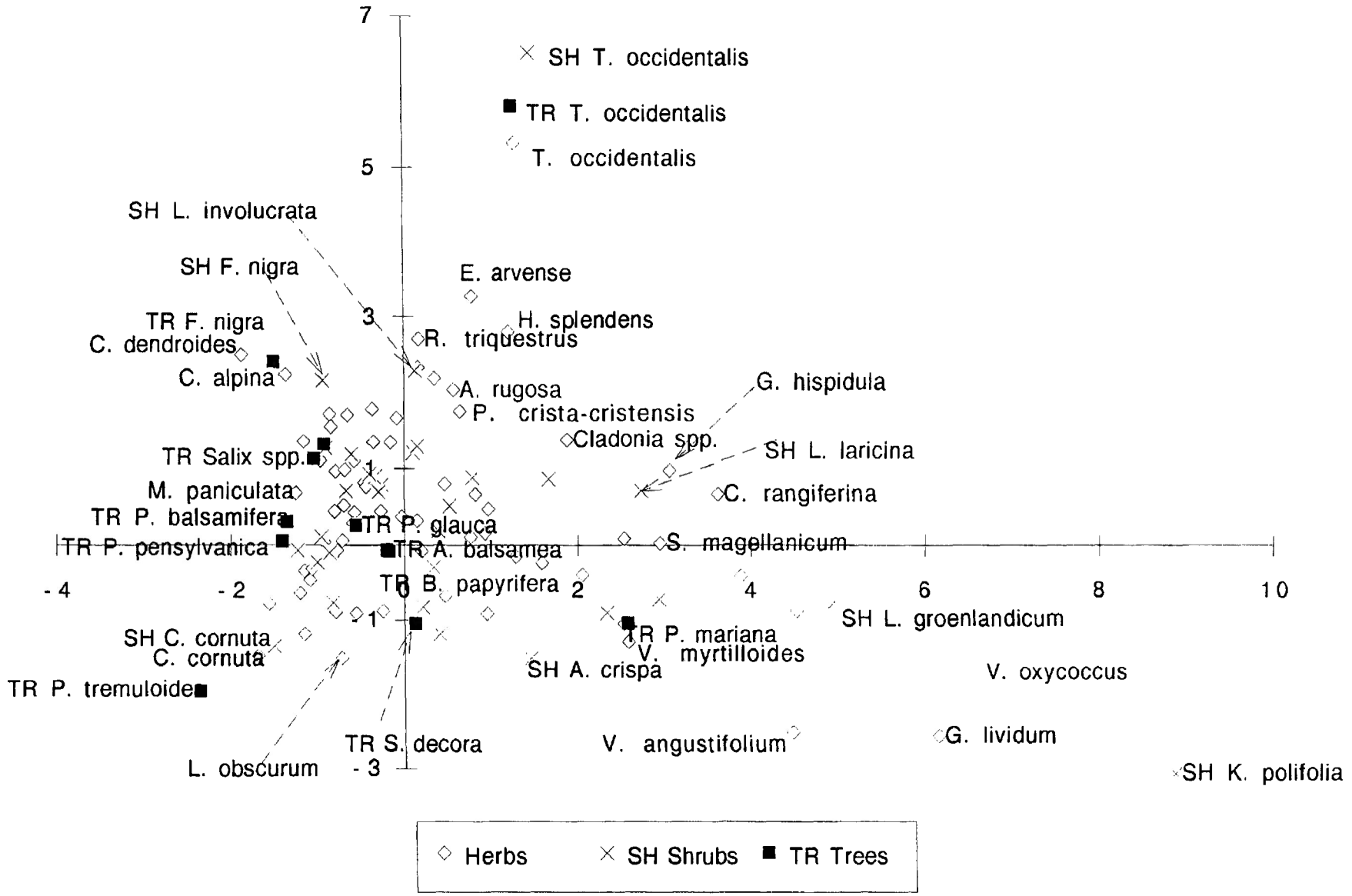


Figure 4.6.1. Species diagram for CA of combined strata cover on the RC17 study area, 1990.

Rhytidiadelphus triquestrus, Climacium dendroides, Epilobium angustifolium and *Circaea alpina*, in descending order. Also occurring in this area of the plot are the shrub stratum representatives of *Lonicera involucrata* (Richards.) Banks and *F. nigra*, and *F. nigra* in the tree stratum. The negative end of axis 2 is dominated by several species that are also at either the positive or negative extremes of axis 1. *Kalmia polifolia* in the shrub stratum is again the most extreme, with *V. angustifolium, G. lividum, V. oxycoccos* and *Lycopodium obscurum* representing the herb stratum. *Populus tremuloides* has the most negative score for tree species on the second axis, followed by *Sorbus decora* and *P. mariana*. *Alnus crispa* and *C. cornuta* of the shrub layer are also prominent.

The CA on shrub cover alone and that on herb cover alone produced species' ordinations similar to that for the combined strata, with the exception of several bog species high on axis 2 as well as on axis 1 of the herb strata CA, and *T. occidentalis* relatively low on axis 2. Thus, these two ordinations are not presented. In the CA of tree cover, most species occupy positions similar (with axis 1 reversed) to those in the CA of the combined strata (Figure 4.6.2). However, some species, e.g. *P. tremuloides, F. nigra* and *P. mariana*, occupy more extreme positions than they did in the CA of combined strata.

According to FEC V-types, the ordination of combined strata shows that *P. mariana* conifer stands (V30 to V35) and *P. mariana* mixedwood stands (V19, V20) fall at the positive end of axis 1, with *A. balsamea /P. glauca* conifer stands (V24, V25) and mixedwood stands (V14, V15, V16) falling near the centre; *B. papyrifera* stands also fell near the centre (V4) (Figure 4.6.3). The mainly hardwood stands, including sites dominated by *P. tremuloides* (V5, V6, V8), *P. balsamifera* (V1) and *F. nigra* (V2), fall at the negative end of axis 1.. Thus, axis 1 appears to represent a gradient of species composition which changes from hardwood-dominated to mixedwood to conifer-dominated stands. Axis 2 of this CA is strongly dominated at the positive end by *T. occidentalis* stands (V21 and V22) as was indicated by the species plot, but the negative end of the

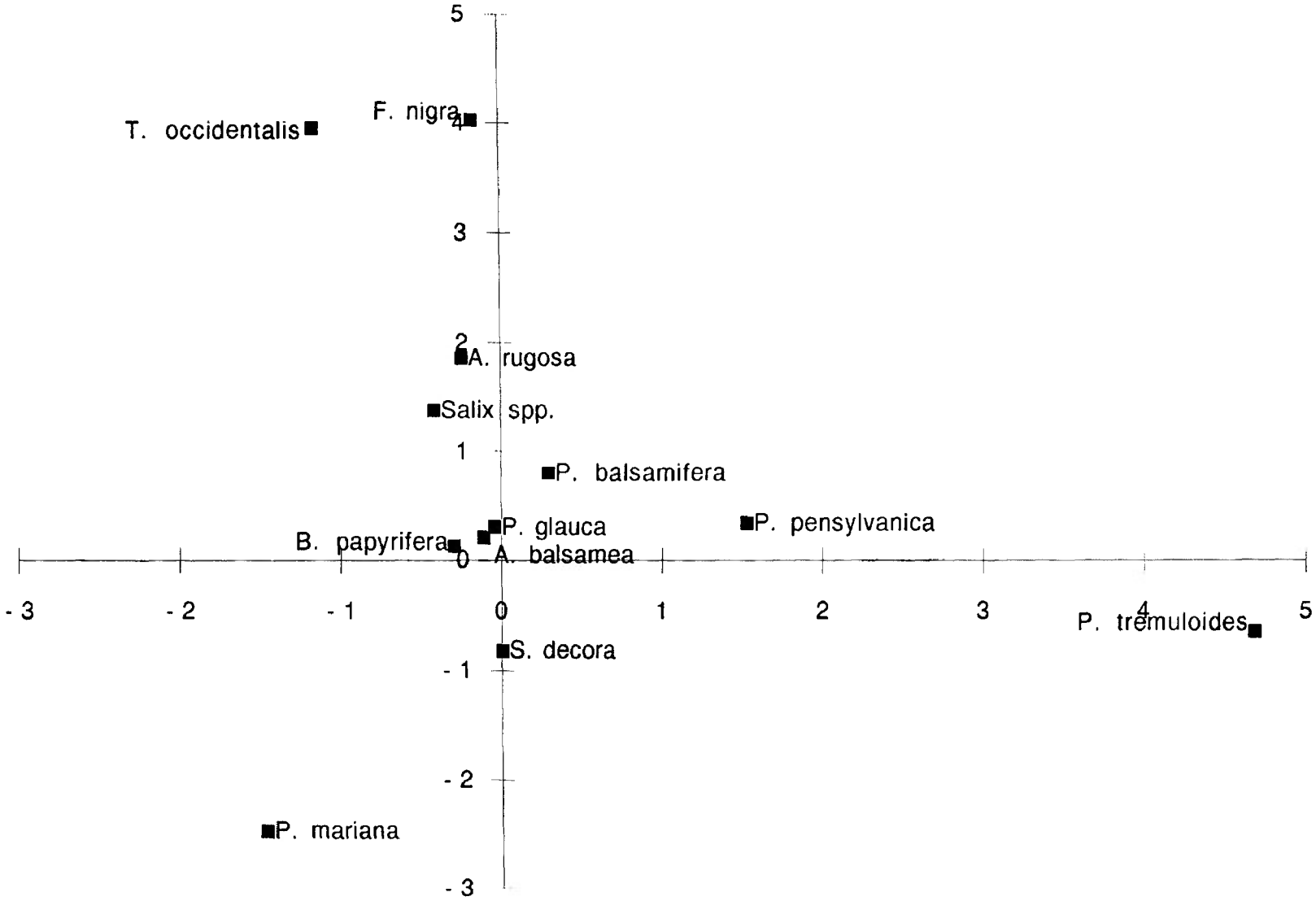


Figure 4.6.2. Species diagram for CA of tree stratum cover on the RC17 study area, 1990.

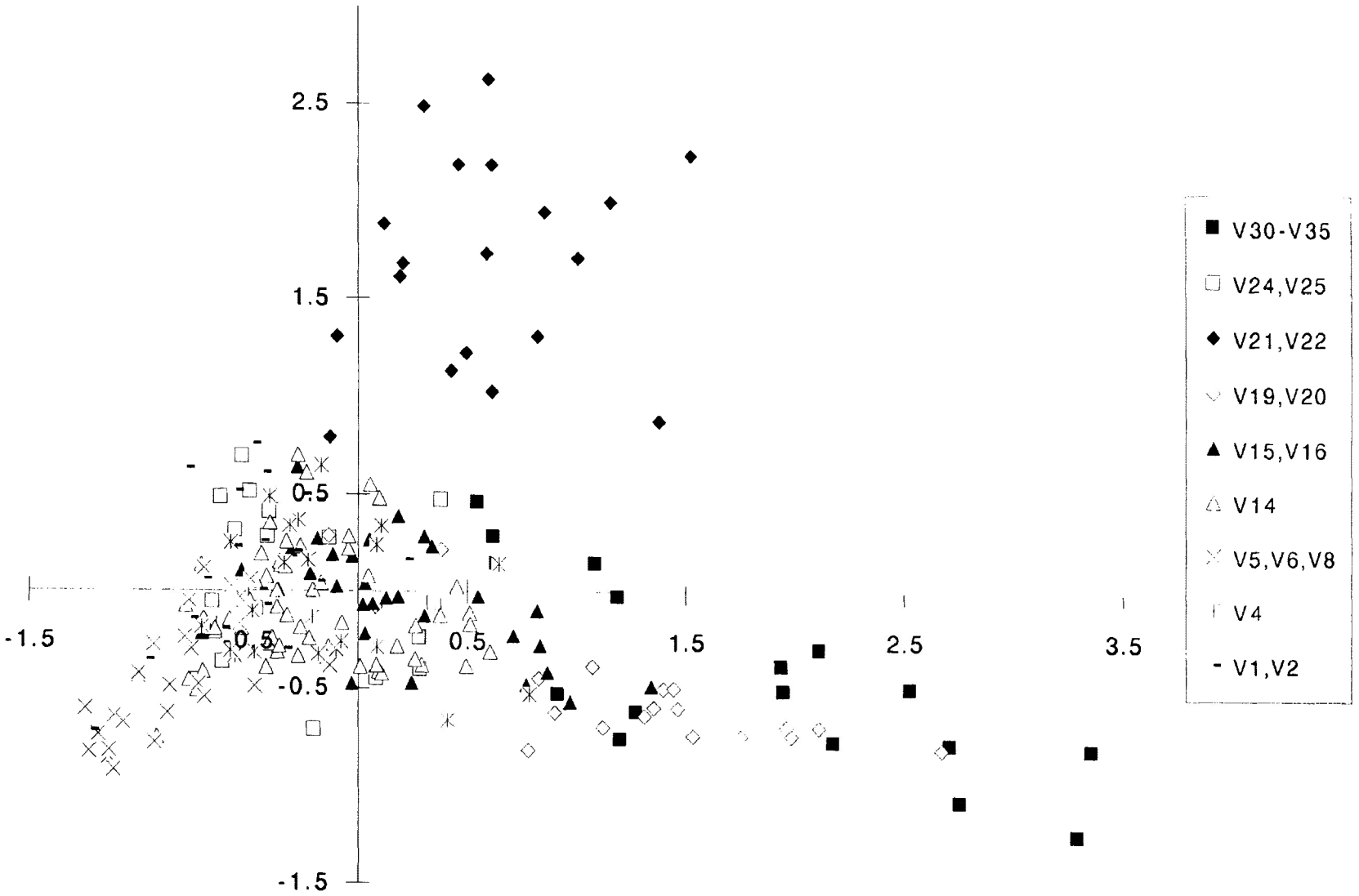


Figure 4.6.3. Sample unit (SU) diagram for CA of combined strata cover, SUs labelled with FEC V-types.

axis encompasses both conifer-dominated stands (V30-V35, V19, V20) and hardwood-dominated stands (V5, V6, V8). Since the particular types of conifer stands occurring at the negative end of axis 2 tend to be wet and nutrient poor, while the hardwood stands falling here tend to be fairly rich and dry, the underlying environmental gradients exhibited by this axis are unclear.

The plot of SUs identified by FEC type for the CA of tree cover confirms that the dominant trend (axis 1) is from conifer-dominated stands (V30 to V35, V19 to V22), to mixedwood stands (V4, V14, V15, V16), to hardwood dominated stands (V5, V6, V8, V1, V2) (Figure 4.6.4). Axis 2 of the CA on tree cover moves from *P. mariana* stands (V30 to V35) (negative end), to mixed and hardwood stands, to *T. occidentalis* stands (V21,V22) (positive end). This axis may be more closely related to moisture (wet to dry) or nutrients (poor to rich) than is axis 2 of the CA of combined strata.

No patterns in harvest treatments were evident from the CA of combined strata (Figure 4.6.5), the SUs from all harvest treatments being widely distributed and intermingled along both of the first two ordination axes. Similarly, when the CA of tree cover is displayed with SUs classified by harvest treatments, it shows no grouping of SUs by harvest treatment and thus no relationship of tree species composition to harvest treatment (Figure 4.6.6). HP SUs occur within a more narrow range than those of the other treatments on axis 1 of both of these ordinations, but are widely distributed on axis 2. The lack of separation of harvest treatments on the first two axes of these ordinations indicates that the main patterns of variance in the species composition and abundance are not due to the harvest treatments.

4.6.2 Canonical Correspondence Analyses With Harvest Treatments as a Canonical Variable

In order to determine whether any of the variation in the species data can be accounted for by the harvest treatments, canonical correspondence analysis (CCA) was

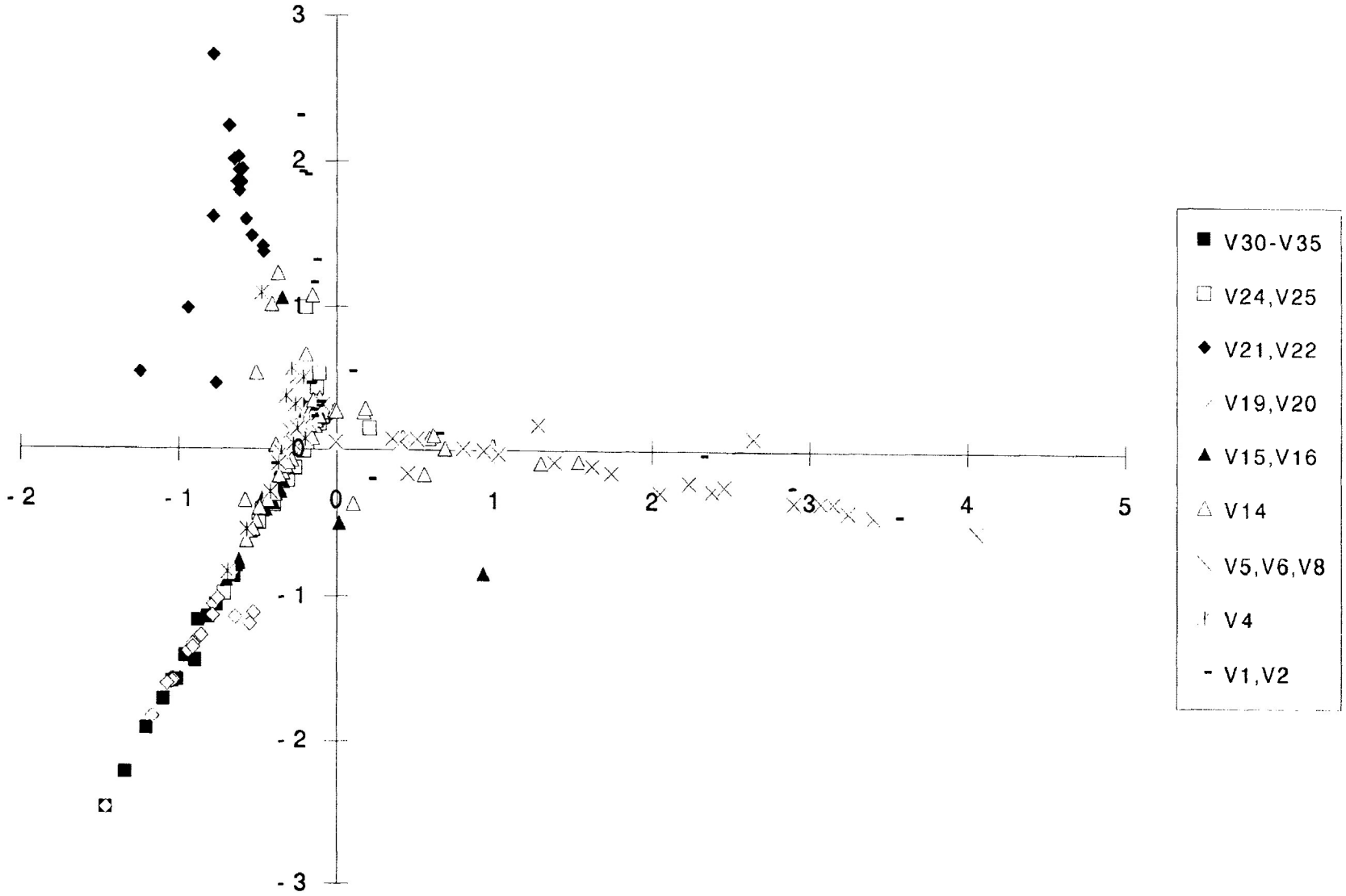


Figure 4.6.4. CA of tree stratum cover on the RC17 study area, 1990, sample units labelled by FEC V-types.

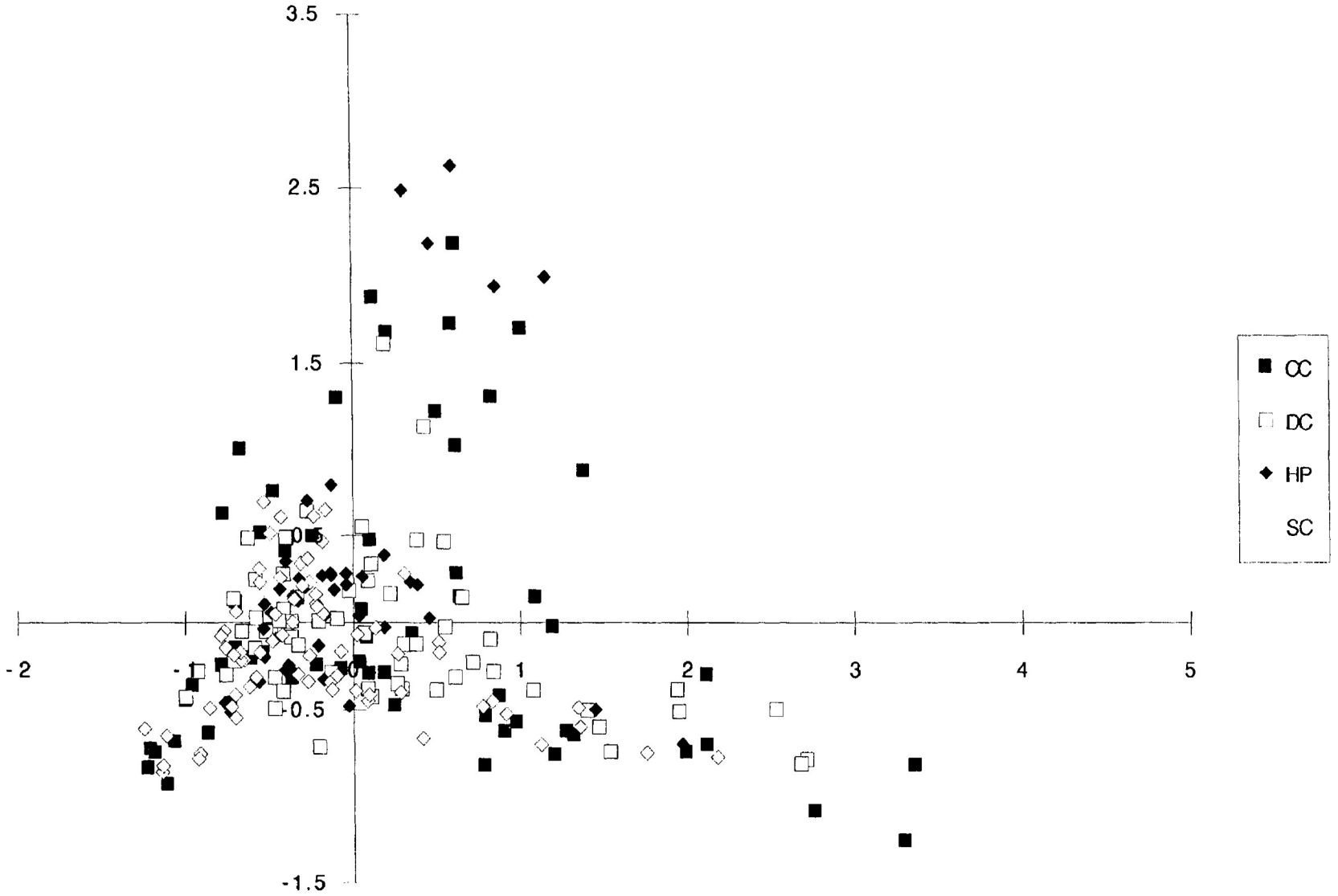


Figure 4.6.5. CA of combined strata cover on the RC17 study area, sample units labelled by harvest treatments.

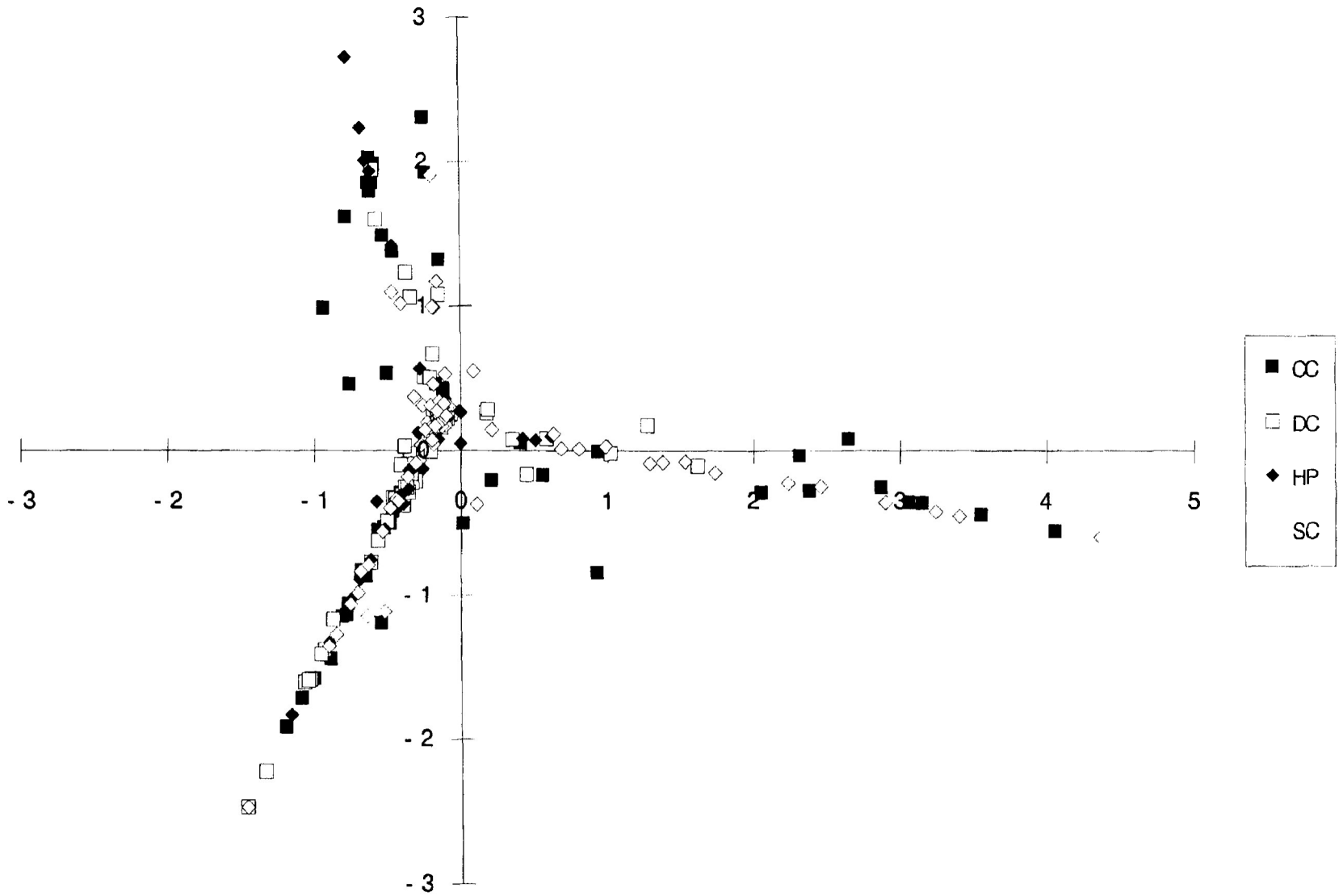


Figure 4.6.6. CA of tree stratum cover on the RC17 study area, sample units labelled by harvest treatments.

run on each of the four data sets (i.e. those for trees, shrubs, herbs and combined strata) using harvest treatment as a nominal (environmental) variable. Since only one variable was used, only one canonical axis was extracted. The multiple correlation coefficient between species and harvest treatment (environmental variable), R, on the canonical axis (axis 1) is fairly high (>0.4) for each of the canonical analyses (Table 4.6.1). However, the eigenvalue of the canonical axis for each of the analyses is very small (<0.10), and the percentage of variance of the species data accounted for by this axis is less than 3.0% for each of the analyses (Table 4.6.1). As mentioned in the methods, the eigenvalues are the true indicators of the influence of the environmental variables. Therefore, as expected from the CAs, very little of the overall variance in the species cover data is associated with harvest treatment.

Due to the use of 'dummy' variables in the program CANOCO to represent the four levels of the nominal variable, harvest treatment, the canonical axis does not represent the entire correlation (R) between the species data and the 'environmental' variable, harvest treatment. However, it does represent much of this correlation : 48.8% in the analysis of combined strata, 70.8% in that of tree cover, 62.7% in that of shrub cover and 52.7% for the analysis of herb cover (R and % in Table 4.6.1). Therefore, the total percentage of variance of the species data accounted for by harvest treatments would likely have been $\leq$ 5.0% even if further canonical axes had been (incorrectly) extracted. The second and further (non-canonical) axes extracted in these CCAs represent the residual variance in the species data after that due to harvest treatments has been extracted. Since so little of the total variance is accounted for by the harvest treatments, the second axes are essentially equivalent to the first CA axes; this was verified by comparison of species plots.

Since the intraset correlations treat each of the harvest 'levels' as variables, due to the 'dummy' variable method, they simply indicate which levels have the most influence on the canonical axis. The CCA of combined strata shows incomplete separation

of SUs by harvest treatments along the canonical axis, the trend being from SC at the negative end, to DC, HP and then CC at the positive end (Figure 4.6.7). This is confirmed by the high positive intraset correlation of CC with this axis (0.93) and the low negative intraset correlation of SC with it (-0.66). The second axis is essentially equivalent to axis 1 of the CA, as evidenced by comparison of species distributions along these axes (Figure 4.6.1, Figure 4.6.8). The slight separation of the treatments along axis 1 of the CCA clarifies trends in axis 2, and thus in axis 1 of the CA. For example, the CCA ordination diagram shows that CC SUs are the most scattered of the four treatment levels across axis 2 and that SUs from the HP level have the narrowest range on this axis, occurring centrally (Figure 4.6.7). This diagram, in combination with its corresponding FEC V-types diagram (Figure 4.6.9), highlights other important aspects of the data. For example, the CC SUs evidently belong to two groups of FEC V-types. The first group is primarily conifer-dominated, including *Thuja occidentalis* stands (V21, V22), *Picea mariana* mixedwood (V19, V20), and *P. mariana* conifer (V30 to V35) stands; these lie on the positive side of axis 2. The second group is primarily hardwood, consisting of wet hardwood stands (V1, V2) and *Populus tremuloides* (V5, V6 and V8); these SUs lie at the low (negative) end of axis 2. The SUs from the DC treated stands fall into two similar categories. The conifer-dominated stands, including *P. mariana* conifer (V30 to V35), *P. mariana* mixedwood (V19, V20) and *Picea glauca-Abies balsamea* conifer (V24, V25) are again at the positive end of axis 2 while the hardwood-dominated stands, including *Betula papyrifera* hardwood and mixedwood (V4) and *P. tremuloides* hardwoods (V5, V6, and V8) as well as some conifer-dominated mixedwoods (V14, V15, V16) are at the negative end of axis 2. Similarly, for the SC SUs at the negative end of axis 1, the lower (on axis 2) ones tend to belong to hardwood FEC V-types (e.g. V5, V6, V8) while the upper ones belong to conifer mixedwood V-types (e.g. V15, V16, V19, V20) . Thus, axis 2 of this CCA clarifies that the main trend in the data is from hardwood to mixedwood to conifer (Figure 4.6.8 and Figure 4.6.9) and that this trend

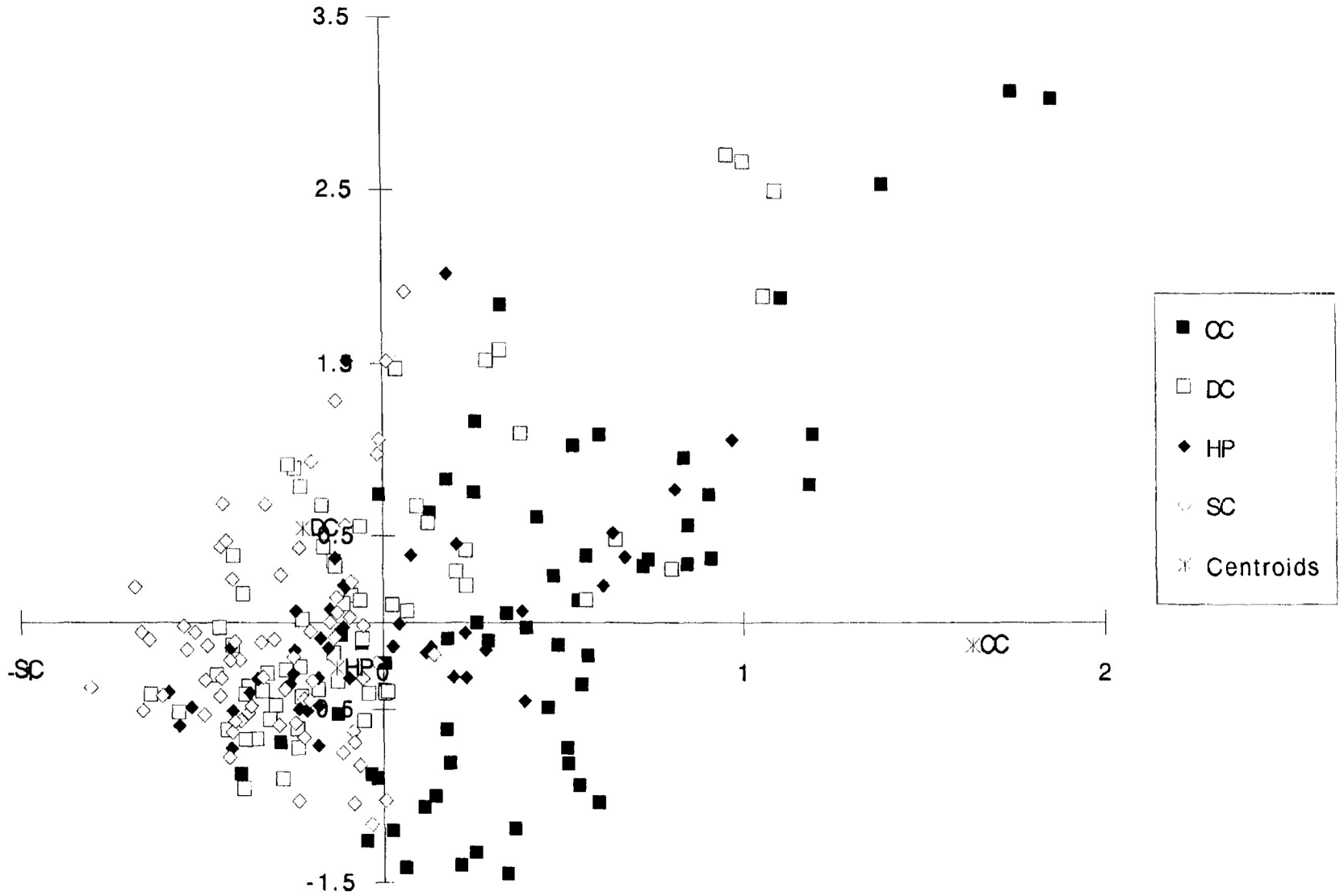


Figure 4.6.7. CCA of combined strata cover on the RC17 study area, harvest treatment as a canonical variable, sample units labelled by harvest treatment. (Harvest treatment centroids are multiplied by 4).

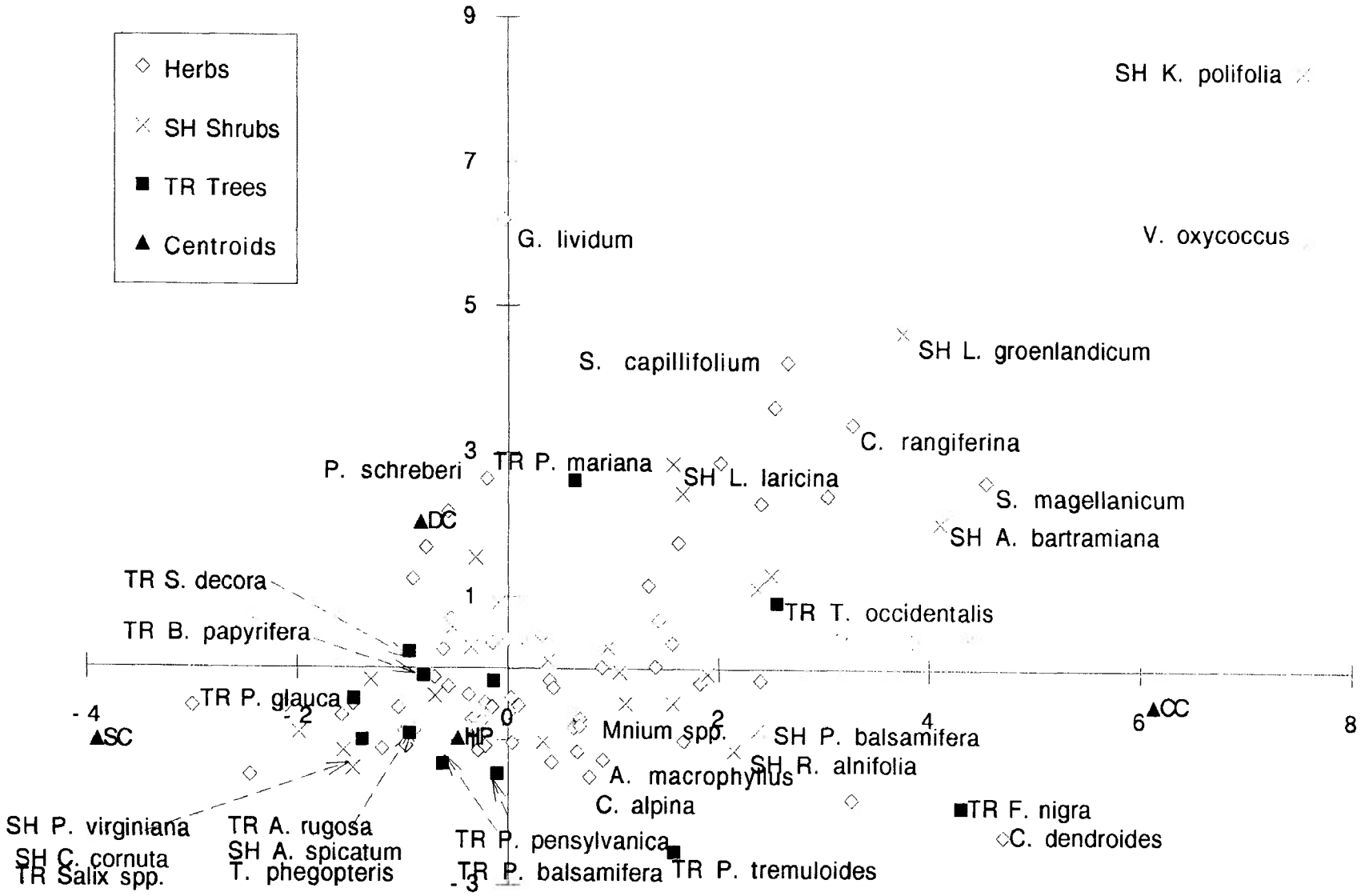


Figure 4.6.8. Species diagram for CCA of combined strata cover on the RC17 study area, 1990, harvest treatment as the canonical variable (Harvest treatment centroids multiplied by 15).

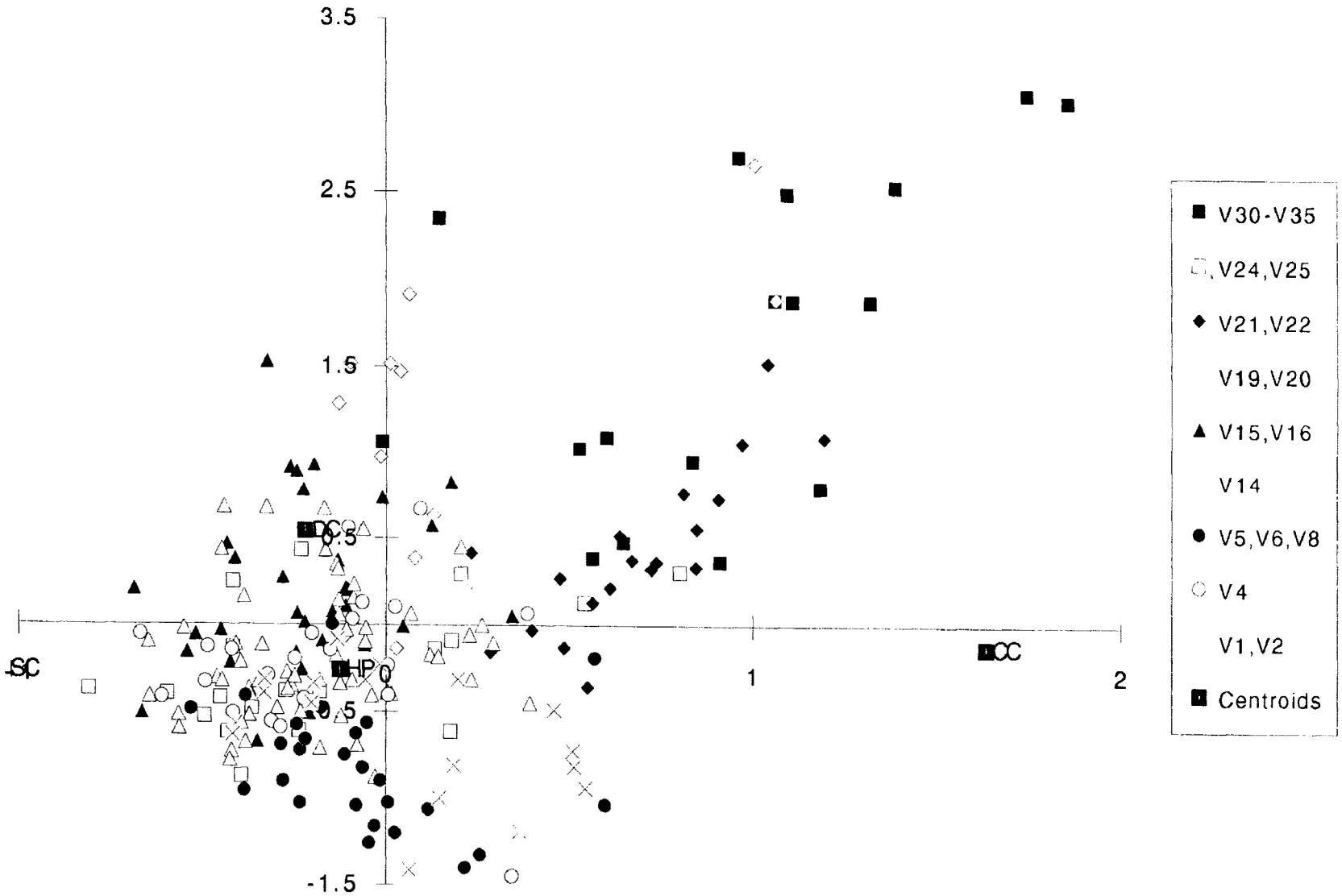


Figure 4.6.9. CCA of combined strata cover, harvest treatment as the canonical variable, sample units labelled by FEC V-type. (Harvest treatment centroids multiplied by 4).

has little to do with harvest treatments: SUs of all four treatments are scattered, with no separation, along the second axis (Figure 4.6.7).

This CCA also shows some evidence of a gradient from dry site species to wet site species (left to right) on axis 1 (Figure 4.6.8). For example, at the negative end of axis 2 (the hardwood end), the left to right sequence includes: *Corylus cornuta* (shrub and herb), *Prunus virginiana* (shrub), *Alnus rugosa* (tree), *Acer spicatum* (shrub), *Thelypteris phegopteris* (L.) Slosson, *Populus balsamifera* (tree), *Prunus pensylvanica* (tree), *Aster macrophyllus, Circaea alpina, Mnium* spp., *Rhamnus alnifolia* L'Hér. (shrub), *P. balsamifera* (shrub), *Fraxinus nigra* (tree) and *Climacium dendroides*. However this trend is less evident at the positive (conifer) end of axis 2; some species more typical of wet sites, e.g. *P. mariana* (tree) and *Larix laricina* (shrub), appear further to the left than species typical to drier sites, e.g. *T. occidentalis* (this species was located more often on upland sites than wetland sites in this study). This may be due to the occurrence of *P. mariana* in several upland mixedwood SUs as well as in the boggy areas. If axis 1 does represent a gradient of dry to wet sites, the ordination emphasizes the unequal distribution of soil moisture types among the treatment levels and SUs. This was already confirmed in Table 3.2.1: most SC SUs fell on fresh to dry soils; most CC SUs were on moist sites, with several on mucky peat sites; DC SUs were spread throughout moisture types and HP SUs were mainly on fresh and moist soils. This CCA, with SUs classified by moisture type (Figure 4.6.10), shows some evidence of this trend from dry to wet along axis 1, although there is a lot of intermingling of moisture types.

For the CCA of tree species cover with harvest treatment as the canonical variable, distinctions among harvest treatments are absent (Figure 4.6.11). Although the HP SUs are placed mostly to the left of axis 1 (the canonical axis), the other three treatment levels are spread broadly over this axis. This is somewhat unexpected since the location of tree species along axis 1 (Figure 4.6.12) is similar to that for the CCA on combined strata (Figure 4.6.8). The CCAs on the shrub stratum and on the herb stratum

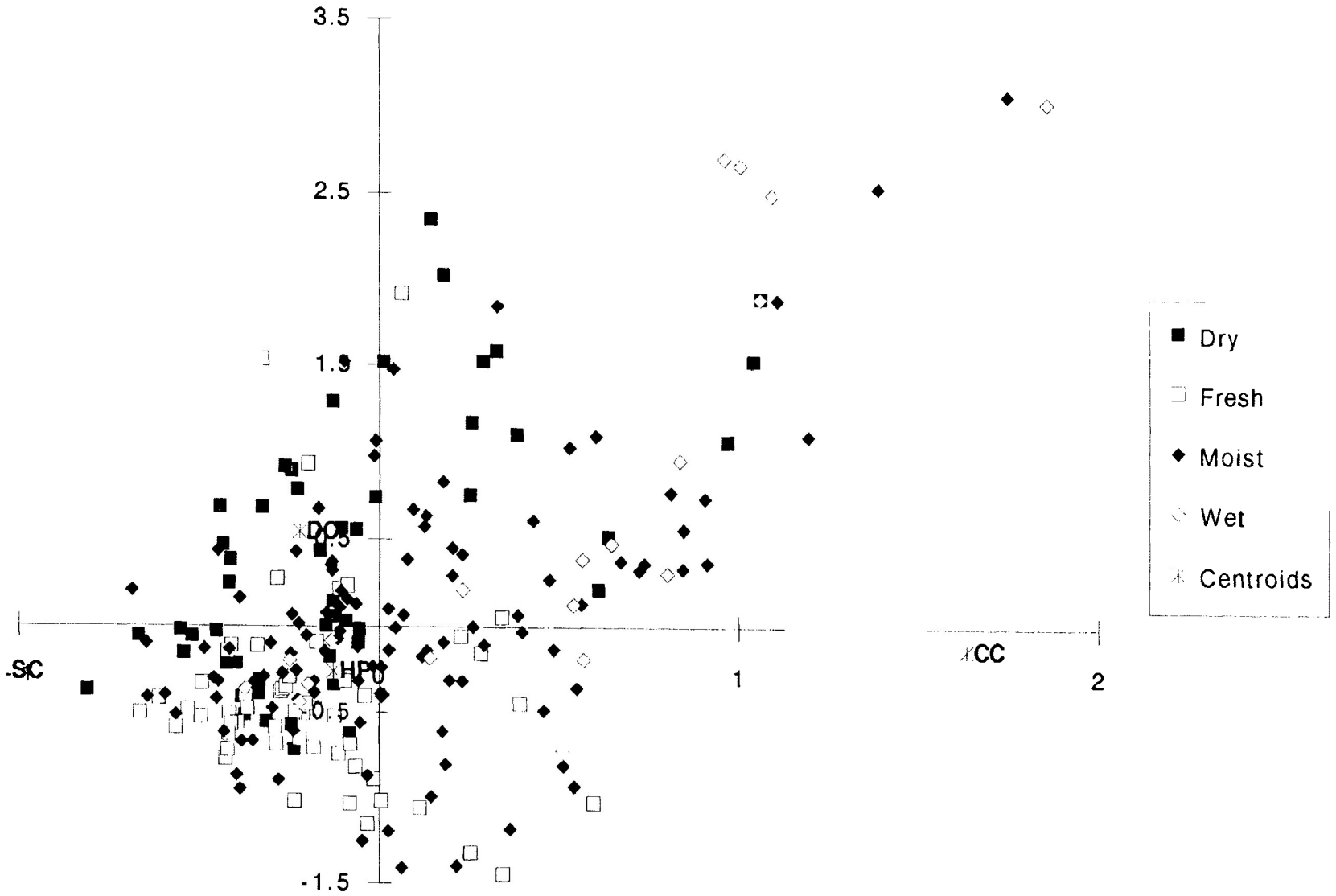
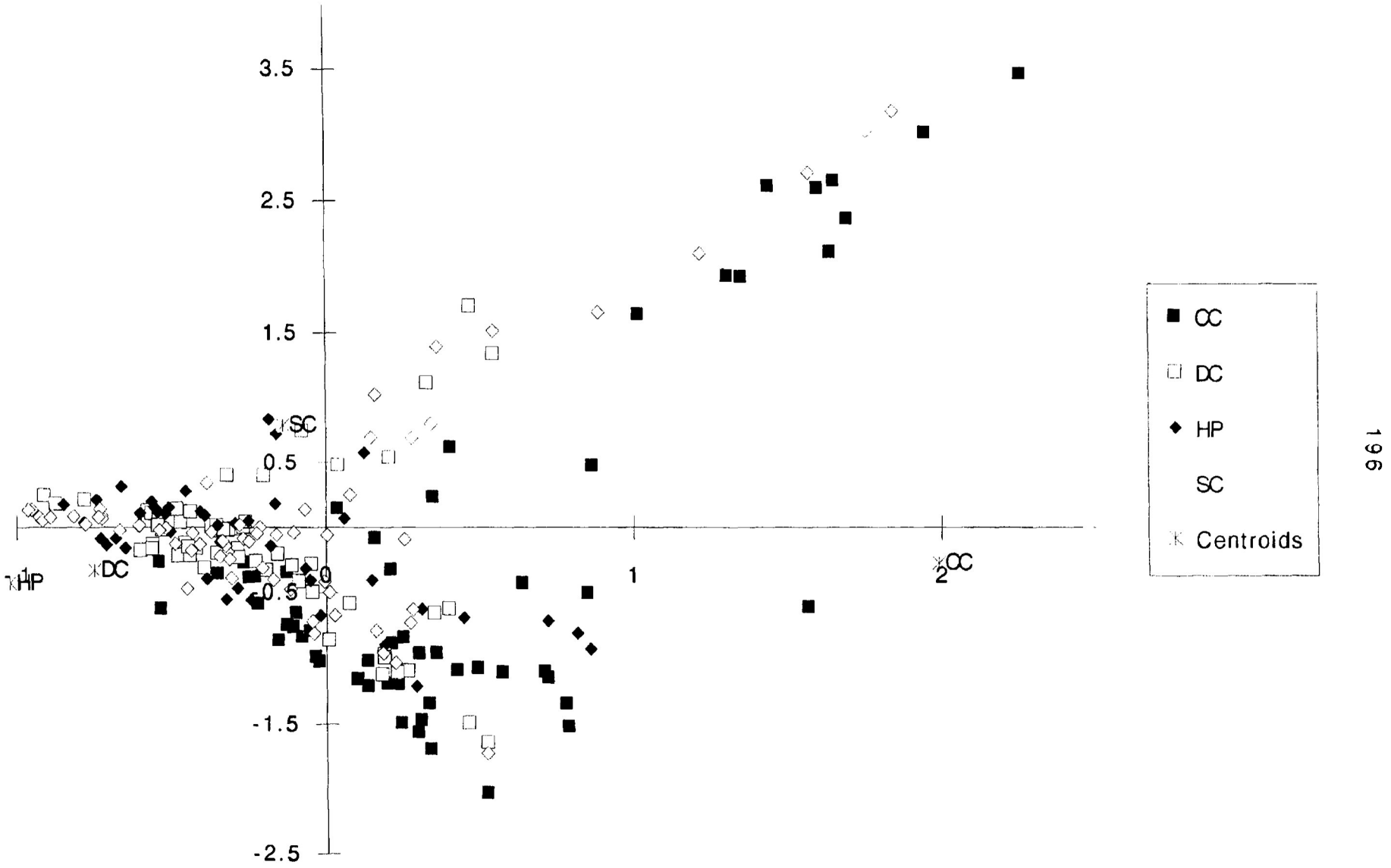
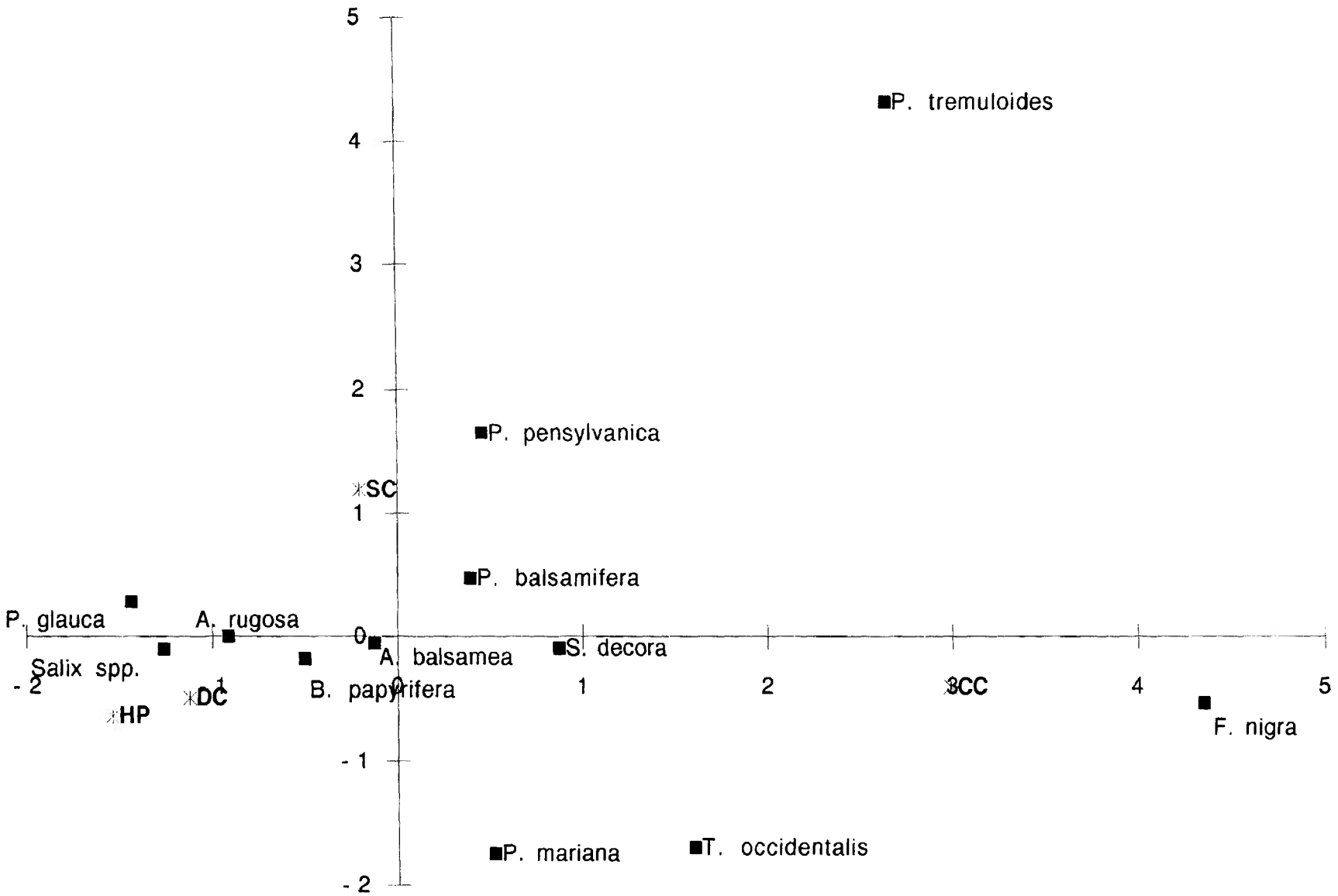


Figure 4.6.10. CCA of combined strata cover, harvest treatment as the canonical variable, sample units labelled by soil moisture. (Harvest treatment centroids multiplied by 4).



Harvest treatment (canonical variable) centroids multiplied by 4.

Figure 4.6.11. SU diagram for CCA of tree stratum cover, harvest treatment as canonical variable, SUs labelled by treatment.



Harvest treatment (canonical variable) centroids multiplied by 6.

Figure 4.6.12. Species diagram for CCA of tree stratum cover, harvest treatments as canonical variables.

produced an ordination of species and SUs very similar to that of the CCA on combined strata. Therefore, these two ordinations are not included.

The low eigenvalues and percentages of variance accounted for by axes, and the lack of strong clustering of SUs by harvest treatments in the ordination diagrams, confirmed that harvest treatment had little influence on species' distributions and abundances in this post-harvest boreal mixedwood.

4.6.3 Soil Moisture and Soil Depth in CA and CCA ordinations

Correspondence analysis of combined strata, with SUs classified by soil moisture categories, did not show a distinct relationship of species composition to soil moisture (Figure 4.6.13). There is some congregation of SUs belonging to the fresh and moist soil types around the negative part of axis 1, but both the dry and wet site SUs tend to extend along the positive end of this axis, although the wet sites are slightly above the dry sites on axis 2. Generally, there is mixing of all site types throughout.

Since CA tends to be strongly influenced by rare species in atypical plots (ter Braak 1987), and since the intent of the original RC-17 project was to examine treatment effects on upland mixedwood sites (Hughes 1967), correspondence analysis was attempted excluding the wet (mucky peat) sites. These sites contain species rare to this study, which were drawn out on both axes of the original CA, particularly the positive end of axis 1 (Figure 4.6.1). In the species diagram of the ordination resulting from the exclusion of these sites, four species present in the original correspondence analysis were absent: one herb stratum species, *Vaccinium oxycoccus* and three shrub stratum species: *Kalmia polifolia, Larix laricina* and *Lonicera villosa* (Michx.) R. & S. The overall appearance of the ordination diagram did not change dramatically, with axis 1 simply shortened and some slight shifting of species. Axis 1 had a slightly smaller eigenvalue, 0.331 compared to 0.379 (Table 4.6.1) accounting for only 0.1% less of the overall species variance. Therefore, the diagrams for this ordination were not

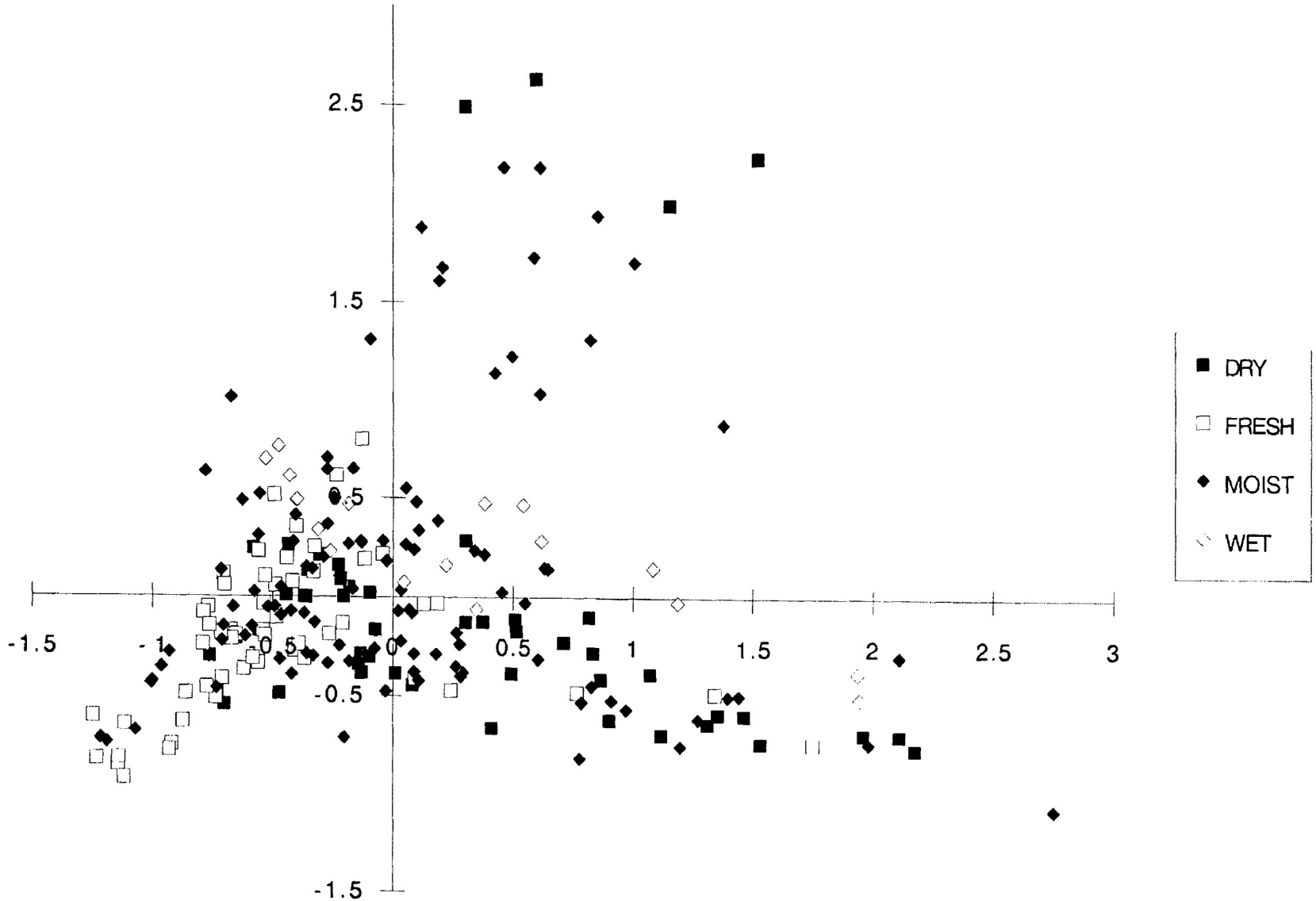


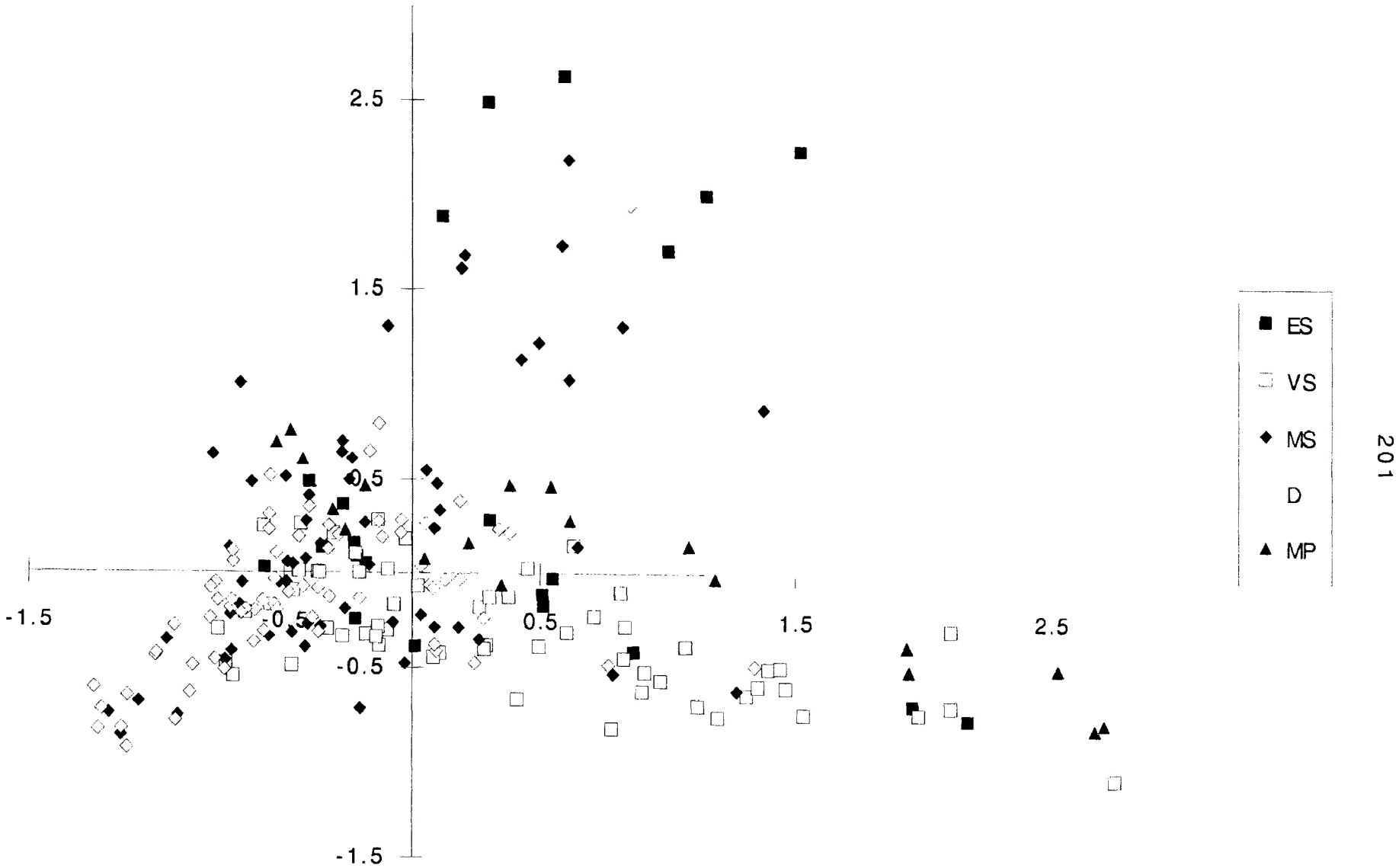
Figure 4.6.13. Sample unit (SU) diagram for CA of all strata cover on the RC17 study area, 1990, SUs labelled by soil moisture.

included.

With SUs classified by soil depth, there is some evidence of a pattern in the CA of combined strata: most deep SUs cluster at the negative end of axis 1, very shallow SUs cluster at the centre of the ordination and extend along the positive end of axis 1, and mucky peat (wet) site SUs also extend along the positive end, but above the SUs located on very shallow sites (Figure 4.6.14). The SUs located on extremely shallow and medium shallow site types tend to be scattered throughout the ordination. The cluster of SUs high on axis 2 are located on a mixture of soil depth and soil moisture types (Figure 4.6.13 and 4.6.14).

No pattern was evident with the SUs classified by both soil depth and moisture categories for the CA of combined strata. With SUs classified by either soil depth, soil moisture, or both categories, CAs performed on each of the three strata separately showed no discernible patterns. Thus these ordination diagrams were not included.

The CCAs performed on the four data sets, with soil depth and soil moisture as ordinal environmental variables, all have very low eigenvalues on the two canonical axes (axes 1 and 2); in all four analyses these axes account for <6.0% of the total variance in the species data (Table 4.6.1). The CCA on shrub cover had the highest percentage of variance explained by the canonical axes (5.1%), that for herb cover had the lowest (2.6%). For all four analyses, soil depth and soil moisture had a fairly high correlation (approximately 0.5) with each other. The intraset correlations (IC) for these two variables with the two canonical axes are very similar for three of the data sets: shrub cover, herb cover, and combined strata cover. For these analyses, both variables have high positive ICs on axis 1, with moisture having a stronger influence (IC≈0.650). Soil depth had a stronger influence on axis 2 (IC≈-0.750) compared to that of soil moisture (IC≈0.100) (Table 4.6.1). For the CCA on tree cover, the axes seem to be flipped, so that both soil moisture and depth have high positive ICs with axis 2, and only soil depth has a strong (negative) IC with axis 1 (Table 4.6.1).



ES=extremely shallow, VS=very shallow, MS=medium shallow, D=deep, MP=mucky peat.

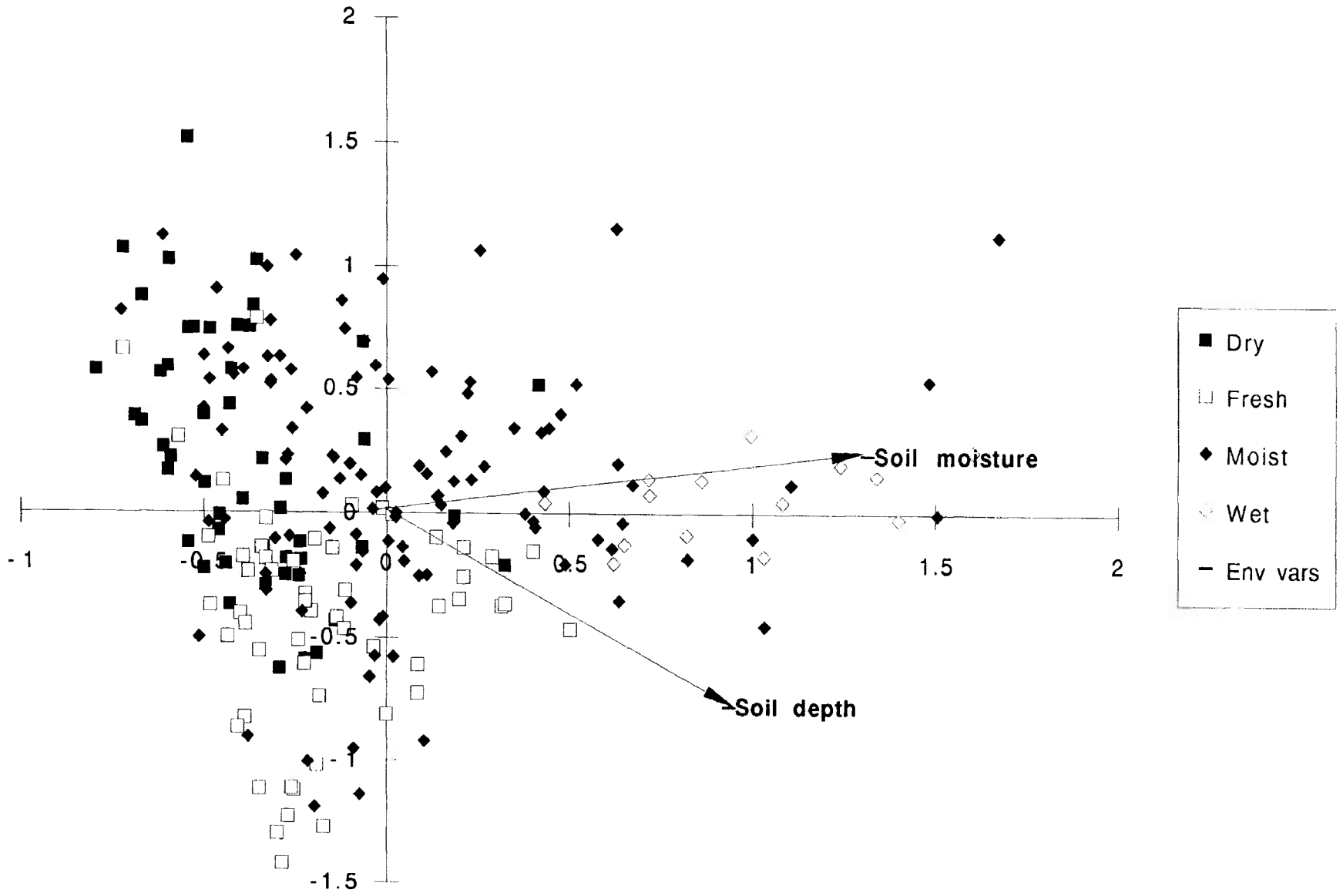
Figure 4.6.14. Sample unit (SU) diagram for CA of all strata cover on the RC17 project, 1990, SUs labelled by soil depth.

The CCAs on shrub cover and on herb cover had ordination diagrams very similar to that of the CCA of combined strata. Therefore only the latter is presented. The corresponding CCA of tree cover was quite different from the other three, but it showed no evident pattern for soil depth and soil moisture, and the SUs did not follow the environmental vectors closely. Thus, this ordination is not displayed.

As indicated by the ICs, soil moisture followed the first canonical axis closely (Figure 4.6.15). Dry site SUs tended to occupy the negative extreme of axis 1 and wet site SUs occupied the right end. However, the relation of species to soil moisture was evidently not strong, since the SUs on fresh and moist sites lay along the same area of axis 1 (and along the moisture vector) and even the dry site SUs were strongly mixed with these two categories (Figure 4.6.15). Axis 2 appeared to separate the fresh sites from the others to some extent.

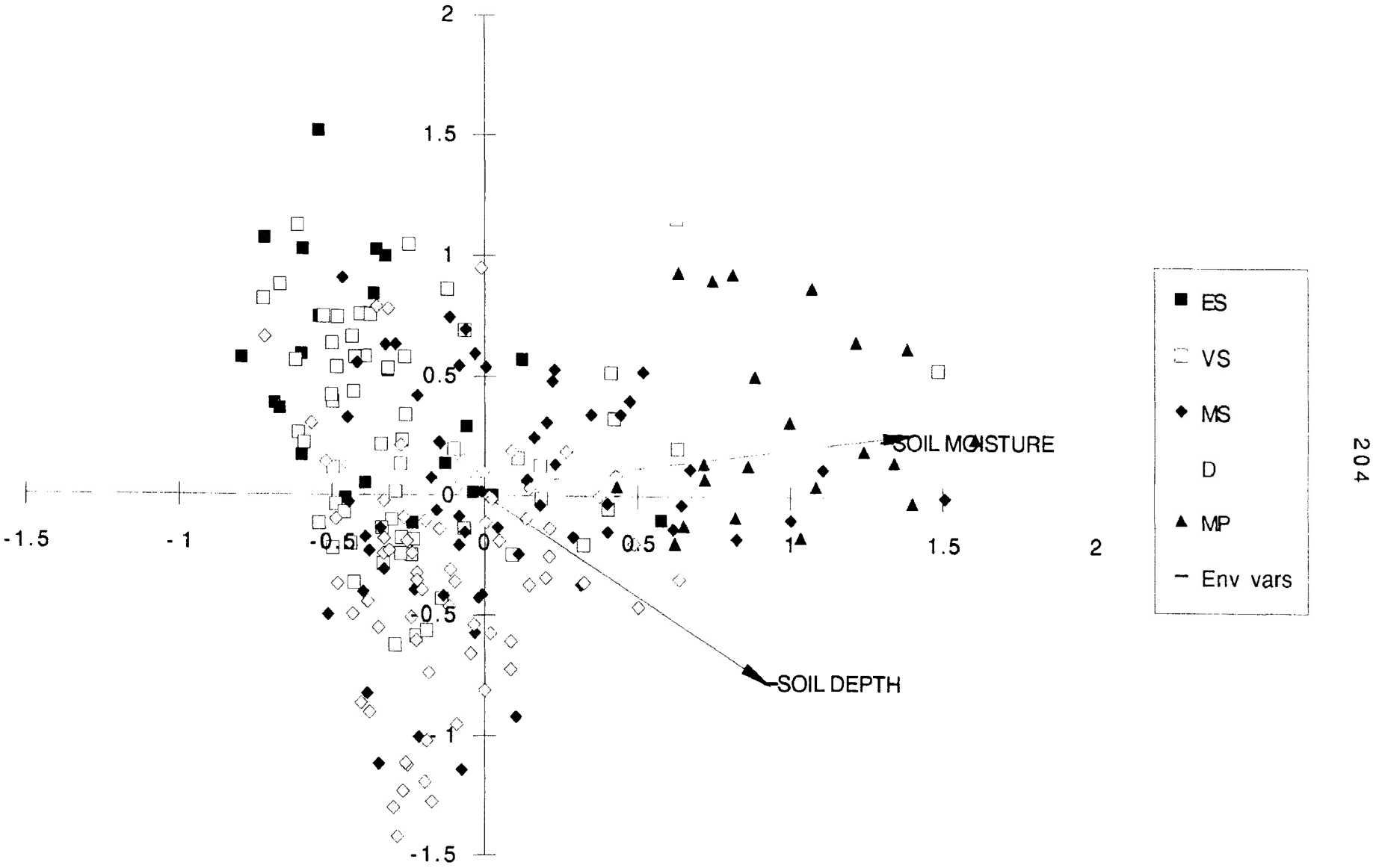
With SUs labeled according to soil depth, there was some evidence of a trend from 'extremely shallow' SUs in the upper left quadrant of the ordination through to 'deep' SUs in the lower left quadrant and to 'mucky peat' SUs in the upper right quadrant (Figure 4.6.16). However, there was still mixing of depth types along the depth vector and along axis 2. Labelling of the SUs by both soil moisture and soil depth did not make the ordination easier to interpret, and therefore this display is not included.

A classification of the SUs by FEC V-types shows that *Picea mariana* mixedwoods (V19, V20) and *Thuja occidentalis* stands (V21, V22) ordinate mostly at the negative end of both environmental vectors, as do *Abies balsamea-Picea glauca* mixedwoods (V14, V15 and V16), but in a less extreme position (Figure 4.6.17). *Populus tremuloides* and hardwood stands (V5, V6 and V8) ordinate at the low end of the soil moisture vector but at a more central position on the depth vector. *Populus balsamifera* and *Fraxinus nigra* hardwoods and mixedwoods (V1 and V2) ordinate mainly at the positive end of both environmental vectors and SUs belonging to *P. mariana*-dominated conifer sites (V30 to V35) also ordinate mostly at the high end of both environmental vectors (Figure



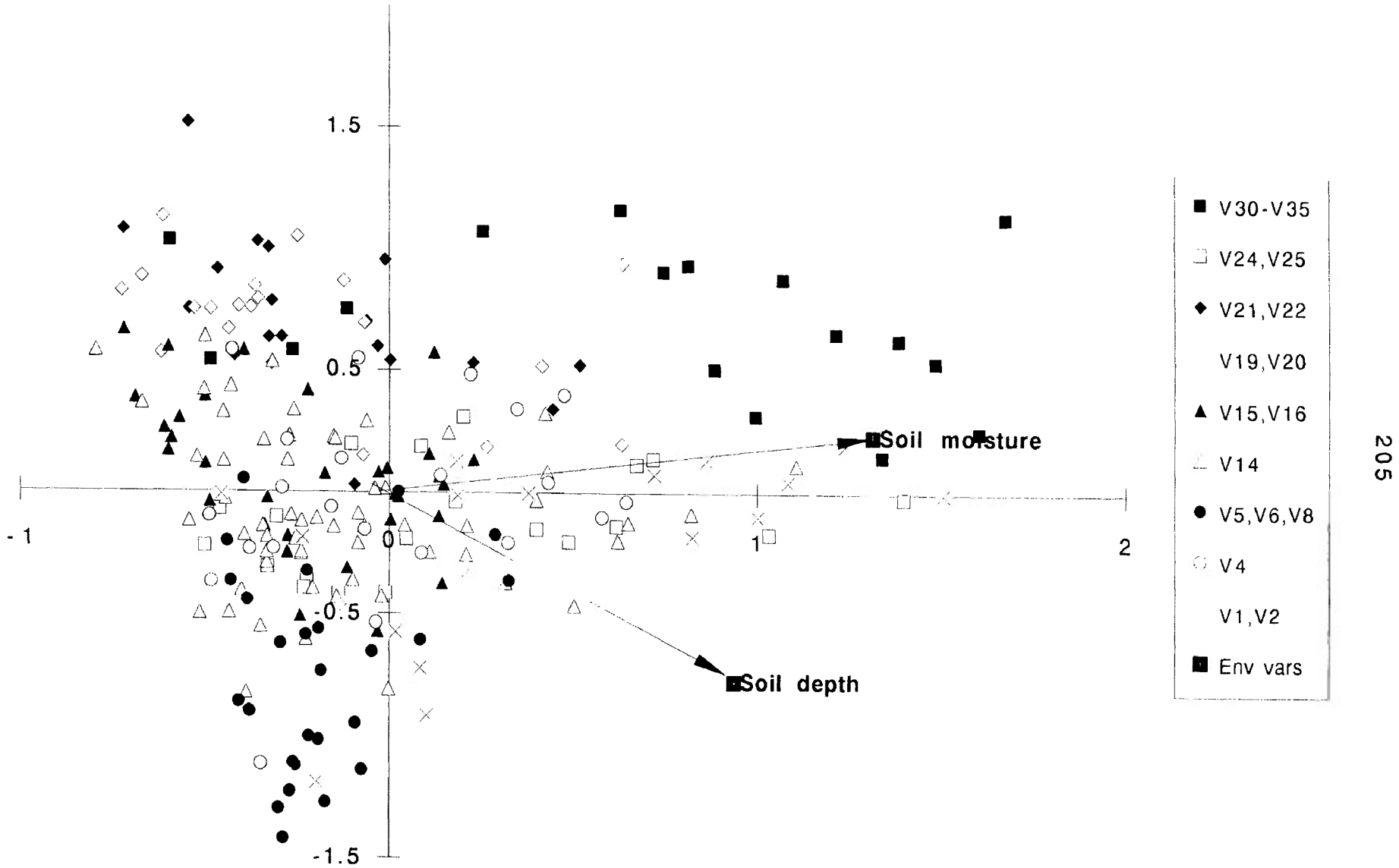
Env vars=Position of environmental (canonical) variables' vector head (multiplied by 5).

Figure 4.6.15. SU diagram for CCA of all strata cover, soil moisture and depth as canonical variables, SUs labelled by soil moisture



ES=extremely shallow, VS=very shallow, MS=medium shallow, D=deep, MP=mucky peat, Env vars=position of environmental (canonical) variables' vector heads (multiplied by 5).

Figure 4.6.16. SU diagram for CCA of all strata cover, soil moisture and depth as canonical variables, SUs labelled by soil depth.



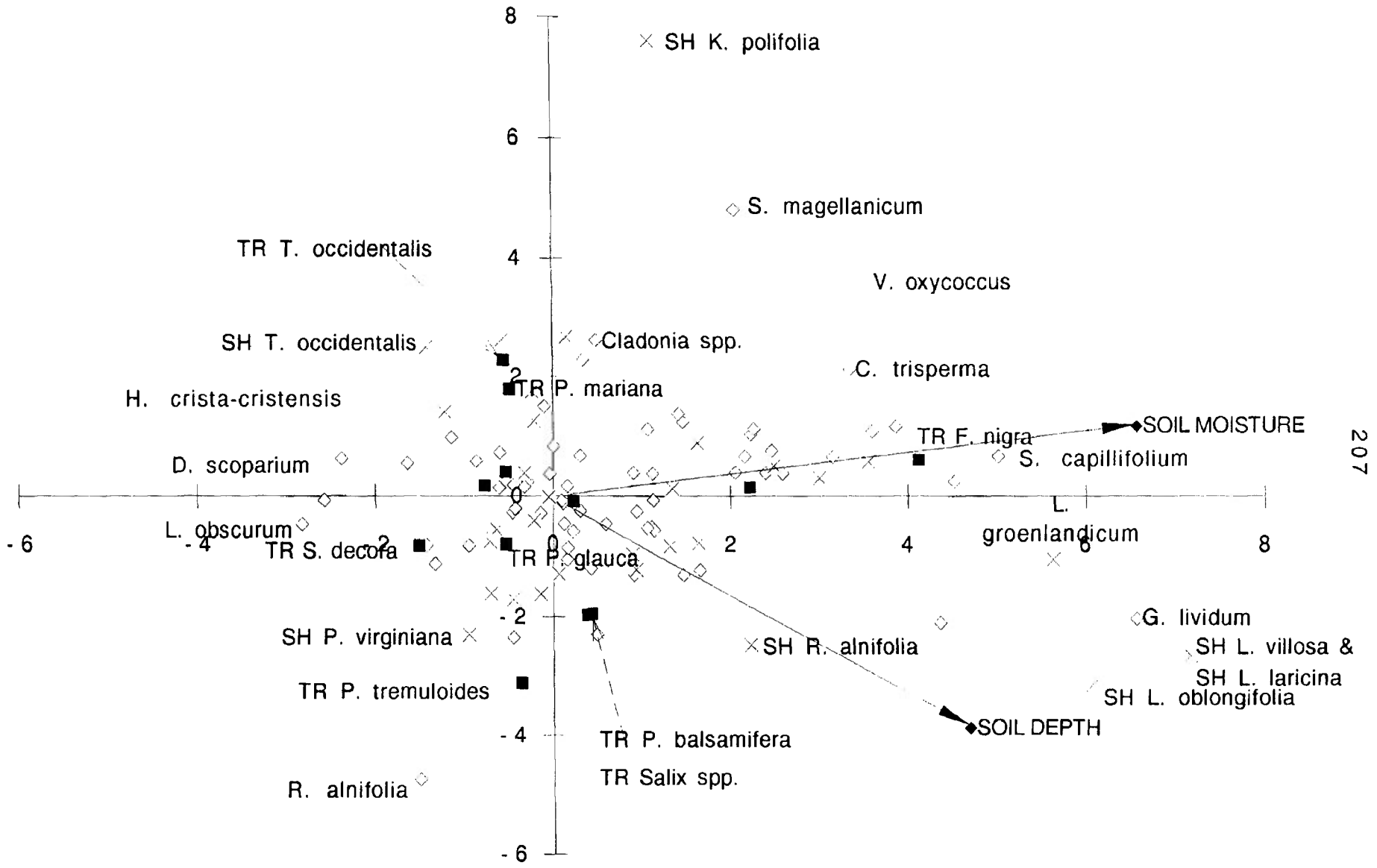
Env vars=position of enviromental (canonical) variables' vector heads (multiplied by 5).

Figure 4.6.17. SU diagram for CCA of all strata cover, soil moisture and depth as canonical variables, SUs labelled by FEC V-types.

4.6.17). This diagram and the corresponding ordination of species (Figure 4.6.18) reflects the tendency of *T. occidentalis* forests and *P. mariana* mixedwoods in this study to be located on shallow, xeric upland sites, as observed during sampling. The deep and wet sites of this study area supported either *P. mariana* bogs or *F. nigra* stands, and the moderately deep-soiled but xeric sites supported mainly *P. tremuloides*-dominated hardwood stands.

4.6.4 Tabular Comparison of Data Organized by CA Axis 1

The cover data of all three vegetation strata, ordered by species scores and SU (SU) scores for the first axis of the CA, are presented in Appendix 12. A tabular comparison of species in each strata revealed three fairly distinct zones along this axis, with boundaries between these zones occurring at about -0.8 standard deviations (s.d.) and 1.2 s.d. for species. The boundaries for SUs are less distinct but some general trends of the three species groups across the SUs are evident (Appendix 12). In general, the herb layer species occurring between *Climacium dendroides* and *Brachythecium* spp. in the ordered table, the shrub layer species from *Corylus cornuta* to *Diervilla lonicera* and the tree species from *Populus tremuloides* to *Alnus rugosa* tend to be most frequent and most abundant in SUs occurring at the negative end of axis 1. The most prominent herbaceous species in these SUs are *Aster macrophyllus, Acer spicatum, Aralia nudicaulis, Anemone quinquefolia, Mitella nuda, Brachythesium* spp., *Galium triflorum, Mnium* spp. and *Mertensia paniculata*. The most frequent and abundant shrubs at this end are *C. cornuta*, *A. spicatum, Lonicera canadensis* and *D. lonicera*. These species tend to decrease in frequency and abundance at about -0.4 along the SU scores, however some of the herbaceous species such as *A. nudicaulis, A. quinquefolia* and *M. nuda* occur infrequently in SUs at the positive end of the axis and *A. spicatum* as a shrub occurs throughout the whole range of SUs, although it is less frequent and less abundant at the extreme positive end (Appendix 12). *Populus tremuloides* is definitely the most



Environmental (canonical) variables' vector heads were multiplied by 25.

Figure 4.6.18. Species diagram for CCA of all strata cover, soil moisture and depth as canonical variables.

dominant tree stratum species in frequency and abundance at the negative end of the SU scores, occurring infrequently after about -0.4, and almost absent from the positive end of the axis. The other trees in this group: *Fraxinus nigra, Prunus pensylvanica, Populus balsamifera, Salix* spp. and *A. rugosa* are most prominent in SUs from about -0.7 s.d. to -0.2 s.d. on the axis.

The second group of species in the ordered table (Appendix 12) are most frequent and abundant in the mid-range of SU scores. These include the herbaceous layer species listed from *Lycopodium obscurum* to *Hylocomium splendens*, the shrub layer species from *Salix* spp. to *Kalmia polifolia* and the tree species from *Picea glauca* to *Sorbus decora*. There is some variation in the boundaries of importance for the different herb stratum species in this group. *Streptopus roseus, Rubus pubescens, Viola renifolia, Gymnocarpium dryopteris*, and a few other species increase first, peaking at about -0.6 in the SU scores and dropping off beyond that. *Clintonia borealis, Carex* spp., *Petasites palmatus, Trientalis borealis, Lycopodium annotinum, Moss* spp., *Rosa* spp., and *Abies balsamea* peak around -0.4 s.d. to -0.3 s.d. Some species including *Maianthemum canadensis, Cornus canadensis* and *H. splendens* peak at about -0.1 s.d. to 0.1 s.d. All of these remain fairly frequent to about 0.6 s.d., but begin to drop in abundance at about 0.1 s.d. in the SU scores. The shrub layer species in the second group increase gradually in frequency and abundance from the most negative SU scores (-1.2 s.d.) to a peak at about -0.4 s.d., and like the herbaceous species drop off at about 0.6 s.d. except for *A. rugosa, A. balsamea* and *Betula papyrifera*. *Abies balsamea* and *B. papyrifera* drop in cover but not frequency at this point, and the reverse is true for *A. rugosa*. In addition to these three species, *Cornus stolonifera, S. decora, Rubus idaeus, P. glauca* and *Rosa acicularis* are also abundant shrubs in this group. In the tree stratum, *P. glauca, A. balsamea* and *B. papyrifera* are most frequent and abundant near the mid-range of SU scores (about -0.5 s.d. to 0.5 s.d.), although they occur throughout the entire range. *Sorbus decora* is also in this second group of tree species, but it occurs infrequently

throughout the entire range of SU scores.

The third group of species are sparse at the negative end of the axis and increase gradually across, peaking at the positive end. In the CA-score ordered table (Appendix 12) these include *Thuja occidentalis* to *Vaccinium oxycoccus* in the herb layer, *Alnus crispa* to *K. polifolia* in the shrub layer and *T. occidentalis* and *P. mariana* in the tree layer. The herb and shrub species are most frequent and abundant from about 0.5 s.d. or 0.6 s.d. on. The dominant herb species in this group are *Dicranum scoparium* Hedw., *Gaultheria hispidula, Vaccinium angustifolium* and *Sphagnum capillifolium*, while the dominant shrubs in this group are *A. crispa*, *Amelanchier bartramiana, P. mariana* and *Ledum groenlandicum*. In the tree stratum, *P. mariana* is almost absent from the SUs at the negative end of the axis, and most frequent and abundant from about 0.4 s.d. and 0.5 s.d. on. *T. occidentalis* is generally less frequent, but has high cover values (about 40% and 50%) near the positive end of the axis, and some near the middle as well.

Thus, as was observed from the FEC plot and the species plot of this CA of combined strata, there is a general trend along axis 1 from species associated with hardwood stands on moist, nutrient rich sites to those more generally common in typical mesic boreal mixedwood sites, to the species occupying boggy, conifer-dominated, more nutrient poor sites. This is the most evident ecological gradient in the data.

4.7 CLUSTER ANALYSIS

The summary dendrograms for the cluster analyses of each data set as produced by Ward's algorithm are presented in Appendix 13. Six clusters were identified for the tree cover analysis, the herb cover analysis and the combined strata analysis, and only five were identified for the shrub cover analysis. The SUs within each cluster in Appendix 13 are ordered first by harvest treatment, then by soil moisture, soil depth and FEC V-type, respectively. Although this sorting of SUs gives the appearance that ecologically significant clusters occurred at lower levels within the larger clusters, this

was not the case. In fact, most smaller clusters contained a mixture of harvest treatment levels, soil moisture and depth categories, and FEC V-types. The four cluster analyses produced somewhat similar clusters of SUs. The analyses of the combined strata and of the tree stratum are the most similar, with clusters 2 to 4 of the tree stratum analysis resembling clusters 1 to 3 of the combined strata analysis in SU content, and cluster 4 of the latter resembling cluster 1 of the former. Clusters 5 and 6 of the tree stratum analysis are similar in SU content to the clusters of the same number in the combined strata analyses (Appendix 13a and b). Each cluster of the shrub stratum analysis and the herb stratum analysis contains SUs from two or three clusters of the combined strata analysis (Appendix 13).

Cluster summaries (Table 4.7.1) showed little evidence of clustering according to harvest treatment in any of the four analyses. Cluster 4 of the analysis on combined strata contains only SUs from CC and DC, and cluster 1 of the tree stratum analysis contains no HP SUs and only one DC SU. However, all other clusters in each analysis have at least one SU from each harvest treatment level, and many contain a fairly even balance of the four levels (Table 4.7.1). There is no evidence that clusters of SUs are due to soil depth and soil moisture classifications, since each cluster of each analysis has a mixture of SUs belonging to several soil depth and moisture classes (Table 4.7.1). Neither do clusters seem to be based upon combinations of harvest treatment levels with soil depth and soil moisture classes (Appendix 13).

There is, however, some evidence that the clusters of the four analyses correspond to similar FEC vegetation-types (Table 4.7.1). For the cluster analysis of all three strata combined, cluster 1 is composed of *Abies balsamea /Picea glauca* dominated stands (V16 and V25) and *Picea mariana* dominated stands (V19, V30 to V37), cluster 2 contains *Thuja occidentalis* dominated stands (V21 and V22) and cluster 4 contains SUs belonging to mostly hardwood stands (including V1 and V2) especially *Populus tremuloides* dominated stands (V5, V6, V8), with some mixedwoods (V14).

Table 4.7.1. Summary information of cluster analyses performed on percentage cover of sample units of the RC-17 project; the number of sample units falling into each treatment, each soil depth and moisture category and each FEC V-type are displayed for each cluster.

		NUMBER OF SAMPLE UNITS																					
Stratum on which the classification was performed:		Combined strata						Tree stratum						Shrub stratum					Herb stratum				
Clusters identified by the classifications:		1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	1	2	3	4	5	6
Total sample units per cluster:		34	18	56	21	61	46	21	35	21	68	39	52	72	16	51	75	22	66	30	42	52	27	19
Treatments	OC	12	10	12	10	5	10	11	11	10	19	1	7	12	1	16	20	10	15	7	10	15	6	6
	DC	11	2	13		21	15	1	10	2	17	12	20	24	4	12	16	6	16	9	12	14	6	5
	HP	2	5	17		12	9		7	6	9	11	12	11	2	14	13	5	8	8	8	8	11	2
	SC	9	1	14	11	23	12	9	7	3	23	15	13	25	9	9	26	1	27	6	12	15	4	6
Soil depth and moisture:	dry-extremely shallow	2	4	1		2	6		2	4	4	1	4	2			9	4	7	5			1	2
	dry-very shallow	10		3	2	15	5	1	7		7	9	11	12	2	3	17	1	8	7	4	10	2	4
	fresh-medium shallow		2	4	2	3	4	2		3	2	3	5	5	3	4	2	1	5	1	1	4	4	
	fresh-deep	4		5	12	16	7	12	3	1	10	9	9	17	6	4	17		13	1	8	10	8	4
	moist-extremely shallow		2	1		1	3			2	2		3	1		2	2	2	3	1	1		2	
	moist-very shallow	11		6		2	7		12		9	2	6	7		4	14	1	8	3	1	8	1	5
	moist-medium shallow	1	8	11	3	13	10	3	1	8	14	8	9	17	4	12	8	5	10	5	12	14	5	
	moist-deep		2	10	2	9	4	3	4	3	5	7	5	10	1	8	6	2	10	6	5	2	4	
	mucky peat	6		15					6		15			1		14		6	2	1	10	4		4
FEC V-types																								
1 Balsam poplar hardwood and mixedwood				5	1	3	3	1			11			5		6	1		3		4		4	
2 Black ash hardwood and mixedwood				6	1			1			6			2		5					7			
3 White birch hardwood and mixedwood				8		8	6			1	16	2	3	7	2	6	7		9		2	7	4	
5 Aspen hardwood					4			4						3	1				1			2	1	
6 Trembling aspen(white birch)-balsam fir/mountain maple					9	6	1	10			2	1	3	9	2	1	4		8		2	4	1	
7 Trembling aspen-balsam fir/balsam fir shrub																								
8 Trembling aspen(white birch)-mountain maple				1	4	1		2			1	3		2	2	1	1		1		2	2	1	
14 Balsam fir mixedwood				8	2	27	24	2	1	1	15	9	33	21	5	8	27		21	1	10	17	12	
15 White spruce mixedwood				5		2	1		1		1	6		2	2	1	3		5		1		2	
16 Balsam fir-white spruce mwd/feathermoss		6		7		5	6	1	3		3	7	10	10		4	10		2	12	2	2		6
19 Black spruce mwd/herb rich		8		2		1	1		12					1		3	8		3	4	1	2		2
20 Black spruce mwd/feathermoss		7							6								5	2				2		5
21 Cedar/mountain maple			17				1			18						4	1	13	7	9				
22 Cedar/speckled alder/labrador tea			1							1								1		1				
24 White spruce-balsam fir/shrub rich				8		7	2				6	9	2	7	1	6	3		4		8	4	1	
25 White spruce-balsam fir/feathermoss		1				1	1					2	1	2	1							2		1
30 Jack pine-black spruce/blueberry/lichen		2									2						1	1						2
31 Black spruce-jack pine/tall shrub/feathermoss		3							3								3					3		
33 Black spruce/feathermoss		2							2								1	1						2
34 Black spruce/labrador tea/feathermoss(sphagnum)		2		1					2		1					1		2			1	1		1
35 Black spruce/speckled alder/sphagnum		2		4					4		2					5		1	2	1	1	2		
37 Black spruce/ericaceous shrub/sphagnum		1							1									1				1		
no I.D.				1							1			1						1				

Clusters 5 and 6, which fuse at the lowest level (Q=74.5, Appendix 13) are similar to each other, dominated by *A. balsamea* mixedwood (V14) and containing several similar V-types with varying compositions of *A. balsamea*, *P. glauca* and *Betula papyrifera* (V3, V6, V15, V16, V19, V24, V25). Cluster 3 has similar FEC V-types to clusters 5 and 6, but contains a greater variety of FEC types, including wet site types (V2, V34, V35). Despite its similarity to clusters 5 and 6 in terms of FEC V-types, cluster 3 fuses with cluster 2 (Q=86.8) and cluster 1 (Q=94.5) before joining with the other clusters (Q=104.8) (Appendix 13a). The clusters of the tree cover analysis show similar groupings of FEC V-types to their corresponding clusters in the combined strata analysis. However, cluster 4 (which corresponds to cluster 3 of the combined strata) has a closer relationship to cluster 5 (Q=186678) and 6 (Q=217161) in this analysis than to the other clusters (Q=256326) (Appendix 13b), as would be expected by the similar V-types of these classes. The classes of the shrub and herb analyses do not show the groupings of these FEC V-types as clearly (Table 4.7.1).

It is important to note that the other attempted cluster analysis algorithms, the centroid and median methods, did not show clearly identifiable clusters. The high degree of chaining and the large number of reversals in the dendrograms produced by these methods indicated that distinctions among ecological types were vague. Therefore, it is likely that the vegetation on the RC-17 site forms broadly recognizable types (as evidenced by clusters in Ward's methods), but that there is a high degree of intergradation among them.

4.8 COMPARISON OF ORDINATION AND CLASSIFICATION RESULTS

Neither the classifications nor the ordinations indicated any noticeable effects of the four harvest treatments on vegetation cover for the RC17 area. In addition, these two genres of vegetation analysis showed a lack of obvious clustering or ordering of the SUs according to soil moisture and soil depth classes, and therefore a low correspondence

between these two environmental variables and vegetative composition and cover.

The indistinct clusters and chaining that occurred in the trial classification methods (centroid and median) and the intermingling of several FEC V-types in the more distinct clusters of Ward's method of classification suggested a continuous pattern of vegetative change throughout the RC-17 site. This continuous nature was reflected in the ordinations as well (Figure 4.6.3). In fact, the six clusters obtained from the classification of the combined strata by Ward's method, overlaid on the CA of the combined strata, show some similarity in SU groupings and intergrading (Figure 4.8.1). Cluster one, the last to fuse with other clusters in the classification (Q=94.5, Appendix 13a), is located along the positive end of axis 1 of the CA, fairly distinct from the other SUs (Figure 4.8.1) and occupying the area that is greatly influenced by conifer wetland species such as *Picea mariana, Ledum groenlandicum*, *Sphagnum* spp., etc. (Figure 4.6.1). Cluster 2, composed completely of *Thuja occidentalis* dominated stands, is the most distinct cluster, occupying the positive end of axis 2. However, it merges with many clusters along axis 1, being closest to cluster 3 on axis 2, as it was in the cluster analysis (Q=86.8, Appendix 13a). Clusters 5 and 6, which are the most similar in the cluster analysis (Q=74.5, Appendix 13a) merge in the CA ordination near the centre of both axes (Figure 4.8.1), and cluster 4, which is more distinct from them in the cluster analysis (Q=80.6, Appendix 13a), is also slightly separated from them in the CA (Figure 4.8.1). Cluster 3 lies between cluster 1 and cluster 2 in the CA, corresponding somewhat with its position in the classification (Appendix 13a). Its intermingling with clusters 5 and 6 reflect its previously mentioned closeness (as cluster number 4) to these clusters in the cluster analysis of tree cover (Appendix 13).

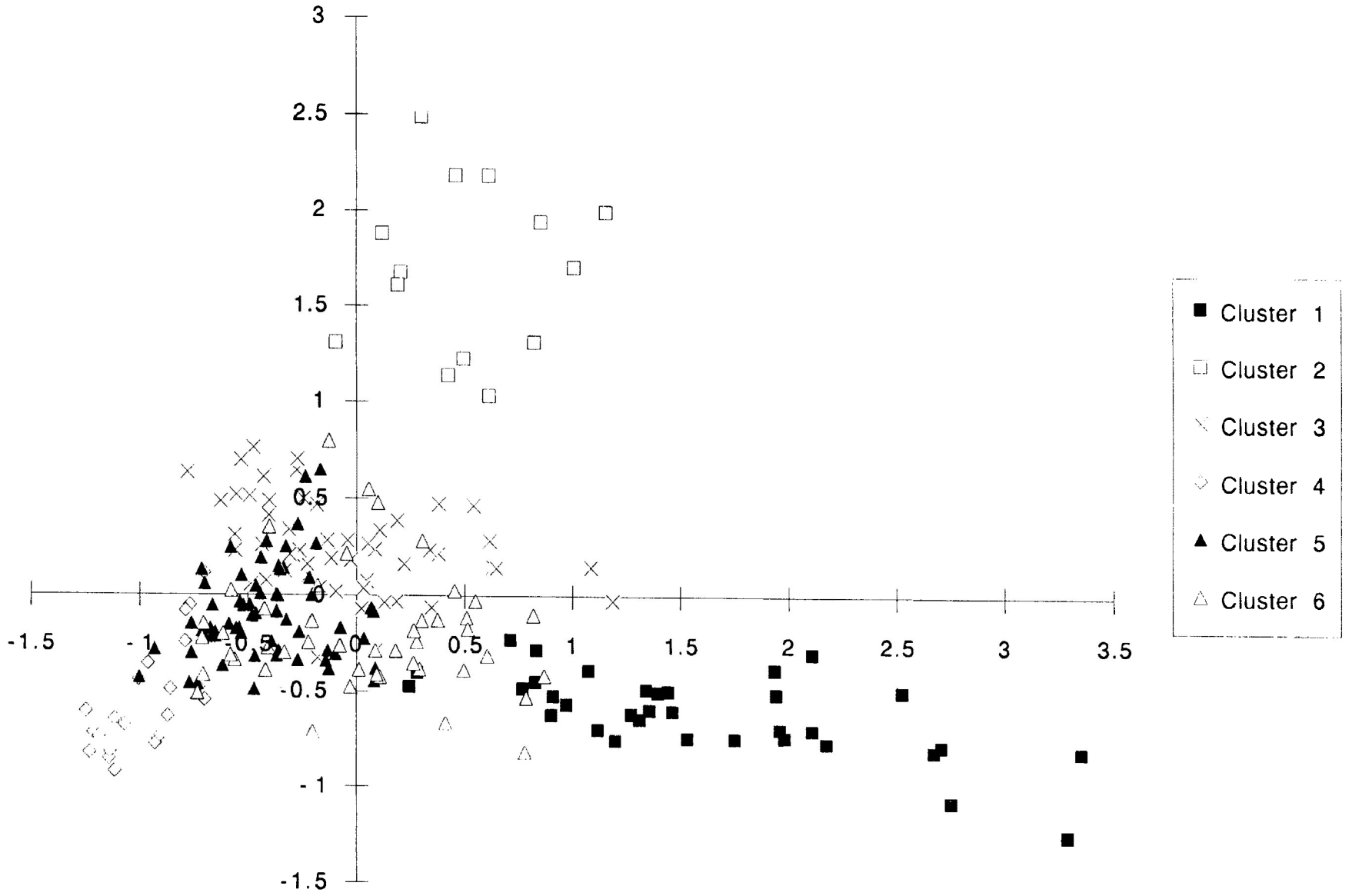


Figure 4.8.1. Overlay of cluster analysis (based on cover data of all strata) clusters on the CA ordination of the RC17 sample units.

CHAPTER 5 - DISCUSSION

5.1 EFFECT OF HARVEST TREATMENTS ON SPECIES COMPOSITION AND ABUNDANCE

The principal conclusion to be drawn from the median polish analyses, the ANOVA tests, the ordinations and the classifications is that naturally regenerating boreal mixedwood communities resulting from the four harvest treatments did not differ substantially from each other. Although median polish treatment effects suggested that tree measures were higher in treatment SC and that shrub densities were somewhat lower in SC and CC than in DC and HP, the differences in t.e. among treatments were very small. Significant treatment differences for individual species, found by ANOVA and Fisher's PLSD, were few for all three strata, and did not occur consistently among the same treatments. Thus, species did not respond in groups to the four harvest treatments. Species composition was very similar among the four treatments, with no evident fidelity of certain species to certain harvest treatments. The dominant species of each stratum were essentially the same for all treatments, and for most species, their values for density, dominance, frequency, cover, and dbh did not differ significantly among treatments.

5.1.1 Tree Stratum

5.1.1.1 Expected Trends

At 27 to 37 years old, natural fire-origin boreal mixedwood stands are generally dominated by *Populus tremuloides* and/or *Betula papyrifera* and a few *Pinus banksiana*, with a secondary canopy of *Picea glauca* and/or *Picea mariana* developing beneath them, a few smaller *Abies balsamea* seedlings in the understorey, and a fairly dense growth of *Acer spicatum* and *Corylus cornuta* (Day and Harvey 1981). The hardwood canopy may be quite dense by this stage (Van Cleve and Viereck 1981). The 27 to 37 year old boreal

mixedwood forest on the RC17 site, of harvest origin, should differ from the above description in several respects. The principal difference should be a much higher presence of *A. balsamea*, since harvesting will not have destroyed all of the abundant *A. balsamea* advance growth that occurs in old stands (Hosie 1954, MacLean 1960). Inter- and intra-specific competition may have reduced the *A. balsamea* component by this stage, to comprise about 21% of the canopy (Morris *et al.* 1988). *Picea* spp. should be a much smaller component of the harvested mixedwood forest than it would be in a burned forest, due to lack of suitable seedbeds, lack of sufficient seed supply, and hardwood competition (Hosie 1954). *Picea* spp. should have been steadily increasing in density and dominance since the harvest, to comprise about 40% of the canopy; hardwoods should comprise the remainder. Many *Picea* spp. stems should also be present in the suppressed subcanopy (Morris *et al.* 1988).

In the clearcut plots (CC), *Populus tremuloides* may be the most dominant hardwood, since cutting of its mature stems stimulates dense suckering (MacLean 1960, Yang and Fry 1981, Jeglum 1983). If some or all hardwoods were left standing, *B. papyrifera* (or *P. tremuloides*) will likely share dominance with *A. balsamea* (Yang and Fry 1981). *B. papyrifera* may be more prominent where only softwoods were cut (SC, DC and HP), since *P. tremuloides* suckering should have been reduced (Schneider 1988, Navratil *et al.* 1991), and mature hardwoods may have sheltered its seedlings and advance growth from environmental extremes (Brace and Bella 1988). Hardwood density should be even lower in HP than in the other 'softwoods only' cuts, due to the expected suppression of suckering by the poisoning.

Since the forest on the RC17 site was horse-logged, *A. balsamea* may be more important than *B. papyrifera*, *P. banksiana* and *P. mariana*, due to a lack of sufficient disturbance to create suitable seedbeds, and lack of destruction of the abundant *A. balsamea* advance growth (Clemmer and Atkins 1980, Jeglum 1983). *Pinus banksiana* will be greatly reduced, since it requires exposure of mineral soil (Ellis and Mattice

1974) and intense heat in order to release seed from its cones (Hosie 1954). In addition, its presence in the canopy of the original stand was low (Hughes 1967) due to the age of the stand and therefore there was little seed supply.

5.1.1.2 Actual Trends

In the tree stratum of this post-harvest boreal mixedwood forest, *Abies balsamea* was the principle softwood component and the most dominant of all species for most measures in all four harvest treatments. The two *Picea* spp. combined generally comprised less than 30% of the canopy for all of the tree stratum measures, and the high relative dominance (basal area) of *Picea glauca* in HP was the only instance in which one of them surpassed *A. balsamea* importance. *Betula papyrifera* was the most dominant hardwood species, generally more important than both *Picea* spp., except in terms of dominance (basal area).

The largest treatment differences in tree measures would be expected between CC and HP, with hardwood dominance being greatest in the former, and softwood dominance in the latter. However, no significant treatment differences (ANOVA) occurred for total density of commercial softwoods or commercial hardwoods. Also, although S:H ratios were higher in HP than in CC, these differences were small, with SC having a lower S:H than CC for all measures, while DC had a higher S:H than HP for density, frequency and overall IV. In addition, none of the dominant tree species had significant treatment differences (ANOVA) that supported the expected trend, and the only species which showed indications of it in the 'unprotected' LSD and/or median polish residuals were *P. glauca* (all measures), *Populus balsamifera* (density and frequency) and *Populus tremuloides* (density, frequency and cover). The overall IVs of these three species also matched the expected trend of hardwoods being most prominent in CC and less so in HP, with the reverse occurring for the softwood.

Betula papyrifera is the only dominant tree species that had any significant

treatment differences when all plots were included, with its density and cover in CC being lower than in the other treatments, including HP. This is contrary to expected results and Lees' (1964) findings in an Alberta study of different harvesting intensities in mixedwoods. In that study, 10 years after harvest, *B. papyrifera* regeneration was best in the most intense cuts, the clearcut and the seed tree cut.

Salix spp. frequency in the tree stratum was significantly higher in HP than in CC and DC, and this trend was also evident in its overall IVs. Navratil *et al.* (1991) noted that harvesting conifers only in boreal mixedwoods promotes invasion of *Salix* spp. on moist sites. However, ecological significance of the observed differences for *Salix* spp. is unclear, as is that of the significantly high cover of *A. balsamea* in DC when mucky peat-dominated plots were excluded from ANOVA. Median polish residuals indicated that even without the exclusion of mucky peat sites, *A. balsamea* had higher values in DC for all measures except dominance and dbh, for which SC had the highest values. Since DC is one of the later-cut treatments, this may suggest that stands in this treatment still have the dense growth of *A. balsamea* that occurs in naturally regenerating cutovers that have not completed the self-thinning process (Richardson 1971, Morris *et al.* 1988).

5.1.1.3 Trends in Spatial Pattern

Payandeh (1973) reported a high degree of clustering in boreal mixedwood stands. In the present study, the overall pattern of trees was significantly clumped in the CC, HP and DC treatments when all plot data for each treatment were combined. However, only five individual plots (one each of HP and DC and three CC plots) supported this, showing significant clumping. During sampling, clumps and 'walls' of trees, separated by open patches and 'strips', were observed in one of these CC plots, where cedar formed a principal part of the canopy. However, although cedar is known to regenerate vegetatively on organic soils (Sims *et al.* 1990), it was not significantly

clumped in this treatment. Examination of the spatial pattern of individual species suggests that clumping may have been largely due to two species, *Abies balsamea* and *Betula papyrifera*. They were both significantly clumped in CC and DC, and *A. balsamea* was also clumped in HP, while *B. papyrifera* was clumped in SC.

Clumping of *B. papyrifera* was expected in CC, since hardwoods were cut in this treatment, and sprouting was likely prolific, forming small groups of several *B. papyrifera* stems around cut stumps. Sprouting may also have occurred to some extent in SC and DC, if *B. papyrifera* stems were damaged during the cut, or if the root collar was exposed to intense radiation following the harvest (MacLean 1960). In HP, the mature *B. papyrifera* stems were destroyed, which should have deterred sprouting, so that any *B. papyrifera* regeneration would have been from seed originating outside plots. Dead *B. papyrifera* stems, with evident girdle marks and no sprouts around them, were observed in HP, while dead birch with clumps of trees around them, evidently stump sprouts, were observed in SC, and clumped young birch were observed frequently throughout the study site. The deterrence of stump sprouting by chemical poisoning was likely the cause of the random distribution of *B. papyrifera* in HP.

Explanation of clumped distribution of *A. balsamea* is more complicated. From the age measurements, it was clear that most *A. balsamea* stems in DC and HP were of advance growth origin, while in CC and SC, most stems originated after the cut. The clumping of *A. balsamea* in DC and HP may therefore be a result of microsite patterns that existed prior to the cut. In undisturbed boreal mixedwoods, the most suitable conifer seedbeds are rotten wood, exposed mineral soil, and mixed mineral soil/humus, created by windfalls or other disturbance (MacLean 1960, Hughes 1967). Conifer regeneration would have been largely restricted to these microsites. In temperate mixedwood forests, the variability of the canopy influences understorey microsites, often resulting in a patchy distribution of herbs; herb species distribution in turn has been shown to influence tree seedling pattern (Maguire and Forman 1983). Therefore,

the clumped pattern of *A. balsamea* stems in the DC and HP plots in 1990 may have been due to the patchy understorey that occurred beneath the mature mixedwood forest in 1961-63, or it may have been due to the pattern of residual conifers left by the harvest. Horse-logged mixedwood forests in the Clay Belt region of Ontario tend to have an alternating pattern of conifer and hardwood strips; presumably the former occurs where conifer advance regeneration survived, the latter where it was destroyed by horses. On the RC17 site, although such strips were not obvious, areas that appeared to be old strip roads were often observed to be open, almost free of a canopy, with low vegetation such as shrubs and grasses. A patchy distribution of tree cover was noted on parts of some plots.

In CC, where *A. balsamea* appears to be mainly of post-harvest origin, the clumped pattern of its trees in 1990 may have been due to the pattern of microsites that were created by harvesting. *Abies balsamea* probably germinated mainly on areas where some mineral soil and humus were exposed, and its survival likely occurred mainly in sheltered areas, possibly under conifer saplings or light slash. The lack of significant clumping of *A. balsamea* in SC, where most stems were of post-harvest origin as in CC, is difficult to interpret. It is possible that residual hardwoods may have influenced the distribution of *A. balsamea* regeneration, but this would likely lead to clumping rather than random distribution, unless the conifers filled into spaces left by a random distribution of mature hardwoods. Payendeh (1973) noted that the hardwood component of boreal mixedwoods was almost randomly distributed, and that dominant conifers in boreal mixedwood stands were clumped. Yet in the current study, the post-harvest growth of *B. papyrifera* in SC of the RC17 site was clumped; therefore the old growth may have had a similar distribution.

The significantly clustered pattern of *Picea mariana* in CC, where it was largely of post-harvest origin, may be due to its establishment on suitable seedbeds, as mentioned for *A. balsamea* above. The lack of significant clumping of *P. mariana* in DC

was surprising, since most of the measured stems in DC were of advance growth origin, and *P. mariana* advance growth is mostly of layer origin in stands undisturbed for long periods of time (Stanek 1968). Layers should have a tendency to be clumped around the trees from which they originate.

5.1.2 Shrub and Herb Strata

5.1.2.1 Expected Trends

At 27 to 37 years old, natural fire-origin boreal mixedwood stands have a secondary canopy of *Picea glauca* and/or *Picea mariana*, a few small *Abies balsamea* seedlings in the understorey, and a fairly dense growth of *Acer spicatum* and *Corylus cornuta* (Day and Harvey 1981). The typically dense hardwood canopy of this stage shades out many early successional herb species, but allows establishment of feathermosses, such as *Pleurozium schreberi* and *Hylocomium splendens* in the understorey (Van Cleve and Viereck 1981).

Many boreal understorey species are capable of vegetative regeneration, from rhizomes or stolons, and several of these grow best under full light; this allows them to expand rapidly following harvesting, due to the increase in light and decrease in root competition caused by overstorey removal (Heinselman 1981, Brumelis and Carleton 1989, Bell 1991). Other understorey species regenerate rapidly after disturbance from seed buried in the forest floor (Heinselman 1981). Therefore many understorey species invade or increase their abundance in harvested boreal stands (Haig and Curtis 1974, Ellis and Mattice 1974, MacLean 1960, Metzger and Schulz 1984, Brumelis and Carleton 1989). Some shrub species are known to invade forests following harvesting (*Amelanchier* spp.), others to increase in abundance (*Alnus rugosa*, *Rubus pubescens*), while several have been cited under both categories (*Corylus cornuta*, *Diervilla lonicera*, *Populus tremuloides*, *Prunus pensylvanica*, *Rubus idaeus* L. var. *strigosus*

(Michx.) Maxim). This is also true for herb stratum species, with invaders (*Athyrium filix-femina* (L.) Roth, *Brachythecium curtum* (Lindb.) Limpr., *Convolvulus sepium*, *Corydalis sempervirens*, *Geranium bicknelli*, *Solidago* spp., *Viola incognita* Brainerd), increasers (*Aralia hispida*, *Aster* spp., *Aulacomnium palustre* (Hedw.) Schwaegr., *Calamagrostis canadensis*, *Cladonia coniocraea* (Flk.) Spreng., *Cornus canadensis*, *Galium* spp., *Polytrichum* spp., *Sphagnum warnstorfii* Russ., *Tetraphis pellucida*), and those referred to as either (*Carex* spp., *Epilobium angustifolium*, *Fragaria* spp., *Pteridium aquilinum*, *Polygonum cilinode*).

There is little documentation of response of the boreal forest understorey to different harvesting methods. However, degree of disturbance seems to influence species composition and structure of forest understories. Following harvest of only softwood species in boreal mixedwoods, *A. spicatum* and *C. cornuta* invade dry sites, while *Salix* spp. and grasses invade moist sites (Navratil *et al.* 1981). On sites selectively cut for large *Picea* spp., shrubs such as *C. cornuta* can become dense and tall, hindering *P. glauca* regeneration (Johnson 1986). Clearcutting has been shown to produce a denser, more diverse shrub layer than various partial cuts (selection, seed tree, shelterwood, etc.) in temperate forests (McDonald 1976, Irwin and Peek 1979). In northern hardwood forests 50 years after harvest, partial harvesting methods (group selection and single tree selection) had produced patchy canopies which maintained a weed/disturbed-forest species component in the understorey, while also supporting a higher proportion (>80%) of herbaceous species typical to undisturbed forests than did clearcut stands (50%)(Metzger and Schulz 1984). Therefore, the partially cut stands had a high herb diversity. Clearcut stands had the greatest number of grasses and sedges and the greatest invasion of weed/disturbed-forest species, such as *Rubus idaeus*, *Epilobium angustifolium*, *Taraxacum* sp., *Cirsium* spp., *Trifolium* spp., and *Anaphalis margaritaceae*. Single-tree and 3-group selection cuts had a higher abundance of *Galium triflorum* than did the other cutting methods, while clearcuts and 8-group selection cuts

had a greater abundance of *Athyrium filix-femina* and *Streptopus roseus* (Metzger and Schulz 1984).

In boreal forests, Brumelis and Carleton (1988) noted that several rhizomatous perennials were more common on horse-skidded sites than on wheel-skidded sites, and Outcalt and White (1981) noted that stands harvested by the full-tree method had more shrub and herb species than controls (unharvested) and than stands harvested by the tree-length method. In a temperate forest, it was noted that residual species dominate areas where the canopy is removed but the ground surface undisturbed, that invaders dominate sites that have been burned following canopy removal, while both residual and invading species make up regeneration of the understorey where the ground has been disturbed, but not burned, following canopy removal (Dyrness 1973). In the latter case, the residual species are principally shrubs, the invaders being herbs. In boreal, upland *P. mariana* stands, feathermosses generally decrease in importance following harvest, while shrubs, herbs and grasses increase, regardless of cutting method (Jarvis 1961). Harvesting boreal mixedwoods may raise the water table, stimulating invasion by *Alnus* spp., *Salix* spp. and *Populus balsamifera* (Navratil *et al.* 1991). In northern hardwood forests 50 years after harvest, more than two-thirds of importance value totals were attributed to species typical to undisturbed forests, regardless of the harvest method (Metzger and Schultz 1984).

5.1.2.2 Actual Trends

There were several shrub and herb species that had significant or nearly significant treatment differences in cover and/or frequency (and/or density, for shrubs), and several more that showed evident treatment contrasts in the median polish residuals, 27 to 37 years after harvest. However, differences did not occur consistently among the same treatments, and no patterns were evident, except for a large number of herb layer species with high values in treatment HP (*Abies balsamea*, *Anemone*

quinquefolia, *Aster macrophyllus*, *Brachythecium* spp., *Carex* spp., *Diervilla lonicera*, *Equisetum pratense*, *Hylocomium splendens*, *Mitella nuda*, Moss species, *Petasites palmatus*, *Rhytidiadelphus triquestrus*, *Rosa acicularis*, *Sorbus decora*, *Streptopus roseus*, *Viola renifolia*). In the shrub stratum, *Cornus stolonifera*, *Diervilla lonicera*, *Rosa acicularis* and *Rubus idaeus*, also had high values in HP. These species noted to have been more abundant in HP include species considered as increasers or invaders (*Aster macrophyllus*, *Brachythecium* spp., *Diervilla lonicera*, *Rubus idaeus*), and species that commonly occur in undisturbed or old, harvested forests (*Abies balsamea*, *Anemone quinquefolia*, *Streptopus roseus*, *Viola* spp.). Poisoning the mature hardwoods may have decreased early competition from *Populus tremuloides* and *Betula papyrifera* regeneration on these sites, and provided a patchy 'canopy' (standing dead *B. papyrifera* and *P. tremuloides*) that allowed a denser, more diverse herb/shrub layer to develop. The only species included in these lists that previously showed a response to different harvest methods were *R. idaeus* (shrub layer) and *S. roseus* (herb layer), which were both more abundant on clearcuts than on single-tree and 3-group selection cuts (Metzger and Schultz 1984), somewhat contrary to the results of the current study.

The only species that seemed to show a previously documented response were *Acer spicatum* in the shrub layer and *Corylus cornuta* in the herb layer. Both have been shown to invade dry boreal forest sites after cutting of only softwoods (Navratil *et al.* 1991) and the latter has also been recorded as very abundant on sites selectively cut for large *Picea glauca* (Johnson 1986). In the current study, both were most abundant in SC.

Reasons for responses of some of the other shrub layer species are uncertain. *L. groenlandicum* is most common on wet sites (Bell 1991); its dominance in CC may be due to the high proportion of mucky peat sites in this treatment. *Abies balsamea* was significantly higher in DC and HP than in the other two treatments, and *Alnus rugosa* also showed a tendency to be higher in these treatments, although it was not significant. DC

and HP were the last cut treatments, and therefore represent a slightly earlier stage of development than the other two. The greater presence of these two species in the shrub layer may be due to a shorter time for interspecific competition to reduce *A. balsamea* density, and to a shorter time for canopy closure to decrease the dominance of *A. rugosa*. However, one of the other most common shrubs, *A. spicatum* showed a non-significant tendency to be higher in DC and SC, stands of different ages, but where only softwoods were cut. The tendency for *Thuja occidentalis* to be higher in CC and HP was unexpected, since extremely shallow sites, on which *T. occidentalis* was most common before harvest (MacLean 1954), were more abundant in SC (Table 3.2.1).

Pleurozium schreberi was the most dominant species in the herb layer. It showed high values in DC compared to CC, according to median polish residuals. However, *H. splendens* had a high cover in HP compared to DC and CC, and *Ptilium crista-cristensis* (Hedw.) De Not. showed no obvious treatment differences. Therefore, feathermosses showed no consistent treatment trends. The other dominant herb layer species, *A. macrophyllus*, *Clintonia borealis*, *Cornus canadensis*, *Maianthemum canadense*, and *Rubus pubescens*, are rhizomatous perennials that can quickly colonize disturbed sites by resprouting (Brumelis and Carleton 1989), but they are a mixture of invader and old forest species. Most were more abundant in horse-skidded than machine logged *Picea mariana* lowland sites (Brumelis and Carleton 1989), but only *A. macrophyllus* and *C. canadensis* showed any response to harvest treatments in the current study, both having low values in SC, but otherwise different trends.

When the two plots with mostly wet, mucky peat sites were removed (CC5A and DC6A), ANOVA results for herb species changed dramatically, with most previously significant or nearly significant differences becoming non-significant or less significant. All species except one, that were significant or nearly significant with all plots included, fell into either the hardwood or the mixedwood section of the CA-ordered table (Table 4.3.3, Appendix 12), and many of the differences noted included CC and/or

DC having lower values than the other treatments. This may indicate that these differences were due to the greater presence of mucky peat sites in DC and CC, and therefore lower proportional abundances of species more common to hardwood and mixedwood sites. This explains the disappearance of these differences when plots 5A and 6A were removed, and suggests that the few species (*Gaultheria hispidula, Ledum groenlandicum, Sorbus decora* and *Streptopus roseus*) that maintained or showed new significant differences after their removal may be the only ones actually affected by the harvest treatments. However, ecological reasons for their treatment differences are unclear, and since they involve such a small proportion of the total number of herbs on the site (4 of 113), it is possible that the differences were simply due to chance factors, rather than true harvest effects.

Overall, species in the shrub and herb strata showed little evidence of clear differences in the understory communities of 27 to 37-year old boreal forests resulting from the different harvest methods. The lack of consistent treatment pairings in the ANOVAs and median polish residuals may indicate that species responded individually to the treatments, or that the boreal mixedwood understorey community was not affected by the harvest treatments applied. However, it may also indicate that the many environmental factors involved in determining shrub and herb distribution in boreal forests confounded the treatment effects.

5.1.3 Species Diversity and Plot Resemblances

As in the analyses of tree, shrub and herb strata separately, the main conclusion of the diversity and plot resemblance measures, calculated from IVs for combined strata, was that there are no treatment trends. Measures of diversity, evenness and abundance varied as much within as among treatments. This contradicts the notion that intermediate levels of disturbance promote higher diversity than more intense disturbance (Fox, 1981), and that clearcuts produce extremely low diversity

(Freedman 1992). Although differences among treatments were small, the order of treatments from highest to lowest diversity for the two measures, λ and H', was CC, HP, DC and SC. This contrasts with studies in northern hardwood stands, where 50 years after harvest, clearcuts had lower diversity thad did single-tree and group selection cuts (Metzger and Schultz 1984), and 10 year-old clearcuts had lower diversity than progressive strip-cuts (Gove *et al.* 1992). In the current study, Hill's diversity numbers emphasized that a few species are strongly dominant (1/4 to 1/5) in the boreal mixedwood forest, and that many species (1/2 to 2/3) are relatively low in abundance and frequency.

In a chronosequence study of postfire succession in *Picea mariana*-dominated boreal forests of the Ontario Clay Belt, H' peaked at approximately 3.5, approximately 8 years after fire, and then decreased to less than 2.0 at 16 years postfire (Shafi and Yarranton 1973). The latter diversity was maintained to the oldest stand (44 years). Diversity (H') of 1 to 45 year-old postfire *Pinus banksiana*, *P. mariana*, *Pinus* spp.-*Picea* spp. and mixedwood (*P. banksiana-Populus tremuloides*) stands in northwestern Ontario ranged from 1.49 to 2.95; most stands had H' between 2.30 and 2.80 (Methven *et al.* 1975). The highest value, 2.95, was for the oldest stand, dominated by *P. banksiana*. Thus, the H' values determined for the RC17 site (3.48 to 3.69, for treatments) are near the high end of the normal range of diversity of boreal stands.

Plot resemblances indicated that all plots were highly similar to each other in terms of species composition and abundance. Chord Distances were larger than Percentage Dissimilarities, indicating that the plots were less similar in terms of proportional abundances than in terms of actual abundances of species. The only discernible patterns for diversity measures and plot resemblances were that pairs involving three SC plots, three DC plots and one HP plot seemed to resemble each other more closely than did other plot pairs, and these pairs also had similar diversity measures. This did not seem to be related to treatments, since three treatments were

involved in the pairings, and the other plots of SC, DC and HP were no more similar to these plots than they were to other plots.

5.1.4 Comparison of 1953 to 1990

Since all comparisons of 1990 data to 1953 data, in order to determine treatment trends, had to be made between 1990 harvest treatment data and 1953 data on the soil site types most prominent in each treatment, treatment differences were difficult to discern, and their validity uncertain. For the tree stratum, *Abies balsamea* density appeared to increase most in SC and DC, *Betula papyrifera* density in SC, and *Populus tremuloides* density in CC and SC. Increase in *A. balsamea* density was expected to be greatest in the least disturbed sites (including SC and DC, but also HP) due to less destruction of its advance growth during harvest. However, both *P. tremuloides* and *B. papyrifera* density would be expected to have the greatest increase in CC. The greatest increase of *B. papyrifera* in SC, and the large increase of *P. tremuloides* in the same treatment were unexpected, although, as mentioned previously, *Populus* spp. have been shown to increase more in partial cuts than in clearcuts in another study (Lees 1964). From the rough comparisons made, *Picea glauca* density decreased in only CC, while it increased in the others. This suggests that the 'only softwoods cut' treatments, including HP, may have improved its regeneration compared to clearcutting.

For softwoods, it seemed that *A. balsamea* advance growth density and frequency had decreased most in CC and SC in the shrub stratum and in DC and SC in the herb stratum. The decrease of *Picea mariana* density in both strata appeared to be greatest in SC (1990 value was 0 stems/ha). *Picea glauca* density in the herb stratum decreased most in CC (1990 value was 0 stems/ha). The reasons for and relevance of these treatment patterns are unknown. *Thuja occidentalis* advance growth density and stocking in 1953 was too variable to determine trends over time due to the treatments. Its presence seemed to be much more dependent on site type than that of other species.

5.1.5 Ordination and Classification

The ordinations and classifications corroborated the main findings of all of the previous analyses, i.e. that the harvest treatments did not greatly influence the vegetational composition and species' abundances of the boreal mixedwood stands. A slight trend of SC to DC to HP to CC was observed on axis 1 of the CCA with harvest treatment as a canonical axis. The order of treatments in this trend matches that of lowest to highest diversity, but does not coincide with the trends of HP and DC contrasting with CC and SC that were observed in S:H, Spr:F, and age for the tree stratum, and *Abies balsamea* values in the shrub stratum. However, there was a great deal of overlap among treatments in the ordinations, and therefore no evident species fidelity to treatments.

5.2 EFFECTS OF HARVEST ON SUCCESSION

5.2.1 Age and Height of Trees

In naturally regenerating harvested mixedwood stands, hardwoods, especially *Populus tremuloides*, generally originate from suckers and sprouts, while conifers, especially *Abies balsamea*, are typically advance growth (Hosie 1954, MacLean 1960), unless a seedbed treatment is applied and a seed supply is available. Therefore, although some *Betula papyrifera* may regenerate prior to harvesting on areas with exposed mineral soil (MacLean 1960) and in open areas of overmature stands (Cogbill 1985), most hardwood stems on harvested sites should be younger than the cut. The greater the degree of disturbance to advance growth and to the seedbed during harvesting, the greater should be the proportion of softwood stems that originate from seed after harvest to those that establish prior to harvest. Thus, in this study, a greater proportion of conifer regeneration would be expected to be of pre-harvest origin in the stands where only softwoods were cut, i.e. in the SC, DC and HP stands, than in the CC stands. Hughes

(1967) noted that following the first harvest on the RC17 site, more large advance growth was destroyed in CC than in SC, in strips receiving seedbed treatment. However, at that time, density of smaller advance growth and total advance growth density were comparable in both SC and CC to those in the uncut stands. If the HP or the SC and DC treatments were successful at inhibiting hardwood reproduction, hardwoods may be a few years younger than the cut, while those in the CC treatment should be as old as the cut.

Comparisons of age ranges and medians did not indicate that the HP or the SC and DC treatments had significantly delayed hardwood reproduction in comparison to the CC treatment. As expected, the age of most hardwood stems in all treatments was less than or equal to the number of years since the cut. However, in keeping with the ability of *B. papyrifera* to establish in openings of old mixedwood stands, several *B. papyrifera* stems in DC, HP and SC originated before harvest.

Most stems of all conifer species in DC and HP were of advance growth origin. In CC, only *Picea glauca* stems appeared to have originated mainly as advance growth in the pre-harvest forest, while *A. balsamea* and *Picea mariana* were principally of post-harvest origin. These findings fit the expectations. However, although the degree of disturbance in SC should have been about the same as in DC and possibly less than in HP, *A. balsamea* and *P. glauca* in SC were mostly of post-harvest origin. Post-harvest seed supply may have been responsible for this difference; SC plots had an available conifer seed supply (unharvested DC and HP plots), while no seed supply was available for DC and HP plots (the area surrounding the project having been cut contemporaneously). It is possible that the post-harvest origin conifers were better competitors than some of the older advance growth, which is often in poor condition (MacLean 1960); thus they predominated where there was a seed supply. Hughes (1967) noted that much of the *A. balsamea* advance growth was in poor condition, some with butt rot, within 3 to 5 years after the initial phase of the harvest. It is also possible that the three 'conifers only'

cuts left different amounts of residual mature *Picea* spp. and *A. balsamea*, therefore varying on-site seed supplies.

Populus tremuloides, *P. glauca* and *B. papyrifera* had the greatest median heights over all treatments, according to median polish, and where it occurred, median height of *P. mariana* was equal to or greater than that of *P. glauca*. At a comparable stage of post-fire boreal mixedwood succession, hardwoods are generally still dominant, in terms of height (Day and Harvey 1981), but conifers are often codominants at about 35 years after harvest (Morris *et al.* 1988). Median polish treatment effects and the 'unprotected' LSD indicated that tree height over all species was slightly higher in CC and SC than in DC and HP. This corresponds with the time since harvest; DC and HP are eight to ten years 'younger'; thus, advance growth have had more time to grow since release from suppression in CC and SC than in DC and HP, as have seedlings that established as a result of harvest. No significant differences in height were noted for individual species, although in a similar study of several harvest treatments in Alberta, *Picea* spp. height 10 years after harvest was greatest in a shelterwood cut (Lees 1964).

5.2.2 Softwood to Hardwood Ratio (S:H)

The original intent of the RC17 study was to find methods to increase the conifer component, particularly the *Picea* spp., of boreal mixedwood stands following harvest (Hughes 1967). The literature indicates that clearcutting mixedwood stands produces more prolific vegetative growth by hardwoods, especially *Populus tremuloides*, than does cutting of softwoods only (Schneider 1988, Navratil *et al.* 1991). Girdling and poisoning of hardwoods kills the mature trees (Waldron 1961), and is expected to prevent suckering and sprouting of new stems (Jarvis *et al.* 1966). Thus, if harvest treatments were successful, the early period of dominance by hardwood suckers and sprouts would have been prevented in HP, and lessened in SC and DC in comparison to CC. This would manifest in the 27- to 37- year old forest as a higher S:H for tree density,

dominance, etc. in HP compared to the other treatments, and in SC and DC compared to CC. As discussed in section 5.1.1.2, the results do not support this well. DC had the highest S:H for density, frequency and overall IV, and this descended through HP, CC and SC. For dominance and cover, the order was the same, except that DC and HP were reversed. This reversal possibly indicates better stem growth of softwoods in HP, but may also simply indicate a reduced number of large, residual hardwoods in HP compared to DC and the other treatments, this being due to the poisoning treatment.

5.2.3 Spruce to Fir (Spr:F) and Spruce to Hardwood (Spr:H) Ratios

The HP and CC methods were attempted particularly to determine their effect on *Picea* spp. growth in comparison to *Abies balsamea* and hardwoods. Spr:F for 1990 tree measures ranged from 0.38 to 1.74, with most being about 0.50. For regenerating clearcut mixedwoods in Ontario, Candy reported a Spr:F (density) of 0.33, less than that for CC of this study (0.51). The ratios in this study suggested that *Picea* spp. growth in comparison to *A. balsamea* was better on treatment HP than on the others, especially CC. Similarly, Spr:H ratios were better on HP and DC than on SC and CC, although the ratio did not descend from HP, to SC and DC, to CC, for all measures. This latter difference runs contrary to the expected trend of hardwoods being more dominant in younger stands and also contrary to seed supplies, since *Picea* spp. seed supplies were higher for the earlier cut stands. However, it coincides with the expected harvest treatment trend, of *Picea* spp. faring better in comparison to hardwoods in HP than in CC, and moderately in the other two treatments. Therefore, these ratios may indicate some success of the HP, and possibly DC, treatments in improving the *Picea* spp. component of post-harvest boreal mixedwoods, in comparison to clearcuts. This was confirmed by harvest treatment trends for density, dominance etc. of *Picea glauca*, *Populus tremuloides*, and *Populus balsamifera* in the tree stratum, though not for *A. balsamea*, *Picea mariana* and *Betula papyrifera*, as noted in section 5.1.1.2.

5.2.4 Tree Species' Reproduction in the Shrub and Herb Strata

Abies balsamea dominated the softwood reproduction in the shrub and herb strata. Both of the *Picea* spp. were relatively unimportant in comparison to it. Its dominance of regeneration was due to a combination of factors. All three of the principal conifer species on this site, *A. balsamea*, *Picea glauca* and *Picea mariana*, are relatively shade-tolerant, allowing them to germinate and survive under a canopy for several years (MacLean 1960, Day and Harvey 1981), but *A. balsamea* is the most tolerant, capable of surviving up to 30 years or more (MacLean 1960). Thus, it is often the dominant tree species in the understorey of boreal stands (Dix and Swan 1971). The pre-harvest forest on the RC17 site was very old (>200 years) and decadent; thus, *A. balsamea* comprised the majority of advance growth in the original forest (Hughes 1967). Horse-skidding was used in the harvest, and this is known to cause little destruction of advance growth (Jeglum 1983, Clemmer and Atkins 1980, Brumelis and Carleton 1989). Observations following the harvest indicated that most small advance growth had survived, and that although some *A. balsamea* had been damaged or died, it was still more abundant than the *Picea* spp. regeneration (Hughes 1967). Much of the 1990 reproduction probably originated from seed produced by the original advance growth crop that survived the harvest. Since that crop was primarily *A. balsamea*, as supported by tree stratum results, and since *A. balsamea* seed seems to have a higher capacity to germinate in hardwood leaf litter than does *Picea* spp. seed (MacLean 1960), the 1990 advance growth was dominated by *A. balsamea*.

Betula papyrifera was the only commercial hardwood species of any importance in the 1990 understorey. It was more abundant than either of the *Picea* spp., but much less so than several hardwood shrub species. Prior to harvest, seedlings of *B. papyrifera* were abundant on exposed mineral soil resulting from windthrown trees, and sprouts were common from root collars of mature trees (Hughes 1967). *Betula papyrifera* is capable of germinating in canopy gaps (Cogbill 1985). The *Populus* spp.

are much more intolerant of shade (Bell 1991), and were therefore scarce in the understorey of this 27 to 37 year old boreal mixedwood.

Abies balsamea and *B. papyrifera* were the only two commercial species to have significant treatment differences in the understorey. In the shrub stratum, *A. balsamea* had significantly high measures in both HP and DC, the latest harvested sites. These sites had no close available seed source after harvest, as did SC and CC. However, *A. balsamea* in the shrub stratum of HP and DC may have seeded in from trees in SC and CC that have matured since harvest; thus its higher values in HP and DC may be due to a shorter time period for reduction of its regeneration by inter- and intra-specific competition. Some of the *A. balsamea* regeneration in HP may be individuals that established from trees on the HP plots after the hardwoods were treated, but prior to the cut. The higher cover of *B. papyrifera* in the shrub stratum of DC compared to other treatments may be related to the time since harvest; DC is ten years younger than SC and CC, and therefore the hardwoods may still be in the process of self-thinning.

5.2.5 Comparison of 1953 to 1990

5.2.5.1 Tree Stratum

The most striking feature in the comparison of the 1990 tree stratum to the 1953 pre-harvest tree stratum was that species' rank orders of importance (density) in most soil site types were very similar for the two dates (Table 4.5.1). This emphasizes the importance of the pre-disturbance community composition in determining the post-disturbance forest composition, and supports the Initial Florisitics hypothesis (Egler 1954). In 1990, *Abies balsamea* was more dominant, in terms of density, than in 1953. It was the most numerous tree species on eight site types in 1990, compared to six site types in 1953. It increased considerably in comparison to other species on some site types. This corresponds to the increase in *A. balsamea* that commonly occurs in harvested boreal stands, especially following horse-

logging (Clemmer and Atkins 1980, Jeglum 1983). *Populus tremuloides* had increased from the 1953 to 1990 forest, although its abundance was still low. Its extremely low density in the 1953 forest was due to the advanced successional stage (~200 years post-fire) of the forest, the relatively short life span of *P. tremuloides*, and its high intolerance to shade. *Betula papyrifera* was obviously more dominant, due to its longer life span, and its ability to regenerate in canopy gaps. During sampling of the RC17 site, large, old *B. papyrifera* and *P. balsamifera* (live and dead), but almost no old *P. tremuloides,*were observed.

In general, densities of all species in 1990 are considerably higher than those in 1953, reflecting the immaturity of the 1990 forest in comparison to that of 1953. The 1990 forest was composed of a large number of individual stems of small size, while the 1953 forest was composed of fewer, but likely larger individuals. A yield table for the *Populus tremuloides-Betula papyrifera-Picea* spp.-*A. balsamea* type in Ontario, reported by MacLean (1960), indicates that young forests of this type (30 years old) have a density of about 5000 small (<10cm dbh) stems per ha, and 600 large (>10cm dbh) stems per ha, while mature stands (130 years old) have a density of about 600 stems per ha each of small and large stems. Morris *et al.* (1988) reported total density of harvested boreal mixedwood stands to be 3500 stems per ha at 35 years, and this had decreased to about 1400 by age 85.

It is notable that *Thuja occidentalis* had become more widely distributed by 1990 than it was in the pre-harvest forest. Previously almost restricted to extremely shallow (-es) sites, it had increased its density considerably in F-ms and M-ms sites, and slightly in F-d and M-d sites by 1990. Prior to harvest, although *T. occidentalis* trees were only common on the extremely shallow sites, *T. occidentalis* seedlings were common on M-ms and M-d soils as well (Hughes 1967). Hughes (1967) noted that the presence of the *T. oocidentalis* seedlings on the other site types corresponded with the tendency for the *T. occidentalis* component of boreal mixedwood stands on moist sites to

increase with old age. Other authors have noted this tendency (Janke *et al.* 1978, Bergeron and Dubuc 1989); it may be related to the increase of well-decomposed wood in old forests, which serves as a good seedbed for *T. occidentalis* (Bergeron and Dubuc 1989). In this study, the continued increase of *T. occidentalis* density in the tree stratum after harvest may be due to two factors: 1) the advance growth noted by Hughes (1967) may have survived harvest, and benefitted from the release, and 2) since the site was not burned, the availability of well-decomposed wood and other suitable seedbeds may not have been reduced greatly by harvesting.

In comparing the S:H of 1953 to 1990, one would expect a decrease, since fast-growing, vegetatively reproducing hardwoods tend to dominate early successional boreal mixedwoods, while slower-growing, more tolerant softwoods gradually replace them. MacLean (1960) reported this shift in a yield table for *P. tremuloides-B. papyrifera-Picea* spp.-*A. balsamea* type stands: at 30 years, S:H for large stems (>10cm dbh) was 0.1, while at 130 years it was 2.0. However, S:H for small stems (<10 cm dbh) was greater than 1.5 even at age 30 and had increased to about 225 by age 130 (MacLean 1960). In the present study, S:H was greater than 1.0 on all site types at both dates, but was lower in 1990 than in 1953, as expected, on all types except the M-vs and all ms types (Table 4.5.1). The decrease in S:H to 1990 was largest on the -es site types, with forests previously considered to be mixed softwoods (Hughes 1967) essentially converted to mixedwoods by harvesting. Jeglum (1983) noted a similar shift in *Picea mariana* stands that were strip-cut near Nipigon, Ontario. Since most of the M-es sites sampled were in treatments CC and DC, while most of the D-es sites sampled were in HP and SC (Table 3.2.1), the type of harvest does not seem to greatly affect the S:H ratios.

Since most of the decreases in S:H from 1953 to 1990 were small, and S:H increased on some site types, it appears that even at this early stage of succession (27 to 37 years post-disturbance), the RC17 forest has shifted from the initial hardwood-dominated phase to a softwood-dominated phase. According to Day and Harvey (1981),

this shift generally occurs at approximately 25 years in fire-origin stands. Horse-skidding tends to favour *A. balsamea* over hardwoods, since advance regeneration is usually preserved (Clemmer and Atkins 1980, Jeglum 1983), and Morris *et al.* (1988) noted that in naturally regenerating harvested boreal mixedwood stands, hardwoods are never more dense than *A. balsamea*, the latter comprising over 50% of the stems even in stands 0-20 years old. Since harvesting on the RC17 site was done with horses, preserving a large amount of advance growth (MacLean 1955), the S:H may not have decreased greatly even initially following harvest.

5.2.5.2 Tree Stratum 1990 vs Advance Growth 1953

Prior to harvest, S:H of advance growth was less than or equal to 1.0 on half of the site types, and less than 4.0 on the others (Table 4.5.2). The lowest ratios were due to a high presence of *Betula papyrifera* advance growth. The post-harvest 1990 tree stratum which regenerated in part from this advance growth had a S:H greater than 1.0 on all site types. *Abies balsamea* and *B. papyrifera* had the highest softwood and hardwood advance growth densities in 1953, and decreased the most to their 1953 tree densities. These trends are part of the self-thinning that takes place in naturally regenerating boreal mixedwood stands, as a result of inter and intra-specific competition, and in the case of the shade-tolerant *A. balsamea* regeneration, mortality due to exposure (Morris *et al.* 1988). The most numerous species were affected the most on a proportional basis. Tree density of two species in 1990 was higher than their 1953 advance growth on particular sites: *Picea glauca* on both es site types, and *Thuja occidentalis* on F-ms sites. These apparent increases were likely due to either suitable seedbeds and available seed following harvest, or presence of residual trees, left uncut at the time of harvest.

5.2.5.3 Tree Species' Reproduction 1990 vs 1953

Density and frequency of reproduction of all commercial tree species in the

shrub and herb strata in 1990 tended to be lower than 1953 advance growth density and stocking. As was noted in comparison of 1990 tree species to 1953 advance growth, the decreases were greatest for the two species with the highest advance growth at both times: *Abies balsamea* and *Betula papyrifera*. The generally lower advance growth abundance in the 1990 forest compared to that of the 1953 forest was probably due to the successional status of the two forests. The 1990 forest was young; the high numbers of stems in the early reproduction phase has begun to decrease due to recruitment of most hardwoods and many conifers to canopy size, and reduction of resources in the understorey as a result of canopy closure. Although all of the principal canopy species (*A. balsamea*, *B. papyrifera*, *Picea glauca*, *Picea mariana*, *Populus tremuloides*) are capable of producing seed by about 15 years (Sims *et al.* 1990), none of them attain optimum seed production before 30 to 40 years, and the *Picea* spp. are much later (60 for *P. glauca*, 150 for *P. mariana*) (Burns *et al.* 1990, Sims *et al.* 1990). Therefore, seed production in the 1990 forest would be low for conifers. Dense mats of leaf litter from the young hardwoods would also inhibit conifer reproduction, especially of the *Picea* spp., which have small seeds and correspondingly small seedling roots (MacLean 1960). Reduced light in the 1990 forest due to the closed canopy would prevent new regeneration of the hardwoods, even if seed prodution was good. In contrast, the 1953 forest, which was approximately 200 years old, was composed of mature trees with high seed production, canopy gaps due to tree mortality, an abundance of exposed mineral soil and humus from wind-felled trees, good growth of moist feathermosses and a large amount of decayed wood on the forest floor (Hughes 1967). The highly-lit gaps were suited to reproduction of *B. papyrifera*, and the exposed mineral soil and humus, the mosses and the decayed wood provided suitable seedbeds for conifer regeneration (Hughes 1967).

5.2.5.4 Herb Stratum 1990 vs 1953

Most species that were abundant in the pre-disturbance forest were still abundant in the 1990 forest, and vice versa. Species lists for the two time periods are also quite similar. Sutton (1964) noted that little change in the understorey had occurred 4 years after harvest on sites of the RC17 project which did not receive seedbed treatments. The changes that did occur, such as an increase in seed-origin *Aster macrophyllus* and vegetative expansion of *Acer spicatum*, seemed to be due to changes in canopy density (light interception) and seed supply. These similarities in species composition and abundance between the late-successional 1953 forest, early post-harvest forest, and the post-harvest mid-successional 1990 forest, correspond with Egler's (1954) Initial Floristics hypothesis, and with findings of other boreal studies that species composition does not change drastically in the herb layer after fire (Morneau and Payette 1989, Black and Bliss 1978) or harvest (Ellis and Mattice 1974, Outcalt and White 1981), and even approaches pre-harvest abundances with time in northern hardwoods stands (Metzger and Schultz 1984). Ellis and Mattice (1974) and Outcalt and White (1981) noted that early successional changes in the understoreys of harvested boreal sites consisted principally of gradual changes in abundance rather than in species composition, and this was expected to continue in response to the gradual closing of the canopy and the accompanying microenvironmental changes (Outcalt and White 1981). The similarity of pre- and post- harvest species lists in the present study corroborates these findings and expectations.

Despite this Initial Floristics character, there were 30 species, infrequent in 1990, that were not present in 1953 or 1957, and 16 species that were present in the 1953 or 1957 tallies, but not in 1990. Many species that were present in the 1953 and 1957 tallies but absent from 1990 lists are species known to invade sites or increase in abundance following harvest: *Corydalis sempervirens*, *Epilobium angustifolium*, *Polygonum cilinode*, *Pteridium aquilinum* (Outcalt and White 1981),

Trifolium pratense, *Rumex acetosella* L. (Metzger and Schulz 1984). Several of these were part of the 1957 general list only (Table 4.5.3), and therefore likely located on already harvested, possibly site-prepared sites in CC and SC plots, not on unharvested sites. Some species more common in the early tallies than in the 1990 tally were observed to decrease in abundance following harvests in Minnesota boreal mixedwood: *Lonicera canadensis*, *Lycopodium obscurum*, *Lycopodium clavatum*, *Petasites palmatus*, and *Vaccinium* spp. (Outcalt and White 1981). Most of the species unique to the 1990 data were very infrequent, and tend to have specific habitat requirements, e.g. *Corallorhiza trifida* Chat., *Moneses uniflora* (L.) Gray (common in shady, moist, conifer-dominated forests), *Trillium cernuum* L. (rich, moist *Populus balsamifera* or *Fraxinus nigra* stands), *Geocaulon lividum*, *Rhamnus alnifolia* L'Hér, *Smilacina trifolia* and *Vaccinium oxycoccus* (common on *Picea mariana* dominated organic soil sites) (Baldwin and Sims 1989). However, some are known to be relatively shade-intolerant species that increase on harvested sites, e.g. *Fragaria vesca* L. and *Prunus* spp. (Outcalt and White 1981). Therefore the species presences and absences in the two forests (time periods) did not seem to correspond well to known successional tendencies. This may be partly due to the patchy nature of the canopy in both forests: many canopy gaps existed in the late-successional, preharvest forest, and numerous gaps and clearings were observed in the mid-successional postharvest forest. These gaps likely maintained early successional species in both forests. This phenomenon has been noted in temperate forests (Glitzenstein *et al.* 1986, Clebsch and Busing 1989).

5.3 INITIAL FLORISTICS CHARACTER OF THE BOREAL MIXEDWOOD

As noted in the previous section, the high similarity of overstorey dominants and understorey composition between 1953 and 1990 indicates that the boreal mixedwood forest on the RC17 site has a strong Initial Floristics (*sensu* Egler 1954) character, i.e. most of the species that comprise the new community were present at the time of

disturbance, and little to no new invasions, *sensu* Relay Floristics, were involved in regeneration. This Initial Floristics character has been previously demonstrated in post-fire boreal forest canopies, via overstorey compositions often being almost identical to the original forest, and via a lack of species replacements over time (Heinselman 1981, Bergeron and Dubuc 1989, Morneau and Payette 1989). As mentioned in the previous section, this phenomenon is also common in boreal post-harvest communities (Ellis and Mattice 1974, Outcalt and White 1981). Post-harvest vegetative composition in 1- to 5-year old Ontario boreal forests was found to be strongly dependent on pre-harvest stand types (Walsh and Krishka 1991). Understorey communities of northern hardwood stands demonstrated the same Initial Florisitics character, with 50th year composition being highly similar to controls and to early postharvest communities (Metzger and Schultz 1984).

This Initial Floristics character of boreal forests, demonstrated by the strong resemblance of the pre- and post-harvest forests of the RC17 site, is likely due to the ability of most boreal species to regenerate rapidly following natural disturbance (Rowe 1961, Carleton 1979, Heinselman 1981). This Initial Floristics nature of boreal forests, i.e the strong tendency for regenerating post-disturbance communities to resemble pre-disturbance communities, may partially explain the lack of evident differences between species composition and abundances among the communities that resulted from the four harvest treatments in this study. However, in northern hardwood communities, although pre- and post- harvest forests were largely similar, as the degree of harvest disturbance increased, the proportion of 'non-forest' or invader species increased in the post-harvest forest, being largest in the clearcuts (Metzger and Schulz 1984).

5.4 PHYTOSOCIOLOGICAL TRENDS

5.4.1 Soil Moisture and Depth

The ordinations and classifications indicated that soil moisture and depth were not the principal environmental factors influencing boreal mixedwood composition. Despite this, the CCA with soil depth and moisture as canonical variables did show that certain FEC V-types tended to occupy certain soil depth and moisture classes: *Thuja occidentalis* stands and *Picea mariana* mixedwoods on shallow, xeric to mesic, upland sites; *P. mariana* bogs on mucky peat sites; *Populus balsamifera* stands and *Fraxinus nigra* stands on deep, moist mineral soil sites; *Populus tremuloides* hardwoods on deep, mesic sites; and *Picea glauca / Abies balsamea / Betula papyrifera* mixedwoods common throughout all types, but mostly in the center of the two gradients.

These trends correspond with known moisture preferences of the dominant tree species in each of these stand types. *Picea mariana* in pure stands is most common on poorly drained, lowland, organic soil sites (Dix and Swan 1971), but occurs on a wide range of sites, including dry, very shallow mineral soils (Sims *et al.* 1990). On the latter type, it is often mixed with the other species of the boreal mixedwood (Sims *et al.* 1990). These two extreme types, pure lowland stands and upland mixedwood stands, were the most common on the RC17 site. In northern Ontario, *T. occidentalis* is located on two site types: wet, organic soils; and moist, well to rapidly drained, mineral soils (Sims *et al.* 1990). On the latter, it is commonly associated with *A. balsamea*, *B. papyrifera*, *P. glauca* and *P. tremuloides* (Sims *et al.* 1990); this corresponds with its occurrence in this study. *Picea glauca* is found mainly on sites with intermediate moisture conditions, on all soil textures except clays; *A. balsamea* occupies dry to mesic, as well as wet-mesic sites, on sandy to loam soils (Dix and Swan 1971). On cutovers in the Manitouwadge area of Ontario, it tends to favour wet, nutrient-poor sites, since it is a poor competitior on richer, dry sites (Yang and Fry 1981). However, Maycock and

Curtis (1960) noted that neither *A. balsamea* nor *P. glauca* reached optimum development on mesic sites, the former growing better on wetter sites, the latter on drier sites. In this study, *A. balsamea* and *P. glauca* were both most typical in the intermediate ranges of soil moisture and depth, as indicated by their central positions on both the CAs and the CCAs for soil moisture and depth. *Betula papyrifera* typically occupies dry to mesic sites, on sandy to sandy-loam soils (Maycock and Curtis 1960, Dix and Swan 1971). In northern Ontario, it is common on sites with stony profiles and on thin till over bedrock (Gordon 1983). On Newfoundland clearcuts, *B. papyrifera* density was highest on dry sites, but its height was greatest on fresh sites (Richardson 1979). On the RC17 site, it seemed to be present on intermediate moisture types, falling near the centre of the soil moisture CCA.

Eigenvalues and intraset correlations indicated that moisture seemed to affect the shrub stratum slightly more than the other strata, while depth seemed to be a greater determining factor in species composition in the tree stratum than in other strata. The greater dependence of tree species on soil depth may be due to the different rooting characteristics of these species. *Populus tremuloides* and *B. papyrifera* growth is better on deep, rich tills than on shallow sites (Jeglum 1983). *Populus tremuloides*, and *Pinus banksiana* roots are concentrated in mineral soil horizons, while those of *P. glauca* and *P. mariana*, *A. balsamea* and *Larix laricina* are concentrated in organic soil horizons (Peterson 1988). Strong and La Roi (1983) have suggested that successional trends in boreal mixedwoods may be controlled by rooting depths to some extent. The shallow roots of the conifer species may deprive the lower roots of *P. banksiana*, *P. tremuloides* and *B. papyrifera* of water and nutrients, thus speeding the decline of these species. In addition, the increasing shade as the conifers develop allows an increase in moss cover, which further limits the amount of water and nutrients reaching the hardwood roots. Thus, early successional species may have a greater advantage on deep, moist sites where they can develop deep roots, and where moisture is not limited, as suggested by the

location of aspen-dominated stands in the current study.

Boreal canopy and understorey species have been shown to be related to soil moisture in other studies, with most species growing best or most abundantly on individual optimum moisture regimes, despite generally wide ecological amplitudes (Rowe 1956, Maycock and Curtis 1960). However, Swan and Dix (1966) found no relationship between vegetation structure and soil moisture factors (drainage regime, moisture content and water-retaining capacity) in western Canadian boreal forests. Rowe (1956) noted that relationships of plant species' distributions and vigour to environmental gradients may often be obscured by the broad but different ecological tolerances of most plants and by the compensating influences of other environmental factors. These may be the reasons for the lack of a strong relationship between plant distribution and soil depth and moisture on the RC17 site. However, it may also be that categories for these two variables were not sufficiently finely divided.

5.4.2 Canopy Composition Influences the Boreal Mixedwood

In the boreal forest, light and moisture conditions are generally correlated, and both related to canopy composition (Larsen 1980). Understories of hardwood canopies receive more light than those under conifer canopies (Rowe 1956) and, since they are more open than conifer canopies, hardwood canopies allow more rainfall to reach the understorey (Larsen 1980). The relationship between moisture and canopy is complicated however, since evaporation is greater in open (hardwood) canopies, but evapotranspiration and root competition for water are higher in dense (conifer) forests (Larsen 1980). Stands of very similar tree composition, but different moisture situations often have very different understorey composition and structure (Maycock and Curtis 1960).

The ordinations and classifications indicated that the most dominant pattern in the vegetation of the RC17 boreal mixedwood site was that of hardwood-dominated, to

mixedwood, to softwood-dominated stands. Rowe (1956) stated that this gradient is principally responsible for the understorey structure of boreal forests, due to its influence on light; the understorey progression from tall shrubs, to medium shrubs and tall herbs, to low shrubs and herbs, to mosses, is essentially a progression of increasing shade tolerance. Shrub and herbaceous layers are generally more vigorous under hardwood canopies, while mosses are more common under conifer canopies (Larsen 1980, Peterson 1988). In the current study, a dense shrub stratum was observed most commonly under canopies of mixedwood NWO FEC types, including White Birch Hardwood and Mixedwood (V4), Balsam Fir-White Spruce Mixedwood/Feathermoss (V16), Balsam Poplar Hardwood and Mixedwood (V1), and especially under canopies of Balsam Fir Mixedwood (V14). Swan and Dix (1966) also stated that the canopy's main influence on understorey vegetation was via light interception, and that conifer canopies with dense shade (*Picea mariana* and *Abies balsamea*) had the smallest number of understorey vascular species and low frequencies of these, but the highest percentage of moss cover, while the reverse was true for thin-canopied stands dominated by *Populus tremuloides*, *Betula papyrifera*, *Pinus banksiana* and to some extent *Picea glauca*. In the current study, the tabular comparison reflected this trend, with a larger number of vascular species being abundant and frequent under the hardwood-dominated canopies and the mosses being most prominent under conifer canopies (principally *P. mariana*).

For the RC17 data, the high degree of similarity between the CA for the tree stratum alone and the CA for all strata combined emphasized the importance of canopy type on the overall composition and structure of the boreal mixedwood. In their study of boreal forests of Saskatchewan, Swan and Dix (1966) noted a high correlation between separate ordinations of canopy and subcanopy. The fact that the separate CAs on shrub and herb strata resembled the CAs of tree stratum and all strata for the RC17 project indicates that the understorey species have some degree of canopy specificity or affinity. The table of cover values, with SUs ordered by CA axis 1, emphasized these affinities,

with most shrub and herb species being more common under one of the three main canopy types. The prominent understorey species in each of the three canopy types (hardwood, mixedwood and softwood) on the RC17 site tended to match the corresponding canopy types of the three-point *B. papyrifera* to *A. balsamea* succession and the two-point *P. tremuloides* to *A. balsamea* succession identified by Carleton and Maycock (1980). *Acer spicatum*, *Aster macrophyllus*, *Brachythesium* spp., *Corylus cornuta*, *Diervilla lonicera*, *Galium triflorum* and *Mertensia paniculata* were more prominent under hardwood canopies in both studies; *Cornus canadensis*, *Clintonia borealis*, *Maianthemum canadense*, *Rubus pubescens*, *Trientalis borealis* and *Viola renifolia* were found to be indifferent to canopy type by Carleton and Maycock (1980) and on the RC17 study area, they were most common under *A. balsamea IB. papyrifera IP. glauca* canopies, the most common stand type. *Coptis trifolia*, *Dicranum* spp. and *Pleurozium schreberi* were most prominent under conifer canopies in both studies. *Ptilium crista-castrensis* and *Hylocomium splendens* favoured conifer canopies and *Aralia nudicaulis* favoured hardwood canopies in Carleton and Maycock (1980), but tended to be more prominent under mixedwood canopies in the present study.

Despite these trends, studies have shown that less than or equal to half of boreal understorey taxa show specificity to only one monodominant canopy type, and that specificity to hardwood canopy types is much more common than to conifer types (Dix and Swan 1971, Carleton and Maycock 1981). Carleton and Maycock (1981) found a large number of species had high affinity to *Populus balsamifera*, but few were specific to *P. tremuloides* or *B. papyrifera* canopies, while Dix and Swan (1971) found that species favoured either *P. tremuloides* or *P. balsamifera*, but few favoured *B. papyrifera*. Carleton and Maycock (1981) noted that the affinities of understorey for canopy types was closely related to shared substrate requirements. They suspected that the dearth of strong affinities may be due to different modes of regeneration: the understorey regenerates almost entirely from on-site sources, i.e. persistent

subterranean parts and seed banks, while some of the canopy species, such as *Picea* spp. and *A. balsamea*, mainly regenerate from surrounding seed sources. They also noted that for both conifer and hardwood canopy types, those that occupied sites with high nutrient imports and rapid cycling (e.g. *P. balsamifera*, *L. laricina*) had more associated understorey species than those occupying sites with low nutrient imports and slow cycling. Although nutrient regimes were not measured on the RC17 site, it is evident that they play an important role in determining species composition. The pure *P. mariana* sites, which extended furthest along CA axis 1, had poor drainage and were likely nutrient poor; the corresponding understorey was evidently poorer in species than those of the drier, more mesic sites.

Since the herb stratum CA is more similar to the tree stratum and all strata CAs than is the shrub CA, herb species seem to be more dependent on canopy composition than are the shrub species. However, the relationships of understorey species to canopy types on the RC17 area are evidently not exclusive, since the separate herb and shrub strata cluster analyses did not greatly resemble the cluster analyses done on the tree stratum alone and on all strata combined. In addition, the table ordered by axis 1 of the CA on all strata showed that species do not form distinct groups, but rather, their distributions merge and overlap in a continuous mosaic. The lower percentage of the variance accounted for by axes of the herb stratum CAs and CCAs, compared to those of the other strata, indicate that a high degree of the variability in the boreal mixedwood forest, in terms of species composition and abundance, is caused by the large number of herbaceous species with low frequency and abundance.

The similarity of all of the CAs suggests that there is some underlying environmental gradient, or composite gradient, that influences overall species composition. However, it is also possible that tree species distribution depends on a combination of environmental factors and stochastic processes of immigration, availability of seed and seedbeds, etc., *sensu* Gleason (1926) and that the other strata

are determined largely by the microenvironments determined by the tree canopies.

5.4.3 Continuum Nature of the Vegetation

The two environmental variables measured on the RC17 site, soil moisture and soil depth, were evidently not sufficient to determine species composition of this boreal mixedwood forest, as indicated by low eigenvalues and percentage variance accounted for by the CCA axes, and also indicated by axis 1 of the CA, which displays species at both ends that are common to both wet and dry habitats. A comparison of the ordination and classification results emphasized the lack of evidence of a strong effect of either harvest treatment or soil characteristics on the species composition and abundance of the boreal mixedwood forests. The overlay of the two analyses indicate that there is a continuous pattern of vegetative cover, with FEC types intergrading into each other.

Although boreal plant communities on opposite extremes of moisture and other environmental gradients are evidently disparate, communities in between these extremes show a continuum of species composition and abundances, with no definite boundaries (Maycock and Curtis 1960). Several studies have shown that distributions of boreal understorey and canopy species cannot be described by simple environmental gradients, and that boreal communities cannot be classified into distinct plant associations (Maycock and Curtis 1960, van Groenewoud 1965, Swan and Dix 1966). Plant species' distributions often do not correspond closely to gradients of individual environmental factors, since many species have broad, but unique, environmental tolerances, and other factors may hide the effects of the one being studied (Larsen 1980). Therefore, boreal forest stands demonstrate a pattern of continuous variation in species composition and abundance, likely determined by a complex gradient of interdependent environmental factors, including light, moisture, organic matter depth, pH, root competition, etc. (Maycock and Curtis 1960, van Groenewoud 1965, Swan and Dix 1966). These multidimensional relationships should be considered carefully in any

interpretation of experimental treatments applied to the boreal forest (Maycock and Curtis 1960), such as those in the current study.

5.5 FUTURE DEVELOPMENT OF THE FOREST

If the boreal mixedwood forest on the RC17 site develops as a natural, post-fire forest would, the fast-growing pioneer species, *Populus tremuloides* and *Betula papyrifera* (and *Pinus banksiana*) will begin to decline in vigour at about 50 years after disturbance, thus releasing the slower-growing pioneers, the *Picea* spp. (Day and Harvey 1981, Van Cleve and Viereck 1981). The *Picea* spp. will gradually take over dominance of the stand, forming the overstorey at about 125 years after disturbance. As the shift from hardwood-dominated to conifer-dominated forest occurs, root competition and light interception will increase, causing the shrub understorey to become less dense, and feathermoss cover to increase (Rowe 1956, Swan and Dix, 1966, Larsen 1980, Peterson 1988). Several studies have indicated that the *Picea* spp. component of naturally regenerating, harvested boreal mixedwood stands will be greatly reduced from pre-harvest levels, while *Abies balsamea* and hardwood densities will increase (Navratil *et al.* 1991, Richardson 1979, Yang and Fry 1981, Morris *et al.* 1988).

At 27 to 37 years after harvest, *A. balsamea* was clearly the most important species of the boreal mixedwood on the RC17 site, with *Picea* spp. being less important than both it and *B. papyrifera*. *Populus tremuloides* was generally less important than the three main conifer species, but where it occurred, it was typically noted to form an overstorey over the suppressed conifer layer. This layered canopy was noted in several stand types, most commonly in NWO FEC type V6 (Trembling Aspen (White Birch)-Balsam Fir/Mountain Maple), but also in V1 (Balsam Poplar Hardwood and Mixedwood), V8 (Trembling Aspen (White Birch)-Mountain Maple), V14 (Balsam Fir Mixedwood), and V16 (Balsam Fir-White Spruce Mixedwood/Feathermoss). Thus, hardwoods will likely maintain a dominant canopy position for about 25 to 30 more years, with some *A.*

balsamea codominants. Then, as *P. tremuloides* and *B. papyrifera* begin to decline in health and vigour, and fall out of the stand, the suppressed *A. balsamea* and *Picea* spp. will take over canopy dominance. Some hardwoods will likely survive for many years after that, but if the forest remains undisturbed to more than 150 years postharvest, there will likely be few surviving *P. tremuloides* stems. However, a small *B. papyrifera* component may be maintained, due to the ability of this species to regenerate in canopy gaps (Cogbill 1985, Sims *et al.* 1990). This corresponds with the hardwood composition noted in the approximately 200 year old forest in 1953 (MacLean 1954)

Due to its prevalence on this site, and its recorded dominance in many harvested boreal stands, *A. balsamea* might be expected to be the principal conifer during the future development period. However, several factors may work against this, in favour of *Picea* spp. dominance. The most important of these factors is that many dead or defoliated stems of *A. balsamea* were observed throughout the RC17 site in 1990, especially on NWO FEC types V16, V24 (White Spruce-Balsam Fir/Shrub Rich), V4 (White Birch Hardwood and Mixedwood), and V14. Spruce budworm moths were often noted on the defoliated stems. In addition, signs of moose browsing were frequently observed, mostly on *Acer spicatum*, *Corylus cornuta* and *Cornus stolonifera*. In Isle Royale upland boreal forests, moose browsing was noted to drastically reduce *A. balsamea* densities, and *Picea glauca*, which is not a favoured browse species, was noted to increase in density, possibly due to reduced competition from the *A. balsamea* (Snyder and Janke 1976, Janke *et al.* 1978). Therefore, it is possible that as this forest ages, the *A. balsamea* component may decrease while the *Picea* spp. component increases.

Canopy cover was quite variable on the RC17 site, with trees often occurring in 'clumps' or 'walls', separated by open areas which were composed principally of grasses, sedges and shrubs. That these sites had not regenerated to tree cover may be due to effects of harvesting on the site, but it may also be due to a combination of ecological factors. It has been observed that many old forests often develop openings (due to tree

mortality) that do not fill in with tree species, often forming areas of long-term 'parkland' (MacLean 1960, Rowe 1961, Cogbill 1985). The clearings noted on the RC17 site may be of this type, since similar areas were noted prior to harvesting (Sutton 1964). Measurements of soil characteristics, such as compaction, development of the humus layer, nutrients, pH, etc. would be necessary to see if these sites differ from the surrounding forest sites, and to surmise whether they will develop tree covers in the future.

5.6 RELEVANCE TO PRESENT DAY PRACTICES

Although the RC17 study was initiated prior to mechanization of harvest in boreal stands, information about its succession is still relevant to present-day boreal mixedwood silviculture. Removing only the softwood component of boreal mixedwoods, where *Betula papyrifera* is the dominant hardwood species, is still currently practiced in Ontario, and some mixedwood forests are still left to regenerate naturally, with no site preparation.[1] In addition, growing concerns about the economic feasibility of intensive silviculture are leading some professionals to reconsider more extensive methods of regenerating boreal forests (Benson 1988).

Studies have shown that horse-skidding is generally less damaging to advance growth, but also creates less beneficial site disturbance, in terms of suitable conifer seedbeds, than mechanical-skidding (Ellice and Mattice 1974, Clemmer and Atkins 1980, Brumelis and Carleton 1989). A shift in dominance of cutover regeneration from *Abies balsamea* to *B. papyrifera* has therefore occurred with the shift from horse to mechanical logging (Clemmer and Atkins 1980, Jeglum 1983). However, some early studies of mechanized harvesting in boreal forests indicated that soil disturbance was not much greater than following horse-logging, and therefore would not be likely to improve

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[1] Personal communication, Mr. R. C. Bowen, Timber Management Planning Forester, Ontario Ministry of Natural Resources, Hearst District, March 16, 1993.

post-harvest establishment of conifer species over horse-logging (Horton 1965, Weetman *et al.* 1973). The common use of scarification in current boreal timber harvesting does, however, destroy some advance regeneration (McNichol and Timmerman 1981, Jeglum 1983) and increase seeding in of conifers (Lees 1970, Jeglum 1983, Roberts and Dong 1991). Therefore, boreal mixedwood sites treated in this way will likely have a higher *Picea* spp. to *A. balsamea* ratio than the RC17 site.

Current harvesting practices in the boreal forest generally involve skidding trees to roadside with limbs and foliage attached (termed full-tree harvesting).[1] This leaves little slash on site, and since a large proportion of canopy nutrients are stored in the foliage and young branches (Weetman and Webber 1972, Mann *et al.* 1988), this may decrease nutrient availability in boreal mixedwoods. Several studies have indicated that nutrient losses to the forest site are 50% to over 200% greater in full-tree harvesting (also termed whole-tree in some studies) than in tree-length harvesting (i.e. delimbing and topping stems before removal to roadside) (Timmer *et al.* 1983, Freedman *et al.* 1986, Maliondo 1988, Mann *et al.* 1988). Although these losses are usually small compared to nutrient reserves in the forest floor (Freedman *et al.* 1986, Gordon 1983) they may be high for particular elements such as phosphorus, potassium (Gordon 1983) and calcium (Freedman *et al.* 1986), and may be greater for particular species and forest types, such as *A. balsamea* (Timmer *et al.* 1983) and hardwoods (Maliondo 1988), due to the high crown to stem ratio for these species. The effects that large-scale practice of full-tree harvesting will have on the boreal mixedwood vegetational community are unknown, but there will likely be compositional and structural changes.

Therefore, there are evidently some important differences between the

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[1]Personal communication, Mr. R. C. Bowen, Timber Management Planning Forester, Ontario Ministry of Natural Resources, Hearst District, May, 1994.

harvesting practices used on the RC17 study and the mechanized harvesting, often with additional site preparation, used currently. The horse-skidding on the RC17 site probably caused less destruction of advance growth and provided less suitable conifer seedbeds than do contemporary practices. Contemporary full-tree harvesting probably causes a greater decrease in available nutrients to the regenerating forest than did the tree-length harvesting done on the RC17 site. Due to these differences, application of the RC17 overstorey removal treatments (clearcut, 'softwoods-only' cut, hardwoods poisoned followed by 'softwoods-only' cut, and deferred 'softwoods-only' cut) to a boreal mixedwood forest using today's practices, i.e. mechanized full-tree harvesting, might produce somewhat different results than were produced in this study, possibly showing more difference between the four overstorey treatments. In assessing the relevance of their study of 50 years of postharvest succession in northern hardwoods, Metzger and Schultz (1984) noted that recent changes in harvesting practices (increase in size and power of harvesting equipment and more complete utilization of wood) had led to greater site disturbance, including uprooting or destruction of perennating organs of many herb species, and reduced slash. However, they judged that since none of the different harvesting methods used in their study caused major changes in composition, or continued dominance by disturbance species, the innovations in harvesting practices that had occurred since their study were also not likely to cause great changes. In light of this judgement, the recent emphasis on natural regeneration, and the similarity of current harvesting practices to the 'softwoods only' cuts of the current study, the knowledge gained from the RC17 project, 37 years after its initiation, provides some valuable insight into the effect of contemporary harvest practices on natural regeneration of boreal mixedwoods.

CHAPTER 6-CONCLUSIONS

The principal conclusion of this study is that the four harvest treatments, clearcutting (CC), deferred 'softwoods only' cutting (DC), 'softwoods only' cutting (SC), and hardwoods poisoned, followed by deferred 'softwoods only' cutting (HP), did not produce significantly different phytosociological communities. Although in all three strata (trees, shrubs and herbs), some differences among treatments were evident for individual species, species did not show evidence of joint responses, i.e. groups of species did not occur exclusively or abundantly in only certain harvest treatments (except for a tendency for several shrubs to have higher abundances, most non-significant, in the HP treatment), as indicated by median polish treatment effects, diversity measures, plot resemblances, and ordination results. Throughout the discussion, several possible reasons for this lack of significant, overall community differences among treatments have been mentioned: 1) the Initial Floristics character of boreal forests, which results from the high capacity of most component species to regenerate following disturbances; 2) the involvement of many chance factors, such as seedfall, mortality, animal browsing, etc., *sensu* Gleason (1926); and 3) the confounding of treatment effects by complex environmental gradients that influence boreal species distributions.

Related to this latter possible reason is the strong connection of phytosociological communities to land type (Rowe 1961). Rowe (1961, 1992) emphasized that a forest community and its structure and dynamics cannot be described or predicted without reference to its specific geographic framework; communities should be studied as 'volumetric landscapes or waterscapes', i.e. geographic ecosystems. Thus, vegetational concepts cannot be simply transferred from one region to another, and thus, plant communities within highly variable geomorphological settings will tend to have highly variable species composition/abundance characteristics (Rowe 1961). The RC17 site,

like many mixedwood sites of the boreal forest, had a complex geomorphology, with varying relief, soil depth, etc., and thus, it likely had a correspondingly complex multidimensional gradient of environmental factors. This may have obscured the effect of harvest treatments on the phytosociological community.

Measures that were intended to indicate whether harvest treatments altered the usual pattern of secondary succession, i.e. of hardwood dominance of the mixedwood forest during the early phase of development, showed mixed results. Although the softwood to hardwood ratio (S:H) did not follow the expected trend of descending from HP, to DC/SC, to CC, the spruce to fir ratio (Spr:F) and spruce to hardwood ratio (Spr:H) did essentially follow this trend. Although these were not tested statistically, they suggest that the HP and possibly DC treatments were somewhat successful at improving the status of *Picea* spp. in the regenerating mixedwood forest, in comparison to clearcutting. This trend, of hardwoods being more prominent in CC, and less so in HP, with the reverse being true for softwoods, was supported by individual species measures (indicated by LSD tests and/or median polish residuals, but not by significant ANOVAs) of *P. glauca, P. tremuloides* and *P. balsamifera*, but not for *A. balsamea, B. papyrifera*, and *P. mariana*. *P. glauca* appeared to have decreased in importance since 1953 in the tree stratum of CC, but not the other treatments, and *P. tremuloides* appeared to have increased in CC. These changes supported the expected trends, but other shifts since 1953 did not. Age trends of tree species seemed to generally match the expected trend, with conifers being mostly advance-growth origin in DC and HP, while most conifers in CC were of post-harvest origin. However, there were no evident supporting trends in tree height. Thus, the results were not conclusive as to the advantage over clearcutting of cutting only softwoods, and of poisoning hardwoods in advance of cutting only softwoods, with the intent of improving *Picea* spp. and softwood quality and quantity in naturally regenerating harvested boreal mixedwood stands.

The strongest trend in the data was represented by canopy composition, with CA

axes representing a turnover of hardwood to mixedwood to softwood canopy types. Occurrence of understorey species was evidently related to either the environmental gradients created by the variations in the canopy, or to some underlying gradients that determined both the canopy and understorey compositions. Soil depth and moisture did not account for this trend, alone or in combination, at least at the level of description applied in this study. Thus, as mentioned above with reference to the lack of overall community differences in response to harvest treatments, it is suspected that the boreal mixedwood community of the RC17 site is best decribed as a continuum of species' presences and abundances, determined by a complex set of interdependent environmental factors. Maycock and Curtis (1960), van Groenewoud (1965), and Swan and Dix (1966) have previously observed this for undisturbed boreal forest communities. Therefore, a more detailed, numerical description of a complex of environmental variables is likely necessary to develop a model capable of predicting species composition and abundance of the boreal mixedwood in relation to environmental gradients, and to distinguish effects of various silvicultural treatments from the naturally high variability of these communities.

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APPENDICES

Appendix 1. Species encountered in each of three vegetation strata on the RC17 project, 1990.

Scientific Names	Common Names
Tree stratum	
Abies balsamea (L.) Mill	Balsam fir
Acer spicatum Lam.*	Mountain maple
Alnus rugosa (DuRoi) Spreng.	Speckled alder
Amelanchier humilis Wieg.*	Shadbush
Betula papyrifera Marsh.	White birch, Paper birch
Fraxinus nigra Marsh.	Black ash
Larix laricina (Du Roi) K. Koch*	Tamarack, Eastern larch
Picea glauca (Moench) A. Voss	White spruce
Picea mariana (Mill.) BSP.	Black spruce
Pinus banksiana Lamb.*	Jack pine
Populus balsamifera L.	Balsam poplar
Populus tremuloides Michx.	Trembling aspen
Prunus pensylvanica L. fil	Pincherry
Prunus virginiana L. fil*	Chokecherry
Salix L. spp.	Willows
Sorbus decora (Sarg.) Schneid.	Mountain ash
Thuja occidentalis L.	Eastern white cedar
Shrub stratum	
Abies balsamea (L.) Mill	Balsam fir
Acer spicatum Lam.	Mountain maple
Alnus crispa (Ait.) Pursh	Green alder
Alnus rugosa (DuRoi) Spreng.	Speckled alder
Amelanchier bartramiana (Tausch) Roem.	Mountain juneberry
Amelanchier humilis Wieg.	Shadbush
Betula papyrifera Marsh.	White birch, Paper birch
Cornus stolonifera Michx.	Red osier dogwood
Corylus cornuta Marsh.	Beaked hazel
Diervilla lonicera Mill.	Bush honeysuckle
Fraxinus nigra Marsh.	Black ash
Kalmia polifolia Wang.	Bog-laurel
Larix laricina (DuRoi) K. Koch	Tamarack, Eastern larch
Ledum groenlandicum Oeder.	Labrador tea
Lonicera canadensis Bartr.	Fly honeysuckle
Lonicera hirsuta Eat.*	Hairy honeysuckle
Lonicera involucrata (Richards.) Banks	Bracted honeysuckle
Lonicera oblongifolia (Goldie) Hook.	Swamp fly honeysuckle
Lonicera villosa (Michx.) R. & S.	Mountain fly honeysuckle
Myrica gale L.*	Sweet gale
Picea glauca (Moench) A. Voss	White spruce
Picea mariana (Mill.) BSP.	Black spruce
Populus balsamifera L.	Balsam poplar
Populus tremuloides Michx.*	Trembling aspen
Prunus pensylvanica L. fil	Pincherry
Prunus virginiana L. fil	Chokecherry

Rhamnus alnifolia L'Hér.	Alder-leaved buckthorn
Ribes glandulosum Grauer*	Skunk currant
Ribes hirtellum Michx.	Wild gooseberry
Ribes hudsonianum Richards.*	Northern wild black currant
Ribes lacustre (Pers.) Poir	Bristly black currant
Ribes oxycanthoides L.*	Bristly wild gooseberry
Ribes triste Pall.*	Wild red currant
Rosa acicularis Lindl.	Prickly wild rose
Rubus idaeus L. var. *strigosus* (Michx.) Maxim	Wild red raspberry
Salix L. spp.	Willows
Sambucus pubens Michx.*	Elderberry
Sorbus decora (Sarg.) Schneid.	Mountain ash
Thuja occidentalis L.	Eastern white cedar
Vaccinium angustifolium Ait.*	Low sweet blueberry
Viburnum edule (Michx.) Raf.	Low-bush cranberry

Herb stratum

Abies balsamea (L.) Mill	Balsam fir
Acer spicatum Lam.	Mountain maple
Alnus rugosa (Du Roi) Spreng.	Speckled alder
Amelanchier bartramiana (Tausch) Roem.*	Mountain juneberry
Amelanchier humilis Wieg.*	Shadbush
*Anaphalis margaritaceae**	
Anemone canadensis L.*	Canada anemone
Anemone quinquefolia L.	Wood anemone
Aquilegia canadensis L.*	Wild columbine
*Aralia hispida**	
Aralia nudicaulis L.	Wild sarsaparilla
Aster ciliolatus Lindl	Ciliolate aster
Aster macrophyllus L.	Large-leaved aster
Aster spp.*	
Athyrium filix-femina (L.) Roth	Lady fern
Aulacomnium palustre (Hedw.) Schwaegr.†**	Ribbed bog moss
Betula papyrifera Marsh.	White birch
Botrychium virginianum (L.) Sw.*	Rattlesnake fern
Brachythecium spp., includes, but possibly not exclusively:	
B. campestre (C. Müll.) B.S.G.†**	
Calamagrostis canadensis†**	Blue-joint grass
Caltha palustris L.*	Marsh marigold? cowslip
Carex disperma Dewey*	Soft-leaved sedge
Carex spp., includes, but probably not exclusively:	
C. arctata†**	
C. vaginata†**	
Carex trisperma Dewey†	Three-fruited sedge
Circaea alpina L.	Dwarf enchanter's nightshade
Cladina mitis (Sandst.) Hale & Culb.*	Reindeer lichen
Cladina rangiferina (L.) Harm.	Reindeer lichen
Cladina stellaris (Opiz) Brodo*	Reindeer lichen
Cladonia spp.	Club lichens
Climacium dendroides (Hedw.) Web. & Mohr†	
Clintonia borealis (Ait.) Raf.	Bluebead lily
Coptis trifolia (L.) Salisb.	Goldthread

*Corallorhiza trifida** Chat.	Early coralroot
Cornus canadensis L.	Bunchberry
Cornus stolonifera Michx.	Red osier dogwood
Corylus cornuta Marsh.	Beaked hazel
Dicranum spp., includes, but probably not exclusively:	
D. fuscescens Turn.†**	Broom moss
D. scoparium Hedw.†**	Broom moss
Diervilla lonicera Mill.	Bush honeysuckle
Dryopteris austriaca (Jacq.) Woynar var. *spinulosa* (Mull.) Fiori	Spinulose shield fern*
Epilobium angustifolium L.	Fireweed
Equisetum arvense L.	Common horsetail
Equisetum pratense Ehrh.	Meadow horsetail
Equisetum scirpoides Michx.*	Dwarf scouring rush
Equisetum sylvaticum L.*	Wood horsetail
Fragaria vesca L.*	Woodland strawberry
Fragaria virginiana Duchesne.	Common strawberry
Fraxinus nigra Marsh.*	Black ash
Galium triflorum Michx.	Sweet scented bedstraw
Gaultheria hispidula (L.) Muhl.	Snowberry
Geocaulon lividum (Richards.) Fern.	Northern comandra
*Geranium bicknelli**	
Glyceria striata†**	
Goodyera repens (L.) R. Brown	Dwarf rattlesnake plantain*
Grass spp., includes, but not exclusively:	
Calamagrostis canadensis†**	Blue-joint grass
Glyceria striata†**	
Gymnocarpium dryopteris (L.) Newm.	Oak fern
Halenia deflexa†*	
Hylocomium splendens (Hedw.) BSG.	Stair-step moss
Larix laricina (Du Roi) Koch*	Tamarack, American larch
Ledum groenlandicum Oeder	Labrador tea
Lichen spp.	
Linnaea borealis L. ssp. *longiflora* (Torr.) Hult.	Twinflower
Lonicera canadensis Bartr.	Fly honeysuckle
Lonicera involucrata (Richards.) Banks*	Bracted honeysuckle
Lonicera villosa (Michx.) R. & S.*	Mountain fly honeysuckle
Luzula acuminata†**	Wood rush
Lycopodium annotinum L.	Stiff club moss
Lycopodium clavatum L.*	Common club moss
Lycopodium complanatum L.	Ground cedar*
Lycopodium obscurum L.	Ground pine
Maianthemum canadense Desf.	Wild lily-of-the-valley
Menyanthes trifoliata L.*	Buckbean
Mertensia paniculata (Ait.) G. Don	Northern bluebell
Mitella nuda L.	Naked mitrewort
Mnium spp.	
Moneses uniflora (L.) Gray	One-flowered wintergreen
Moss spp., may include some:	
Aulacomnium palustre (Hedw.) Schwaegr.†**	Ribbed bog moss
Brachythecium campestre (C. Müll.) B.S.G.†**	
Pohlia nutans (Hedw.) Lindb.†**	
Petasites palmatus (Ait.) Gray	Sweet coltsfoot
Picea glauca (Moench) Voss*	White spruce

Picea mariana (Mill.) BSP.*	Black spruce
Peltigera spp.*	
Pinus banksiana Lamb.*	Jack pine
Pleurozium schreberi (Brid.) Mitt.	Schreber's moss
Pohlia nutans (Hedw.) Lindb.†	
*Polygonum scandens**	
Polytrichum juniperinum Hedw.	Hair cap moss
Populus balsamifera L.*	Balsam poplar
Populus tremuloides Michx.*	Trembling aspen
Prunus pensylvanica L. fil	Pincherry
Prunus virginiana L. fil*	Chokecherry
Ptilium crista-castrensis (Hedw.) De Not.	Plume Moss
*Pyrola rotundifolia**	
Rhamnus alnifolia L'Hér.	Alder-leaved buckthorn
Rhytidiadelphus triquestrus (Hedw.) Warnst.	Electrified cat's tail moss
Ribes glandulosum Grauer*	Skunk currant
Ribes hirtellum Michx.*	Wild gooseberry
Ribes lacustre (Pers.) Poir	Bristly black currant
Ribes triste Pall.*	Wild red currant
Rosa acicularis Lindl.	Prickly wild rose
Rubus hispidus L.*	Swamp dewberry
Rubus idaeus L. var. *strigosus* (Michx.) Maxim	Wild red raspberry
Rubus pubescens Raf.	Dwarf raspberry
Salix L. spp.*	Willows
Smilacina trifolia (L.) Desf.*	Three-leaved false Solomon's seal
Sorbus decora (Sarg.) Schneid.	Mountain ash
Sphagnum capillifolium (Ehrh.) Hedw.†	
Sphagnum magellanicum Brid.†	
Sphagnum spp.*, includes, but not exclusively: *S. palustre* L.†**	
Streptopus roseus Michx.	Rose-twisted stalk
Thelypteris phegopteris (L.) Slosson	Northern beech fern
Thuja occidentalis L.	Eastern white cedar
Trientalis borealis Raf.	Starflower
Trillium cernuum L.*	Nodding trillium
Vaccinium angustifolium Ait.	Low sweet blueberry
Vaccinium myrtilloides Michx.	Velvet-leaf blueberry
Vaccinium oxycoccos L.	Small cranberry
Viburnum edule (Michx.) Raf.	Low-bush cranberry
Viola renifolia Gray	Kidney-leaved violet
Viola spp.*	Violets

†Bryophyte species identified by R. R. Ireland, vascular species identified by A. W. Dugal, both of the National Herbarium of Canada.
*Species with average cover < 5% in that stratum, excluded from ordinations.
**Rare species and species reported in species' groups, abundances not included individually in tabulated data.

Nomenclature of vascular plants follows Scoggan (1978) and Fernald (1950), bryophyte nomenclature follows Ireland and Bellolio-Trucco (1987), lichen nomenclature follows Hale (1979).

APPENDIX 2 - HISTORY OF THE RC17 EXPERIMENTAL AREA

THE CONDITION OF THE STUDY SITE PRIOR TO TREATMENT

Overstorey Composition

At the initiation of RC17, extremely shallow sites of the area supported mixed softwoods, mucky peat sites were occupied by *Picea mariana* stands and the other site types were covered by mixedwoods of various compositions (Hughes 1967). MacLean (1954) reported the common ranges of each species over the soil depth and moisture site types in the period following the fire in 1761. *Picea glauca* , balsam fir and trembling aspen occurred on all site types except dry and moist, extremely shallow sites. White birch occurred on all site types, *P. mariana* on all except fresh and moist, deep sites and balsam poplar occurred on only fresh and moist, medium shallow and deep sites. Cedar occurred only on dry and moist, extremely shallow soils, and jack pine occurred on these soil types as well as on dry and moist, very shallow soils (MacLean 1954).

Seedbed Conditions

Seedbed conditions prior to harvest treatments made the survival of conifer seedlings for more than a few weeks difficult. Leaf litter of broadleaved species including mountain maple and hazel created a mat on the forest floor, and the humus layer below was a poorly decomposed fibrous mor (Hughes 1967). Both did not retain moisture well, and became very dry in periods of drought. Most spruce seedlings died within a few weeks, fir seedling survival was better, but the roots were of poor form, often lying entirely in the leaf litter (Hughes 1967). *P. schreberi* and *Hylocomium splendens* were common, and provided a slightly better seedbed than the leaf litter since they were raised slightly above it. *Ptilium crista-castrensis* provided an even better

seedbed because it was small and compact, and very decayed logs were the best available seedbed for spruce and fir (Hughes 1967).

There was some difference in seedbed availability among site types. Moist, medium-shallow sites and moist, deep sites had better seedbeds created by windthrown trees than did fresh, medium-shallow and fresh, deep sites. The roots of softwood trees on moist sites were more widespread than on fresh sites. Therefore, on moist sites, windthrown trees exposed well-decomposed lower organic layers or mineral soil in fairly large patches, very suitable seedbeds for spruce and fir. On fresh sites, the deeper, less widespread roots of softwoods created deeper, irregular depressions which collected water and leaf litter and were unsuitable seedbeds. Thus, fresh sites had fewer conifer seedlings than moist sites. However, the rotting logs provided good seedbeds on both moisture types, and many seedlings that became established on the moist sites at the base of windthrown trees were quickly smothered by leaf litter. Very-shallow and extremely-shallow sites provided fairly good seedbeds for conifers at the base of windthrown trees, except on very dry sites. Seedlings became established in *Polytrichum spp.*, which grew in crevices of bedrock exposed by the uprooted trees (Hughes 1967).

Hughes (1967) reported that conifer seedling establishment would have been sufficient for a well-stocked stand despite germination problems, if suppression by shrubs (mountain maple and hazel) had not prevented the seedlings from attaining a height at which they would be less affected by animal browsing or trampling. At the initiation of the experiment many *P. glauca* and fir seedlings only a few feet tall were 35 years of age or older, and therefore in poor physical shape (Hughes 1967).

INITIAL RESULTS (1954 - 1965)

Hughes (1967) reported detailed results on the initial 5-year effects of harvesting and seedbed treatments on seedling establishment and on survival of advance

growth of both softwood and hardwood species (prior to cutting of DC and HP plots). These results were based solely on the transects of the seedbed experiment and therefore do not give a complete picture of the response of reproduction to the overstorey treatments alone, on the larger treatment plots. Similarly, Sutton's (1964) report on the response of understorey vegetation to treatments is also based on only transect data. Therefore, this section will only summarize some general trends and observations made by these authors about the effect of the overstorey treatments on the transects, and some general observations about the plots.

Seedbed and Forest Floor

MacLean (1955) reported that there was little direct effect of the initial harvest on the character of the forest floor itself. However, since trees were limbed and topped where they fell, a considerable amount of slash remained from the harvest (MacLean 1955). The slash averaged 0.5 m in depth, and was mostly loose with about 20% moderately compact. It was widely distributed over the plots with about 1/2 of the ground covered in the CC plots and about 1/3 covered in the SC plots. Needles from the spruce slash carpeted the ground beneath, making a poor seedbed. Slash did not appear to have any effect on the spruce advance growth, but protected the balsam fir advance growth from exposure (MacLean 1955).

MacLean (1955) noted that the year after the initial harvest (1954) spruce seedlings had only germinated in the exposed, well-decomposed humus of skid trails, mostly on moist sites, and that no first-year conifer seedlings were located on exposed mineral soil.

Advance Growth Survival

Tallies of advance growth were taken only on unscarified transects, since scarification removed all advance growth (Hughes 1967). In general, a larger number of spruce and fir advance growth survived harvesting on the moist sites than on the fresh

sites, but numbers of advance growth were only somewhat better on transects in the uncut (DC and HP) areas than in the cut (SC and CC) areas (Hughes 1967). MacLean (1955) noted that although larger spruce and fir saplings were cut during the harvest (with more damage in the CC than in the SC block), the smaller advance growth appeared to be undamaged, and the spruce advance growth was little affected by the exposure from cutting. However, exposure did seem to hinder balsam fir advance growth, with some mortality in 1954, thought to be partly due to deformed root systems in hardwood leaf litter (MacLean 1955). Leader growth of fir seedlings also decreased from 1953 rates in the year following cutting in the CC and SC plots, (again moreso in CC), but quickly recovered, surpassing that in the uncut plots (DC and HP) from 1956 to 1959 (Hughes 1967).

Softwood Regeneration

In general, stocking and density of spruce and fir seedlings were significantly higher on the transects of the uncut plots than on those in the cut (CC and SC) plots, and this was attributed mainly to seed availability, which was of course considerably greater in the uncut plots (Hughes 1967). Fir seedlings were also slightly more frequent and abundant on transects in the SC plots than on those in the CC plots (Hughes 1967). This may also have been a result of seed availability, since more seed-producing trees were left on the SC than on the CC plots (Hughes 1967)(as described in the methods of this report).

The ratio of spruce to fir seedlings was generally higher in transects of the CC and SC plots than in those of the uncut (DC and HP) plots, and in the first round of seedbed treatments (1954-1955) the ratio of spruce was much higher (80% of fir seedlings) in the CC plot than in the SC plot (20% of fir seedlings). This difference was attributed to the availability of spruce and balsam fir seed and their relative weights (Hughes 1967). In the CC treatment, seed was only available from the adjacent uncut

plots, while some seed trees were present in the SC plots (see Methods). Fir seed is larger and heavier than the spruce seed and therefore did not move into the CC plots as easily as the spruce seed, as indicated by tallies in 1 chain sections of the 10-chain wide plots (Hughes 1967).

Hardwood Regeneration

Hardwood regeneration was higher (density) than softwood regeneration on CC plots in 1954, most of the stems being aspen and balsam poplar suckers and birch stump sprouts (MacLean 1955). Aspen and balsam poplar had higher stocking on transects in the cut plots (CC and SC) in 1954 than in the uncut plots (DC and HP) but birch stocking was lowest in the CC plots (Hughes 1967). MacLean (1955) noted that birch seedlings were common on mineral soil of strip roads. After the 1956 seedbed treatments, aspen and poplar stocking was much lower in all mainstand treatments than in the previous tally, and lowest in the CC transects (Hughes 1967). Yet even in the CC, hardwood seedlings were much taller (at least 4 to 5 times) than softwood seedlings, and shrub species were even taller (Hughes 1967).

Understorey Composition

Sutton (1964) concluded that in the post-harvest period from 1953 to 1957, the species composition of the understorey vegetation on the transects which received no seedbed treatment (undisturbed forest floor) changed very little in response to the overstorey harvest treatments. The characteristic species of the fresh sites remained, with the perennial herbs *A. macrophyllus, C. borealis*, and *C. canadensis*, the perennial pteridophyte *L. obscurum*, and the shrubs *A. spicatum, C. cornuta* dominating the community. Some differences did occur, and were likely due to changes in canopy density (and therefore available light) and seed supply (Sutton 1964). *A. macrophyllus* seemed to be stimulated by light to produce more seed than typical of undisturbed areas while *A. spicatum* seemed to reproduce by vegetative means more frequently (Sutton 1964).

Appendix 3. Soil profile descriptions of representative fresh and moist, deep soils on the RC17 project (Hughes 1967)*.

(A) FRESH DEEP SITE

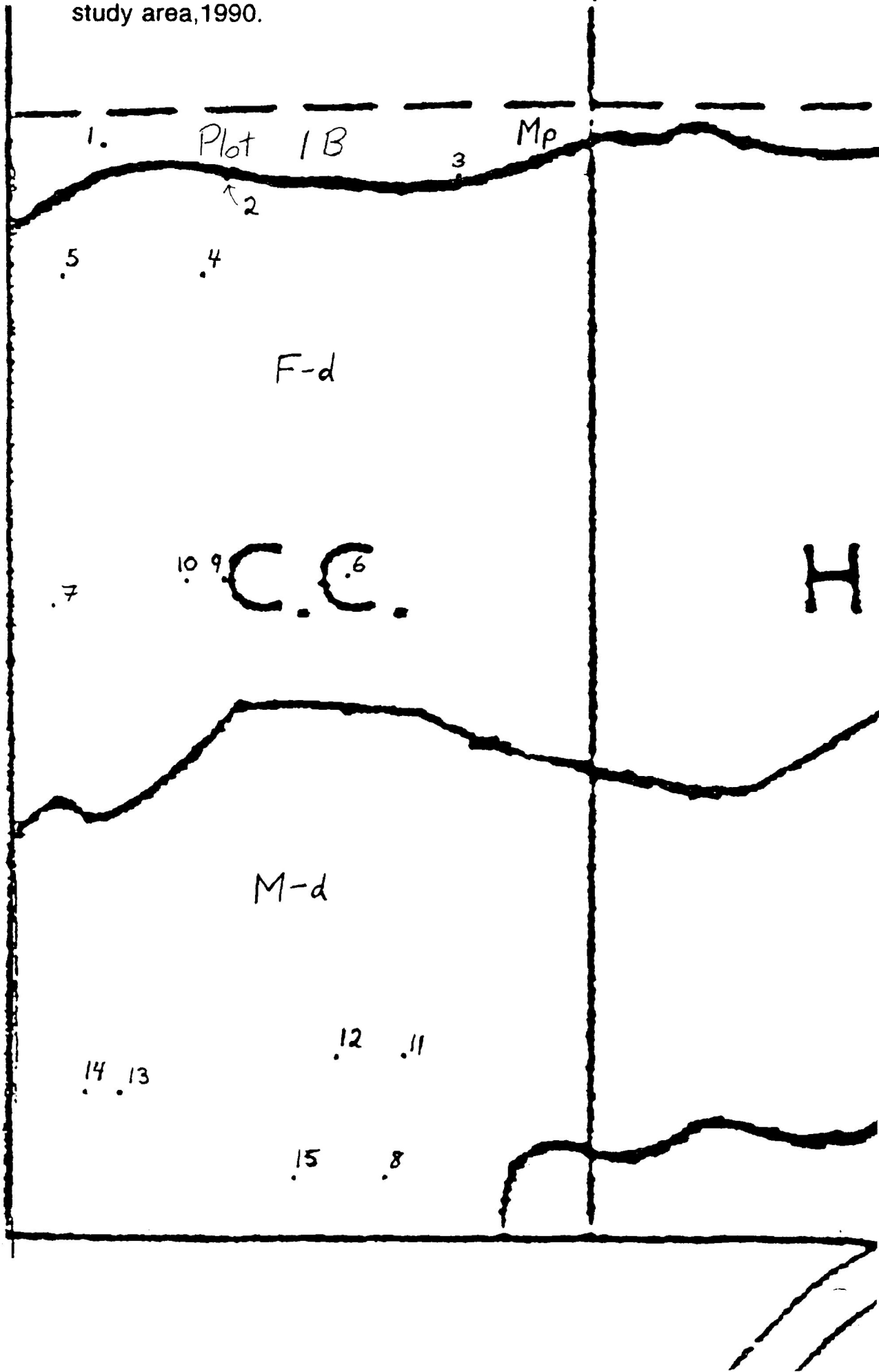
Horizon	Thickness (In.)	Lower limit (In.)	Color	Texture	Structure	Remarks
L	½	½				
F	2	2½			Fibrous mor	
H	trace					
A_2	4	7	Light gray	Fine sand	Single grain	0.6% organic material
B_2	"	14	Orange brown	" "	" "	1.8% organic material
B_3	4	18	Yellow "	Silty "	Somewhat platy	
C_{1_g}	10	28	Gray "	Silt loam	" "	No free carbonate
C_{2_g}	12	40				Free carbonate present
C_2	8+	48+	"	" " "	" "	" "

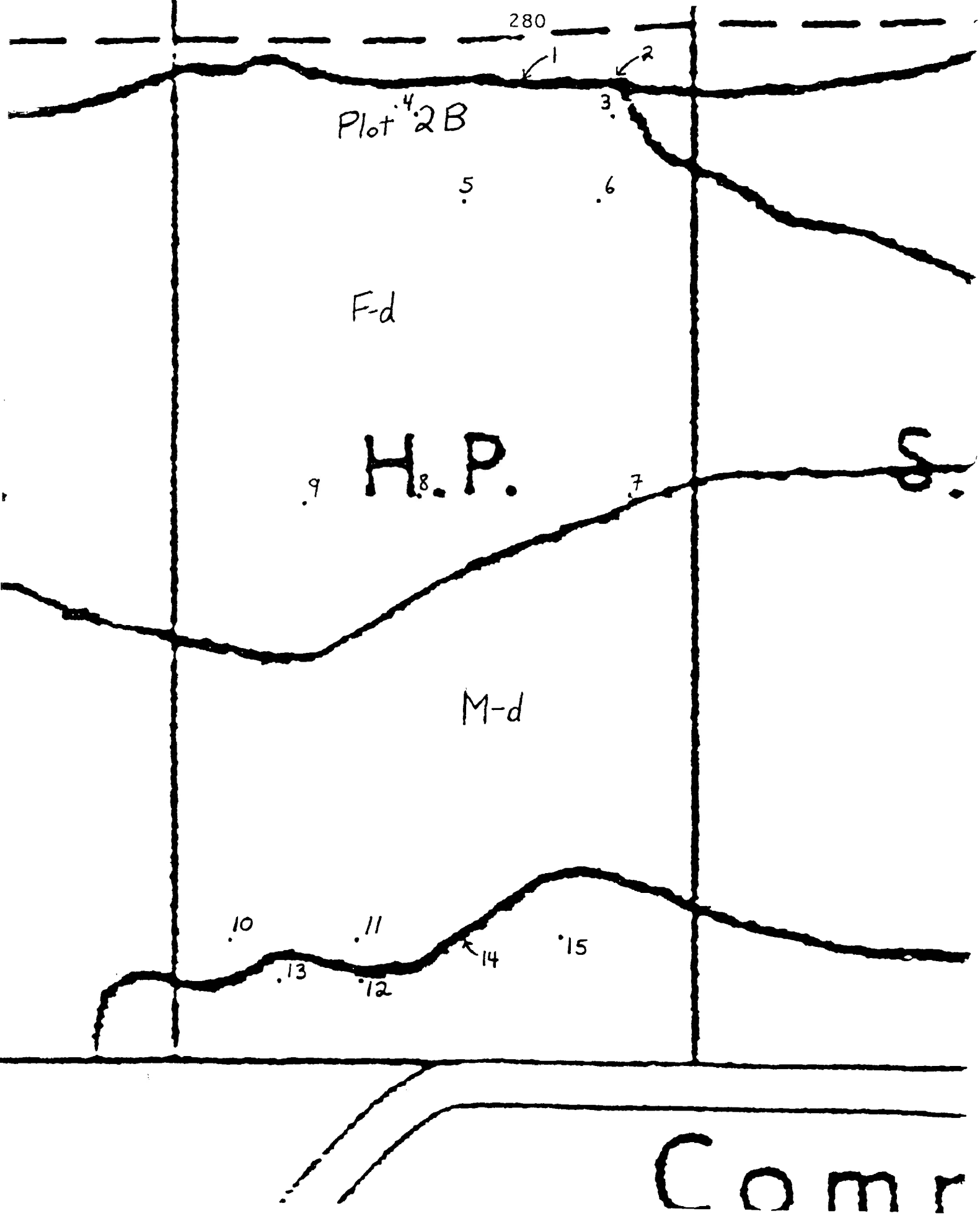
(B) MOIST DEEP SITE

Horizon	Thickness (In.)	Lower limit (In.)	Color	Texture	Structure	Remarks
L	½	½				
F	3½	4			Fibrous mor	
H	4	8				
A_1	8	16	Black			
A_{2_g}	2	18	Dark gray-brown	Sandy silt	Single grain	0.4% organic material
B_{2_g}	3	21	Brown			No free carbonate, 0.2% organic material
B_{3_g}	4	25	Light brown	Silty sand	"	Free carbonate present
G	11+	36+	Gray "	" "	" "	" "

* Determinations of per cent organic material were carried out by dichromate oxidation and each value represents the average of 10 individual soil samples.

Appendix 4. Location of sample units on the treatment plots of the RC17 study area,1990.




280
1
2
3
4
Plot 2B
5
6
F-d
H. P.
S.
7
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9
M-d
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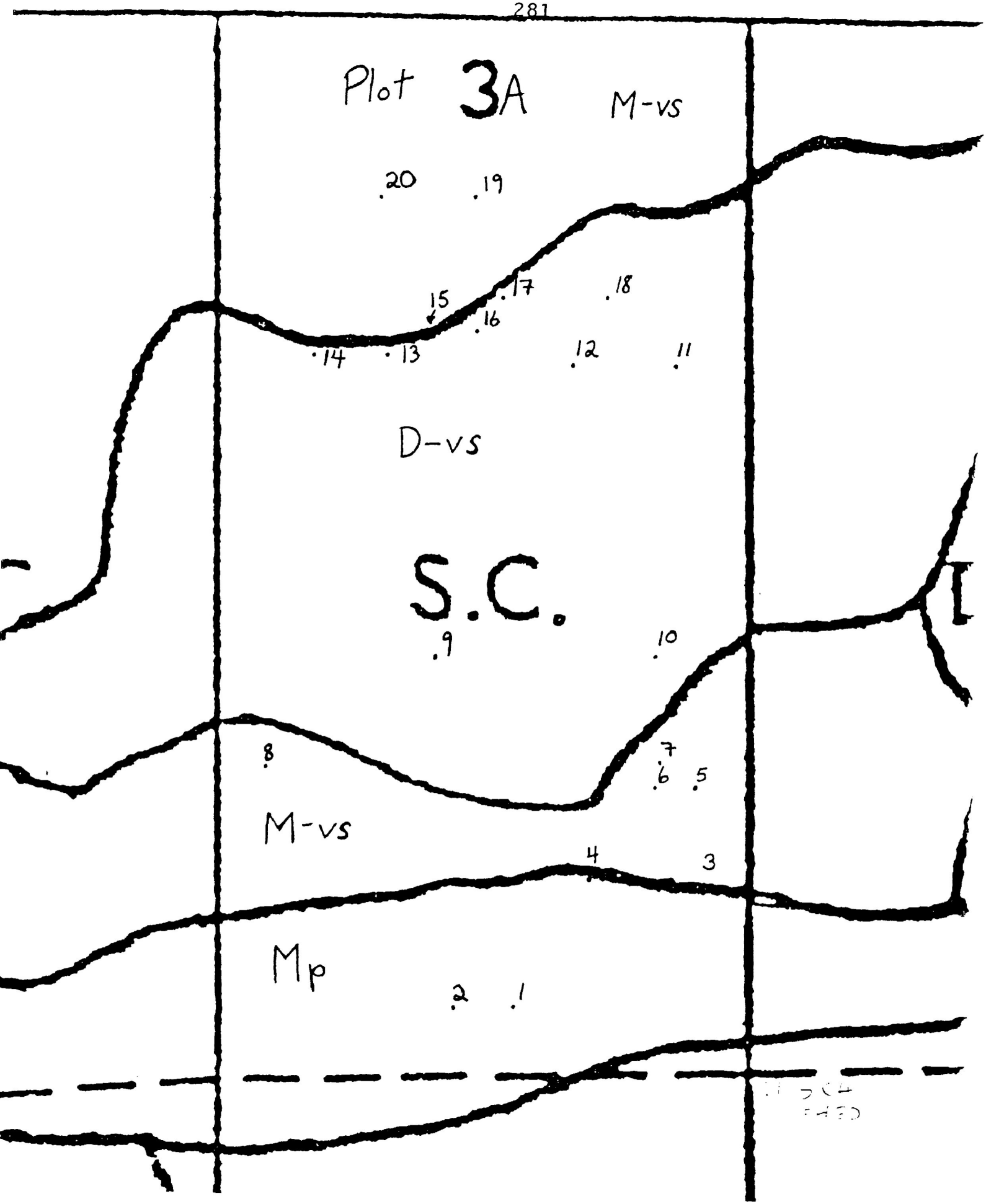
Comr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M-vs
20
19
15
17
18
16
14
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D-vs
S.C.
9
10
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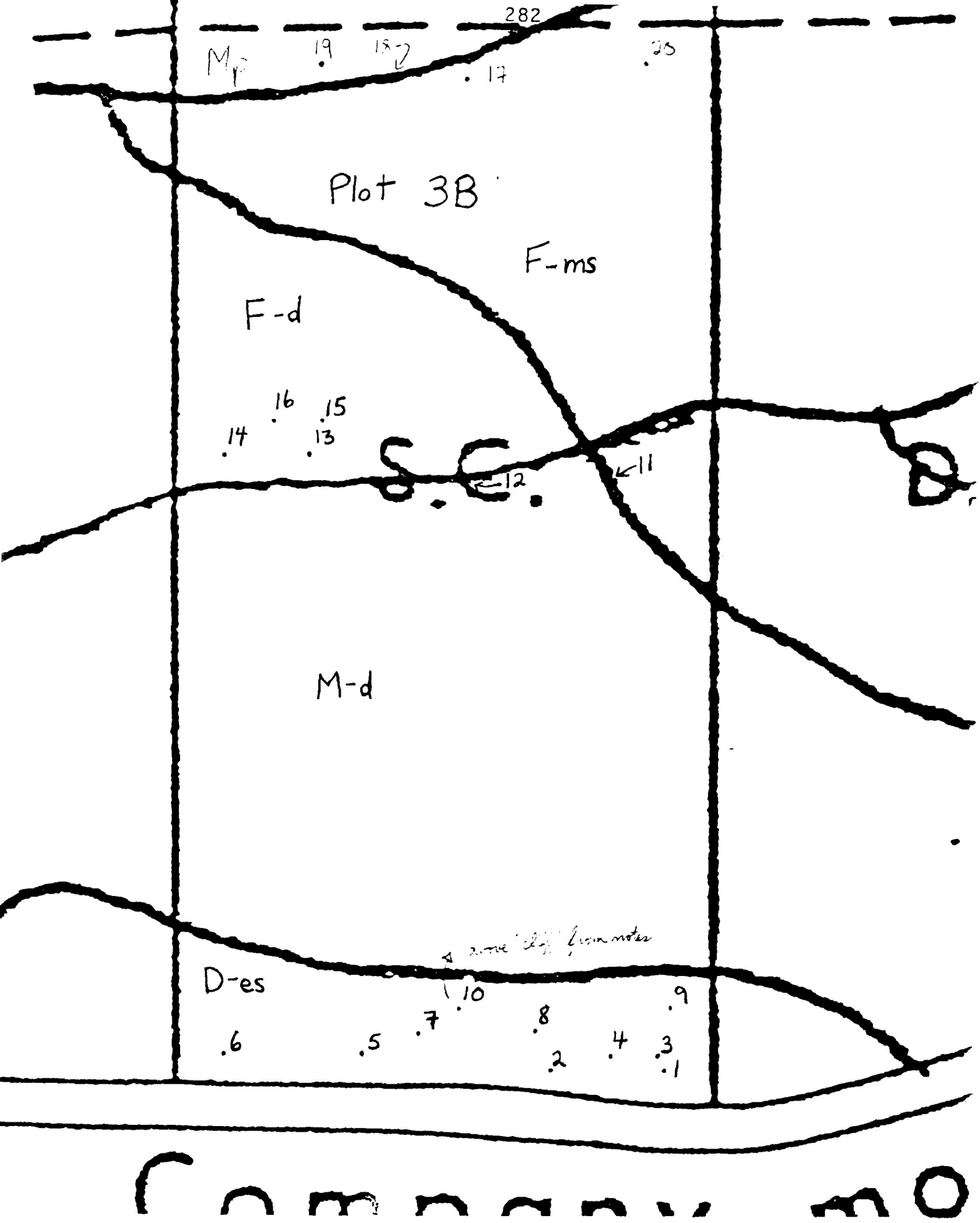
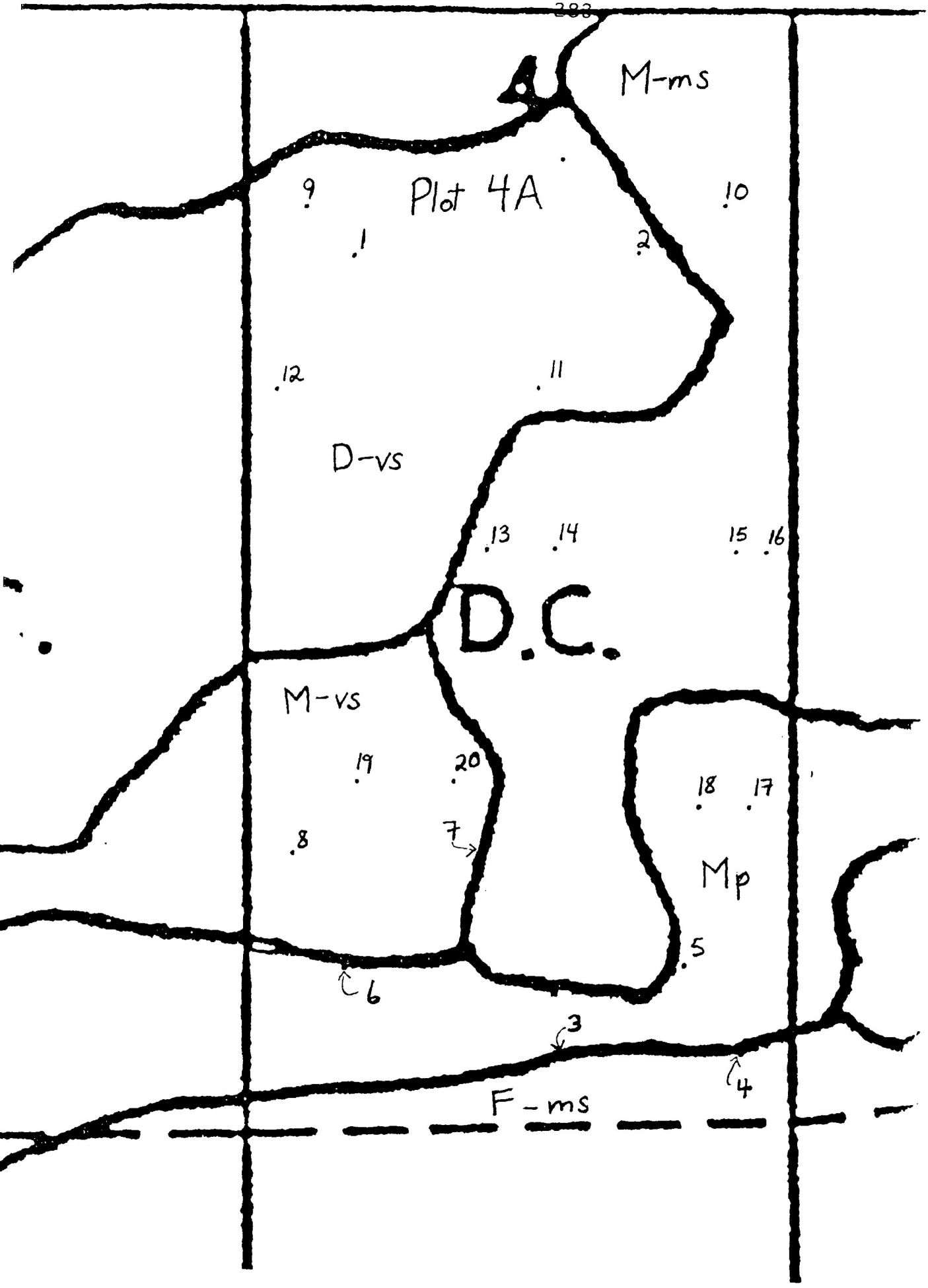
3
Mp
2
1


282
Mp
19
18-2
17
35
Plot 3B
F-ms
F-d
16
15
14
13
12
11
M-d
D-es
10
9
8
7
6
5
4
3
2
1


M-ms
Plot 4A
9
10
1
2
12
11
D-vs
13
14
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16
D.C.
M-vs
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18
17
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7
Mp
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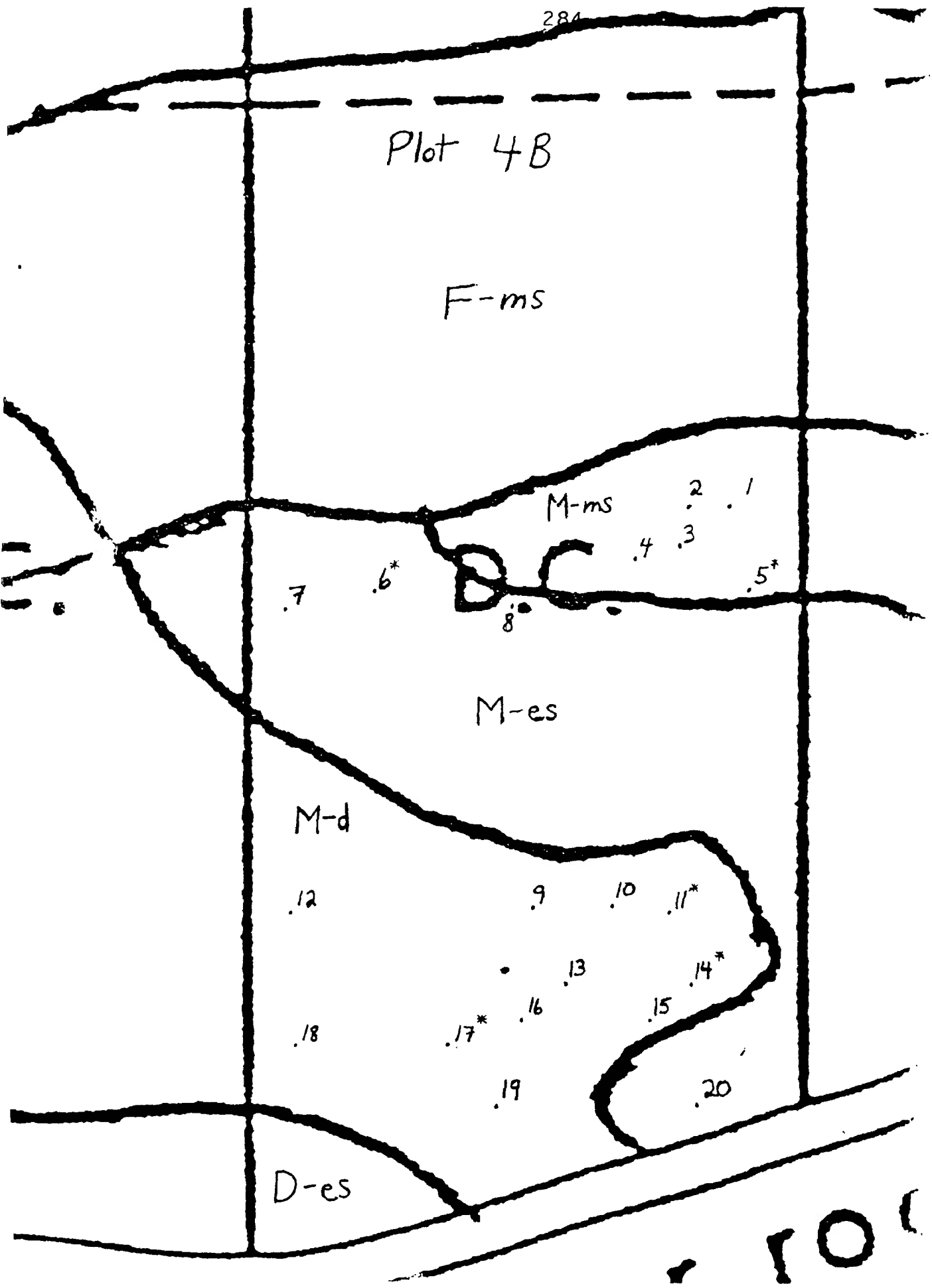
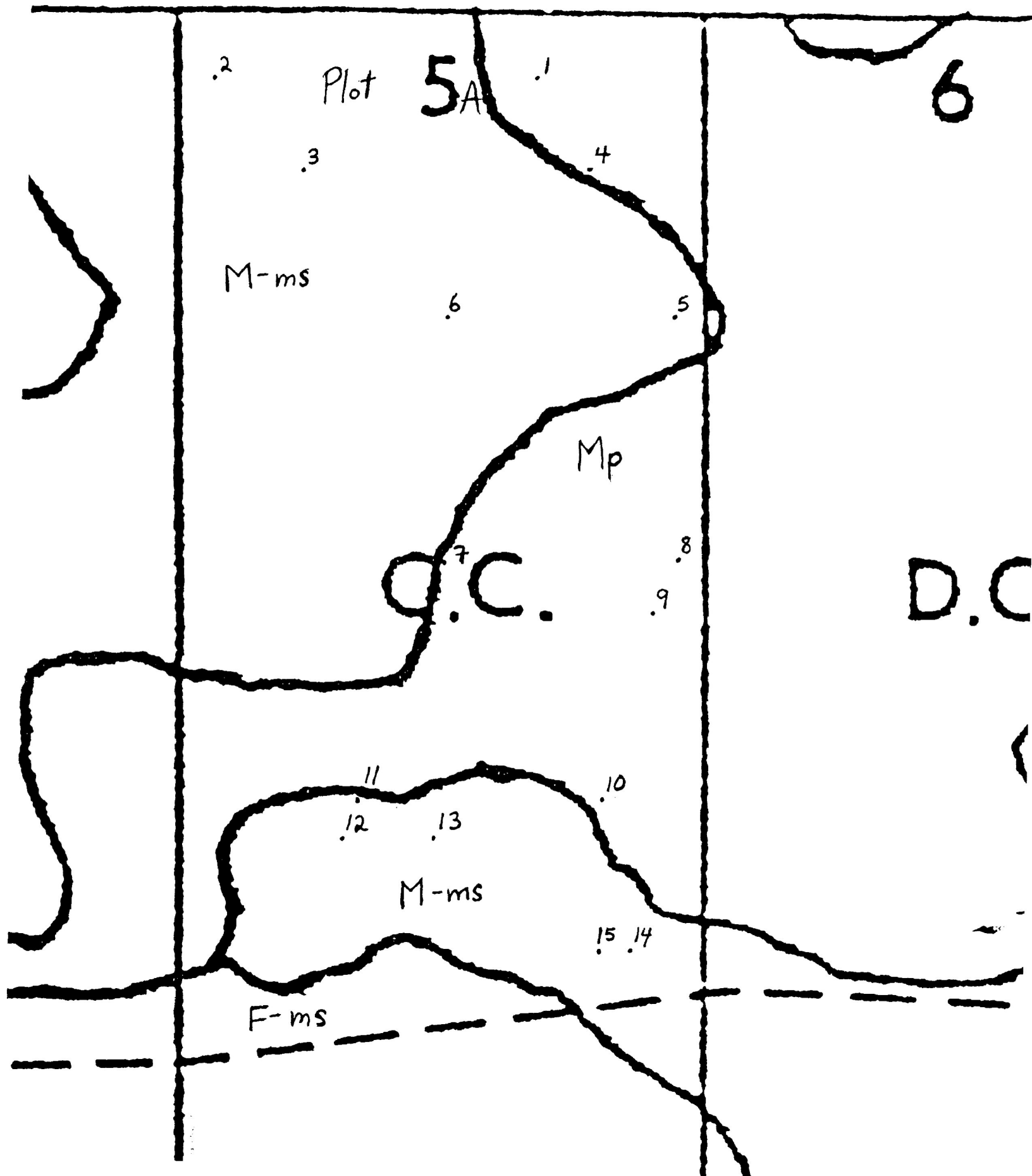
6
3
4
F-ms


284
Plot 4B
F-ms
M-ms
.2
.1
.4
.3
.7
.6*
.5*
.8
M-es
M-d
.12
.9
.10
.11*
.13
.14*
.16
.15
.18
.17*
.19
.20
D-es

y ..d F-Q data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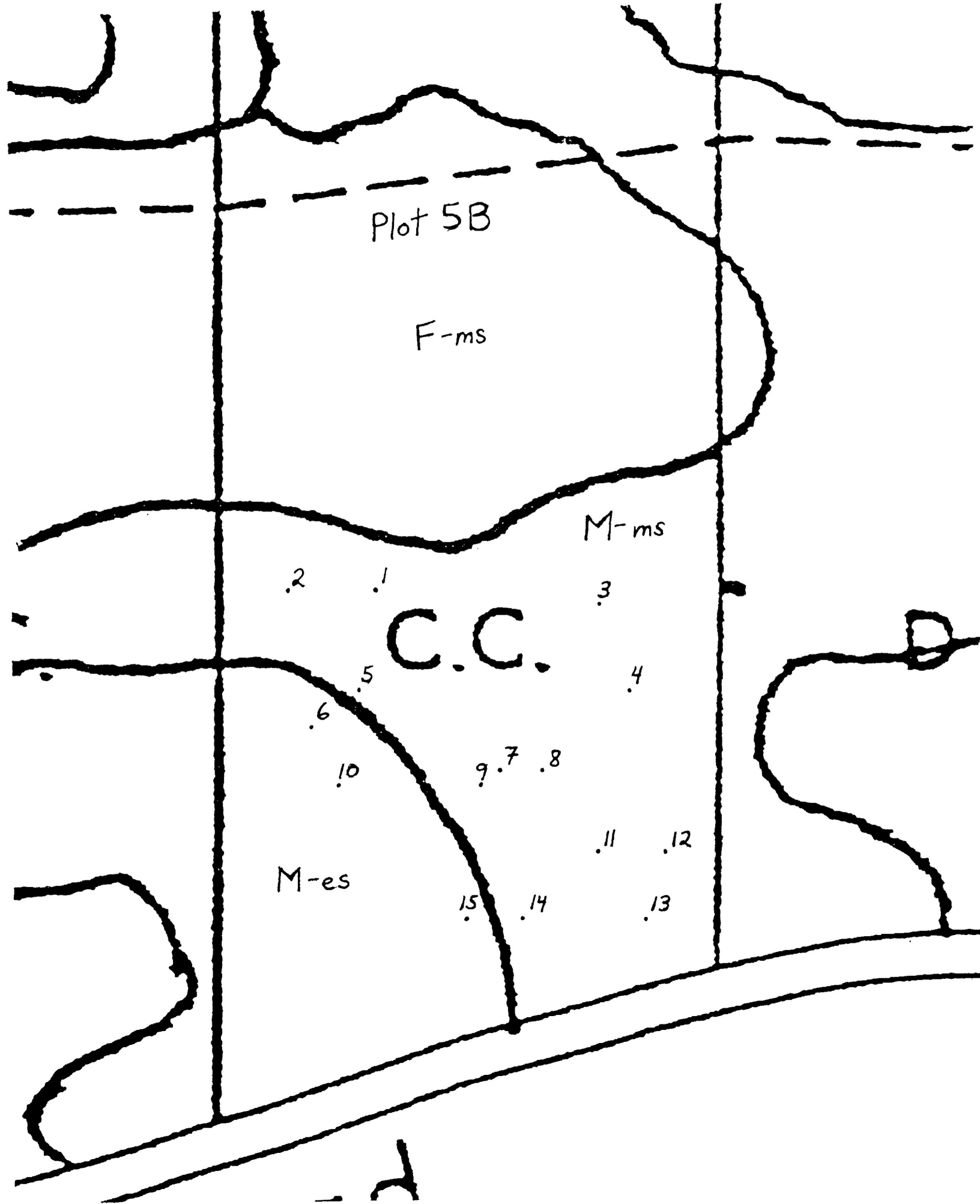
.2
.3
.4
.5
.6
M-ms
Mp
.7
.8
.9
D.C.
D.C
.10
.11
.12
.13
M-ms
.14
.15
F-ms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F-ms
M-ms
.2
.1
.3
C.C.
.5
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.10
.9
.7
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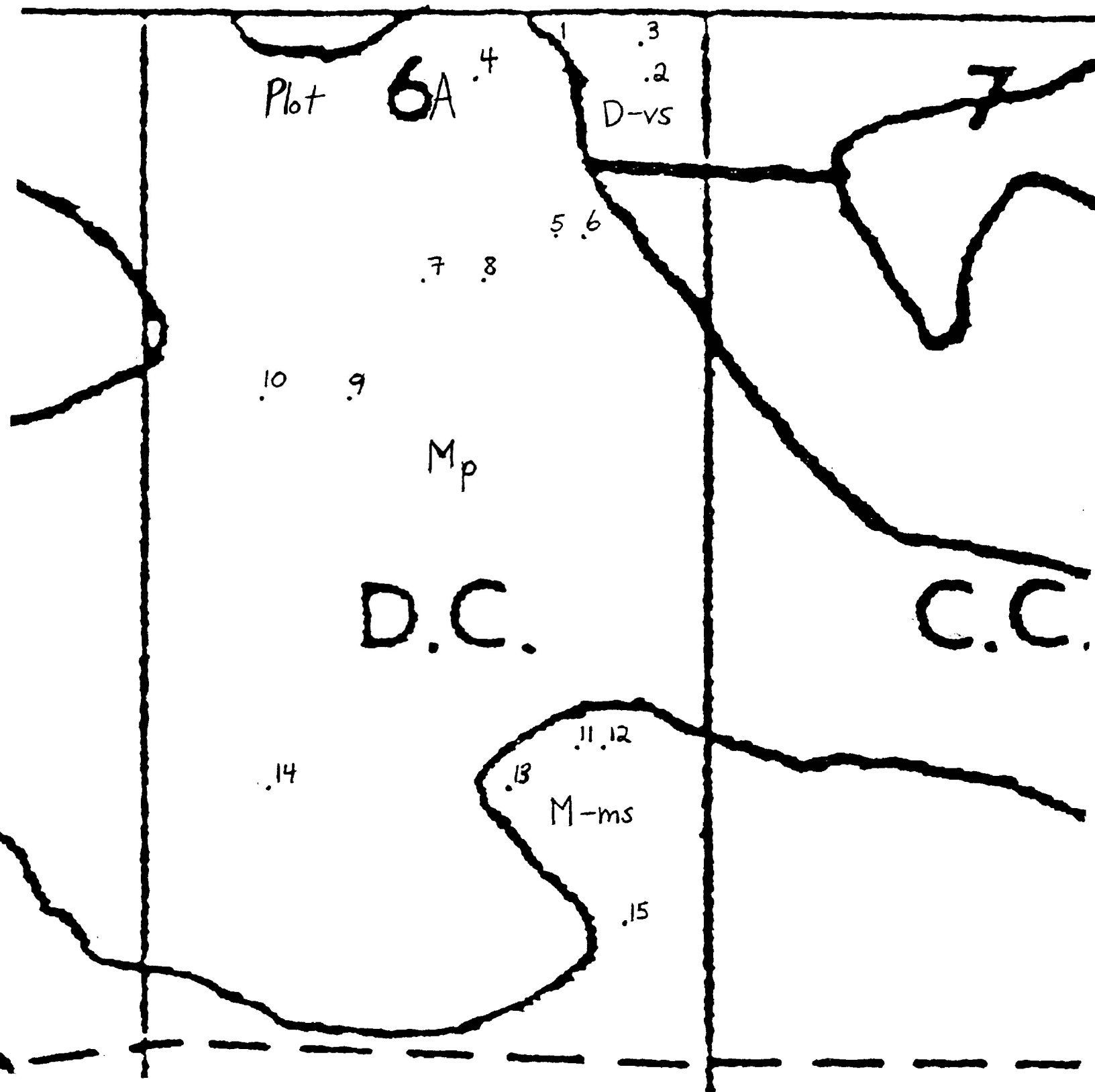
.11
.12
M-es
.15
.14
.13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.3
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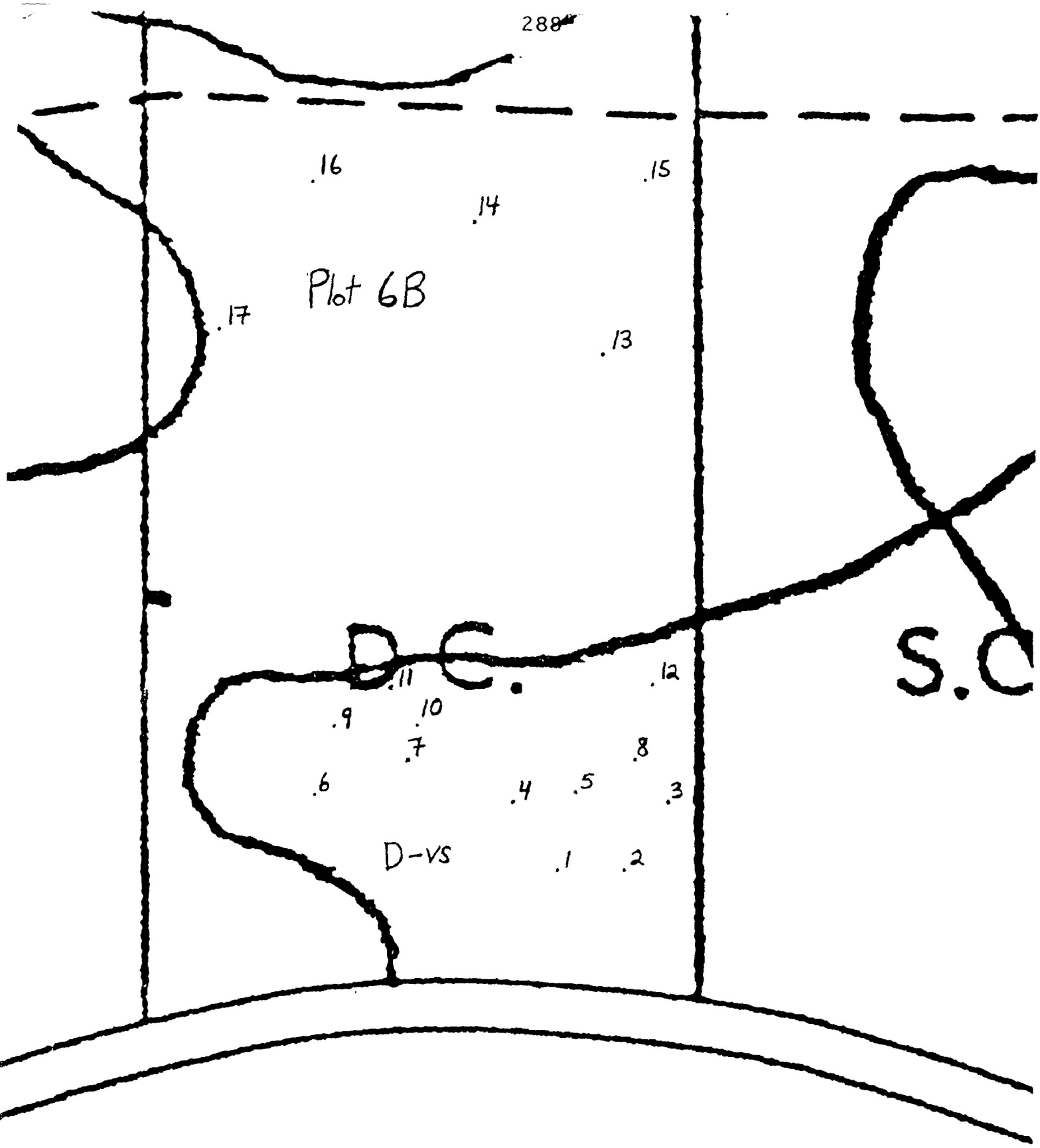
.4
D-vs
7
.5
.6
.7
.8
.10
.9
Mp
D.C.
C.C.
.11
.12
.14
.13
M-ms
.15


288
16
15
14
Plot 6B
17
13
B.C.
S.C
11
12
9
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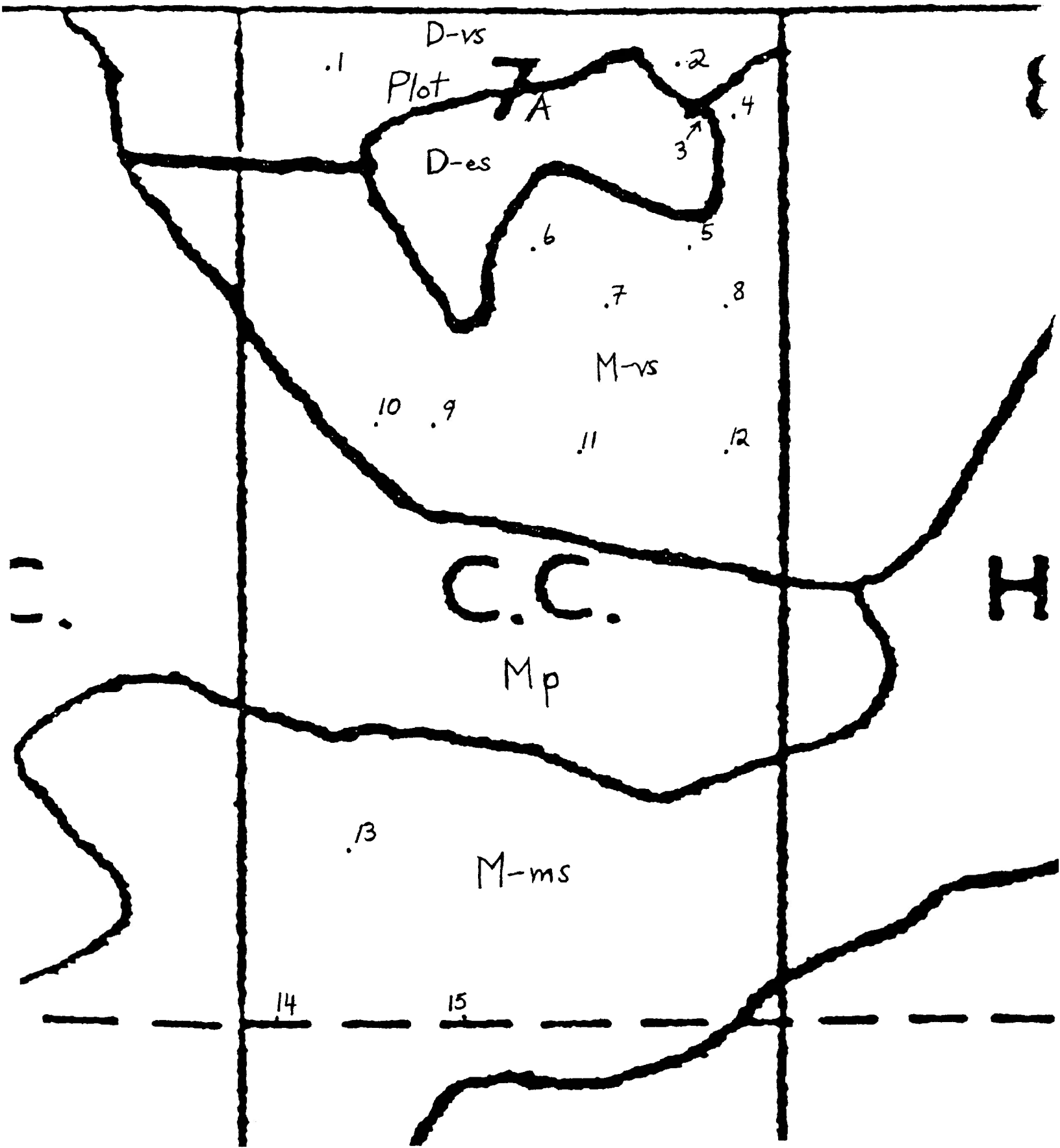
7
8
6
4
5
3
D-VS
1
2


D-vs
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Plot
A
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M-vs
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.12
C.C.
Mp
.13
M-ms
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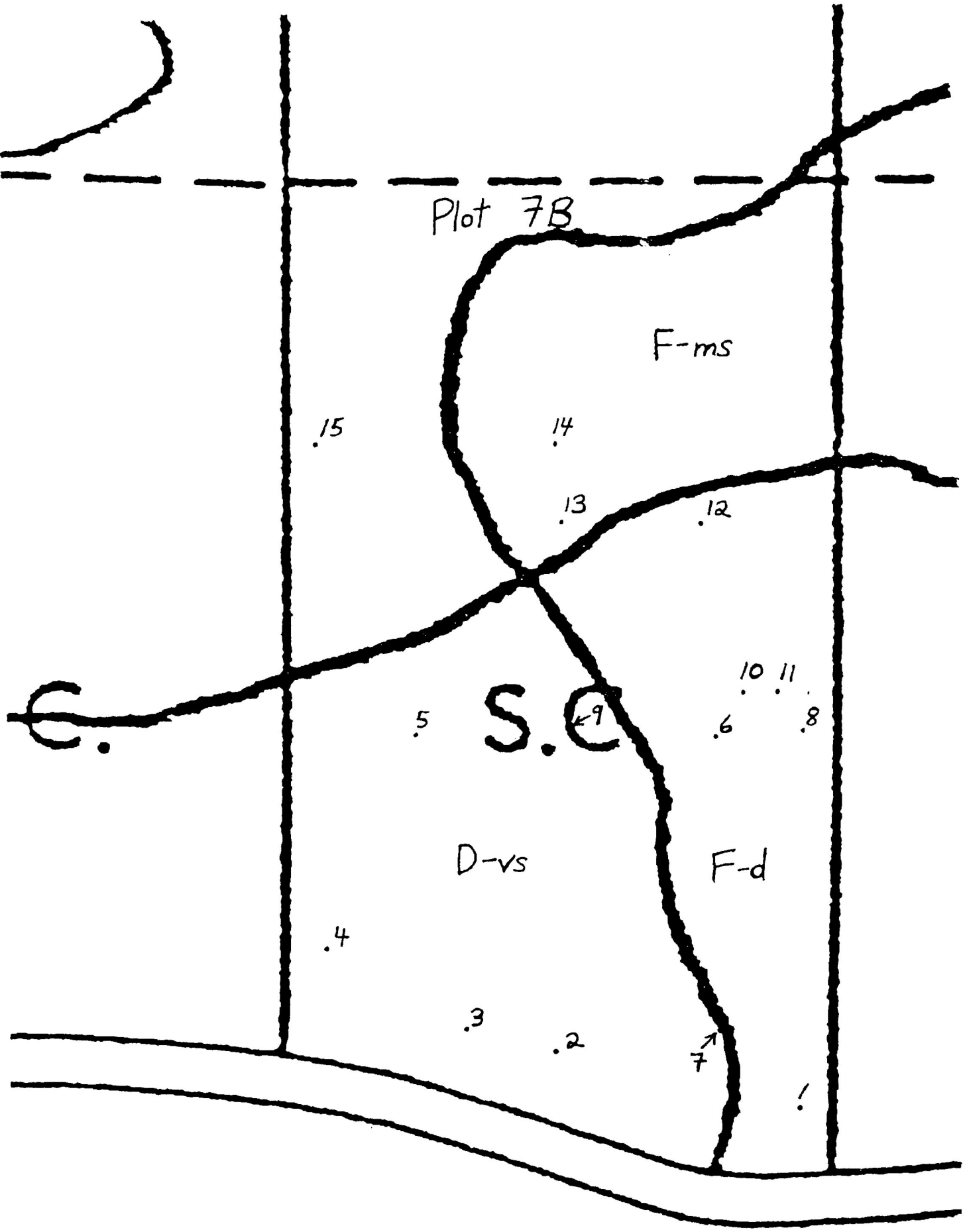
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F-ms
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S.C
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D-vs
F-d
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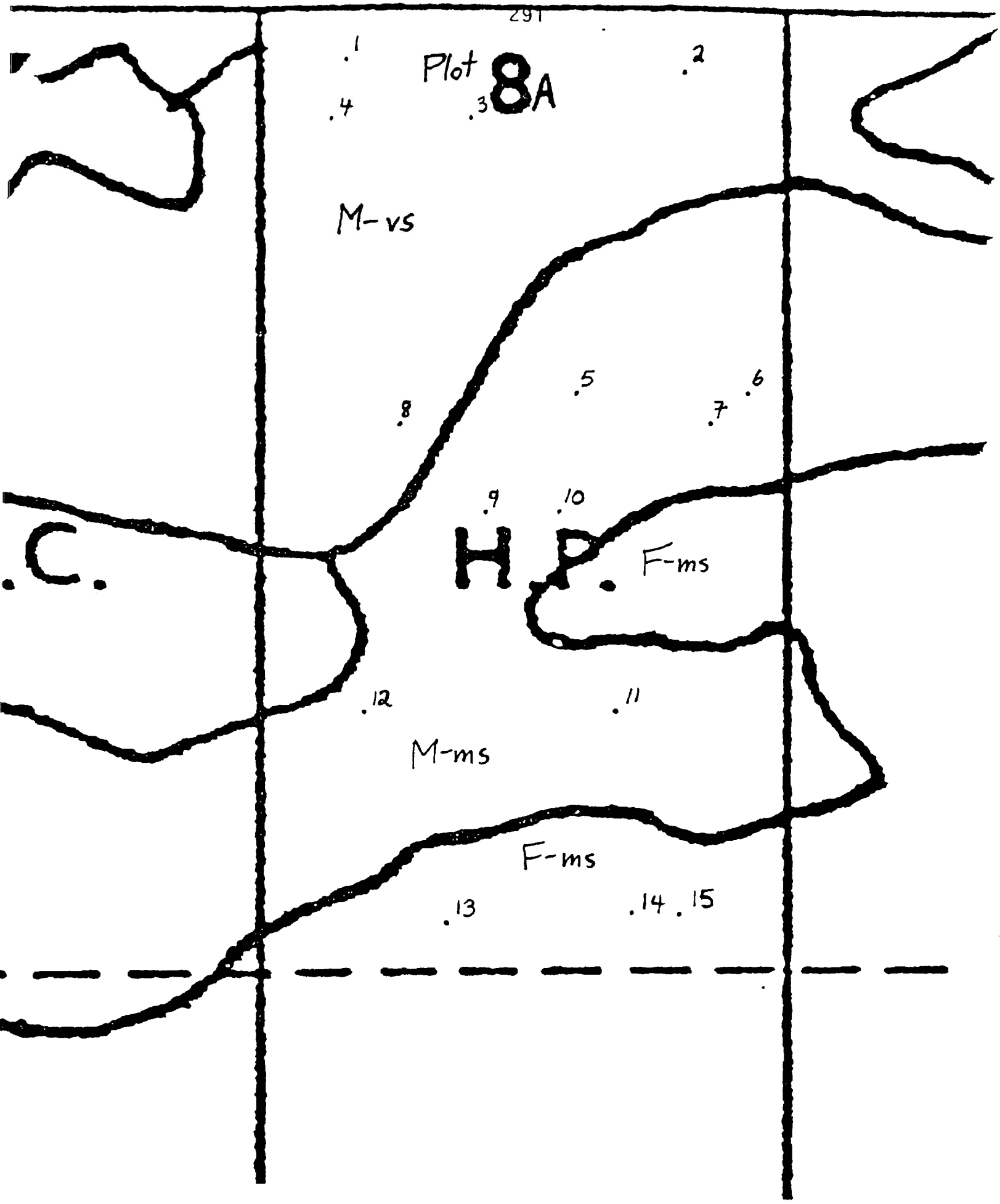
1


Plot 8A
1
2
3
4
M-vs
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H.P.
F-ms
C.
11
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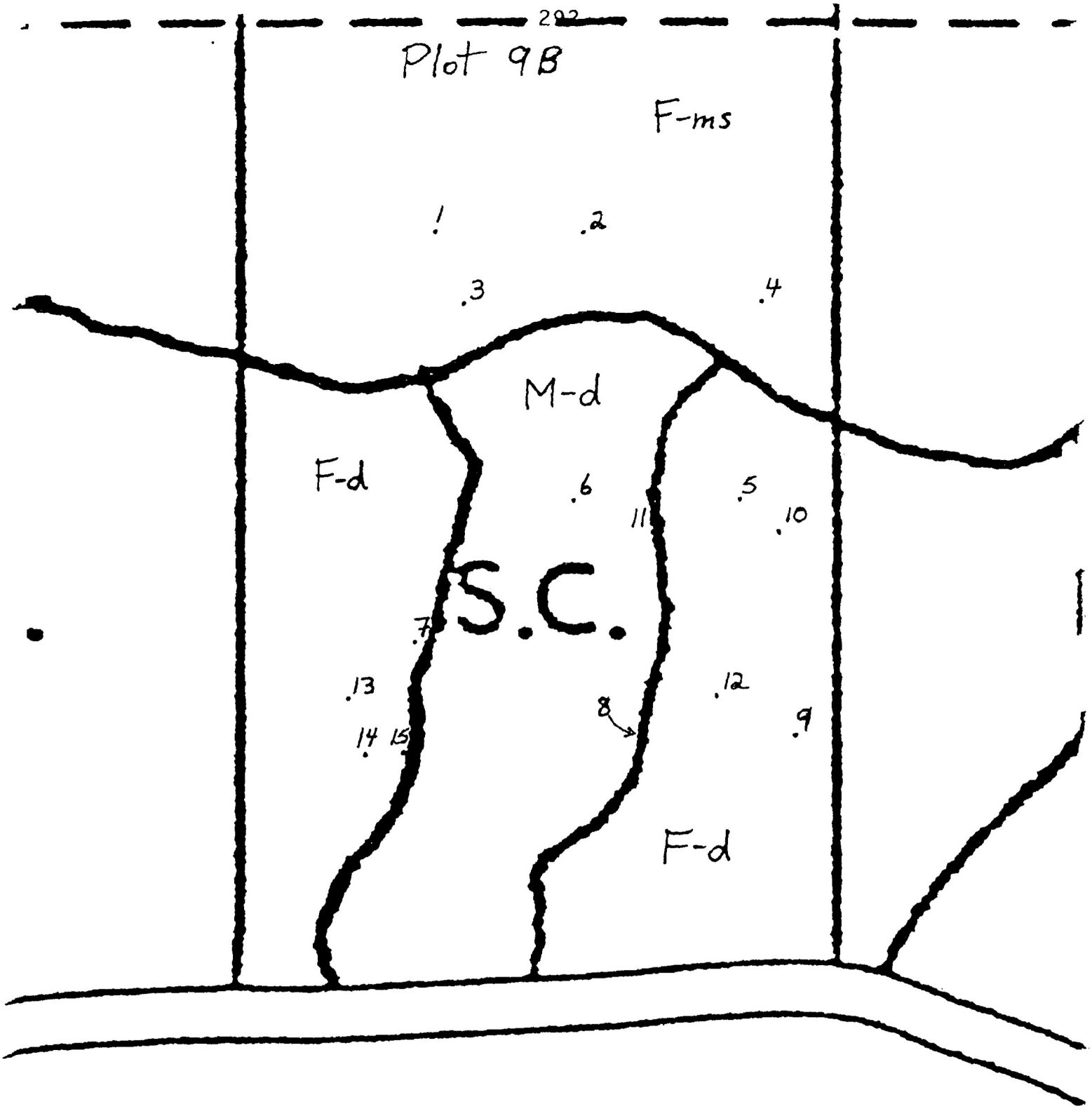
M-ms
F-ms
13
14
15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F-ms
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F-d
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S.C.
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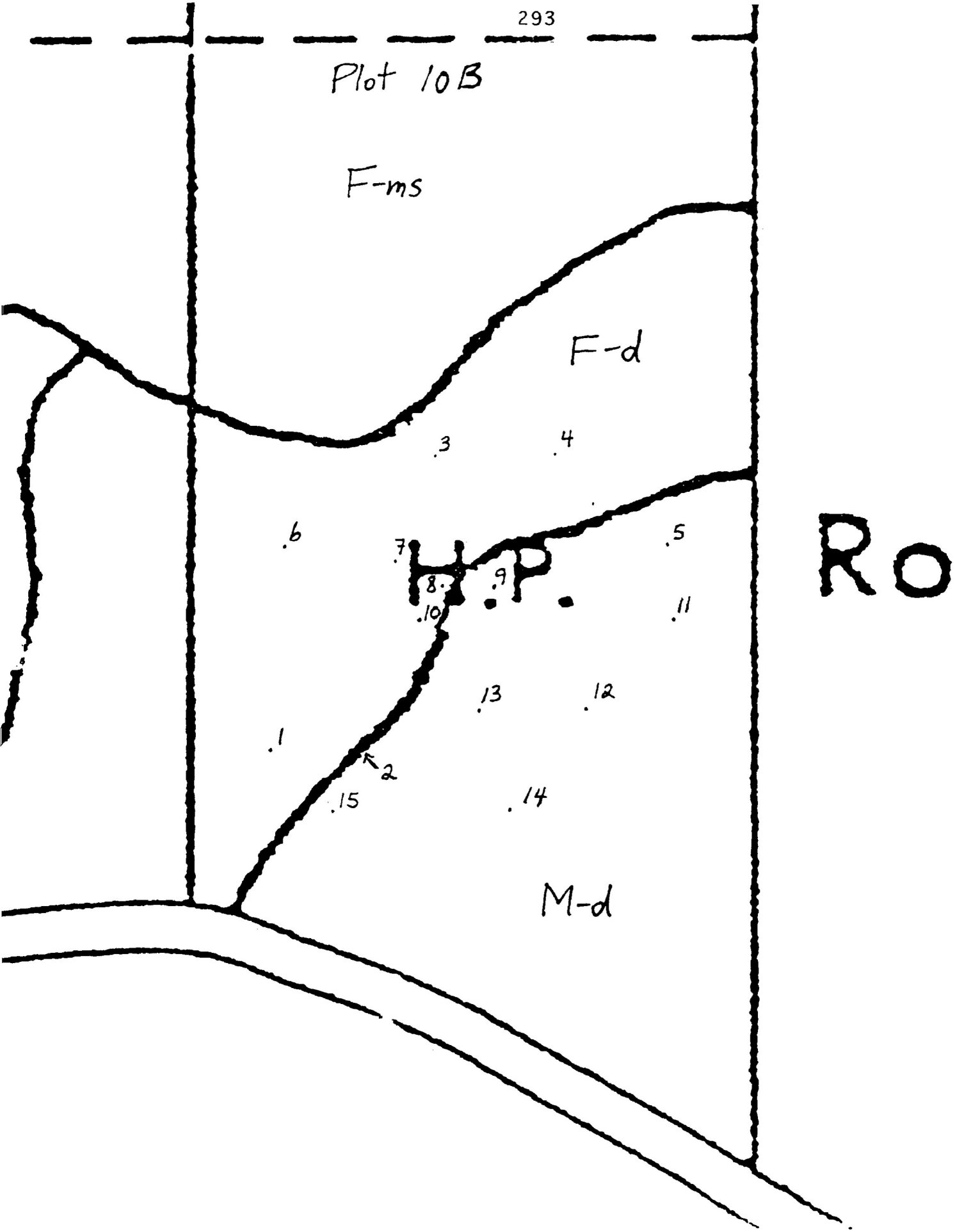
F-d


Plot 10B
F-ms
F-d
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H.P.
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RO
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M-d

Appendix 5. Plot values for density, dominance, frequency, cover and DBH of species in the tree stratum on the RC-17 project, 1990 (species ordered by overall importance values in Table 4.1.2).

a) Density (trees/ha).

Treatment	CC				SC				DC				HP		
Plot	1B	5A	5B	7A	3A	3B	7B	9B	4A	4B	6A	6B	2B	8A	10B
Abies balsamea	1003.6	558.1	462.6	585.0	1063.1	1062.3	702.1	383.4	959.8	978.1	212.8	1633.4	993.7	592.7	410.4
Betula papyrifera	215.1	232.5	330.4	292.5	408.9	516.0	501.5	287.5	319.9	366.8	328.8	466.7	478.5	395.1	273.6
Picea glauca	71.7	23.3	132.2	-	54.5	121.4	334.3	191.7	137.1	244.5	19.3	272.2	147.2	65.9	547.2
Picea mariana	71.7	162.8	99.1	760.5	190.8	212.5	100.3	-	182.8	152.8	580.2	77.8	110.4	131.7	82.1
Thuja occidentalis	35.8	-	793.1	-	-	121.4	-	-	-	244.5	-	-	331.2	-	27.4
Populus tremuloides	430.1	139.5	-	-	136.3	60.7	33.4	407.3	22.9	152.8	-	38.9	36.8	22.0	-
Alnus rugosa	35.8	46.5	66.1	-	163.6	91.1	133.7	24.0	137.1	214.0		-	-	22.0	82.1
Populus balsamifera	215.1	-	66.1	-	27.3	30.4	133.7	-	-	30.6		116.7	-	-	54.7
Salix	-	23.3	33.0	-	-	121.4	-	71.9	-	-	-	38.9	110.4	43.9	54.7
Sorbus decora	35.8	23.3	-	58.5	54.5	30.4	33.4	47.9	45.7	30.6	-	-	-	-	109.4
Fraxinus nigra	-	162.8	-	-	27.3	60.7	-	-	22.9	-	19.3	-		22.0	-
Prunus pensylvanica	35.8	-		-	54.5	-	33.4	-	-	-	-	-		22.0	-
Prunus virginiana	-	-		58.5	-	-	-	-		-	-	-		-	-
Larix laricina	-	23.3		-				-		-		-			-
Acer spicatum	-	-	-	-		-		24.0		30.6	-	-			-

b) Dominance (m2/ha)

Treatment	CC				SC				DC				HP		
Plot	1B	5A	5B	7A	3A	3B	7B	9B	4A	4B	6A	6B	2B	8A	10B
Abies balsamea	13.15	5.41	3.57	6.11	9.80	12.72	8.47	7.65	9.95	7.70	1.71	9.07	7.23	5.41	1.99
Betula papyrifera	1.57	2.47	3.34	1.91	4.00	0.81	3.69	8.75	5.20	2.37	3.54	1.91	3.21	3.36	1.98
Picea glauca	0.17	0.80	1.20	-	2.44	0.48	7.10	10.96	4.73	3.61	0.18	8.58	3.79	1.23	14.73
Picea mariana	0.54	2.00	0.72	5.61	5.73	1.28	0.72	-	3.60	1.24	7.67	0.64	0.70	3.24	1.84
Thuja occidentalis	0.36	-	9.42	-	-	3.40	-	-	-	11.54	-	-	5.13	-	0.13
Populus tremuloides	5.69	2.90	-	-	2.11	2.54	1.10	11.47	0.57	0.93	-	0.09	1.52	0.13	-
Alnus rugosa	0.07	0.14	0.14	-	0.42	0.20	0.30	0.07	0.38	0.56		-	-	0.06	0.20
Populus balsamifera	1.17	-	0.71	-	0.08	2.00	1.77	-	-	1.22		1.47	-	-	0.58
Salix	-	0.15	0.07	-	-	0.59	-	0.37	-	-	-	0.24	0.49	0.20	0.15
Sorbus decora	0.10	0.05	-	0.16	0.27	0.17	0.09	0.22	0.24	0.09	-	-	-	-	0.44
Fraxinus nigra	-	1.95		-	0.43	1.74	-	-	0.19	-	0.06	-		0.11	-
Prunus pensylvanica	0.11	-		-	0.14	-	0.14	-	-	-	-	-		0.15	-
Prunus virginiana	-	-		0.16	-	-	-	-	-	-	-	-		-	-
Larix laricina	-	0.06		-	-		-	-		-		-			-
Acer spicatum	-	-	-	-	-	-	-	0.05		0.06	-	-	-		-

Appendix 5 (cont.)

c) Frequency (%).

Treatment	CC				SC				DC				HP		
Plot	1B	5A	5B	7A	3A	3B	7B	9B	4A	4B	6A	6B	2B	8A	10B
Abies balsamea	86.7	86.7	53.3	80.0	85.0	80.0	73.3	53.3	95.0	80.0	46.7	94.1	86.7	80.0	66.7
Betula papyrifera	33.3	46.7	53.3	53.3	55.0	55.0	66.7	60.0	50.0	35.0	66.7	47.1	46.7	60.0	53.3
Picea glauca	6.7	6.7	13.3	-	10.0	20.0	46.7	33.3	20.0	40.0	6.7	41.2	26.7	13.3	73.3
Picea mariana	6.7	33.3	13.3	80.0	30.0	15.0	13.3	-	25.0	20.0	73.3	11.8	6.7	13.3	20.0
Thuja occidentalis	6.7	-	73.3	-	-	15.0	-	-	-	20.0	-	-	33.3	-	6.7
Populus tremuloides	33.3	20.0	-	-	10.0	5.0	6.7	46.7	5.0	15.0	-	5.9	6.7	6.7	-
Alnus rugosa	6.7	13.3	13.3	-	15.0	10.0	20.0	6.7	20.0	20.0		-	-	6.7	6.7
Populus balsamifera	26.7	-	13.3	-	5.0	5.0	13.3	-	-	5.0		11.8	-	-	13.3
Salix spp	-	6.7	6.7	-	-	10.0	-	20.0	-	-	-	5.9	13.3	13.3	13.3
Sorbus decora	6.7	6.7	-	13.3	5.0	5.0	6.7	13.3	10.0	5.0	-	-	-	-	13.3
Fraxinus nigra	-	6.7	-	-	5.0	5.0	-	-	5.0	-	6.7	-		6.7	-
Prunus pensylvanica	6.7	-		-	10.0	-	6.7	-	-	-	-	-		6.7	-
Prunus virginiana	-	-		6.7	-	-	-	-	-	-	-	-		-	-
Larix laricina	-	20.0		-	-			-		-		-			-
Acer spicatum	-	-	-	-	-	-		6.7		5.0	-	-			

d) Cover (%).

Treatment	CC				SC				DC				HP		
Plot	1B	5A	5B	7A	3A	3B	7B	9B	4A	4B	6A	6B	2B	8A	10B
Abies balsamea	23.7	16.2	25.7	19.2	26.5	23.8	19.7	20.8	33.7	34.7	8.8	35.3	30.2	30.7	14.2
Betula papyrifera	11.7	9.3	15.4	11.0	18.9	24.0	23.2	14.3	23.7	24.0	16.0	21.6	16.0	19.5	18.0
Picea glauca	4.3	0.7	5.7	-	5.3	7.6	17.8	8.7	7.5	10.7	1.3	17.4	10.3	7.0	23.0
Picea mariana	4.7	8.7	6.5	23.0	13.9	8.0	5.7	-	10.3	5.0	21.5	7.4	2.7	8.0	12.3
Thuja occidentalis	1.0	-	32.9	-	-	5.6	-	-	-	11.0	-	-	17.5	-	2.7
Populus tremuloides	34.7	12.3	-	0.3	5.6	1.5	2.0	27.0	-	7.0	-	3.8	1.7	0.7	1.0
Alnus rugosa	0.3	2.2	1.1	0.7	2.3	2.3	3.0	0.3	7.7	5.7		0.9	0.7	2.7	1.7
Populus balsamifera	4.2	-	1.8	-	0.6	0.3	2.7	7.0	-	2.0		4.0	-	0.3	1.7
Salix	-	0.7	0.5	-	-	1.5	0.7	1.7	2.0	0.7	-	-	2.0	1.3	1.0
Sorbus decora	0.5	1.2	0.4	1.7	2.9	0.4	0.8	2.8	0.2	0.7	-	0.6	-	-	1.3
Fraxinus nigra	-	11.7	-	-	1.0	1.3	-	-	1.3	-	0.3	-		0.3	-
Prunus pensylvanica	1.3	-	-	-	0.8	-	1.0	-	-	-	-	-		1.0	0.7
Prunus virginiana	-	-		0.7	-	-	-	-	-	-	-	-		-	-
Larix laricina		0.3		-	-			-		-		-			-
Acer spicatum		0.3		-	-	-		0.3		0.7	-	-			

Appendix 5 (cont.)

e) DBH (cm).

Treatment	CC				SC				DC				HP		
Plot	1B	5A	5B	7A	3A	3B	7B	9B	4A	4B	6A	6B	8A	2B	10B
Abies balsamea	12.0	10.4	9.5	10.7	10.1	10.9	11.0	15.0	10.5	9.4	9.4	7.9	10.2	9.0	7.6
Alnus rugosa	*5.1	*6.1	*5.1	-	5.7	6.4	5.3	6.1	5.9	5.7	-	-	*6.1	-	5.5
Betula papyrifera	9.0	10.7	10.7	8.4	10.8	15.5	9.2	15.4	12.5	8.4	10.5	6.9	10.2	8.6	8.9
Fraxinus nigra	-	11.7	-	-	*14.2	-	-	-	*10.2	-	*6.5	-	*8	-	-
Picea glauca	*5.6	*20.9	10.4	-	*23.5	11.2	14.8	24.9	19.0	12.7	*10.9	17.8	13.4	16.9	16.9
Picea mariana	*9.1	11.5	9.1	9.1	18.6	13.4	9.5	-	15.6	9.3	11.9	*10.2	16.9	8.7	16.6
Populus balsamifera	7.9	-	*11.55	-	*6.3	*14.1	-	-	-	*22.5	-	11.5	-	-	*11.5
Populus tremuloides	12.7	15.3	-	-	13.4	*23.1	*20.5	17.4	*17.8	8.4	-	*5.4	*8.6	*22.9	-
Prunus pensylvanica	*6.2	-	-	-	*5.7	-	*7.4	-	-	-		-	*9.3	-	-
Salix spp.	-	*9	*5.1	-	-	12.6	-	7.9	-	-		*8.8	*7.55	7.5	*5.85
Sorbus decora	*5.9	*5.1	-	*5.85	*7.95	*5.6	*5.8	*7.6	*8.05	*6.1		-	-	-	7.1
Thuja occidentalis	*11.3	-	11.1	-	-	13.4	-	-	-	16.9		-		12.1	*7.7

* Sample size ≤2

Appendix 6. Total tree density, conifer density and hardwood density, on plots of the RC-17 project, 1990 *(conifer= P. mariana, P. glauca, A. balsamea; hardwood = b. papyrifera, P. tremuloides, P. balsamifera).*

TREATMENT	PLOT	TOTAL	CONIFER	HARDWOOD
CC	1B	2150.6	1147.0	860.3
	5A	1395.2	744.2	372.0
	5B	1982.6	693.9	396.5
	7A	1755.1	1345.5	292.5
SC	3A	2180.8	1308.4	572.5
	3B	2428.2	1396.2	607.1
	7B	2006.1	1136.7	668.6
	9B	1437.7	575.1	694.8
DC	4A	1828.2	1279.7	342.8
	4B	2445.3	1375.4	550.2
	6A	1160.5	812.3	328.8
	6B	2644.6	1983.4	622.3
HP	2B	2208.3	1251.3	515.3
	8A	1317.0	790.3	417.1
	10B	1641.5	1039.7	328.3
CC	Mean	1820.9	982.7	480.3
	Std. dev.	396.6	248.4	275.1
SC	Mean	2013.2	1104.1	635.8
	Std. dev.	420.9	368.8	55.9
DC	Mean	2019.7	1362.7	461.0
	Std. dev.	670.0	481.4	147.7
HP	Mean	1722.3	1027.1	420.2
	Std. dev.	451.1	230.8	93.5

Appendix 7. Tree age and height data, collected at 5 points per plot, via the point-centred quarter method, on the RC17 project, 1990.

Treatment CC

PLOT	TREE SPECIES	HGT	AGE
1B CC	Abies balsamea	11.5	34
		5.3	28
		8.4	41
		13.3	36
		7.4	36
		11.7	68
		8.4	52
		9.0	38
		10.9	36
		8.8	38
		5.4	32
	Betula papyrifera	11.7	21
	Picea mariana	9.1	35
	Populus balsamifera	8.7	22
	Populus tremuloides	9.9	21
		14.1	39
		9.5	25
		15.2	32
		22.0	35
	Thuja occidentalis	6.5	30
5A CC	Abies balsamea	11.0	43
		12.0	32
		13.9	39
		5.0	28
		5.2	29
		6.4	42
		3.6	33
	Betula papyrifera	9.1	30
		10.1	32
		12.8	36
		12.5	22
		13.5	32
		3.6	30
	Fraxinus nigra	11.0	51
		8.5	24
		12.0	52
	Larix laricina	5.0	26
	Picea mariana	5.0	20
		6.4	25
	Salix spp.	8.3	30
5B CC	Abies balsamea	7.2	28
		8.3	35
		6.8	35
		5.8	38
		11.9	36
		12.4	31
	Betula papyrifera	10.8	36
		12.5	28
	Picea glauca	9.3	49
		7.6	39
		9.2	45
	Salix spp.	6.1	20
	Thuja occidentalis	7.0	38
		4.6	38
		4.9	29
		3.7	34
		3.5	33
		4.0	23
		5.8	29
		6.5	31
7A CC	Abies balsamea	9.2	36
		5.8	38
		6.0	34
		11.0	55
		12.5	57
		12.0	41
		6.8	33
	Betula papyrifera	10.7	37
		3.2	20
	Picea mariana	10.0	44
		10.8	35
		9.8	33
		8.6	40
		5.5	27
		4.0	26
		8.0	43
		11.8	59
	Prunus vir	6.0	25
		6.2	30
	Sorbus decora	7.4	26

Treatment DC

PLOT	TREE SPECIES	HGT	AGE
4A DC	Abies balsamea	8.0	31
		8.2	26
		5.1	29
		10.4	45
		4.9	35
		8.6	38
		6.2	38
	Alnus rugosa	5.6	24
		7.1	25
		7.0	20
	Betula papyrifera	16.0	50
		8.9	49
		6.3	26
		8.3	26
	Fraxinus nigra	9.5	74
	Picea glauca	11.5	42
		7.9	38
	Picea mariana	11.8	79
		11.0	73
	Sorbus decora	7.5	31
4B DC	Abies balsamea	8.4	30
		6.4	26
		7.6	32
		9.8	41
		7.2	43
		9.2	32
		9.3	41
		6.8	32
		9.6	44
	Alnus rugosa	6.0	21
		7.3	19
		7.9	18
	Betula papyrifera	7.5	26
		7.7	22
		10.7	40
		7.4	20
		8.9	23
		9.0	20
	Picea glauca	8.7	36
	Populus tremuloides	7.8	26
6A DC	Abies balsamea	4.4	39
		8.4	38
		3.5	35
	Betula papyrifera	8.0	40
		8.8	43
		11.0	53
		11.0	56
		10.5	50
		6.3	31
		8.7	36
	Picea glauca	6.3	38
	Picea mariana	10.4	81
		4.3	33
		7.1	64
		10.4	72
		13.0	92
		10.5	48
		4.8	32
		4.7	31
		12.3	78
6B DC	Abies balsamea	4.8	23
		4.8	29
		12.3	37
		6.1	30
		4.0	31
		6.7	25
		5.6	24
		4.7	21
		5.5	28
		5.5	25
		5.0	25
		4.6	17
		4.8	20
		5.5	26
	Betula papyrifera	7.8	24
		8.0	23
	Picea glauca	5.6	25
		5.8	27
		7.0	30
	Salix spp.	6.0	17

Appendix 7 (cont.)

Treatment HP

PLOT	TREE SPECIES	HGT	AGE
10B HP	Abies balsamea	5.1	23
		7.6	30
		6.7	25
		7.3	45
		4.5	30
		8.7	52
	Alnus rugosa	6.5	23
		5.2	23
		7.3	23
	Betula papyrifera	11.0	44
		8.2	33
	Picea glauca	9.1	45
		5.5	35
		11.4	33
		13.0	68
		11.2	37
	Sorbus decora	6.7	
		7.6	28
		8.2	29
	Thuja occidentalis	5.8	28
2B HP	Abies balsamea	10.4	39
		6.5	38
		10.4	40
		8.2	49
		6.0	39
		7.0	35
		6.0	37
		7.2	30
	Betula papyrifera	13.0	39
		7.4	31
		6.5	27
		9.2	28
	Picea glauca	16.0	50
		4.5	29
	Populus tremuloides	16.7	25
	Salix spp.	7.1	24
		6.9	25
	Thuja occidentalis	4.9	33
		4.0	43
		6.7	56
8A HP	Abies balsamea	6.7	35
		6.5	35
		5.6	28
		8.4	36
		7.8	36
		5.3	27
		6.8	30
		6.4	34
		7.5	56
		5.7	33
		7.5	36
	Betula papyrifera	7.0	23
		9.6	26
		7.1	17
		9.6	20
		10.2	27
	Picea glauca	3.6	26
	Populus tremuloides	9.8	28
	Prunus pensylvanica	7.8	29
	Salix spp.	6.6	21

Treatment SC

PLOT	TREE SPECIES	HGT	AGE
3A SC	Abies balsamea	11.0	45
		5.4	41
		7.3	34
		10.8	36
		9.3	29
		11.7	33
		5.4	27
		11.0	34
		10.4	27
	Alnus rugosa	7.0	19
		7.2	18
		7.4	18
		8.2	15
	Betula papyrifera	16.2	39
	Picea glauca	14.6	73
	Picea mariana	13.2	55
		15.5	50
	Populus tremuloides	17.6	39
	Sorbus decora	7.6	41
		7.9	30
3B SC	Abies balsamea	6.8	26
		4.8	22
		5.5	26
		8.1	46
		12.9	38
		4.0	20
		7.2	36
		6.2	45
		6.0	34
		9.9	40
		9.7	38
		6.1	29
		4.5	33
		7.8	33
		7.8	27
	Betula papyrifera	13.3	
		12.5	28
		6.4	29
	Picea glauca	5.2	30
	Thuja occidentalis	4.8	34
7B SC	Abies balsamea	22.0	55
		7.4	38
		12.9	44
		4.3	29
	Alnus rugosa	9.4	18
	Betula papyrifera	10.0	18
		10.5	29
		10.3	27
		10.1	30
		8.4	26
		8.6	24
		8.4	28
		12.7	
	Picea glauca	10.0	35
	Picea mariana	9.0	32
	Populus balsamifera	12.3	
		9.5	24
		11.5	
		13.1	24
	Prunus pensylvanica	6.7	27
9B SC	Betula papyrifera	13.0	34
		15.6	29
		8.6	26
		14.6	36
		8.4	35
		6.7	
	Picea glauca	4.5	33
	Populus tremuloides	19.4	29
		19.8	31
		19.2	29
		12.4	25
		13.9	22
		15.5	
		17.8	29
		20.6	35
		19.8	
		22.0	33
		20.8	36
	Salix spp.	8.2	23
	Sorbus decora	9.2	27

Appendix 8. Distance pairs for spatial pattern analysis of trees by the T-square and the Johnson and Zimmer indices. (x-distance from point to tree, y-distance from tree to nearest neighbor).

a) Plot data for spatial pattern analysis of all trees.

CC							
1B		5A		5B		7A	
x	y	x	y	x	y	x	y
1.28	2.90	0.80	1.73	0.79	0.58	0.52	0.51
1.72	1.59	1.25	0.44	1.20	1.75	1.84	2.00
0.86	0.97	1.40	0.85	0.50	0.80	1.47	0.17
1.21	1.83	1.39	1.54	2.31	2.19	0.71	1.39
0.27	1.34	1.22	1.73	0.75	0.50	0.75	0.13
0.83	1.81	0.46	4.28	0.87	0.58	0.68	1.46
1.18	1.67	4.74	0.84	0.65	0.50	1.42	2.25
0.72	0.61	1.00	2.90	1.67	0.38	1.08	0.34
0.32	0.42	0.37	1.66	1.58	2.15	1.78	0.45
1.35	1.87	1.04	0.58	0.65	0.27	1.96	1.24
1.89	1.68	0.49	0.92	1.09	1.14	1.48	0.30
1.76	1.63	0.41	2.43	0.68	1.91	2.59	1.68
0.73	0.51	0.82	2.48	0.65	0.39	0.31	2.89
0.70	0.94	0.77	2.23	0.48	1.33	0.76	1.48
0.66	0.47	0.73	0.77	0.94	0.66	1.34	1.59

CC							
4A		4B		6A		8B	
x	y	x	y	x	y	x	y
0.60	0.54	0.40	0.84	0.97	1.65	0.68	2.08
1.90	3.98	1.04	1.75	0.82	3.45	0.52	1.38
0.26	1.92	0.63	0.95	0.53	2.22	0.55	0.95
0.84	1.17	1.21	1.53	1.93	2.14	1.23	0.88
2.14	0.20	0.36	3.03	0.79	1.05	0.75	0.74
0.50	1.59	1.09	1.74	0.87	0.93	0.63	2.30
0.45	1.45	0.30	0.91	3.48	5.35	1.05	1.52
0.50	0.74	2.30	0.76	1.62	0.32	0.43	1.81
0.37	0.19	0.45	0.51	2.05	1.00	1.00	0.58
2.64	0.83	0.50	1.81	2.66	1.51	0.69	1.44
1.76	2.72	1.22	0.63	2.37	0.33	1.73	1.25
0.40	0.17	0.60	0.94	2.40	0.71	1.84	1.80
1.15	3.54	0.40	2.07	0.77	1.26	1.11	3.63
1.57	1.49	1.54	0.78	1.24	0.51	1.37	2.82
0.86	3.84	1.50	1.94	1.35	1.28	1.38	2.35
0.92	0.67	0.30	1.13			1.20	1.36
0.74	0.58	1.46	3.80			1.44	2.43
1.51	3.42	1.18	0.75				
1.23	0.94	2.11	2.04				
1.38	1.96	1.20	2.97				

HP					
10B		2B		8A	
x	y	x	y	x	y
2.14	2.15	0.95	1.41	0.89	0.53
1.13	1.39	1.00	1.04	0.94	5.65
1.66	2.12	1.97	2.02	1.91	0.37
0.97	2.18	0.78	1.92	4.95	1.75
1.97	0.95	0.52	0.84	1.46	0.53
2.05	3.11	1.83	1.57	0.94	0.64
1.86	2.56	1.45	2.02	1.61	1.66
0.30	1.50	1.15	0.78	0.35	1.18
0.78	1.76	0.53	1.19	1.50	1.31
1.62	0.86	0.72	1.84	3.09	3.26
0.47	3.00	1.45	2.30	1.20	0.92
2.30	3.44	2.65	1.69	2.42	0.65
0.60	1.09	0.53	0.16	1.26	1.47
0.81	1.52	0.64	0.97	1.62	1.35
1.25	0.21	1.25	0.43	1.70	3.85

SC							
3A		3B		7B		9B	
x	y	x	y	x	y	x	y
0.69	1.85	1.50	0.48	1.23	0.71	0.98	0.71
0.81	0.56	0.25	0.84	0.38	1.91	1.07	1.57
1.72	0.72	0.17	0.41	1.70	3.50	0.92	1.09
0.14	1.62	0.80	0.59	1.25	1.14	2.34	3.56
1.23	0.45	0.48	3.98	2.06	3.47	0.74	1.83
0.58	0.79	0.50	0.93	0.53	1.52	2.30	2.15
0.33	2.66	0.76	1.61	0.22	0.56	0.51	3.24
3.06	0.97	1.16	2.20	1.48	0.78	1.78	2.75
0.55	1.21	0.75	3.08	0.86	2.24	0.70	2.62
1.00	0.65	1.13	0.41	0.76	1.25	0.89	1.67
0.93	1.10	0.30	1.21	1.69	1.22	0.27	2.02
1.60	1.95	0.34	1.04	1.24	0.62	1.53	1.79
1.20	1.40	1.20	4.33	0.78	1.52	1.17	1.89
1.57	0.93	2.30	4.29	0.90	2.52	1.98	2.62
1.27	0.49	1.34	1.40	1.72	1.81	2.30	0.45
0.88	3.25	1.63	1.32				
1.26	0.88	1.17	0.85				
1.15	1.37	1.18	1.16				
2.53	2.14	0.20	2.15				
1.33	1.79	1.39	3.44				

Appendix 8 (cont.).

b) Data for spatial pattern analysis of each tree species in each treatment.

Abies balsamea

CC		DC		HP		SC	
x	y	x	y	x	y	x	y
2.77	1.24	2.36	1.30	2.57	1.57	2.02	1.11
2.40	1.73	2.76	3.33	6.39	6.09	1.72	0.96
1.97	0.90	0.84	1.17	1.66	2.12	0.14	1.62
2.16	2.77	2.40	1.39	3.43	3.65	1.23	0.45
0.27	2.37	0.50	3.97	1.86	2.75	0.58	0.79
1.18	4.95	3.36	1.35	1.62	2.28	0.55	1.21
0.72	0.61	0.50	0.74	2.98	0.63	1.63	3.36
1.61	0.92	0.53	1.97	3.59	2.78	0.93	2.70
1.35	1.87	5.56	2.95	2.64	1.72	1.60	2.78
7.18	0.90	1.76	2.72	4.76	1.26	1.20	3.99
1.76	3.07	0.54	2.97	0.95	1.41	1.67	1.16
0.73	5.39	1.15	3.30	1.00	1.35	2.33	1.94
2.02	4.17	1.57	1.49	1.97	2.02	0.88	3.25
2.40	2.38	0.86	3.84	0.76	1.92	1.35	1.99
3.34	4.94	1.46	4.17	0.52	1.16	1.15	2.55
2.30	1.39	0.74	0.78	1.83	1.57	2.53	2.14
1.65	7.46	1.64	0.38	1.45	2.02	2.39	1.64
2.58	3.93	1.23	0.94	1.15	2.89	1.50	1.82
1.78	2.23	4.26	0.93	1.55	4.14	1.93	1.55
5.03	0.51	0.40	4.45	2.65	1.92	0.17	2.74
1.00	5.73	1.10	0.99	1.61	5.02	0.80	0.59
0.37	1.66	3.16	0.55	0.64	3.03	0.48	3.98
3.26	7.91	3.17	2.27	1.84	8.45	1.52	2.15
1.10	2.68	0.30	0.91	0.69	0.53	1.16	2.20
1.38	1.24	2.30	7.80	5.86	1.43	3.05	0.33
1.12	0.87	0.45	6.10	3.24	0.84	0.35	3.86
3.61	1.62	1.16	0.43	6.36	1.42	2.35	1.10
0.75	0.50	0.60	0.94	2.15	2.62	1.67	1.00
2.18	0.96	1.15	1.27	0.94	0.64	2.30	4.75
1.85	1.35	1.54	0.87	1.61	1.84	1.34	1.40
0.65	2.49	1.50	3.11	0.35	1.66	4.06	1.38
2.18	2.28	0.43	0.79	1.50	1.45	1.17	1.37
0.68	2.21	1.46	3.80	3.09	3.26	2.08	1.28
1.00	1.37	1.18	0.75	1.20	0.92	1.23	1.58
1.90	2.09	2.45	3.81	2.43	0.63	1.70	5.84
2.46	4.25	2.85	3.64			1.25	1.14
1.47	0.17	4.52	0.27			2.34	2.53
1.71	0.42	4.05	3.91			2.01	3.10
0.68	2.26	2.40	0.71			2.21	2.24
2.02	2.94	1.23	4.38			1.28	2.04
2.44	1.34	2.83	2.25			1.69	1.22
6.36	2.91	1.35	1.28			0.78	2.54
1.98	0.65	0.68	2.08			1.75	1.45
0.31	4.06	0.96	1.35			1.72	1.61
0.76	1.48	1.23	0.88			0.98	9.27
1.34	1.59	0.75	0.74			1.07	1.57
		1.29	4.90			3.54	4.61
		1.05	2.03			2.34	3.56
		1.16	3.04			0.51	4.98
		1.00	0.58			1.35	4.00
		0.69	1.44			1.65	4.27
		1.73	1.25			1.17	1.89
		2.38	1.24				
		1.11	4.84				
		1.60	1.54				
		1.86	1.08				
		1.20	1.36				
		1.56	3.56				

Betula papyrifera

CC		DC		HP		SC	
x	y	x	y	x	y	x	y
1.60	6.56	0.60	5.50	1.25	1.66	0.61	0.56
0.32	0.42	1.90	3.96	2.25	7.87	3.65	0.91
3.36	0.34	0.76	0.88	2.32	2.77	3.56	5.17
1.03	5.73	0.37	1.66	2.80	0.68	1.00	0.65
0.66	0.47	0.40	0.17	1.65	2.32	2.07	0.90
0.80	6.37	2.79	0.31	0.47	7.76	3.70	0.67
1.25	0.44	1.76	12.15	2.86	4.35	1.70	2.67
1.40	1.66	0.92	0.87	2.56	2.37	1.57	0.93
4.41	3.70	1.40	1.66	1.32	4.48	1.27	4.84
3.35	6.98	2.16	4.60	1.16	5.54	3.67	0.48
6.20	5.19	4.01	1.42	2.78	0.47	0.25	1.40
1.15	9.02	1.09	6.38	3.94	0.42	4.00	2.52
0.79	0.58	0.82	3.56	1.06	0.20	1.65	3.61
1.80	7.61	4.67	1.59	0.80	3.21	1.86	2.24
1.42	3.94	0.42	0.30	2.68	3.04	0.76	1.61
1.14	6.11	2.40	7.20	3.41	6.27	0.75	3.08
5.77	0.68	2.74	2.12	5.24	1.94	0.34	1.04
0.65	0.39	0.97	1.83	1.46	4.23	2.52	3.24
4.90	0.37	0.82	3.45	2.02	2.75	2.59	1.12
2.51	2.00	0.53	2.22	2.47	4.83	1.76	2.05
1.88	1.89	1.21	11.00	2.42	0.65	2.92	5.20
1.77	0.77	6.75	1.91	1.26	2.47	4.55	1.58
0.71	2.15	3.82	16.40	2.02	3.14	0.45	0.33
0.83	4.71	2.37	0.33	1.70	4.95	1.70	5.84
1.42	2.48	2.92	1.38			3.72	6.65
1.08	0.34	0.77	2.30			2.06	6.36
4.52	3.46	2.16	0.19			0.98	0.49
2.59	2.81	0.52	1.42			0.22	0.56
		1.72	5.11			1.48	0.78
		3.90	0.31			1.55	3.38
		0.63	2.30			2.61	0.70
		0.43	1.81			2.75	4.90
		2.41	5.05			3.33	4.10
		1.90	2.24			0.74	1.83
		2.44	1.67			2.30	2.15
						5.23	10.20
						7.38	1.98
						0.75	2.67
						0.98	5.92
						3.52	0.44
						3.36	0.59

Picea mariana

CC		DC	
x	y	x	y
1.28	8.65	3.20	4.64
1.80	0.60	2.33	9.72
1.30	1.84	1.51	3.42
1.39	6.08	1.38	2.97
1.22	2.83	3.15	5.15
0.46	3.90	0.95	1.78
4.74	0.84	1.67	0.76
2.67	2.16	2.11	2.04
2.70	3.21	1.93	2.14
0.52	0.51	0.79	2.34
1.84	2.20	0.87	0.93
2.70	0.54	1.85	5.95
0.75	1.08	2.33	5.23
2.67	0.55	1.12	1.42
5.17	0.55	5.16	4.63
1.82	3.60	1.62	0.32
1.78	0.45	2.05	1.00
1.96	1.24	2.66	1.51
1.48	0.30	0.77	12.90
2.92	0.93	2.64	3.55
1.61	3.34	1.86	0.65

Picea glauca

DC		HP	
x	y	x	y
2.14	2.17	3.25	4.76
3.60	7.18	1.13	2.53
2.84	0.83	0.97	4.59
4.40	6.25	1.97	1.80
1.18	1.65	2.05	3.11
1.21	10.30	2.32	2.40
3.97	2.60	0.78	1.76
2.17	3.00	1.84	1.15
1.55	1.73	2.30	3.44
2.40	6.54	0.92	2.25
0.30	5.08	3.24	0.80
2.35	0.57	1.00	3.42
0.55	7.09	1.23	1.19
4.16	8.00	0.53	6.18
1.96	2.13	0.75	4.83
2.34	2.17	3.55	5.25
1.37	4.15	1.91	0.37
1.36	4.96	2.43	8.10
4.40	4.95		

Thuja occidentalis

CC	
x	y
4.03	3.88
1.86	4.20
1.20	1.75
2.31	3.14
1.05	5.98
0.87	0.58
0.65	0.50
1.67	0.38
1.58	2.15
1.09	1.14
3.35	1.51
0.94	0.66

Appendix 9. Plot means of shrub percentage cover, percentage frequency and density on the RC-17 project, 1990.

a) Shrub cover (%).

Treatment	CC	CC	CC	CC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	5A	3B	7B	9B	3A
Abies balsamea	3.0	6.2	11.3	2.7	12.3	14.8	12.7	21.2	12.8	15.7	10.8	13.1	6.6	3.5	6.4
Acer spicatum	33.7	18.3	10.0	5.8	37.7	44.0	5.5	45.9	28.2	24.0	30.7	29.0	33.3	41.3	31.5
Alnus crispa	-	3.3	1.8	4.7	5.5	4.7	4.3	-	-	-	-	2.1	2.0	-	7.8
Alnus rugosa	11.0	15.8	12.0	8.7	13.0	13.3	18.7	2.1	21.7	2.0	20.3	7.0	5.0	3.3	4.3
Amelanchier bartramiana	0.5	5.8	1.0	1.8	0.5	0.2	2.3	0.1	0.5		1.7		-		0.3
Amelanchier humilis	0.3		0.7	-	-	1.0		0.1	0.7	0.2	1.0	-	0.3	-	0.9
Betula papyrifera	1.5	1.3	3.2	7.2	9.0	8.7	4.3	5.4	2.8	3.3	3.3	4.0	3.5	0.3	4.4
Cornus stolonifera	2.8	3.8	3.7	0.3	0.8	3.2	1.7	1.6	9.3	3.0	1.8	0.8	1.5	1.5	0.4
Corylus cornuta	5.2	2.8		2.0	2.3	4.3	4.7	13.5	0.3	8.3	8.3	5.0	4.0	20.3	3.1
Diervilla lonicera	0.7	1.0	1.3	0.2	-	3.3	0.7	0.7	1.2	0.3	3.8	0.3	2.5	1.7	0.1
Fraxinus nigra	-	0.3	-	-	0.8	-	0.3	-	-	-	0.7	0.8	-	-	0.6
Kalmia polifolia		-		0.2	-		-				-	-			-
Larix laricina	-	0.3	-	-			0.7		-		-				-
Ledum groenlandicum	0.7	5.0	6.5	9.2	-	-	15.2	-	0.3	0.3	1.3	-	-	-	-
Lonicera canadensis	2.7	0.2	1.0	0.2	0.5	2.7	0.2	3.1	2.0	2.5	1.8	0.5	1.2	2.2	1.1
Lonicera hirsuta	-	-	-	-	-	0.3	-	0.3	0.2	-	0.3	-	-	-	-
Lonicera involucrata	0.2	0.5	1.0	-		-	-	0.6	0.8	0.7	0.2	0.1	0.3		
Lonicera oblongifolia	0.2	0.7	-				0.3		0.2						
Lonicera villosa	-	1.8					2.7	-	-						
Myrica gale	-	0.3				-	-	-	-		-		-	-	
Picea glauca	0.5	-	0.5	-	2.0	0.8	0.7	1.5	3.3	0.5	1.0	2.1	0.3	0.5	0.3
Picea mariana	1.2	3.7	0.7	5.0	1.2	0.7	10.0	2.2	1.8	1.7	0.7	0.8	0.7	-	0.5
Populus balsamifera	0.8		0.7	-		-	-	0.6	0.2		-	-	0.3	0.3	-
Populus tremuloides	-	-	-	-		-	-	-	-			-	0.2	0.2	-
Prunus pensylvanica	1.5	0.2	0.3	2.2		0.8	0.3	0.1	0.2		-	0.5	-	0.3	0.6
Prunus virginiana	-	-	-	0.7		-	-	0.6	1.2		0.5	-	0.7	1.7	0.1
Rhamnus alnifolia	0.2	0.8	0.7	-		-		-	1.5		0.2		0.7	-	-
Ribes glandulosum			-			-		-	-		-		-	0.2	0.1
Ribes hirtellum		-		-		0.3		0.1	1.3		-		-	-	-
Ribes hudsonianum		0.2	-	-		-		-	-	-	-	-	-	-	-
Ribes lacustre		-	1.0	-		0.5		1.2	1.2	0.8	0.3	0.1	0.2	0.2	-
Ribes oxycanthoides			0.2	-		-		-	-				0.3	-	-
Ribes triste	-	-	-	-		-	-	0.3	0.2	-	-	-	-	-	0.1
Rosa acicularis	0.3	0.7	2.0	0.3	-	1.3	1.0	0.7	3.2	1.0	0.7	0.3	0.8	0.2	-
Rubus idaeus var. strigosus	0.5	0.8	0.3	0.3	0.2	-	0.7	0.1	1.2	0.5	1.0	0.1	0.2	0.2	0.1
Salix	1.0	-	1.0	-	-	2.3	-	0.7	1.3	1.8	1.2	0.4	0.3	0.2	0.5
Sambucus pubens	0.3	-	-	0.2	-	-	-	-	-	-	-	-	-	0.3	-
Sorbus decora	0.8	1.5	1.0	2.5	1.2	2.2	2.8	1.6	2.8	0.8	1.3	1.3	2.3	1.2	0.5
Thuja occidentalis	0.7		16.7	-	-	3.5	-	0.3	1.3	16.0		2.6			
Vaccinium angustifolium		-	-	-	-	-	0.3	-	-	-	0.2	-	-	-	-
Viburnum edule	1.2	1.5	0.3	0.3	0.2	0.2	0.5	1.0	1.2	0.3	2.0	0.6	0.5	1.3	0.6

Appendix 9 (cont.)

b) Shrub frequency (%).

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3B	7B	9B	3A
Abies balsamea	60.0	66.7	86.7	60.0	73.3	93.3	86.7	113.3	93.3	93.3	73.3	85.0	73.3	46.7	70.0
Acer spicatum	86.7	80.0	86.7	26.7	80.0	100.0	46.7	113.3	100.0	86.7	100.0	90.0	86.7	100.0	100.0
Alnus crispa	-	26.7	20.0	33.3	40.0	20.0	33.3	-	-	-	-	10.0	13.3	-	35.0
Alnus rugosa	33.3	60.0	40.0	26.7	73.3	53.3	80.0	20.0	86.7	20.0	53.3	35.0	26.7	13.3	15.0
Amelanchier bartramiana	13.3	60.0	13.3	53.3	20.0	6.7	53.3	6.7	20.0	-	20.0		-		10.0
Amelanchier humilis	13.3	-	6.7		-	13.3	-	6.7	20.0	6.7	33.3		6.7	-	20.0
Betula papyrifera	26.7	40.0	33.3	73.3	40.0	53.3	53.3	73.3	40.0	46.7	33.3	55.0	66.7	13.3	40.0
Cornus stolonifera	33.3	53.3	46.7	13.3	13.3	33.3	20.0	46.7	60.0	53.3	40.0	15.0	26.7	33.3	15.0
Corylus cornuta	46.7	26.7	-	6.7	20.0	33.3	6.7	86.7	13.3	53.3	53.3	35.0	46.7	93.3	30.0
Diervilla lonicera	26.7	20.0	20.0	6.7		13.3	6.7	20.0	20.0	6.7	33.3	5.0	40.0	40.0	5.0
Fraxinus nigra	-	6.7		-	13.3		6.7				6.7	10.0	-	-	10.0
Kalmia polifolia		-		6.7	-		-	-			-				-
Larix laricina		6.7		-			20.0	-	-	-	-		-		-
Ledum groenlandicum	13.3	33.3	40.0	46.7	-	-	60.0	-	6.7	6.7	6.7	-	-	-	-
Lonicera canadensis	53.3	6.7	33.3	6.7	20.0	46.7	6.7	73.3	40.0	73.3	20.0	10.0	33.3	40.0	20.0
Lonicera hirsuta	-	-	-		-	13.3	-	13.3	6.7	-	6.7	-	-	-	-
Lonicera involucrata	6.7	13.3	20.0			-	-	20.0	20.0	20.0	6.7	5.0	6.7		-
Lonicera oblongifolia	6.7	6.7					6.7		6.7		-				-
Lonicera villosa	-	20.0					13.3	-	-		-				-
Myrica gale	-	6.7	-		-	-	-	-	-	-	-	-	-	-	-
Picea glauca	13.3	-	20.0	-	33.3	13.3	13.3	20.0	66.7	20.0	13.3	40.0	13.3	20.0	10.0
Picea mariana	13.3	46.7	13.3	53.3	33.3	20.0	86.7	26.7	46.7	20.0	6.7	20.0	6.7	-	20.0
Populus balsamifera	26.7	-	20.0		-	-	-	6.7	6.7	-	-	-	13.3	13.3	-
Populus tremuloides	-		-	-		-	-	-	-			-	6.7	6.7	-
Prunus pensylvanica	20.0	6.7	13.3	26.7		13.3	6.7	6.7	6.7		-	10.0	-	6.7	15.0
Prunus virginiana	-	-	-	6.7		-		20.0	33.3		13.3		6.7	13.3	5.0
Rhamnus alnifolia	6.7	13.3	6.7	-				-	20.0		6.7		6.7	-	-
Ribes glandulosum	-			-		-		-	-				-	6.7	5.0
Ribes hirtellum		-		-		6.7		6.7	53.3				-		-
Ribes hudsonianum		6.7	-	-		-		-	-	-	-	-	-	-	-
Ribes lacustre		-	40.0	-		13.3		46.7	40.0	26.7	13.3	5.0	6.7	6.7	-
Ribes oxycanthoides		-	6.7	-		-		-	-	-	-	-	6.7	-	-
Ribes triste	-	-	-	-		-	-	13.3	6.7	-	-	-	-	-	5.0
Rosa acicularis	13.3	20.0	53.3	13.3	-	26.7	40.0	33.3	66.7	6.7	20.0	10.0	33.3	6.7	-
Rubus idaeus var. strigosus	20.0	33.3	13.3	13.3	6.7	-	20.0	6.7	26.7	13.3	33.3	5.0	6.7	6.7	5.0
Salix	20.0	-	20.0	-		13.3	-	33.3	33.3	20.0	20.0	15.0	6.7	6.7	15.0
Sambucus pubens	13.3	-	-	6.7	-	-	-	-	-	-	-	-	-	13.3	-
Sorbus decora	20.0	40.0	20.0	46.7	33.3	40.0	73.3	46.7	66.7	33.3	40.0	45.0	66.7	26.7	20.0
Thuja occidentalis	6.7		73.3			26.7	-	6.7	6.7	46.7	-	20.0			
Vaccinium angustifolium	-	-	-	-	-	-	6.7	-	-	-	6.7	-	-	-	-
Viburnum edule	26.7	53.3	13.3	13.3	6.7	6.7	13.3	46.7	46.7	13.3	60.0	20.0	20.0	40.0	25.0

Appendix 9 (cont.)

c) Shrub density (shrubs/ha).

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3B	7B	9B	3A
Abies balsamea	1127	515	991	135	2108	2736	1917	5286	3599	1509	3271	676	1176	1549	407
Acer spicatum	4508	515	1652	1886	4105	6449	1917	11562	4370	4024	7269	2434	2416	3217	6519
Alnus crispa	-	343	165	404	111	195	1150			-	-	338	65	119	-
Alnus rugosa	966	343	1652	1078	444	1564	5751	-		1006	5815	68	196	238	204
Amelanchier bartramiana	161	86		674	444	195	767	330		-		135		-	
Amelanchier humilis			-		-	-	-			503	-	-	-	119	
Betula papyrifera	322	944	330	135	666	782	767	330	-	168	727	203	261	596	
Corylus cornuta	805	86	165	269	555	586	-	2973	1285	838	-	609	327	-	3056
Cornus stolonifera	161	86	165	539		586	767		514	168	2181			238	-
Diervilla lonicera		-	-	539					257	335	364	-	131	119	204
Fraxinus nigra		-	-	135			-	-		-	-	135	65	-	-
Ledum groenlandicum	-	1030	1156	943		-	4600	-	-	-			-		-
Lonicera canadensis	805		330	-		391		330	257	-					-
Lonicera hirsuta			-	-				330		168				-	-
Lonicera involucrata			165	-			-	991		-				238	-
Lonicera villosa	-		-	269	-		1150	-	-			-	-	-	-
Picea glauca	161	-	165		111		383	-	257			135	327		
Picea mariana		429	-		111		3067		514		-	135			
Populus balsamifera		-		-	-	-					364	-			
Prunus pensylvanica		343		135		391				-	-	135			-
Prunus virginiana		172				195				168	364	68		-	204
Rhamnus alnifolia		-		-				-		-	364	-		119	-
Ribes hudsonianum			-	269				-			-			-	-
Ribes lacustre		-	165	-	-			-	-	-	-			-	-
Rosa acicularis		86	165	135	111				514	168	727			119	-
Rubus idaeus var. strigosus	-	-	165	135		-		-	-	335					-
Salix	161		-	-		195		-	257	168					204
Sambucus pubens	-	-	-	-	-	-	-					-		-	204
Sorbus decora		172	-	269	111	195	383		-			68	-	238	-
Thuja occidentalis	-	-	2478	-	-	977	-	-	3599	-	-	-	196	-	-
Viburnum edule	483	-	-	135	-	195	-	330	-	503	364	270	65	238	1222

Appendix 10. Plot means of herb percentage cover and frequency in the RC-17 project, 1990.

a) Plot means of percentage cover.

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B
Species with mean I.V. ≥3.0															
Abies balsamea	1.0	2.5	1.6	2.0	0.7	2.5	1.0	1.3	1.5	1.8	1.2	0.4	0.6	1.3	0.3
Acer spicatum	4.5	0.7	1.1	0.3	2.5	4.2	-	3.7	3.0	3.5	3.7	1.5	2.9	4.5	4.8
Anemone quinquefolia	0.8	0.8	2.0	0.2	2.7	0.5		1.2	1.8	1.2	0.7	2.8	-	0.8	1.0
Aralia nudicaulis	12.0	1.8	3.4	0.2	4.7	3.3	0.7	5.6	4.7	5.2	4.3	1.0	2.1	2.2	7.0
Aster macrophyllus	11.7	4.0	6.8	2.3	5.3	4.0		11.2	12.3	9.0	6.3	1.8	4.3	1.5	4.2
Brachythesium sp.	3.8	-	1.4	1.2		0.3	-	1.5	3.8	1.3	5.3	-	-	2.0	3.2
Carex spp.	3.2	2.2	3.0	3.7	5.3	4.2	5.7	3.5	10.2	1.0	4.7	4.4	1.5	2.8	5.2
Clintonia borealis	9.2	6.7	2.9	7.5	5.8	5.8	5.0	3.2	5.0	5.7	11.3	9.1	3.9	5.3	14.5
Cornus canadensis	4.8	6.5	4.1	7.8	5.0	5.2	8.2	6.6	2.0	3.8	4.8	6.6	0.8	3.0	2.7
Dicranum scoparium	0.5	2.2	4.1	2.5	2.3	1.5	4.0	7.5	1.3	5.2	2.3	5.0	3.3	4.7	0.3
Grass sp.	1.8	2.3	1.8	0.3	0.7	2.5	2.0	2.1	1.5	1.3	0.5	1.3	0.5	0.3	1.0
Gymnocarpium dryopteris	1.5	1.3	0.4	0.3	3.3	2.5	1.0	0.7	3.7	0.8	2.2	3.4	3.3	1.0	2.5
Linnaea borealis	1.0	4.2	3.9	1.5	1.2	2.0	3.0	2.6	2.3	2.2	1.2	3.1	1.5	2.7	0.7
Lycopodium annotinum	4.2	6.3	0.4	8.5	7.3	-	4.0	5.0	1.3	5.7	2.7	4.4	1.0	6.8	5.5
Maianthemum canadense	3.0	4.7	2.3	4.3	5.8	3.0	2.8	3.4	4.7	0.8	1.8	4.9	1.5	3.5	2.3
Mitella nuda	5.0	2.8	3.4	1.0	4.0	4.0	0.5	4.6	6.8	3.3	2.3	0.5	3.4	4.3	7.3
Moss spp.	0.7	1.0	1.4	-	1.7	1.2	2.7	2.2	2.7	4.0	1.3	1.1	1.8	1.7	0.2
Pleurozium schreberi	4.2	5.0	3.0	18.7	6.2	4.8	19.7	12.1	9.8	9.2	10.0	12.0	7.6	15.0	0.2
Rubus pubescens	10.7	9.0	5.2	3.0	7.2	8.3	4.8	6.9	7.0	4.8	3.7	5.0	3.5	4.3	6.3
Streptopus roseus	2.0	4.3	1.6	1.0	5.8	3.3	0.7	5.1	5.5	3.5	5.7	1.6	1.5	2.5	4.8
Trientalis borealis	0.7	0.3	1.8	0.7	2.3	1.3	1.5	1.6	0.7	0.8	1.2	1.0	1.4	0.8	1.7
Viola renifolia	2.8	2.2	1.6	0.8	2.8	2.2	2.2	1.0	3.5	2.5	3.0	2.4	3.4	2.0	1.7
Species with mean I.V. <3.0															
Alnus rugosa		-	1.8	0.2		0.3	1.0	-	1.0	0.3	1.0	0.1	0.1	-	-
Amelanchier bartramiana		0.3	-	0.3		-	0.2	-	0.3	-	0.2	-	-	0.2	-
Amelanchier humilis			-	-			-	-	-		0.3			-	-
Anaphalis margaritaceae			-	-				0.1			-				-
Anemone canadensis	-		0.7	-				0.1			0.2				-
Aquilegia canadensis	0.7					-		-		-	-				-
Aralia hispida	-		-		-	0.2		-	-	-	-			-	0.7
Aster ciliolatus	0.7		0.4		0.8	0.2		0.4	2.0	0.5	0.3	-	-	0.2	0.7
Aster spp.		-	0.2		-	-	-	-	-	-	0.2	0.1	0.4	-	-
Athyrium filix-femina		2.3	0.2		7.7	1.0	1.0	1.2	1.7		2.3	2.5	0.8	-	3.0
Betula papyrifera		0.3	0.4		-	0.2	0.2	0.6	0.2		0.2	-	-	0.5	-
Botrychium virginianum		-	0.7			0.3		0.5			-				-
Caltha palustris		1.7	-			-		-			-				0.7
Carex disperma		0.7		-			-	-			-				
Carex trisperma		0.7		0.7			2.0	-			-		-		-
Circaea alpina		1.5	-	-			-	-			-		0.9		0.7
Cladina mitis		1.3	0.4	0.7			0.7	-	-	-	-		0.5		
Cladina rangiferina		0.3	1.4	1.3			0.7	0.9	0.3	1.0	-		-		-
Cladina stellaris		-	-	0.3	-	-	-	-	-	1.3	-	-	-		-
Cladonia sp		0.8	1.8	-	0.3	0.3	0.8	0.4	0.2	0.8	0.2	0.6	0.1	-	-
Climacium dendroides		1.3	-	-	-	-	-	-	-	-	-	-	0.1	0.2	-
Coptis trifolia		5.2	1.3	1.0	1.5	2.0	3.5	0.7	1.3	0.2	2.0	1.0	1.3	-	-
Corallorhiza trifida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
Cornus stolonifera	0.3	1.5	-	0.3		-	1.2	-	0.5	-	-	-	-	0.3	-
Corylus cornuta	0.2	-	0.2	-	-	0.3	-	0.3	-	0.7	0.3	0.5	0.1	1.0	1.0
Diervilla lonicera	3.0	0.7	1.3	0.7	1.3	1.3	0.7	2.1	1.7	3.3	5.3	2.0	1.5	1.3	2.0
Dryopteris austriaca		1.3	-			-	-		-		0.7	-	0.3		-
Epilobium angustifolium		-	0.7			-		-	0.7	-	-		-	-	0.2
Equisetum arvense	-	0.3	3.6	-	-	1.3		-	0.7	0.2	-		-	0.3	-
Equisetum pratense	0.2	0.2	1.4	-	0.8	0.5	-	0.7	1.8	1.0	0.5		0.6	-	0.2
Equisetum scirpoides	-	-	-	-	-	-	-	-	0.5	0.3			-		-
Equisetum sylvaticum	0.2	0.2	-	0.7	0.3	0.8	0.3	-	-	-	-		0.5		-
Fragaria vesca	-		0.4	-	-	0.2	-	0.1	-		-	-	1.0		0.2
Fragaria virginiana			0.7	-	0.3	0.3	0.2	0.3	2.0		-	0.3	0.1		-
Fraxinus nigra	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-
Galium triflorum	1.8	0.8	0.9	-	1.5	0.5	0.3	0.9	1.5	1.2	2.2	0.5	0.5	0.7	2.0
Gaultheria hispidula	0.2	1.8	2.3	2.3	0.2	0.8	3.7	0.3	1.2	1.7	0.5	0.1	0.5	0.8	-
Geocaulon lividum	-	0.2	-	-	-	-	1.5	-	-	-	-	-	-	-	-
Geranium bicknelli	-	0.7		-		-	-	-	-	-	-		-	-	-
Goodyera repens	0.3	-		-	-	0.2	-	-	0.2	-	-		0.1	0.2	-
Halenia deflexa	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
Hylocomium splendens	-	0.2	2.5	-	0.3	0.2	0.7	1.2	8.0	3.8	0.2	0.3	2.6	2.7	-
Hypnum crista-castrensis	0.8	0.7	0.4	0.7	0.3	0.5	-	0.1	0.5	1.3	0.3	0.4	2.3	0.8	0.2

Appendix 10 (cont.).

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B
Larix laricina		-		0.2			0.2								
Ledum groenlandicum	0.7	2.8	1.4	3.3		-	9.2	-	1.0	0.7	1.0		-	-	
Lichen spp.	-		0.7			0.2	0.2	0.9	0.3	1.5	0.2	0.1	0.3	0.2	-
Lonicera canadensis	0.2						-	0.4		0.3	1.0	0.5	0.1		0.2
Lonicera involucrata		-	-				0.3	0.4	0.3						
Lonicera villosa	-	0.5	0.4	-			0.3								
Lycopodium clavatum	0.3			0.8			0.7					0.1			
Lycopodium complanatum	-			-	0.2		-			0.2	-	0.3		-	-
Lycopodium obscurum	0.7			0.2	1.0					1.5	1.0	2.4		1.3	0.7
Menyanthes trifoliata	-	-	-	0.3	-	-		-	-	-	-			-	-
Mertensia paniculata	1.8	0.8	0.7	1.0	3.2	2.3		2.6	2.3	0.3	2.5	-	-	1.0	1.7
Mnium spp.	0.3	6.3	0.9	2.7	3.0	0.3		1.2	2.2	1.5	4.3	0.5	0.9	1.0	1.5
Moneses uniflora	-		0.5		0.3	0.3		0.6	-	0.3	0.3		-	0.2	0.5
Peltigera spp.	-	-	-		0.3	-	-	0.3	-	-	0.8	-	0.5	1.0	
Petasites palmatus	1.3	0.2	2.3	0.3	0.7	1.8	1.5	1.8	2.2	3.0	1.7	0.5	0.3	3.3	
Picea glauca	-		-	-	-	0.2	-	-	-		-	-	-	0.2	-
Picea mariana			0.4	-		-	0.5		0.2		0.2			-	-
Pinus banksiana				-		0.2	-		-		-				-
Polygonum scandens			-	-	-	-	-	-	-		1.3	-	-	-	-
Polytrichum juniperinum	-		0.4	0.3	0.2	0.5	0.2	0.3	0.3			0.8	0.3	0.2	
Populus balsamifera	0.2		0.7										-	-	-
Populus tremuloides	-			-		-		-					0.1	0.2	0.2
Prunus pensylvanica	0.2			0.2		0.2		0.1	-		-	-	-	-	-
Prunus virginiana						-		-	0.2		-	0.3			0.3
Pyrola rotundifolia									-	-	0.2				-
Rhamnus alnifolia			-	-	-	-		-	0.7	0.3	-			1.3	-
Rhytidiadelphus triquestrus			3.4	0.2	1.7	1.2		0.3	2.3	1.5	0.2	-	-	0.8	
Ribes glandulosum			-					-	0.2		-	0.3	0.3		
Ribes hirtellum			-			-		-	0.7		-	-	-	-	-
Ribes lacustre	-	-	0.4			0.2	-	-	0.2	-	0.7	-	0.1	0.7	-
Ribes triste	0.7	0.2	0.2	-	-		0.2	1.3	1.8	0.2	-	1.3	-	-	1.0
Rosa acicularis	2.0	-	3.6	0.7	1.0		1.0	4.1	1.5	1.7	2.5	-	-		0.2
Rubus hispida	-	-	-	-	-	-	-	-	-		-	0.8	-		-
Rubus idaeus var. strigosus	1.0	1.0	-	-	0.7	0.3	1.3	0.4			1.2	-	0.8		0.3
Salix	-	-	0.7	-	-	0.3	-	-			-		-		-
Smilacina trifolia	-		-	1.0		-	0.7				-	-	-	-	-
Sorbus decora	0.3	-	0.4	0.7		-	0.5	-			0.2	0.5	0.9	0.3	0.5
Sphagnum capillifolium	-	3.0	0.7	7.7		0.2	14.0	-			-	-	-	-	-
Sphagnum magellanicum		1.3		6.7		-	4.3								-
Sphagnum spp.		0.3			-	-	-	-	-		1.0	-	-		-
Thelypteris phegopteris	-	1.3	-	-	2.0	0.3		-	0.5	-	4.7	0.5	1.8		0.2
Thuja occidentalis	0.2	-	1.3	-	-	-		-	0.2	0.8	-	-	-		-
Trillium cernuum	-	0.2	-	-	-		-	-		-	-			-	
Vaccinium angustifolium	-	6.7	1.1	7.8	1.5	2.0	4.7	0.9	-	0.7	1.5	1.3		0.7	
Vaccinium myrtilloides	0.7	0.8	1.1	0.7	0.2	-	1.8	-	0.7	0.2	0.5			0.2	
Vaccinium oxycoccos	-	0.2	-	0.3	-	-	-	-	-	-	-	-	-	-	-
Viburnum edule	1.8	2.0	-	-		0.5	0.7	0.1	0.3	0.8	0.8	2.1	1.4	0.5	0.8
Viola spp.	-	-	0.2			0.3		-	-	-		0.1	0.1	-	0.3

Appendix 10 (cont.).

b) Plot means of percentage frequency.

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B
Species with mean I.V. ≥3.0															
Abies balsamea	33.3	33.3	42.9	53.3	6.7	33.3	13.3	52.9	33.3	53.3	25.7	15.0	20.0	53.3	13.3
Acer spicatum	60.0	20.0	21.4	6.7	26.7	53.3		58.8	33.3	46.7	46.7	30.0	45.0	66.7	66.7
Anemone quinquefolia	33.3	26.7	57.1	6.7	20.0	20.0		35.3	66.7	40.0	20.0	40.0	-	26.7	33.3
Aralia nudicaulis	86.7	20.0	57.1	6.7	26.7	46.7	13.3	76.5	53.3	53.3	33.3	15.0	20.0	33.3	53.3
Aster macrophyllus	46.7	26.7	35.7	13.3	20.0	33.3		47.1	60.0	40.0	40.0	15.0	30.0	33.3	33.3
Brachythesium sp.	60.0	-	14.3	20.0	-	13.3	-	17.6	60.0	20.0	46.7	-	-	13.3	60.0
Carex spp.	33.3	33.3	64.3	33.3	46.7	60.0	26.7	41.2	86.7	40.0	46.7	35.0	25.0	46.7	46.7
Clintonia borealis	86.7	46.7	28.6	53.3	60.0	60.0	66.7	47.1	53.3	40.0	80.0	75.0	45.0	53.3	80.0
Cornus canadensis	40.0	46.7	57.1	60.0	53.3	60.0	66.7	70.6	53.3	53.3	53.3	65.0	20.0	60.0	40.0
Dicranum scoparium	20.0	33.3	57.1	40.0	20.0	13.3	46.7	47.1	33.3	26.7	20.0	50.0	25.0	46.7	13.3
Grass sp.	33.3	40.0	42.9	13.3	15.0	26.7	20.0	41.2	40.0	20.0	20.0	30.0	15.0	5.0	25.0
Gymnocarpium dryopteris	20.0	13.3	7.1	13.3	33.3	40.0	33.3	17.6	53.3	13.3	26.7	35.0	40.0	13.3	40.0
Linnaea borealis	13.3	40.0	50.0	33.3	26.7	20.0	53.3	52.9	46.7	20.0	20.0	50.0	25.0	33.3	13.3
Lycopodium annotinum	26.7	46.7	7.1	53.3	53.3	-	40.0	17.6	20.0	40.0	26.7	50.0	25.0	46.7	20.0
Maianthemum canadense	46.7	60.0	71.4	40.0	53.3	46.7	40.0	64.7	73.3	33.3	40.0	55.0	40.0	66.7	46.7
Mitella nuda	53.3	40.0	57.1	6.7	40.0	60.0	20.0	47.1	73.3	60.0	33.3	15.0	55.0	33.3	40.0
Moss spp.	20.0	6.7	21.4	-	26.7	33.3	26.7	35.3	33.3	46.7	13.3	25.0	20.0	20.0	6.7
Pleurozium schreberi	20.0	46.7	42.9	66.7	60.0	33.3	66.7	58.8	60.0	46.7	66.7	55.0	60.0	53.3	6.7
Rubus pubescens	80.0	66.7	50.0	20.0	53.3	73.3	33.3	58.8	80.0	33.3	40.0	50.0	35.0	40.0	53.3
Streptopus roseus	60.0	40.0	21.4	13.3	53.3	53.3	6.7	52.9	80.0	60.0	73.3	30.0	30.0	40.0	60.0
Trientalis borealis	20.0	13.3	50.0	20.0	40.0	40.0	46.7	41.2	26.7	33.3	33.3	30.0	40.0	26.7	40.0
Viola renifolia	60.0	46.7	50.0	13.3	40.0	46.7	33.3	29.4	66.7	66.7	40.0	40.0	55.0	40.0	40.0
Species with mean I.V. < 3.0															
Alnus rugosa		-	21.4	6.7		6.7	20.0		13.3	6.7	13.3	5.0	5.0	-	-
Amelanchier bartramiana		6.7	-	13.3		-	13.3		6.7	-	6.7	-	-	6.7	-
Amelanchier humilis		-		-			-	-	-		13.3			-	-
Anaphalis margaritaceae			-	-				5.9			-				-
Anemone canadensis	-		7.1	-				5.9			6.7				-
Aquilegia canadensis	6.7		-	-		-		-			-			-	-
Aralia hispida	-		-	-	-	6.7		-	-	-	-		-	-	6.7
Aster ciliolatus	20.0		14.3	-	13.3	6.7		17.6	20.0	13.3	6.7	-	-	6.7	20.0
Aster spp.	-	-	7.1			-	-	-	-	-	6.7	5.0	10.0		-
Athyrium filix-femina		13.3	7.1		26.7	20.0	6.7	5.9	13.3		13.3	5.0	5.0	-	20.0
Betula papyrifera		13.3	14.3		-	6.7	6.7	17.6	6.7		6.7	-	-	20.0	-
Botrychium virginianum		-	21.4			6.7		11.8							-
Caltha palustris		6.7	-			-		-							6.7
Carex disperma		6.7		-		-	-	-							
Carex trisperma		6.7		6.7		-	20.0	-			-		-		-
Circaea alpina		20.0	-	-			-	-			-		15.0		6.7
Cladina mitis		13.3	7.1	6.7			6.7	-	-	-	-		5.0		
Cladina rangiferina		13.3	28.6	6.7			20.0	29.4	6.7	26.7	-		-		
Cladina stellaris		-	-	6.7	-	-	-	-	-	6.7	-	-	-		-
Cladonia sp		33.3	28.6	-	6.7	13.3	26.7	17.6	6.7	26.7	6.7	20.0	5.0	-	-
Climacium dendroides		13.3	-	-	-	-	-	-	-	-	-	-	5.0	6.7	
Coptis trifolia		46.7	21.4	6.7	13.3	40.0	26.7	11.8	26.7	6.7	33.3	20.0	40.0	-	-
Corallorhiza trifida	-	-	-	-		-	-	-	-					-	6.7
Cornus stolonifera	6.7	20.0	-	6.7		-	13.3	-	13.3	-	-	-	-	6.7	-
Corylus cornuta	6.7	-	7.1	-	-	13.3	-	5.9	-	6.7	6.7	5.0	5.0	13.3	26.7
Diervilla lonicera	20.0	6.7	14.3	6.7	13.3	13.3	6.7	11.8	13.3	20.0	26.7	5.0	5.0	6.7	13.3
Dryopteris austriaca	-	13.3	-	-	-	-		-	-		6.7	-	5.0		-
Epilobium angustifolium		-	7.1	-		-		-	6.7	-				-	6.7
Equisetum arvense	-	6.7	50.0	-	-	26.7		-	20.0	6.7	-		-	6.7	-
Equisetum pratense	6.7	6.7	35.7	-	13.3	13.3		23.5	66.7	20.0	13.3		20.0	-	6.7
Equisetum scirpoides	-	-	-	-	-	-	-	-	20.0	13.3	-		-		-
Equisetum sylvaticum	6.7	6.7	-	6.7	6.7	13.3	6.7	-	-	-	-		15.0		-
Fragaria vesca	-	-	7.1	-	-	6.7	-	5.9	-		-	-	10.0		6.7
Fragaria virginiana	-	-	7.1	-	6.7	6.7	6.7	5.9	26.7	-	-	5.0	5.0		-
Fraxinus nigra	-	-	-	-	6.7	-	-	-	-	-	-	-	-	-	-
Galium triflorum	33.3	20.0	35.7	-	33.3	13.3	13.3	35.3	46.7	26.7	33.3	10.0	20.0	26.7	46.7
Gaultheria hispidula	6.7	20.0	21.4	26.7	6.7	13.3	40.0	11.8	33.3	26.7	13.3	5.0	10.0	13.3	-
Geocaulon lividum	-	6.7	-	-	-	-	13.3	-	-	-	-	-	-	-	-
Geranium bicknelli	-	6.7		-		-	-	-	-		-		-	-	-
Goodyera repens	6.7	-		-	-	6.7	-	-	6.7	-	-		5.0	5.0	-
Halenia deflexa	-	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-

Appendix 10 (cont.)

Treatment	OC	OC	OC	OC	DC	DC	DC	DC	HP	HP	HP	SC	SC	SC	SC
Plot	1B	5A	5B	7A	4A	4B	5A	6B	10B	2B	8A	3A	3B	7B	9B
Hylocomium splendens		6.7	42.9		6.7	5.7	6.7	23.5	53.3	33.3	6.7	5.0	15.0	20.0	-
Hypnum crista-castrensis	13.3	6.7	7.1	13.3	6.7	13.3	-	5.9	13.3	6.7	6.7	10.0	30.0	13.3	6.7
Larix laricina	-	-	-	6.7			6.7		-	-	-			-	-
Ledum groenlandicum	6.7	26.7	14.3	20.0			60.0		6.7	6.7	6.7	-	-	-	-
Lichen spp.			21.4			6.7	6.7	23.5	6.7	33.3	6.7	5.0	5.0	6.7	-
Lonicera canadensis	6.7						-	11.8	-	6.7	6.7	5.0	5.0		6.7
Lonicera involucrata		-	-	-			6.7	11.8	6.7		-		-		
Lonicera villosa	-	13.3	7.1	-			6.7	-	-		-	-			
Lycopodium clavatum	6.7			13.3	-		6.7				-	5.0			
Lycopodium complanatum	-			-	6.7					6.7	-	10.0		-	-
Lycopodium obscurum	20.0			6.7	20.0			-		20.0	13.3	35.0		6.7	13.3
Menyanthes trifoliata	-	-	-	6.7	-	-		-	-	-	-			-	-
Mertensia paniculata	33.3	13.3	7.1	6.7	6.7	13.3		23.5	20.0	13.3	26.7	-	-	20.0	13.3
Mnium spp.	6.7	26.7	14.3	6.7	20.0	6.7		29.4	20.0	26.7	33.3	10.0	15.0	20.0	13.3
Moneses uniflora	-	-	21.4		13.3	13.3		23.5	-	13.3	13.3		-	6.7	20.0
Peltigera spp.	-	-	-	-	6.7	-	-	5.9	-	-	20.0	-	5.0	6.7	-
Petasites palmatus	20.0	6.7	35.7	13.3	13.3	20.0	13.3	23.5	33.3	33.3	20.0	5.0	5.0	26.7	
Picea glauca		-	-	-		6.7	-		-	-	-	-		6.7	
Picea mariana			14.3			-	13.3		6.7		6.7			-	-
Pinus banksiana						6.7					-				-
Polygonum scandens			-	-	-	-	-	-	-		6.7	-		-	-
Polytrichum juniperinum	-		14.3	13.3	6.7	13.3	6.7	5.9	13.3		-	10.0	10.0	6.7	
Populus balsamifera	6.7		7.1			-	-				-		-	-	-
Populus tremuloides	-			-		-		-					5.0	6.7	6.7
Prunus pensylvanica	6.7			6.7		6.7		5.9	-			-	-	-	-
Prunus virginiana				-					6.7		-	5.0			6.7
Pyrola rotundifolia				-					-	-	6.7			-	-
Rhamnus alnifolia			-	-	-	-		-	6.7	6.7	-			6.7	
Rhytidiadelphus triquestrus			28.6	6.7	13.3	20.0		5.9	33.3	33.3	6.7	-	-	13.3	-
Ribes glandulosum			-	-		-			6.7		-	5.0	5.0		-
Ribes hirtellum			-	-		-		-	20.0		-	-	-	-	-
Ribes lacustre	-	-	7.1	-		6.7	-	-	6.7	-	6.7	-	5.0	6.7	-
Ribes triste	20.0	6.7	7.1	-	-	-	6.7	17.6	40.0	6.7	-	15.0		-	26.7
Rosa acicularis	20.0		35.7	6.7	13.3		13.3	35.3	33.3	20.0	26.7	-			6.7
Rubus hispida	-	-		-	-	-	-	-	-	-	-	5.0	-		-
Rubus idaeus var. strigosus	6.7	6.7	-	-	13.3	6.7	13.3	11.8			13.3	-	10.0		6.7
Salix			7.1	-	-	6.7	-	-			-	-			-
Smilacina trifolia	-		-	6.7		-	6.7	-			-	-	-	-	-
Sorbus decora	13.3		14.3	26.7		-	13.3				6.7	15.0	35.0	13.3	13.3
Sphagnum spp.		6.7	-	-		6.7	-				13.3				
Sphagnum capillifolium		13.3	7.1	26.7			40.0				-				
Sphagnum magellanicum		6.7	-	20.0	-	-	20.0		-		-	-	-		-
Thelypteris phegopteris		13.3	-	-	6.7	6.7			13.3	-	20.0	10.0	10.0		6.7
Thuja occidentalis	6.7	-	14.3						6.7	33.3	-	-			
Trillium cernuum	-	6.7	-	-	-	-	-	-	-	-	-	-		-	-
Vaccinium angustifolium	-	40.0	14.3	66.7	26.7	26.7	33.3	-	-	13.3	13.3	25.0		6.7	-
Vaccinium myrtilloides	6.7	13.3	14.3	26.7	6.7		26.7	-	6.7	6.7	13.3	-		6.7	
Vaccinium oxycoccos	-	6.7	-	6.7	-	-	-	-	-	-	-	-	-	-	-
Viburnum edule	26.7	6.7	-	-		13.3	13.3	5.9	6.7	20.0	13.3	25.0	15.0	13.3	20.0
Viola spp.	-	-	7.1	-		6.7	-	-	-	-	-	5.0	5.0		13.3

Appendix 11. Total species' importance values, across all three strata, for treatments and plots of the RC-17 project.

Treatment	CC				DC				HP			SC				TOTAL IVs			
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B	CC	DC	HP	SC
Abies balsamea	113	94	73	98	119	98	64	135	63	116	106	109	122	94	60	94	104	95	96
Acer spicatum	70	37	26	17	54	65	12	63	41	48	53	74	66	73	83	37	51	47	74
Alnus crispa	-	8	5	15	14	7	9	-	-	-	-	19	5	5	-	7	8	0	7
Alnus rugosa	24	35	30	22	41	33	34	4	36	6	34	21	23	22	10	28	28	25	19
Amelanchier bartramiana	3	16	3	15	5	1	11	1	3		5	3		1	-	9	4	3	1
Amelanchier humilis	3		2	-		3		1	3	-	7	5		2	-	1	1	4	2
Anaphalis margaritaceae				-				1			-				-	0	0	0	0
Anemone canadensis	-		1	-	-	-		1	-		1	-		-	-	0	0	0	0
Anemone quinquefolia	3		6	1	4	2		3	5	4	2	7		3	4	3	2	4	3
Aquilegia canadensis	1		-	-	-	-		-	-	-	-	-		-	-	0	0	0	0
Aralia hispida	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	0	0	0	0
Aralia nudicaulis	18	3	7	1	7	7	2	10	6	9	6	2	5	5	12	7	6	7	6
Aster ciliolatus	2	-	1	-	2	1		1	2	1	1	-	-	1	2	1	1	2	1
Aster macrophyllus	14	5	9	3	6	7		12	12	11	8	3	9	4	7	8	6	10	6
Aster spp.		-	1	-	-		-	-	-	-	1	1	2	-	-	0	0	0	1
Athyrium filix-femina	-	3	1	-	9	3	1	1	2	-	3	3	2	-	5	1	4	2	2
Betula papyrifera	28	42	47	62	58	41	71	47	37	49	64	54	48	63	48	45	54	50	53
Botrychium virginianum	-		2	-		1		1	-	-	-			-	-	1	1	0	0
Brachythesium sp.	3	-	2	3		1		2	6	3	6			3	8	3	1	5	3
Caltha palustris		2		-				-	-		-			-	1	0	0	0	0
Carex disperma	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0
Carex spp.	6	4	7	7	9	9	7	6	12	4	7	8	5	7	9	6	8	8	7
Carex trisperma	-	1		1	-	-	3	-			-		-		-	1	1	0	0
Circaea alpina		3	-	-			-	-			-		3		1	1	0	0	1
Cladina mitis		2	1	1			1	-		-	-		1		-	1	0	0	0
Cladina rangiferina		1	3	2			2	3	1	3	-				-	2	1	1	0
Cladina stellaris		-	-	1			-	-	-	2	-	-			-	0	0	1	0
Cladonia sp		3	4	-	1	1	3	1	1	3	1	2	1	1	-	2	2	1	1
Climacium dendroides	-	2	-	-	-	-	-	-	-	-	-	-	1	1	-	1	0	0	0
Clintonia borealis	15	9	5	12	11	11	9	6	6	8	15	16	10	10	22	10	9	10	14
Coptis groenlandica		-	-	-	-	-	-	-	-	-	-	-	-		-	0	0	0	0
Coptis trifolia		8	3	2	3	5	5	1	2	1	4	3	6		-	3	4	2	2
Corallorhiza trifida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0
Cornus canadensis	8	9	8	13	9	10	12	10	4	7	8	13	3	8	6	9	10	6	7
Cornus stolonifera	10	15	11	4	4	8	7	7	16	12	8	4	4	7	8	10	6	12	6
Corylus cornuta	16	7	1	5	7	10	6	23	2	19	17	12	14	15	45	7	11	12	22
Dicranum scoparium	2	4	8	6	4	3	7	9	3	7	3	10	7	9	1	5	6	4	7
Diervilla lonicera	10	5	7	3	2	7	3	5	5	6	15	4	4	12	12	6	4	9	8
Dryopteris austriaca		2		-	-	-	-	-	-	-	1		1	-	-	1	0	0	0
Epilobium angustifolium		-	1	-		-		-	1	-	-		-	-	1	0	0	0	0
Equisetum arvense		1	7	-	-	4		-	2	1	-		-	1	-	2	1	1	0
Equisetum pratense		1	4	-	2	2		2	5	2	1		3		1	1	1	3	1
Equisetum scirpoides			-	-	-	-		-	1	1	-		-		-	0	0	1	0
Equisetum sylvaticum	1	1	-	1	1	2	1	-	-	-	-		2		-	1	1	0	1
Fragaria vesca	-	-	1	-	-	1	-	1	-		-	-	2		1	0	0	0	1
Fragaria virginiana		-	1	-	1	1	1	1	3		-	1	1		-	0	1	1	0
Fraxinus nigra		19	-	-	7	-	5	-	-	-	5	6	11	-	-	5	3	2	4
Galium triflorum	4	2	3	-	4	2	1	3	4	3	4	1	3	3	6	2	3	4	3
Gaultheria hispidula	1	3	4	5	1	2	6	1	3	3	1	1	2	2	-	3	2	2	1
Geocaulon lividum	-	1		-	-	-	2	-		-	-			-	-	0	1	0	0
Geranium bicknelli	-	1		-		-	-	-	-		-		-	-	-	0	0	0	0
Goodyera repens	1	-	-	-	-	1	-	-	1	-	-	-	1	1	-	0	0	0	0
Grass spp.	4	5	4	2	2	5	3	4	3	3	2	4	2	1	3	4	4	3	2
Gymnocarpium dryopteris	3	2	1	2	6	6	4	2	6	2	4	7	8	2	6	2	4	4	6
Halenia deflexa		-	-	-	-	-	-	-	-	1	-	-	-	-	-	0	0	0	0
Hylocomium splendens		1	5	-	1	1	1	3	9	6	1	1	5	4	-	1	1	5	3
Kalmia polifolia		-		2	-	-	-	-	-		-	-	-	-	-	0	0	0	0
Larix laricina	-	8	-	1			4	-	-	-	-				-	2	1	0	0
Ledum groenlandicum	4	15	16	30		-	37	-	2	3	4	-	-	-	-	16	9	3	0
Lichen spp.	-	-	2	-	-	1	1	2	1	4	1	1	1	1	-	1	1	2	1
Linnaea borealis	2	7	7	5	4	4	7	6	4	3	3	8	5	6	2	5	5	3	5
Lonicera canadensis	13	1	6	2	5	10	1	12	6	15	6	7	3	7	11	5	7	9	7
Lonicera hirsuta	-	-	-	-	-	2	-	2	1	-	1	-	-	-	-	0	1	1	0
Lonicera involucrata	1	3	4	-		-	1	4	3	4	1		1	2	-	2	1	3	1
Lonicera oblongifolia	1	2	-	-			1	-	1		-		-	-	-	1	0	0	0
Lonicera villosa	-	6	1	-	-		5	-	-	-	-	-	-	-	-	2	1	0	0
Lycopodium annotinum	6	9	1	13	11		6	5	2	8	4	9	4	11	7	7	6	5	8
Lycopodium clavatum	1	-		2	-		1	-	-	-	-	1	-	-	-	1	0	0	0
Lycopodium complanatum	-			-	1		-	-		1	-	1	-	-	-	0	0	0	0
Lycopodium obscurum	2	-	-	1	3	-	-	-	-	3	2	6	-	2	2	1	1	2	2
Maianthemum canadense	6	9	7	8	10	7	5	7	7	3	4	10	6	9	6	7	7	5	8
Menyanthes trifoliata	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0

Appendix 11 (cont.).

Treatment	OC				DC				HP			SC							
Plot	1B	5A	5B	7A	4A	4B	6A	6B	10B	2B	8A	3A	3B	7B	9B	OC	DC	HP	SC
Mertensia paniculata	4	2	1	2	3	4		4	3	1	4	-		3	3	2	3	3	1
Mitella nuda	9	5	7	2	7	9	2	7	9	7	4	2	10	7	11	6	6	7	7
Mnium spp.	1	7	2	3	4	1		3	3	3	6	1	3	3	3	3	2	4	2
Moneses uniflora	-		2	-	2	1		2	-	1	1			1	2	0	1	1	1
Moss spp.	2	1	3	-	4	4	4	4	4	7	2	3	4	3	1	2	4	4	3
Myrica gale	-	1	-	-			-	-		-	-	-		-	-	0	0	0	0
Peltigera spp.	-	-		-	1			1	-	-	2		1	2	-	0	0	1	1
Petasites palmatus	3	1	4	2	2	4	2	3	3	5	3	1	1	6	-	2	3	4	2
Picea glauca	8	6	16	-	32	29	7	49	95	28	16	13	21	47	41	7	29	46	30
Picea mariana	10	36	13	98	32	16	121	13	21	13	29	34	13	11	-	39	45	21	16
Pinus banksiana	-	-	-	-	-	1	-	-	-	-	-	-		-	-	0	0	0	0
Pleurozium schreberi	5	8	6	23	11	8	21	14	10	12	13	18	15	20	1	10	13	12	14
Polygonum scandens	-			-				4			2	5	-	4	1	0	1	1	2
Polytrichum juniperinum	-		1	2	-	2	1	1	1		-	2	1	1	-	1	1	0	1
Populus balsamifera	24	-	13	-		5		12	8	-	-	3	8	16	3	9	4	3	7
Populus tremuloides	40	24	-	-	4	10		3	-	8	4	13	10	8	53	16	4	4	21
Prunus pensylvanica	10	1	2	10		3		1	1		4	9	3	3	2	6	1	2	4
Prunus virginiana	-			7				3	5	-	2	2		2	5	2	1	2	2
Ptilium crista-castrensis	2		1	2		2		1	1	2	1	1	5	2	1	1	1	1	3
Pyrola rotundifolia				-				-	-		1				-	0	0	0	0
Rhamnus alnifolia	1	3	2	-	-	-		-	4	1	1			4	-	1	0	2	1
Rhytidiadelphus triquestrus			5	1	3	3		1	3	4	1	-		2	-	1	2	3	0
Ribes glandulosum			-	-		-		-	1	-	-	2			1	0	0	0	1
Ribes hirtellum				-		1		1	8		-	-			-	0	1	3	0
Ribes hudsonianum			-	-		-		-	-	-	-			-	-	0	0	0	0
Ribes lacustre			7	-		3		6	6	5	3		2	3	1	2	2	5	1
Ribes oxycanthoides	-	-	1	-			-	-	-	-	-	-		2	-	0	0	0	0
Ribes triste	2	1	1	-	-	-	1	4	4	1	-	4	-	-	3	1	1	2	2
Rosa acicularis	6	4	15	4	2	5	8	10	12	5	7	-	2	7	2	7	6	8	3
Rubus hispida	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	0	0	0	0
Rubus idaeus var. strigosus	5	7	2	3	3	1	6	2	4	3	8	1	3	1	2	4	3	5	2
Rubus pubescens	16	13	8	5	11	15	6	10	9	7	6	10	6	8	11	10	10	7	9
Salix spp.	5	4	8	-		5		8	10	14	12	4	11	2	11	4	3	12	7
Sambucus pubens	3	-	-	2			-	-	-	-	-	-			3	1	0	0	1
Smilacina trifolia	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	0	0	0	0
Sorbus decora	9	10	5	23	13	10	14	7	18	6	8	10	18	19	14	12	11	11	15
Sphagnum capillifolium	-	3	1	10		1	14	-	-	-	2	-			-	4	4	1	0
Sphagnum magellanicum		2		8			5	-			-				-	2	1	0	0
Sphagnum spp.		1		-				-			-				-	0	0	0	0
Stereocaulon paschale	-	-	-	-	-	-		-	-	-	-	-		-	-	0	0	0	0
Streptopus roseus	6	7	3	2	10	8		8	8	7	10	4	5	6	10	5	7	8	6
Thelyptens phegopteris	-	2	-	-	2	1		-	1	-	5	1	4		1	1	1	2	1
Thuja occidentalis	7		113	-	-	45	-	1	6	65	-		24		-	30	12	23	6
Trientalis borealis	2	1	5	3	6	5	5	4	2	3	3	4	6	3	5	3	5	3	4
Trillium cernuum	-	1	-	-	-	-	-	-	-	-	-	-		-	-	0	0	0	0
Vaccinium angustifolium	-	9	2	14	4	4	8	1	-	2	3	4		1	-	6	4	2	1
Vaccinium myrtilloides	1	2	2	3	1	-	4	-	1	1	1			1	-	2	1	1	0
Vaccinium oxycoccos	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0
Viburnum edule	10	11	2	3	2	3	4	7	6	5	12	10	8	6	11	7	4	8	9
Viola spp.	-	-	1	-	-	1	-	-	-	-	-	1	1	-	1	0	0	0	1
Viola renifolia	7	5	5	2	6	6	4	3	6	7	5	6	10	5	5	5	5	6	7
Sums of Importance Values	599	600	600	601	600	598	599	600	599	601	601	599	599	599	600	600	599	600	599

Appendix 12. Tabular comparison of species cover in all three vegetation strata on the RC-17 project, species and sample units are ordered by their scores on axis 1 of the CA performed on this data.

(Underlining separates the three 'groups' identified in the text).

Sample scores:	Axis 1	-1.2	-1.2	-1.2	-1.2	-1.1	-1.1	-1.1	-1.1	-1.1	-1.0	-1.0	-1.0	-0.9	-0.9	-0.9	-0.9	-0.9	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7
	FEC V-type	5	5	1	6	5	5	6	6	6	8	8	2	6	8	14	6	6	6	14	2	14	8	6	1	14	24	6	14	4	15	14	14
	Treatment	SC	OC	OC	OC	SC	SC	OC	SC	OC	OC	DC	OC	DC	SC	SC	OC	SC	OC	SC	OC	HP	SC	DC	SC	HP	OC	SC	DC	SC	DC	SC	OC
Species scores:	Point	9B10	1B6	1B14	5A15	9B1	9B15	1B2	9B9	5A14	1B13	4B9	5A11	4B13	9B12	9B4	1B4	3B14	1B3	9B13	5A13	2B6	9B8	6B3	9B14	2B4	7A14	3A16	6B17	9B5	6B16	9B2	1B8
Axis 1	Herb stratum species																																
-1.9	CLIM DEN*																				15												
-1.7	CORY COR																					10											
-1.6	PRUN PEN			3																													
-1.4	CIRC ALP																				10												
-1.2	MERT PAN										5		10										10						10		10		5
-1.2	ASTE MAC	10	30	15	15					15	5	15	20					10	20					10	5	40	25	5		25	40	20	60
-1.2	ATHY FEL								5												15								20	25			
-1.2	ACER SPI	25	10	5	3	15	5		3	3		20	5				3		15	3				10		5	5	3		3		10	
-1.2	DIER LON		15				15			10																25	10				20	15	
-1.1	ARAL NUD	10	30	5			15	15		3	5		20		10		25	20	10	25		20		10		25			15	15		15	
-1.1	VIBE EDU							5	3								5	10			30		5		5			10					
-1.0	GAL TRIF	3							5											5	5		3	3					3				
-0.9	RIBE TRI	5																										10					
-0.9	THEL PHE																				15		3										
-0.8	MNIUM SP																				15								3	3			5
-0.8	ANEM QUI	3								5		3	3						3								3	25	5	3			3
-0.8	LONI CAN								3								3	3															
-0.8	MITE NUD	15									10	5	10	10			10	5	5	25	10		20						15		10		
-0.8	BRACH SP		5						10							5			5	5		5		15	3				5	3		3	3
-0.7	LYCO OBS					5		5									3					10						10			5		
-0.7	STREP RO	10		3	5		3			5	3	3	25	3				3	5	5		3	10	10			5	10	10	15	10	5	3
-0.7	RUB PUBE	10		5	5			5		10	15	3	20		10		5	3		10	15	3	10	3	25			5	10	5	20		5
-0.7	VIOL REN				10				3	5							3			10	5		3					3					5
-0.7	RHAM ALN																																
-0.6	RUB IDAE																						5										
-0.6	GYMN DRY								10				10		5			10		15			3										
-0.6	RIBE LAC																																
-0.6	CLIN BOR	3	10	15	15	40	25	15		5	10		10		25	20	30	20	10	5		30		5	15		20		10	15		10	3
-0.5	ASTE CIL	5									3												3		3						3		
-0.4	CAREX SP	5			3		10				15		3										3		20			25	5	10	10		5
-0.4	MONE UNI																							3									
-0.4	PETA PAL										3		3																10		5		3
-0.3	TRIE BOR					3	3				5	3						3				3			3		3		5		3		
-0.2	LYCO ANN				15			15	10				5				3	10				3				30	15	5					
-0.2	MOSS SPP						3					3					3				15					3		3					
-0.1	EQUI PRA																			3													
0.0	ROSA ACI																							10						3			
0.1	GRASS SP																			3			3							5	10		
0.2	EPIL ANG																																
0.2	RHYT TRI																																
0.2	SORB DEC								5		3																						
0.3	LICH SP																																
0.5	FRAG VIR																																
0.5	MAIA CAN	3						5		10	15		5				10							3	10					10			
0.6	ALNU RUG																																
0.6	HYPN CRI																																
0.8	ABIE BAL												3																				
0.8	EQUI ARV																																
0.8	CORN STOL												5																				
0.9	LINN BOR														5					5						3				5			
0.9	CORN CAN				3	3	3	10							25		3			5					3	5	3	3			10	3	
1.0	BETU PAP																																
1.2	HYLO SPL																																
1.3	THUJ OCC																																
1.3	COPT TRI																																
1.6	POLY JUN																																
1.9	CLADO SP																																
2.0	DICR SCO																																
2.5	PLEU SCH																																
2.5	CAREX TR																																
2.6	VACC MYR																																
2.9	SPHA MAG																																
3.1	GAUL HIS																																
3.6	CLAD RAN																																
3.9	LEDU GRO																																
4.5	VACC ANG																																
4.5	SPHA CAP																																
6.1	GEOC LIV																																

Appendix 12 (cont.).

Sample scores:	Axis 1	-1.2	-1.2	-1.2	-1.2	-1.1	-1.1	-1.1	-1.1	-1.1	-1.0	-1.0	-1.0	-0.9	-0.9	-0.9	-0.9	-0.9	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.8	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7
	FEC V-type	5	5	1	6	5	5	6	6	6	8	8	2	6	8	14	6	6	6	14	2	14	8	6	1	14	24	6	14	4	15	14	14
	Treatment	SC	CC	CC	CC	SC	SC	CC	SC	CC	CC	DC	CC	DC	SC	SC	CC	SC	CC	SC	CC	HP	SC	DC	SC	HP	CC	SC	DC	SC	DC	SC	CC
Species scores:	Point	9B10	1B6	1B14	5A15	9B1	9B15	1B2	9B9	5A14	1B13	4B9	5A11	4B13	9B12	9B4	1B4	3B14	1B3	9B13	5A13	2B6	9B8	6B3	9B14	2B4	7A14	3A16	6B17	9B5	6B16	9B2	1B8
Axis 1	**Shrub stratum species**																																
-1.5	SH* Co co	30			5	15	40	15	10	30		15		15	40	40	15	5		5	3	15	15	15	25	50	30	25		20	60	25	10
-1.2	SH Pr vi						15																							10			
-1.0	SH Ac sp	70	50	90	50	60	40	30	40	30	90	70	30	70	30	30	15	50		30	40	70	25	70	50	20	60	25	80	60	30	25	20
-1.0	SH Vi ed	3			3					3	3		3		5					5	5				3		3	3			3	3	
-0.9	SH Fr ni																																
-0.9	SH Rh al																				3												
-0.9	SH Lo ca		3	3		3		3	5	3		5		10	3		10	5		5				5	15	5	3	5			10		
-0.8	SH Di to	3	3		3	3				3					3				3						3	5					3	10	
-0.7	SH Salix																		5							15							
-0.6	SH Po ba																3																3
-0.4	SH Ri hi																														3		
-0.3	SH Co st												10							5	5		3	3						10			
-0.3	SH Ru id																				3									3	3		
-0.3	SH Pi gl																			3			3	5									
0.1	SH Al ru													10							5		10										
0.1	SH Lo in																				3												
0.1	SH Ri la																																
0.2	SH Am hum																																
0.3	SH So de			5					5				3																				
0.4	SH Ro ac		3																														
0.4	SH Pr pe					5					10																						
0.5	SH Ab	10				3		5	3		3	10	3	3					10				15	10		5		10		20	5	3
0.8	SH Lo ob																																
0.8	SH Be pa																	5	15					5	3			20					3
1.5	SH Al cr																											15					
1.5	SH Th oc																		10														
1.7	SH Lo vi																																
2.3	SH Am ba																																
2.7	SH La la																																
2.9	SH Pi ma																																
5.0	SH Le gr																																
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR* Po tr	80	80	70	80	70	50	80	60	40	70	50	60	40	60	20	60	30	70	30		10	30	30				50					
-1.5	TR Fr ni												10								75												
-1.4	TR Pr pen			10																													
-1.4	TR Po ba			5													3								70				40			20
-1.0	TR Salix																																
-0.9	TR Al ru				5									25							3												
-0.6	TR Pi gl				10			10			20	30			20		15		5	15			20	10		10			20		30		10
-0.2	TR Ab	5			15	5		25	15	30	10	15	30	50	15	40	40	25	20	30		50	15	40	3	20	40	40	50	20	15	50	60
-0.2	TR Be pa		10	15		20	15		15			30		15	10			15	5	5	15	15	20	30	15	15	20	5	5	30	15	30	10
0.1	TR So de				10					5	3					5							3							10			
1.3	TR Th oc																		15														
2.6	TR Pi ma																5																

Appendix 12(cont.).

Sample scores:	Axis 1	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5
	FEC V-type	6	8	1	24	2	15	24	14	14	24	24	1	14	4	4	6	4	24	1	24	1	6	6	24	15	14	14	24	14	8	4	2
	Treatment	CC	SC	SC	SC	CC	SC	DC	SC	HP	DC	SC	CC	DC	SC	DC	DC	HP	SC	SC	SC	CC	CC	HP	SC	HP	HP	DC	SC	DC	HP	SC	CC
Species scores:	Point	1B7	7B5	9B7	9B3	5A12	3B16	6B15	3A17	2B5	4A10	3B13	1B15	4B12	3B15	4A2	4B20	8A15	9B6	7B12	7B3	1B11	1B9	10B4	3B19	10B7	2B3	6B14	7B14	4A15	8A14	7B7	5A10
Axis 1	Herb stratum species																																
-1.9	CLIM DEN					5																											
-1.7	CORY COR		10		3		3							3				5															
-1.6	PRUN PEN																																
-1.4	CIRC ALP					10													10						3								
-1.2	MERT PAN	10			15	3		20			15			15			20																
-1.2	ASTE MAC				3		25					20	40	10	3		15	20		5						30	35				20	5	
-1.2	ATHY FEL										75					15			15							15							20
-1.2	ACER SPI	3			3		10	20	3	15			10		3		5	15	3	3	3		15	10					3	20		5	
-1.2	DIER LON		20														5	15				10					10				20		
-1.1	ARAL NUD		10	10	5			5	5				25		10			5				15	15				15	10				10	
-1.1	VIBE EDU						3											10					3				5					3	
-1.0	GAL TRIF	15		10		5		3			10					3	3		3			5			3			3			15		
-0.9	RIBE TRI	5			3			10											3					5				3					
-0.9	THEL PHE					5																			20								
-0.8	MNIUM SP					15		10	5		15								20	3					3			3	10				40
-0.8	ANEM QUI		3					3			10					25						3											
-0.8	LONI CAN																																
-0.8	MITE NUD			20	15	5		5	5		10						5		15			20	20		5	5	5	10	20			5	3
-0.8	BRACH SP	5		5	5								20				3		10			5	3			15						
-0.7	LYCO OBS								10	3											20		3				10						
-0.7	STREP RO		5		10		3	10			15	5	5	3		10	20	10	10				3	3		5	10	3	10				
-0.7	RUB PUBE	20	25	10		10		15	5		10	5	25	10		20	5			10		30	5		20	3		10	20				20
-0.7	VIOL REN	10		5	3	5	10	5	5	3	20	3	3	5			5		3	3			5		15		3	3	5		10		3
-0.7	RHAM ALN																			20													
-0.6	RUB IDAE	15						5			5																						
-0.6	GYMN DRY	10			3		3		10															10				10				
-0.6	RIBE LAC																																
-0.6	CLIN BOR	10	15		40		15	5	10	15		5	15	15	5	15		10	10				10	3		3	15	10	3		10		
-0.5	ASTE CIL										10																						
-0.4	CAREX SP				10			10	10		20		3	3		30	15		20			15				5			5		10	10	
-0.4	MONE UNI			3				3						3					3														
-0.4	PETA PAL	15														5													15				
-0.3	TRIE BOR		5				5		5							10		3										3					
-0.2	LYCO ANN		25				3														10						10	35					
-0.2	MOSS SPP									15					10						10			10				5					
-0.1	EQUI PRA							3					3															3					
0.0	ROSA ACI							5					5			5																	
0.1	GRASS SP							3	3				3			5												3					
0.2	EPIL ANG																																
0.2	RHYT TRI																10																
0.2	SORB DEC																																
0.3	LICH SP																																
0.5	FRAG VIR																																
0.5	MAIA CAN		5																3				3										
0.6	ALNU RUG																																
0.6	HYPN CRI																		3				3										
0.8	ABIE BAL	3	3																3														
0.8	EQUI ARV																																
0.8	CORN STOL																																
0.9	LINN BOR		5						3																				3				
0.9	CORN CAN		15						5	3				5									5				3	3					
1.0	BETU PAP							3																								3	
1.2	HYLO SPL																																
1.3	THUJ OCC																																
1.3	COPT TRI						3					3			3																		
1.6	POLY JUN																																
1.9	CLADO SP																																
2.0	DICR SCO																						3	5									
2.5	PLEU SCH																						3	3									
2.5	CAREX TR																																
2.6	VACC MYR																																
2.9	SPHA MAG																																
3.1	GAUL HIS																																
3.6	CLAD RAN																																
3.9	LEDU GRO																																
4.5	VACC ANG																																
4.5	SPHA CAP																																
6.1	GEOC LIV																																

Appendix 12 (cont.).

Sample scores:	Axis 1	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.7	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.6	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5	-0.5
	FEC V-type	6	8	1	24	2	15	24	14	14	24	24	1	14	4	4	6	4	24	1	24	1	6	6	24	15	14	14	24	14	8	4	2
	Treatment	CC	SC	SC	SC	CC	SC	DC	SC	HP	DC	SC	CC	DC	SC	DC	DC	HP	SC	SC	SC	CC	CC	HP	SC	HP	HP	DC	SC	DC	HP	SC	CC
Species scores:	Point	1B7	7B5	9B7	9B3	5A12	3B16	6B15	3A17	2B5	4A10	3B13	1B15	4B12	3B15	4A2	4B20	8A15	9B6	7B12	7B3	1B11	1B9	10B4	3B19	10B7	2B3	6B14	7B14	4A15	8A14	7B7	5A10
Axis 1	**Shrub stratum species**																																
-1.5	SH Co co	10	30	15	20		20	40	3	10		30		10	35			20			3				3		10	10			15	5	
-1.2	SH Pr vi							3																		3							
-1.0	SH Ac sp	30	40	50	50	15	40	70	80	25	70	40	30	70	20	90	30	40	20	40	60	15	30	60	30	50	40	70	20	30	15	60	40
-1.0	SH Vi ed	10				3		3			3							3		3		3		3	3	3	3	3				3	
-0.9	SH Fr ni					5																			10								
-0.9	SH Rh al																			10													10
-0.9	SH Lo ca				3			3		3											5		3	5			3	5	3			3	
-0.8	SH Di lo		3	5													40	3		3		3									10	10	
-0.7	SH Salix			3													15	3		5		5					3	3			10		
-0.6	SH Po ba	3			3															3		5											
-0.4	SH Ri hi																									3							
-0.3	SH Co st					5		5			10						20			5		20					3						3
-0.3	SH Ru id	3														3				3		3				3							3
-0.3	SH Pi gl						10															3		3	5	3	3			3			
0.1	SH Al ru	15				20					30					20				15		80		15	40	20			20		25		50
0.1	SH Lo in					5																						5	5				
0.1	SH Ri la																									3						3	
0.2	SH Am hum																10																
0.3	SH So de			3												5	5									3						5	
0.4	SH Ro ac			3				3									3	3								3						3	
0.4	SH Pr pe	3					5																										
0.5	SH Ab			3	15			10		10		3				10	10	5				3	3		5	3	30	15	5		10	15	
0.8	SH Lo ob																																
0.8	SH Be pa		5				5						3					15	3	3			3										
1.5	SH Al cr																																
1.5	SH Th oc																																
1.7	SH Lo vi																																
2.3	SH Am ba																																
2.7	SH La la																																
2.9	SH Pi ma																																5
5.0	SH Le gr																																
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR Po tr	15	20		5				20	15			10									15	10	15									
-1.5	TR Fr ni					50																											
-1.4	TR Pr pen	5																		5		5											
-1.4	TR Po ba			25									15							30		20						5					
-1.0	TR Salix			10		10	3													5					20		10			20			
-0.9	TR Al ru					15										10									20				20	10	25		10
-0.6	TR Pi gl		20		25		40	20	20	30	30			30					50		30			20	10	30	10	20	40	3			
-0.2	TR Ab	30		40	40		10	30	40	40	20	60	25	40	40	5	40	40	20		30		25	25	10	10	30	60	20	50		20	20
-0.2	TR Be pa	15	20	20		3	30			5			30	30	50	20	30	60	15	40	5	5	35	35		30	15	10	5	40	40	60		
0.1	TR So de				5							3		10						3													
1.3	TR Th oc																																
2.6	TR Pi ma							5					10								5					15							

Appendix 12(cont.).

Sample scores:	Axis 1	-0.5	-0.5	-0.5	-0.5	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3
	FEC V-type	6	4	14	24	1	14	1	2	1	14	14	24	14	24	4	14	14	14	14	14	14	16	14	14	14	4	1	14	14	14	4	16
	Treatment	DC	DC	SC	HP	DC	HP	SC	SC	SC	DC	DC	DC	HP	CC	DC	HP	DC	HP	DC	DC	CC	SC	HP	HP	SC	DC	SC	HP	HP	DC	SC	SC
Species scores:	Point	6B12	4A14	7B15	8A3	6B2	2B2	7B2	3A1	9B11	6B13	4A4	4A5	8A13	7A15	4B8	10B1	4A3	2B1	6B1	4B10	1B10	7B4	8A7	8A11	3B5	4A16	3A8	10B8	2B8	4B15	3A2	7B9
Axis 1	Herb stratum species																																
-1.9	CLIM DEN																																
-1.7	CORY COR																																
-1.6	PRUN PEN										5				3																3		
-1.4	CIRC ALP																																
-1.2	MERT PAN						3	5				3	20		15		15							5						3			
-1.2	ASTE MAC		60			15	10	5			50	5		15	10		20		30	15					10	3		10	10	5	10		
-1.2	ATHY FEL								50			15						10											10				
-1.2	ACER SPI	10	10	10	3	5	10	25		5						15			5	3	10		3	5	10	5	5						5
-1.2	DIER LON		10								15			15			15		15			20						40	10				
-1.1	ARAL NUD	15				5	5					40		10				10	10	15	3	20	5		40			5	10				5
-1.1	VIBE EDU								5											3	3			3				15					
-1.0	GAL TRIF						3	3		3			5			5	5					3	3					5					3
-0.9	RIBE TRI								10																								
-0.9	THEL PHE								5									30						15								5	
-0.8	MNIUM SP				5								15		40									20					3				3
-0.8	ANEM QUI						5		3				5	5			3		3	3									3		3	10	5
-0.8	LONI CAN													15					5														
-0.8	MITE NUD		5	15		5	3		3			5	20	3	15	15	3	5		15	3	3	10			5			3	15	5		15
-0.8	BRACH SP				5									10		3	5		5					5	15				5	10			
-0.7	LYCO OBS				10																												
-0.7	STREP RO		5	3			10		5	5	10	25	15	10	10		15	10	5	10			5						3	5	5	3	10
-0.7	RUB PUBE		10	5		10	5	3	3	15		15	20		15	40	5	20	10	20		15	3	5				15	5	15	5		
-0.7	VIOL REN		5				3	3	3			3			10	3	5	5	3	3		5	3	5					5		5	3	15
-0.7	RHAM ALN																												10				
-0.6	RUB IDAE															5																	
-0.6	GYMN DRY		5		5	3	3	5	5	3		10	10			5		15				10								10		3	
-0.6	RIBE LAC							10																									
-0.6	CLIN BOR		10	10	3	10	5		5	10	3	10		10	10			10	10					15					15		10	5	15
-0.5	ASTE CIL		3			3		3																									
-0.4	CAREX SP		15	3	3	10	3	10	15			3	5		40									15				20	10			5	5
-0.4	MONE UNI																										3						3
-0.4	PETA PAL						5	5					5		3	15	5						20	5						3			10
-0.3	TRIE BOR	3	3				3			10			5					10		5			3	3						5	3		
-0.2	LYCO ANN	20		20						70	30	5	10		10				15			25				10							
-0.2	MOSS SPP			10		5	5		5									10		5						10			5				
-0.1	EQUI PRA												3				3	10											3	3			
0.0	ROSA ACI										15		10				5			10													
0.1	GRASS SP										5	3				20	10													3			
0.2	EPIL ANG																10																
0.2	RHYT TRI														3														10	3			
0.2	SORB DEC																																
0.3	LICH SP					5	3													5										10			
0.5	FRAG VIR		5														10											5					
0.5	MAIA CAN	3			3							40	5	5			3	10		5			3					3	5				
0.6	ALNU RUG																																
0.6	HYPN CRI																			3			10										
0.8	ABIE BAL	3	10	3				3												3										5			
0.8	EQUI ARV																3													3			
0.8	CORN STOL																												3				
0.9	LINN BOR		3		10						3	3					3			5							20		5			3	
0.9	CORN CAN	3	5								5	10	15	5				3	10	15		35	3	3	15					10	10	3	3
1.0	BETU PAP																						3										
1.2	HYLO SPL																			3			5										25
1.3	THUJ OCC																																
1.3	COPT TRI								10		3							3											3				
1.6	POLY JUN		3												3																		
1.9	CLADO SP																			3													
2.0	DICR SCO	3															5		10					5	10								
2.5	PLEU SCH	10	10												15			3		5		3	15	10	10								
2.5	CAREX TR																																
2.6	VACC MYR																																
2.9	SPHA MAG																																
3.1	GAUL HIS																																
3.6	CLAD RAN																																
3.9	LEDU GRO																																
4.5	VACC ANG																																
4.5	SPHA CAP																							10									
6.1	GEOC LIV																																

Appendix 12 (cont.).

Sample scores:	Axis 1	-0.5	-0.5	-0.5	-0.5	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.4	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3
	FEC V-type	6	4	14	24	1	14	1	2	1	14	14	24	14	24	4	14	14	14	14	14	14	14	16	14	14	14	4	1	14	14	14	4	16
	Treatment	DC	DC	SC	HP	DC	HP	SC	SC	SC	DC	DC	DC	HP	CC	DC	HP	DC	HP	DC	DC	CC	SC	HP	HP	SC	DC	SC	HP	HP	DC	SC	SC
Species scores:	Point	6B12	4A14	7B15	8A3	6B2	2B2	7B2	3A1	9B11	6B13	4A4	4A5	8A13	7A15	4B8	10B1	4A3	2B1	6B1	4B10	1B10	7B4	8A7	8A11	3B5	4A16	3A8	10B8	2B8	4B15	3A2	7B9
Axis 1	**Shrub stratum species**																																
-1.5	SH Co co	20	10	3			5			5	30	15		15					10	5		3	15	10	10	5					5		3
-1.2	SH Pr vi														10					3				3					3				10
-1.0	SH Ac sp	70	80	50	60	60	35	30	25	40	25	20	50	20	20	40	15	40	50	50	40	50	70	50	30	40	60	10	30	50	70	25	40
-1.0	SH Vi ed					3	3			3				3	3					3	3			5		3		3				3	3
-0.9	SH Fr ni								10				3					10														3	
-0.9	SH Rh al																								10				10				
-0.9	SH Lo ca						3					3		10					3	5	5			15	3		3			3	5	3	3
-0.8	SH Di lo	3						15			3			5			3					3	3						5				
-0.7	SH Salix					3											5			3						3		5		10			
-0.6	SH Po ba					10		3		3							3																
-0.4	SH Ri hi																3																
-0.3	SH Co st						5	5				3				5	70											3					
-0.3	SH Ru id														3		10			3								3					
-0.3	SH Pi gl			3								3					3	10						10		5	5				3		
0.1	SH Al ru			10				30	25	40	10	40	15		25	50	5	20						10		3	40		40			40	
0.1	SH Lo in					3	5																										
0.1	SH Ri la					3	3			3							3			3					3								
0.2	SH Am hum																				5				3								
0.3	SH So de	5	5		3		3										3				10		3						15		3		
0.4	SH Ro ac							3									20						3						3		3		
0.4	SH Pr pe	3															3				5					5		5			10		
0.5	SH Ab	5		5	3	15	20	15	10		10	10	20	20		10	5	30	40	10	20			20		5		10	10	15	15	5	3
0.8	SH Lo ob																3																
0.8	SH Be pa			5		15	10	10			5			20		5				3	10								5	5	15		10
1.5	SH Al cr		30																								3	40					
1.5	SH Th oc						3																			5				3			
1.7	SH Lo vi																																
2.3	SH Am ba																																
2.7	SH La la																																
2.9	SH Pi ma																																
5.0	SH Le gr																																
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR Po tr	15																										3					
-1.5	TR Fr ni								15									20															
-1.4	TR Pr pen							10									10							15				15				
-1.4	TR Po ba					20		10		10							10				30			5		5		3					
-1.0	TR Salix							5		15		30														3				15			
-0.9	TR Al ru			10				15	15	5	15	25			10	20		60														10	
-0.6	TR Pi gl			20	20		30	3					40			5	10	20			25			35	15	10			15	15	5		50
-0.2	TR Ab	25	20	35	40	30	50		15	15	25	50	40	50	30	20	15	30	50	50	40	50	60	40	60	20	30	5	30	40	50	10	10
-0.2	TR Be pa	40	30	20		40	5	50		20	25	10		40		30	10		40	30	10	20	10		15	20	40	10	35	20	40	50	40
0.1	TR So de	10								20					5								3				3		20				5
1.3	TR Th oc						3																										
2.6	TR Pi ma	5									10																						

Appendix 12(cont.).

Sample scores:	Axis 1	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
	FEC V-type	1	15	14	4	14	14	14	1	14	4		14	16	4	14	25	16	2	14	4	14	4	14	19	14	24	21	6	16	4	16	21	
	Treatment	HP	DC	HP	SC	SC	SC	SC	CC	SC	SC	SC	CC	SC	HP	DC	DC	HP	SC	SC	HP	HP	SC	SC	HP	DC	HP	HP	SC	HP	SC	DC	CC	
Species scores:	Point	10B2	4B4	8A10	3B11	3A19	7B13	3B20	5B14	3B17	3B2	3A7	5B10	3B8	2B9	6B9	6A15	8A6	3B18	3B1	8A4	8A9	3B12	3A10	8A2	6B4	10B12	10B3	3A15	10B6	3A14	6B8	5B2	
Axis 1	Herb stratum species																																	
-1.9	CLIM DEN																																	
-1.7	CORY COR					10																												
-1.6	PRUN PEN																																	
-1.4	CIRC ALP				5														10															
-1.2	MERT PAN			10														20							3				5			10	
-1.2	ASTE MAC	25					5		20				20		15	15										30	30	50		10				
-1.2	ATHY FEL		5		15													20															3	
-1.2	ACER SPI		5				10			3		5		10	10	3		3	3	20					5							3	10	
-1.2	DIER LON												15				10																	
-1.1	ARAL NUD							10		3			10			5	5									3	20	15		5	10	15	5	
-1.1	VIBE EDU							15				10					5																	
-1.0	GAL TRIF			10				3		3		5				3		3							3		3	3		3		3	3	
-0.9	RIBE TRI																										3			3				
-0.9	THEL PHE			25															15						30									
-0.8	MNIUM SP			10							10								5			10			20			15		15		3		
-0.8	ANEM QUI					5									3	5											3	3		3	3	3		
-0.8	LONI CAN											10																						
-0.8	MITE NUD		5	3	15					3	10				5	3		15	5	10		5	5		10		5	10		20		15	5	
-0.8	BRACH SP						15														20	10					10			3				
-0.7	LYCO OBS																												5					
-0.7	STREP RO	10		5			5	5								15		15			5	10			15		3	5		3		10		
-0.7	RUB PUBE	5	20	15				20	25	3		5				10		10	10			5	10		15	10	5	15	15		15	10	20	
-0.7	VIOL REN	3	10	15	5			5	3	5		25				5		5	5	5		5	10		5	3		10		5	3		5	
-0.7	RHAM ALN																																	
-0.6	RUB IDAE							5											10		15													
-0.6	GYMN DRY		15		15					3		5						3	15	10		10	5		15		3			10		5	5	
-0.6	RIBE LAC		3							3												10					3							
-0.6	CLIN BOR	10	15	10	5	10	20	5				10	10		10		10			3	25	25	10		5				5	10	10	10		
-0.5	ASTE CIL																	5									10					3		
-0.4	CAREX SP	20	15	20				10	10			10			3	15		15				3			5	5	30		3	3		5		
-0.4	MONE UNI																	3								3						3		
-0.4	PETA PAL								3						10	10		15					5		5		15			3		5		
-0.3	TRIE BOR					3	3			5			5		3							5	3		5				3	5	5		
-0.2	LYCO ANN						10	3				10	5		25		20					5	3		30		10		5		20			
-0.2	MOSS SPP		3	15						15	5		5		3										5		5	5	5			15		
-0.1	EQUI PRA							5								3						3	3				3	3		3				
0.0	ROSA ACI	10														15					5	3				15								
0.1	GRASS SP							3	3						3	10						3			3	3	3	3	3	3				
0.2	EPIL ANG																																	
0.2	RHYT TRI																											5		10				
0.2	SORB DEC																																	
0.3	LICH SP														3																			
0.5	FRAG VIR															5																		
0.5	MAIA CAN						3	10	3				5		3	3							3		3	15	10		5	3	20	10	5	
0.6	ALNU RUG		5	10					15			3															5						5	
0.6	HYPN CRI											3		20									10						5	5				
0.8	ABIE BAL								3				3									10												
0.8	EQUI ARV		5						3																									
0.8	CORN STOL																																	
0.9	LINN BOR				3	3	15						10									3		10		5				5	3	3		
0.9	CORN CAN					5	5	3						5		3	15	3				15	5			15		3	15		25	10	5	
1.0	BETU PAP																								3									
1.2	HYLO SPL													3	3													3	5	5				
1.3	THUJ OCC																													3				
1.3	COPT TRI				5			5		3			3					3	3		3	5						5						
1.6	POLY JUN										3															5	3							
1.9	CLADO SP													3			5																	
2.0	DICR SCO						3				5				20		5							5		15		5	10	3		5		
2.5	PLEU SCH						10			3	3	30		3			25	20	20	5	25			5	10	15	10	10	20	20		20		
2.5	CAREX TR																																	
2.6	VACC MYR												5					3									10							
2.9	SPHA MAG																																	
3.1	GAUL HIS																	3									3							
3.6	CLAD RAN																																	
3.9	LEDU GRO	15																																
4.5	VACC ANG																10																	
4.5	SPHA CAP		3																			5												
6.1	GEOC LIV																																	
6.6	VACC OXY																																	

Appendix 12 (cont.).

Sample scores:	Axis 1	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.3	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1	-0.1
	FEC V-type	1	15	14	4	14	14	14	1	14	4		14	16	4	14	25	16	2	14	4	14	4	14	19	14	24	21	6	16	4	16	21
	Treatment	HP	DC	HP	SC	SC	SC	SC	CC	SC	SC	SC	CC	SC	HP	DC	DC	HP	SC	SC	HP	HP	SC	SC	HP	DC	HP	HP	SC	HP	SC	CC	CC
Species scores:	Point	10B2	4B4	8A10	3B11	3A19	7B13	3B20	5B14	3B17	3B2	3A7	5B10	3B8	2B9	6B9	6A15	8A6	3B18	3B1	8A4	8A9	3B12	3A10	8A2	6B4	10B12	10B3	3A15	10B6	3A14	6B8	5B2
Axis 1	Shrub stratum species																																
-1.5	SH Co co														20	15	70			3		20				20	3		10	3	3	3	
-1.2	SH Pr vi	3		5																				3						5		5	
-1.0	SH Ac sp	20	60	20	50	90	40	40	15	40	30	50	15	40	20	60	20	40	50	20	50	20	40	5	50	30	3	30	30	50	40	70	20
-1.0	SH Vi ed			3				3								3			5		3	3			5			3		3	3	3	
-0.9	SH Fr ni			10															5														
-0.9	SH Rh al	10							10									3															
-0.9	SH Lo ca	5							5	5		10	3		10	5										5			5			5	
-0.8	SH Di lo	10											15				10									5							
-0.7	SH Salix	3	5																	3		5									3		5
-0.6	SH Po ba																																
-0.4	SH Ri hi	3	5																														
-0.3	SH Co st	15		10				10	5				20		3	5		5			3	5			3			3		15		5	
-0.3	SH Ru id			3					3		3				3						5	3			3								3
-0.3	SH Pi gl	5			3			5		10								5									5	3				15	
0.1	SH Al ru	25	30	70	5			40	60	10		20						20	40			50			60		60			20			50
0.1	SH Lo in																	3	3														
0.1	SH Ri la															3				3		3				5						3	
0.2	SH Am hum	3											10																3				
0.3	SH So de			3	3					3			10			3	3			3	3	5	3		5	10	3		3				
0.4	SH Ro ac	5						3	5				5			3	3					3				3				3			
0.4	SH Pr pe												3																				
0.5	SH Ab	5	10	5	15	20	5	3	3	20	20		5	3	15	40	3	20	30	40			15	3	15	25	20	40		10	10	30	
0.8	SH Lo ob																																
0.8	SH Be pa		30		5						5		5		20	15		10		10		3	5			5				20	5	
1.5	SH Al cr					40			3				20																				
1.5	SH Th oc		15		5																							20					25
1.7	SH Lo vi																																
2.3	SH Am ba	3																															
2.7	SH La la																																
2.9	SH Pi ma																																
5.0	SH Le gr	5																															
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR Po tr																																
-1.5	TR Fr ni																																
-1.4	TR Pr pen																																
-1.4	TR Po ba	10							5				5			3																	
-1.0	TR Salix	5	10					5					5																				
-0.9	TR Al ru		20						10	5		20							20														
-0.6	TR Pi gl	15	20		10	5	40				30		15	10	30		15	25					5		10	20	40	15		40		40	
-0.2	TR Ab	5		20	25	20	40	20	20	15	10	15	30	40	40	40	40	60	5	30		25	10	40	5	40	20	30	50	10	25	15	20
-0.2	TR Be pa	15	30		50	15	15	10	15	25	40	3	10	20	60	25		15		40	3	15	50	20	15	15		15	20	15	40	40	20
0.1	TR So de										3													3									
1.3	TR Th oc		15		10					15				3									30				40					30
2.6	TR Pi ma				3			10						3		10						15			20		10			15	3	20	

Appendix 12(cont.).

Sample scores:	Axis 1	-0.1	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.2
	FEC V-type	4	14	14	14	16	16	14	15	16	16	14	15	14	16	19	25	14	4	24	4	14	14	14	14	4	21	15	14	15	16	21	21	2
	Treatment	CC	SC	HP	HP	HP	DC	SC	SC	HP	CC	CC	HP	DC	DC	CC	SC	DC	DC	CC	HP	SC	CC	DC	DC	DC	CC	SC	CC	HP	HP	DC	CC	DC
Species scores:	Point	5B3	3A12	2B7	10B13	8A5	4A7	3B9	3A3	10B9	5A6	1B1	10B15	4B3	4B18	1B12	3A9	4B16	6A12	7A13	8A12	7B10	5B5	4A19	6A11	5B6	7B6	5A3	10B10	10B5	4B1	5B13	6A14
Axis 1	Herb stratum species																																
-1.9	CLIM DEN																																
-1.7	CORY COR																																
-1.6	PRUN PEN																																
-1.4	CIRC ALP																																
-1.2	MERT PAN				15		10									5																	
-1.2	ASTE MAC					20		25							10	5							10	15				10					
-1.2	ATHY FEL																								15								
-1.2	ACER SPI			3				3		5		5					15	3					3			3			20				
-1.2	DIER LON					30		30																									
-1.1	ARAL NUD			10	3	5	5			10		3	5	15		3		5					10			5			3				
-1.1	VIBE EDU			5						5																							
-1.0	GAL TRIF			10	3		3					3											3			3							
-0.9	RIBE TRI																													10			
-0.9	THEL PHE									5																			3				
-0.8	MNIUM SP						15				25																						
-0.8	ANEM QUI	3	5		5	3				3	3	3																					
-0.8	LONI CAN																																
-0.8	MITE NUD	3		5	5		15	3		3		5			3	3			3				5						20			10	3
-0.8	BRACH SP				3	15						3	3			10				5		15				10			5				
-0.7	LYCO OBS					5											3							10									
-0.7	STREP RO	15		3		5	3	5		15	5	3		10		3	5					5	3	5				15		5			
-0.7	RUB PUBE		30	40	10		10			15		15	3	5	5				10	15	5		10	3	3			10	15	15	3		15
-0.7	VIOL REN	3	3	10	3		5	3		3		5	5		3	5			5				3	5	3		3						10
-0.7	RHAM ALN																																
-0.6	RUB IDAE					3																						15					10
-0.6	GYMN DRY				3		10		3	15		3	3	5	3				3	3									10			3
-0.6	RIBE LAC																						5										
-0.6	CLIN BOR	15	25			40	5	10	5	15		3		10	10	3	25	10		20	15		10	15				20	15	5	10		15
-0.5	ASTE CIL			5	15							5				3																	
-0.4	CAREX SP	3		3	5		5	5		5		10	30	3	3					3			3	3	20		5	3	3	3	3		15
-0.4	MONE UNI													3											10	3							
-0.4	PETA PAL		10	20						5				10					3				5										
-0.3	TRIE BOR			3			3					3		3					3						3	3			3	3			
-0.2	LYCO ANN									5	20	20							5	40	3	30		10	10		5	20		5			
-0.2	MOSS SPP												15						5						5					5	5	10	
-0.1	EQUI PRA	3		10	5								3										5						3				
0.0	ROSA ACI	10		15		25						15											5										
0.1	GRASS SP	5	5	15								10		5															3				
0.2	EPIL ANG																																
0.2	RHYT TRI						20																			3			5				
0.2	SORB DEC		5																							3							
0.3	LICH SP																									5					3		
0.5	FRAG VIR				3																									3			
0.5	MAIA CAN		10		3	5				10	3							5		3	10		5	10		3	10	3	10	3		3	
0.6	ALNU RUG																																
0.6	HYPN CRI										10			5	3	10																5	
0.8	ABIE BAL									3			10	10	5			5									3			3		3	5
0.8	EQUI ARV													3									3							3	10		
0.8	CORN STOL																										5		5				3
0.9	LINN BOR		5	20			10	3		5			5			5				3	5		5			15	5		5				5
0.9	CORN CAN	5	20	15		3		3		5		5	3	15	5		15	5		3	20		10	15			5	20	5	5	5			
1.0	BETU PAP										3			3															3			3	
1.2	HYLO SPL						5			20	3		5													5			3	50			
1.3	THUJ OCC			3																													
1.3	COPT TRI							3	3					5	5		3			15	15		10	20	5			15	10	3	10		5
1.6	POLY JUN												3						3														
1.9	CLADO SP										3		3															3			3		
2.0	DICR SCO								10		5						10	20				10					15	3	3				
2.5	PLEU SCH			25		20	20	5	5	30	10			3	20	10	25				3	3					5	3	10	10				
2.5	CAREX TR																		15						10								
2.6	VACC MYR	10		3		5						10																					
2.9	SPHA MAG																		20						30								
3.1	GAUL HIS									5																							3
3.6	CLAD RAN												5																				
3.9	LEDU GRO											10													3			3					10
4.5	VACC ANG										3							5						3				5					
4.5	SPHA CAP																																20
6.1	GEOC LIV																											3					
6.6	VACC OXY																																

Appendix 12 (cont.).

Sample scores:	Axis 1	-0.1	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2	0.2	0.2
	FEC V-type	4	14	14	14	16	16	14	15	16	16	14	15	14	16	19	25	14	4	24	4	14	14	14	4	21	15	14	15	16	21	21	2
	Treatment	CC	SC	HP	HP	HP	DC	SC	SC	HP	CC	CC	HP	DC	DC	CC	SC	DC	DC	CC	HP	SC	CC	DC	DC	CC	SC	CC	HP	HP	DC	CC	DC
Species scores:	Point	5B3	3A12	2B7	10B13	8A5	4A7	3B9	3A3	10B9	5A6	1B1	10B15	4B3	4B18	1B12	3A9	4B16	6A12	7A13	8A12	7B10	5B5	4A19	6A11	5B6	7B6	5A3	10B10	10B5	4B1	5B13	6A14
Axis 1	Shrub stratum species																																
-1.5	SH Co co			5		10					5	10						20			25			10			3						
-1.2	SH Pr vi																																
-1.0	SH Ac sp	20	40	30	20	20	60	20	15	40	40	5	25	10	60	50	40	50	25	5	15		20	10	3	15	15	5	30	20	20		20
-1.0	SH Vi ed	3	3		3	5				3											3							3		3			3
-0.9	SH Fr ni																																5
-0.9	SH Rh al											3																					
-0.9	SH Lo ca			3	3		3			10		5	5		10	5							3			5				3			3
-0.8	SH Di lo	3	3			30		5													10						5					3	
-0.7	SH Salix		3									5	5	15																5	3	5	
-0.6	SH Po ba																															3	
-0.4	SH Ri hi				3								3																	3	3		
-0.3	SH Co st			20						3		5	15		10											10				15			10
-0.3	SH Ru id			5									3															3					3
-0.3	SH Pi gl									5				10					5										10	5	3	3	5
0.1	SH Al ru				20		10			20		50			20	10		5	40	10	40				40	10		10	15	30	40	15	20
0.1	SH Lo in			3								3	3																	5		3	
0.1	SH Ri la			5	3					3			3	5																		3	
0.2	SH Am hum		3			3							5																				
0.3	SH So de			3				3		3		3	3		10				10								3	3		5		3	
0.4	SH Ro ac	5		15		5		3		3		3	3		10												3	3		5			
0.4	SH Pr pe		3									10																					
0.5	SH Ab	3	10	10	10	15	20	30	10	10	3	5	15	15	30	5		10	15	3		5	15	15	30	5	15		5	15	15	10	15
0.8	SH Lo ob											3																					5
0.8	SH Be pa	30	15	5		3			3	3	5		10	10				20	15			3		40			5	3	10	10		5	15
1.5	SH Al cr							40			10			20				10						20				5					
1.5	SH Th oc													3									5			15					15	30	
1.7	SH Lo vi																																
2.3	SH Am ba	10										3									20									3			5
2.7	SH La la																																
2.9	SH Pi ma				3	10	5					15	10					5	10														10
5.0	SH Le gr											5																					
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR Po tr										5	10																					
-1.5	TR Fr ni																																
-1.4	TR Pr pen																																
-1.4	TR Po ba								10																							10	
-1.0	TR Salix												5																	5		3	
-0.9	TR Al ru				25		10					5		20							15											5	
-0.6	TR Pi gl	30			20		20	5	30	30			25	10		5	20	5				15				10	30		25	35	20		
-0.2	TR Ab	10	50	30	15	50	25	20	20	3	20	20	5	40	60	25	20	40	25	25		20	60	40	5	10	20	40	10	10	20	30	5
-0.2	TR Be pa	50	50	15	10	20	5	20	20	30	10	10	30	15	30	10	10	40	30	20	30	25	20	40	75	30	15	40	10	5	10	30	30
0.1	TR So de											5								5						5							
1.3	TR Th oc													30									30			60					60	40	
2.6	TR Pi ma	20	15		30	20	20	5		15	10	5	10		20	25		10		15		15	15		5			10	35	15			5

Appendix 12(cont.).

Sample scores:	Axis 1	0.2	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
	FEC V-type	16	14	14	24	25	14	21	16	16	16	24	14	24	19	4	21	14	21	14	21	14	14	34	16	21	21	14	21	21	35	35	4
	Treatment	CC	DC	SC	DC	SC	DC	HP	DC	SC	HP	CC	DC	DC	HP	SC	DC	HP	HP	DC	CC	SC	SC	DC	DC	CC	HP	DC	CC	CC	CC	CC	DC
Species scores:	Point	1B5	4A17	3A5	4B19	3A20	4A6	2B13	8B5	3B3	10B14	5A1	8B6	6A7	10B11	3A13	4B2	8A8	2B10	4A1	5B12	3B4	3B7	6A10	4B7	5B7	2B12	4A8	5B11	5B4	5A9	7A9	6A13
Axis 1	Herb stratum species																																
-1.9	CLIM DEN																																
-1.7	CORY COR																																
-1.6	PRUN PEN																																
-1.4	CIRC ALP																																
-1.2	MERT PAN																																
-1.2	ASTE MAC					20							15																				
-1.2	ATHY FEL																	15															
-1.2	ACER SPI	3		3				5					3				3			3													
-1.2	DIER LON		10		15																3												
-1.1	ARAL NUD	10			15			3					5				5		5	15	5												
-1.1	VIBE EDU	15			5	3																											
-1.0	GAL TRIF							3			3																						
-0.9	RIBE TRI					5		3	10		3																						
-0.9	THEL PHE																																
-0.8	MNIUM SP					5															10						10						
-0.8	ANEM QUI					3		3			3		3								3					3			3				
-0.8	LONI CAN												3																				
-0.8	MITE NUD			3				10			15			3	15		10				10					5	3		5		5		
-0.8	BRACH SP								5		10																		10				
-0.7	LYCO OBS															10				3								3					
-0.7	STREP RO	5			5	5					3				15	5	3	3	10							5							
-0.7	RUB PUBE	15		3	15	5								30	10						3			15	15	3				3	15	15	
-0.7	VIOL REN					5					5			5	10		3		3		3			10							3	3	
-0.7	RHAM ALN																																
-0.6	RUB IDAE													10																			
-0.6	GYMN DRY					40							5	3	3		5														10	3	3
-0.6	RIBE LAC																																
-0.6	CLIN BOR	5	15		5	20						40		3		20	3	10														10	
-0.5	ASTE CIL				3										5																		
-0.4	CAREX SP				3			3			10				25		5				3			45	15			3	10	10	5	
-0.4	MONE UNI																		3		3					3							
-0.4	PETA PAL							5							5				5					20		10			10		3		
-0.3	TRIE BOR	5			5	3		3				3		5	3						3								5		3	3	
-0.2	LYCO ANN		3	5		10	50					15				15		3		20								3			40	15	
-0.2	MOSS SPP				5			10	5	5															3		20	3				25	
-0.1	EQUI PRA							3			3				3											3			5	3			
0.0	ROSA ACI	10						5			3			10	3											10			20				
0.1	GRASS SP	10			10								3	10	3									15					5	3			
0.2	EPIL ANG																																
0.2	RHYT TRI							3	5						5						40					3	10		3				
0.2	SORB DEC									3																							
0.3	LICH SP							3		5			3				3										5						
0.5	FRAG VIR				5										15																		
0.5	MAIA CAN			3	15	15						10	5	3	20	20	10	3								3							
0.6	ALNU RUG										10			10				5	5														
0.6	HYPN CRI						5			5					3												20						
0.8	ABIE BAL				15						5								3								3		3	3			
0.8	EQUI ARV											5														5			10				
0.8	CORN STOL											3		15																			
0.9	LINN BOR	10			10	20			3				3	10	10		5						3	15	15	10			10				3
0.9	CORN CAN	15	20	3	20				5		3	5	15		5	10	3	10	5	5	3				10	5		5		15			5
1.0	BETU PAP																							3									
1.2	HYLO SPL							10	3	30	25				10		3				3					10	40		3	10			
1.3	THUJ OCC	3						3											3		3					15							
1.3	COPT TRI					5						3	10				3	5							3					5			
1.6	POLY JUN																						3		3								
1.9	CLADO SP			3			5									3			3							3	3	3		3			3
2.0	DICR SCO	3		10			10		5	5			5				3			10	5	20	15			5	5		3	3			5
2.5	PLEU SCH	40	15			80	10		35	15	20		15		35		25		5	5	10	10	3		20	5			3	5			15
2.5	CAREX TR																																
2.6	VACC MYR																																
2.9	SPHA MAG																														20	30	15
3.1	GAUL HIS	3											3	10			3								10						10		
3.6	CLAD RAN																		5							3				5			
3.9	LEDU GRO													10				15													15	25	
4.5	VACC ANG		5		20											5		3		10										5			
4.5	SPHA CAP													5										40								20	
6.1	GEOC LIV																																
6.6	VACC OXY																																

Appendix 12 (cont.).

Sample scores:	Axis 1	0.2	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
	FEC V-type	16	14	14	24	25	14	21	16	16	16	24	14	24	19	4	21	14	21	14	21	14	14	34	16	21	21	14	21	21	35	35	4
	Treatment	CC	DC	SC	DC	SC	DC	HP	DC	SC	HP	CC	DC	DC	HP	SC	DC	HP	HP	DC	CC	SC	SC	DC	DC	CC	HP	DC	CC	CC	CC	CC	DC
Species scores:	Point	1B5	4A17	3A5	4B19	3A20	4A6	2B13	6B5	3B3	10B14	5A1	6B6	8A7	10B11	3A13	4B2	8A8	2B10	4A1	5B12	3B4	3B7	6A10	4B7	5B7	2B12	4A8	5B11	5B4	5A9	7A9	6A13
Axis 1	Shrub stratum species																																
-1.5	SH Co co	15				20			5				3			3																	
-1.2	SH Pr vi										5																						
-1.0	SH Ac sp			25	20	50	50	5	30	10	15	10	15	5	15	20	20	20	10	5	10	10	10	5	30	10							
-1.0	SH Vi ed	3										3		5																			
-0.9	SH Fr ni																																
-0.9	SH Rh al																																
-0.9	SH Lo ca	10			3								3				3		3								3		3				
-0.8	SH Di lo				10																												
-0.7	SH Salix								3														3			5							
-0.6	SH Po ba																																
-0.4	SH Ri hi														3																		
-0.3	SH Co st	10			10	3					3	15		10	3				3														
-0.3	SH Ru id	3										3		5	3																3		
-0.3	SH Pi gl			3						3	10									10	3		3			3							
0.1	SH Al ru		3							3	20	40	5	40	35			30	10	3	30			40	40				15	30	80	30	
0.1	SH Lo in														5											3							
0.1	SH Ri la										3				5						3					3			3				
0.2	SH Am hum										3					10																	
0.3	SH So de				3						3	10	3		3											3							
0.4	SH Ro ac				5						3		3		3											3				3			
0.4	SH Pr pe				3											5																	
0.5	SH Ab	10	10	25	40	3	5	10	40	10	30	20	40	10	15		20	40	25	25	10	40	10	3	15	30	20	20	20	25	15		40
0.8	SH Lo ob																														10		
0.8	SH Be pa		10	3			5	3	10	10			20		5	15	10			15	5	10	20	3	30			15		3	5	3	
1.5	SH Al cr			15	40					3						20				15								5					
1.5	SH Th oc							50					5				20		50		20		3			40	50		40	15			
1.7	SH Lo vi											15		30										10									
2.3	SH Am ba	5										15						3		3											3	3	3
2.7	SH La la													5										3									
2.9	SH Pi ma		5								5	15	5	10										15	3					10	5	15
5.0	SH Le gr											5		5				20						15							5	5	5
8.9	SH Ka po																																
	Tree stratum species																																
-2.4	TR Po tr	30																															
-1.5	TR Fr ni																																
-1.4	TR Pr pen																																
-1.4	TR Po ba										5																						
-1.0	TR Salix							5																									
-0.9	TR Al ru																																
-0.6	TR Pi gl			10	10			10	15	10	20		35	5	5				20		20	20	3										
-0.2	TR Ab	25	60	25	15	50	40	15	30	50	10	20	40	5	15	10	30	50	10	50	20	40	40		60	30	30	25	30	15	15	5	10
-0.2	TR Be pa	10	50	50			30	20	25	40	20	15	30		10	40	40	30	20	40	10	30	40	5	10			40			10	5	40
0.1	TR So de															5							3								3		
1.3	TR Th oc							60		5							60		60		40					40	50		50	30			
2.6	TR Pi ma	25		20	5	40	30				30	10	25	3	25	30		10		30	30	10	20	5	40			15	10	15	5	20	5

Appendix 12 (cont.).

Sample scores:	Axis 1	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.9	0.9	0.9	1.0	1.0	1.1	1.1	1.1	1.2	1.2	1.2	1.3	1.3	1.3	1.4	1.4	1.4	1.4	1.5	1.5	1.5	1.8
	FEC V-type	16	16	19	4	16	21	19	16	21	16	19	31	16	21	19	35	19	21	35	31	31	19	16	19	22	19	20	19	21	20	20
	Treatment	DC	SC	CC	CC	DC	CC	SC	DC	HP	CC	CC	SC	CC	CC	DC	CC	SC	HP	CC	CC	CC	CC	SC	SC	CC	DC	HP	DC	SC	DC	SC
Species scores:	Point	6B10	7B11	7A7	5A2	6B7	5B9	3A6	6B11	2B11	7A3	7A1	3A4	7A8	5B15	6A1	5A8	3A18	2B14	5A4	7A6	5A5	7A4	7B8	3A11	5B8	4A20	8A1	6A3	3B6	6A2	7B1
Axis 1	Herb stratum species																															
-1.9	CLIM DEN																															
-1.7	CORY COR																															
-1.6	PRUN PEN																															
-1.4	CIRC ALP																															
-1.2	MERT PAN																															
-1.2	ASTE MAC		3																													
-1.2	ATHY FEL																															
-1.2	ACER SPI		3																													
-1.2	DIER LON																															
-1.1	ARAL NUD	5	3																													
-1.1	VIBE EDU		5																													
-1.0	GAL TRIF																															
-0.9	RIBE TRI																															
-0.9	THEL PHE																															
-0.8	MNIUM SP																															
-0.8	ANEM QUI																			3												
-0.8	LONI CAN	5																														
-0.8	MITE NUD									3							10		3							5				3		
-0.8	BRACH SP										10	3																				
-0.7	LYCO OBS													3				5							5							
-0.7	STREP RO									5									3	10								3				
-0.7	RUB PUBE						10										25			5												
-0.7	VIOL REN									5							3		5													
-0.7	RHAM ALN																		5													
-0.6	RUB IDAE																															
-0.6	GYMN DRY																															
-0.6	RIBE LAC																															
-0.6	CLIN BOR		5	30			5					3	25	5		10																
-0.5	ASTE CIL						3			3																3						
-0.4	CAREX SP			3			5			3							15									5						
-0.4	MONE UNI									3																						
-0.4	PETA PAL																									5						
-0.3	TRIE BOR	5					3						3			3										5						
-0.2	LYCO ANN				10					3	10		3			5			10			3	10									
-0.2	MOSS SPP	3					5						5																				
-0.1	EQUI PRA																									5						
0.0	ROSA ACI																						10			5						
0.1	GRASS SP						5										10					3				5						
0.2	EPIL ANG						10																									
0.2	RHYT TRI																															
0.2	SORB DEC															3																
0.3	LICH SP	3											3			3																
0.5	FRAG VIR																									10						
0.5	MAIA CAN	5	10	10	20							3	15	10		3				5	15	10		3		3					20	10
0.6	ALNU RUG															3																
0.6	HYPN CRI		3																										5		5	
0.8	ABIE BAL	3			25																10		5			10			3	10		
0.8	EQUI ARV						15																			10						
0.8	CORN STOL																15															
0.9	LINN BOR	15	3		3		5		5				3	3	5	3	10	10	10	25		15	10			10			3		3	
0.9	CORN CAN	10	3	15	30		5		20				20	10		25	10	5		5	40	25	20	5	3	10			10		20	5
1.0	BETU PAP	3					3		5													3										3
1.2	HYLO SPL	5							10	3									3					10		5		3		20		
1.3	THUJ OCC									3									3													
1.3	COPT TRI				25			5									10		3	10		10				5						
1.6	POLY JUN						3						5		3										10							3
1.9	CLADO SP					3	10	3		5					10					3		3			5			3				
2.0	DICR SCO	20	15			60	10	5	15	10	15	3	5		20	3		30	20	5		10		20	15	10	15	20	15		20	5
2.5	PLEU SCH	40	40		5	20	10	10	40	15	20		25	50		10		40	15	20	15	10	50	60	15	10	25	40	20	10	30	90
2.5	CAREX TR																10															
2.6	VACC MYR											3		3						3		10					3		3			3
2.9	SPHA MAG																															
3.1	GAUL HIS					3	20			10							3		10	15						10						
3.6	CLAD RAN					3	10			3					3				5			3								3		
3.9	LEDU GRO																20		10	5						15						
4.5	VACC ANG				5				10									10		3	3	15	10		5	10					15	10
4.5	SPHA CAP																30			15						10						
6.1	GEOC LIV																															
6.6	VACC OXY																3															

Appendix 12 (cont.).

Sample scores:	Axis 1	0.7	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.9	0.9	0.9	0.9	1.0	1.0	1.1	1.1	1.1	1.2	1.2	1.2	1.3	1.3	1.3	1.4	1.4	1.4	1.4	1.5	1.5	1.5	1.8
	FEC V-type	16	16	19	4	16	21	19	16	21	16	19	31	16	21	19	35	19	21	35	31	31	19	16	19	22	19	20	19	21	20	20
	Treatment	DC	SC	CC	CC	DC	CC	SC	DC	HP	CC	CC	SC	CC	CC	DC	CC	SC	HP	CC	CC	CC	CC	SC	SC	CC	DC	HP	DC	SC	DC	SC
Species scores:	Point	6B10	7B11	7A7	5A2	6B7	5B9	3A6	6B11	2B11	7A3	7A1	3A4	7A8	5B15	6A1	5A8	3A18	2B14	5A4	7A6	5A5	7A4	7B8	3A11	5B8	4A20	8A1	6A3	3B6	6A2	7B1
Axis 1	Shrub stratum species																															
-1.5	SH Co co	5																														
-1.2	SH Pr vi																															
-1.0	SH Ac sp	15	30		5	25	5	20	10									30										10				
-1.0	SH Vi ed						3										3															
-0.9	SH Fr ni																															
-0.9	SH Rh al																															
-0.9	SH Lo ca	5							3						3				3													
-0.8	SH Di lo													3								10										
-0.7	SH Salix								3																							
-0.6	SH Po ba						3																			5						
-0.4	SH Ri hi																															
-0.3	SH Co st						5							3	10		10															
-0.3	SH Ru id																3															
-0.3	SH Pi gl								5	3																						
0.1	SH Al ru					20				15						20	40		5	40							10					
0.1	SH Lo in																									10						
0.1	SH Ri la	3				3	3																			3						
0.2	SH Am hum	3																														
0.3	SH So de		3	5	3	3						10		3		3					10										5	10
0.4	SH Ro ac		3				5		3					3		3				5		3		5		3						
0.4	SH Pr pe			3	3							5		20	3								5								5	
0.5	SH Ab	20	5	3	3	40	20	5	20	10	5	5	10	3	10	10	10	3	5	30		5		10	5	15	20	10	15	5	10	20
0.8	SH Lo ob																															
0.8	SH Be pa	5	5	10		5				3	5	15	10	15		5				3	10	3	10	5	3		50		5	3	15	3
1.5	SH Al cr			50	25			3				3			5			20		10	5		10	15			10			10	15
1.5	SH Th oc						20			25					30				60							10			40		
1.7	SH Lo vi																10															
2.3	SH Am ba			3	5									3	5	3	20	3		25	5	3							3		3	
2.7	SH La la																5															
2.9	SH Pi ma			5	3	20								5	5	5	15	3		5	10	3			3	5			3	3	20	10
5.0	SH Le gr						15								15	3	20		5	15	3					50						
8.9	SH Ka po																															
	Tree stratum species																															
-2.4	TR Po tr																															
-1.5	TR Fr ni																															
-1.4	TR Pr pen																															
-1.4	TR Po ba																									5						
-1.0	TR Salix																															
-0.9	TR Al ru									10																						
-0.8	TR Pi gl	20				35			30				15		5			5						20								
-0.2	TR Ab	40	20	10	15	50	30	30	20	15	30	20	30	40	25	20	5	15	30	10	20	20	25	5	20	30	20	20	10	5		15
-0.2	TR Be pa	3	15	15	40	15	15	10	20		25	15	10	35	15	15	3	5		5			15	25	20		10	10	15		20	3
0.1	TR So de		3									5						40			10				10							
1.3	TR Th oc						50			50					50				40							40			50			
2.6	TR Pi ma	15	20	15	20	20	1	40	15		20	40	50	20		50	20	30		15	35	40	35	20	50		60	40	50	40	40	25

Appendix 12 (cont.).

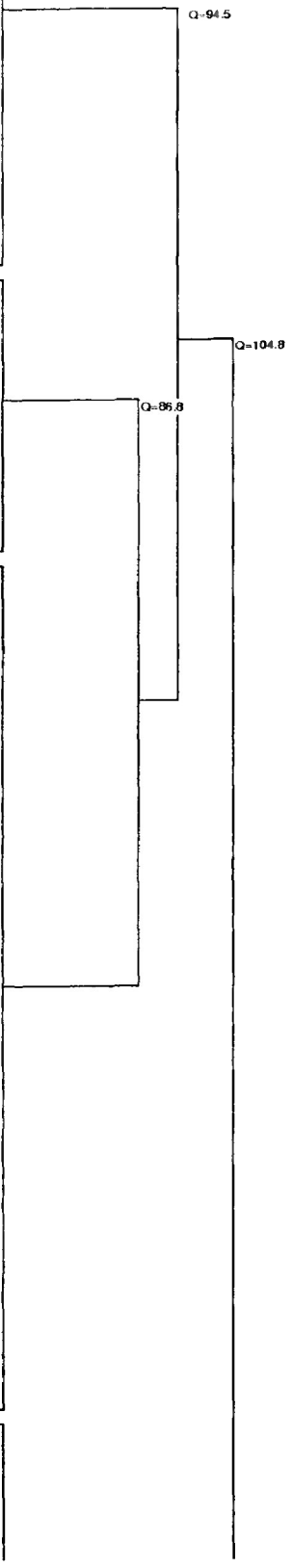
Sample scores:	Axis 1	1.9	1.9	2.0	2.0	2.1	2.1	2.2	2.5	2.7	2.7	2.8	3.3	3.4
	FEC V-type	35	34	20	20	20	35	33	34	20	33	30	30	37
	Treatment	DC	DC	HP	CC	CC	CC	SC	DC	DC	DC	CC	CC	CC
Species scores:	Point	6A5	6A9	2B15	7A5	7A2	7A12	3B10	6A4	6A8	6A6	7A10	5A7	7A11
Axis 1	Herb stratum species													
-1.9	CLIM DEN													
-1.7	CORY COR													
-1.6	PRUN PEN													
-1.4	CIRC ALP													
-1.2	MERT PAN													
-1.2	ASTE MAC													
-1.2	ATHY FEL													
-1.2	ACER SPI													
-1.2	DIER LON													
-1.1	ARAL NUD													
-1.1	VIBE EDU													
-1.0	GAL TRIF													
-0.9	RIBE TRI													
-0.9	THEL PHE													
-0.8	MNIUM SP													
-0.8	ANEM QUI													
-0.8	LONI CAN													
-0.8	MITE NUD													
-0.8	BRACH SP													
-0.7	LYCO OBS													
-0.7	STREP RO		10					10						
-0.7	RUB PUBE													
-0.7	VIOL REN													
-0.7	RHAM ALN													
-0.6	RUB IDAE													
-0.6	GYMN DRY													
-0.6	RIBE LAC													
-0.6	CLIN BOR	10	3											
-0.5	ASTE CIL													
-0.4	CAREX SP		5											
-0.4	MONE UNI													
-0.4	PETA PAL													
-0.3	TRIE BOR													
-0.2	LYCO ANN													
-0.2	MOSS SPP													
-0.1	EQUI PRA													
0.0	ROSA ACI													
0.1	GRASS SP													
0.2	EPIL ANG													
0.2	RHYT TRI													
0.2	SORB DEC													
0.3	LICH SP													
0.5	FRAG VIR													
0.5	MAIA CAN	3	10			25								
0.6	ALNU RUG	3					3							
0.6	HYPN CRI				5		5							
0.8	ABIE BAL						3							
0.8	EQUI ARV													
0.8	CORN STOL													
0.9	LINN BOR						3		5					
0.9	CORN CAN	15	15	10	5	20	3		5	10	3			
1.0	BETU PAP													
1.2	HYLO SPL									10				
1.3	THUJ OCC													
1.3	COPT TRI	3	40											
1.6	POLY JUN													3
1.9	CLADO SP								3		3		3	
2.0	DICR SCO			10		5	3	20	10		3	10	10	
2.5	PLEU SCH	5	10	70	50	30	20	75	50	60	70	20	25	10
2.5	CAREX TR													10
2.6	VACC MYR	5			3				10		10			
2.9	SPHA MAG						60							10
3.1	GAUL HIS	10	5		3	3	20	5	25		3			10
3.6	CLAD RAN			3						5	3	20	3	
3.9	LEDU GRO	20	15			5			15	30	30			20
4.5	VACC ANG		10	5	3	5	10			30		80	70	15
4.5	SPHA CAP	70	50		15		10		25					70
6.1	GEOC LIV	3									20			
6.6	VACC OXY													5

Appendix 12 (cont.).

Sample scores:	Axis 1	1.9	1.9	2.0	2.0	2.1	2.1	2.2	2.5	2.7	2.7	2.8	3.3	3.4
	FEC V-type	35	34	20	20	20	35	33	34	20	33	30	30	37
	Treatment	DC	DC	HP	CC	CC	CC	SC	DC	DC	DC	CC	CC	CC
Species scores:	Point	6A5	6A9	2B15	7A5	7A2	7A12	3B10	6A4	6A8	6A6	7A10	5A7	7A11
Axis 1	Shrub stratum species													
-1.5	SH Co co													
-1.2	SH Pr vi													
-1.0	SH Ac sp													
-1.0	SH Vi ed													
-0.9	SH Fr ni													
-0.9	SH Rh al													
-0.9	SH Lo ca													
-0.8	SH Di lo													
-0.7	SH Salix													
-0.6	SH Po ba													
-0.4	SH Ri hi													
-0.3	SH Co st													
-0.3	SH Ru id		3											
-0.3	SH Pi gl			3										
0.1	SH Al ru	15	10											
0.1	SH Lo in													
0.1	SH Ri la													
0.2	SH Am hum			3										
0.3	SH So de	3	3	3		5								
0.4	SH Ro ac	3	3							3				
0.4	SH Pr pe													
0.5	SH Ab	25	5	20	5	5	10	10		10			3	3
0.8	SH Lo ob													
0.8	SH Be pa	3	5	5	25	3	10	3				3	3	
1.5	SH Al cr	10			3				20	15	10			
1.5	SH Th oc													
1.7	SH Lo vi												3	
2.3	SH Am ba	3	15			5	3				3	5	10	
2.7	SH La la								3					
2.9	SH Pi ma		15	20	5		10	3	5	15	25	10		25
5.0	SH Le gr	40	30		10	60	15		50	40	40	5	30	40
8.9	SH Ka po													3
	Tree stratum species													
-2.4	TR Po tr													
-1.5	TR Fr ni													
-1.4	TR Pr pen													
-1.4	TR Po ba													
-1.0	TR Salix													
-0.9	TR Al ru													
-0.6	TR Pi gl													
-0.2	TR Ab	10	3	3	10	15	3					15	3	
-0.2	TR Be pa	10		10	10		5							
0.1	TR So de													
1.3	TR Th oc													
2.6	TR Pi ma	30	30	40	40	15	30	70	20	40	40	10		50

Appendix 13a. Condensed dendrogram for cluster analysis of cover of all three vegetation strata (trees, shrubs and herbs) on the RC-17 project sample units within clusters ordered by harvest treatment, soil moisture, soil depth and FEC V-type, in that order).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
1	CC	7A1	19	D	vs
1	CC	7A4	19	D	vs
1	CC	7A2	20	D	vs
1	CC	1B5	16	F	d
1	CC	5A5	31	M	ms
1	CC	7A8	16	M	vs
1	CC	7A5	20	M	vs
1	CC	7A10	30	M	vs
1	CC	7A6	31	M	vs
1	CC	7A12	35	M	vs
1	CC	7A11	37	M	vs
1	CC	5A7	30	W	mp
1	DC	6B10	16	D	vs
1	DC	6B11	16	D	vs
1	DC	6A1	19	D	vs
1	DC	6A3	19	D	vs
1	DC	6A2	20	D	vs
1	DC	4A20	19	M	vs
1	DC	6A8	20	W	mp
1	DC	6A6	30	W	mp
1	DC	6A4	34	W	mp
1	DC	6A9	34	W	mp
1	DC	6A5	35	W	mp
1	HP	2B15	20	D	es
1	HP	8A1	20	M	vs
1	SC	3B10	33	D	es
1	SC	3A11	19	D	vs
1	SC	3A18	19	D	vs
1	SC	7B8	16	F	d
1	SC	7B11	16	F	d
1	SC	7B1	20	F	d
1	SC	3A6	19	M	vs
1	SC	3A20	25	M	vs
1	SC	3A4	31	M	vs
2	CC	5B6	21	M	es
2	CC	5B15	21	M	es
2	CC	5B2	21	M	ms
2	CC	5B4	21	M	ms
2	CC	5B7	21	M	ms
2	CC	5B9	21	M	ms
2	CC	5B11	21	M	ms
2	CC	5B12	21	M	ms
2	CC	5B13	21	M	ms
2	CC	5B8	22	M	ms
2	DC	4B1	21	F	ms
2	DC	4B2	21	F	ms
2	HP	2B12	21	D	es
2	HP	2B13	21	D	es
2	HP	2B14	21	D	es
2	HP	2B10	21	M	d
2	HP	2B11	21	M	d
2	SC	3B6	21	D	es
3	CC	1B11	1	M	d
3	CC	5B14	1	M	ms
3	CC	5A12	2	M	ms
3	CC	5A13	2	M	ms
3	CC	7A15	24	M	ms
3	CC	7A9	35	M	vs
3	CC	5A10	2	W	mp
3	CC	1B1	14	W	mp
3	CC	5A1	24	W	mp
3	CC	5A4	35	W	mp
3	CC	5A8	35	W	mp
3	CC	5A9	35	W	mp
3	DC	6B8	16	D	vs
3	DC	4A4	14	F	ms
3	DC	4B4	15	F	ms
3	DC	4B8	4	M	es
3	DC	6A11	4	M	ms
3	DC	6A12	4	M	ms
3	DC	6A13	4	M	ms
3	DC	4A10	24	M	ms
3	DC	4A7	16	M	vs
3	DC	6A14	2	W	mp
3	DC	4A3	14	W	mp
3	DC	6A7	24	W	mp
3	DC	6A10	34	W	mp
3	HP	10B8	14	F	d
3	HP	10B10	15	F	d
3	HP	10B6	16	F	d
3	HP	8A14	8	F	ms
3	HP	10B2	1	M	d
3	HP	10B13	14	M	d
3	HP	10B15	15	M	d
3	HP	10B5	16	M	d
3	HP	10B9	16	M	d
3	HP	10B14	16	M	d
3	HP	10B11	19	M	d
3	HP	10B12	24	M	d
3	HP	8A12	4	M	ms
3	HP	8A9	14	M	ms
3	HP	8A10	14	M	ms
3	HP	8A4	4	M	vs
3	HP	8A2	19	M	vs
3	SC	3B2	4	D	es
3	SC	7B2	1	D	vs
3	SC	7B9	16	D	vs
3	SC	7B12	1	F	d
3	SC	7B6	15	F	d
3	SC	7B14	24	F	ms
3	SC	9B6	24	M	d
3	SC	3A3	15	M	vs
3	SC	3A7		M	vs
3	SC	3A1	2	W	mp
3	SC	3B18	2	W	mp
3	SC	3A2	4	W	mp
3	SC	3B20	14	W	mp
3	SC	3B19	24	W	mp
4	CC	1B6	5	F	d
4	CC	1B2	6	F	d
4	CC	1B3	6	F	d
4	CC	1B4	6	F	d
4	CC	1B7	6	F	d
4	CC	1B14	1	M	d
4	CC	1B13	8	M	d
4	CC	5A11	2	M	ms
4	CC	5A14	6	M	ms



LEGEND

Harvest treatments
- CC clear cut
- DC deferred cut
- HP hardwoods poisoned
- SC softwoods cut

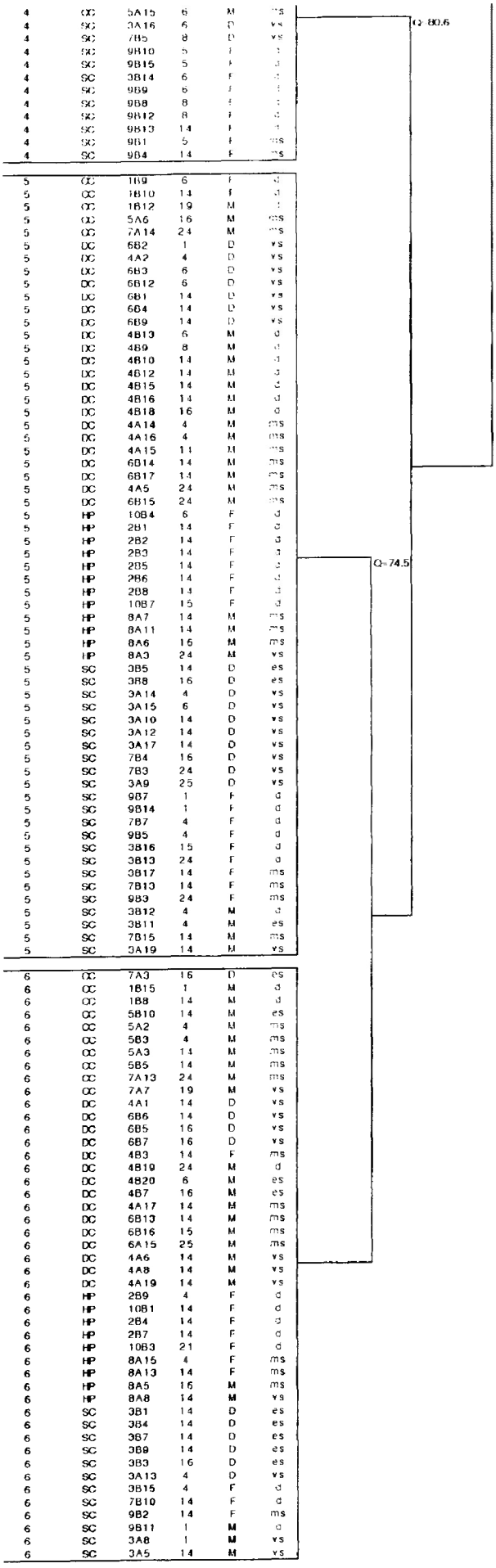
FEC V-types
- 1 Balsam poplar hardwood and mixedwood
- 2 Black ash hardwood and mixedwood
- 4 White birch hardwood and mixedwood
- 5 Aspen hardwood
- 6 Trembling aspen(white birch)-balsam fir/mountain maple
- 7 Trembling aspen-balsam fir/balsam fir shrub
- 8 Trembling aspen(white birch)-mountain maple
- 14 Balsam fir mixedwood
- 15 White spruce mixedwood
- 16 Balsam fir-white spruce mwd/feathermoss
- 19 Black spruce mwd/herb rich
- 20 Black spruce mwd/feathermoss
- 21 Cedar/mountain maple
- 22 Cedar/speckled alder/labrador tea
- 24 White spruce-balsam fir/shrub rich
- 25 White spruce-balsam fir/feathermoss
- 30 Jack pine-black spruce/blueberry/lichen
- 31 Black spruce-jack pine/tall shrub/feathermoss
- 33 Black spruce/feathermoss
- 34 Black spruce/labrador tea/feathermoss(sphagnum)
- 35 Black spruce/speckled alder/sphagnum
- 37 Black spruce/ericaceous shrub/sphagnum

Soil moisture
- D dry
- F fresh
- M moist
- W wet

Soil depth
- es extremely shallow
- vs very shallow
- ms medium shallow
- d deep
- mp mucky peat

Q within cluster dispersion (variance) of newly formed cluster

Appendix 13a (cont.).



4	CC	5A15	6	M	ms
4	SC	3A16	6	D	vs
4	SC	7B5	8	D	vs
4	SC	9B10	5	F	d
4	SC	9B15	5	F	d
4	SC	3B14	6	F	d
4	SC	9B9	6	F	d
4	SC	9B8	8	F	d
4	SC	9B12	8	F	d
4	SC	9B13	14	F	d
4	SC	9B1	5	F	ms
4	SC	9B4	14	F	ms
5	CC	1B9	6	F	d
5	CC	1B10	14	F	d
5	CC	1B12	19	M	d
5	CC	5A6	16	M	ms
5	CC	7A14	24	M	ms
5	DC	6B2	1	D	vs
5	DC	4A2	4	D	vs
5	DC	6B3	6	D	vs
5	DC	6B12	6	D	vs
5	DC	6B1	14	D	vs
5	DC	6B4	14	D	vs
5	DC	6B9	14	D	vs
5	DC	4B13	6	M	d
5	DC	4B9	8	M	d
5	DC	4B10	14	M	d
5	DC	4B12	14	M	d
5	DC	4B15	14	M	d
5	DC	4B16	14	M	d
5	DC	4B18	16	M	d
5	DC	4A14	4	M	ms
5	DC	4A16	4	M	ms
5	DC	4A15	14	M	ms
5	DC	6B14	14	M	ms
5	DC	6B17	14	M	ms
5	DC	4A5	24	M	ms
5	DC	6B15	24	M	ms
5	HP	10B4	6	F	d
5	HP	2B1	14	F	d
5	HP	2B2	14	F	d
5	HP	2B3	14	F	d
5	HP	2B5	14	F	d
5	HP	2B6	14	F	d
5	HP	2B8	14	F	d
5	HP	10B7	15	F	d
5	HP	8A7	14	M	ms
5	HP	8A11	14	M	ms
5	HP	8A6	16	M	ms
5	HP	8A3	24	M	vs
5	SC	3B5	14	D	es
5	SC	3B8	16	D	es
5	SC	3A14	4	D	vs
5	SC	3A15	6	D	vs
5	SC	3A10	14	D	vs
5	SC	3A12	14	D	vs
5	SC	3A17	14	D	vs
5	SC	7B4	16	D	vs
5	SC	7B3	24	D	vs
5	SC	3A9	25	D	vs
5	SC	9B7	1	F	d
5	SC	9B14	1	F	d
5	SC	7B7	4	F	d
5	SC	9B5	4	F	d
5	SC	3B16	15	F	d
5	SC	3B13	24	F	d
5	SC	3B17	14	F	ms
5	SC	7B13	14	F	ms
5	SC	9B3	24	F	ms
5	SC	3B12	4	M	d
5	SC	3B11	4	M	es
5	SC	7B15	14	M	ms
5	SC	3A19	14	M	vs
6	CC	7A3	16	D	es
6	CC	1B15	1	M	d
6	CC	1B8	14	M	d
6	CC	5B10	14	M	es
6	CC	5A2	4	M	ms
6	CC	5B3	4	M	ms
6	CC	5A3	14	M	ms
6	CC	5B5	14	M	ms
6	CC	7A13	24	M	ms
6	CC	7A7	19	M	vs
6	DC	4A1	14	D	vs
6	DC	6B6	14	D	vs
6	DC	6B5	16	D	vs
6	DC	6B7	16	D	vs
6	DC	4B3	14	F	ms
6	DC	4B19	24	M	d
6	DC	4B20	6	M	es
6	DC	4B7	16	M	es
6	DC	4A17	14	M	ms
6	DC	6B13	14	M	ms
6	DC	6B16	15	M	ms
6	DC	6A15	25	M	ms
6	DC	4A6	14	M	vs
6	DC	4A8	14	M	vs
6	DC	4A19	14	M	vs
6	HP	2B9	4	F	d
6	HP	10B1	14	F	d
6	HP	2B4	14	F	d
6	HP	2B7	14	F	d
6	HP	10B3	21	F	d
6	HP	8A15	4	F	ms
6	HP	8A13	14	F	ms
6	HP	8A5	16	M	ms
6	HP	8A8	14	M	vs
6	SC	3B1	14	D	es
6	SC	3B4	14	D	es
6	SC	3B7	14	D	es
6	SC	3B9	14	D	es
6	SC	3B3	16	D	es
6	SC	3A13	4	D	vs
6	SC	3B15	4	F	d
6	SC	7B10	14	F	d
6	SC	9B2	14	F	ms
6	SC	9B11	1	M	d
6	SC	3A8	1	M	vs
6	SC	3A5	14	M	vs

Appendix 13b. Condensed dendrogram for cluster analysis of tree cover measured for sample units on the RC-17 project (sample units within clusters ordered by harvest treatment, soil moisture, soil depth and FEC V-type, in that order).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
1	CC	1B6	5	F	d
1	CC	1B2	6	F	d
1	CC	1B3	6	F	d
1	CC	1B4	6	F	d
1	CC	1B7	6	F	d
1	CC	1B5	16	F	d
1	CC	1B14	1	M	d
1	CC	1B13	8	M	d
1	CC	5A11	2	M	ms
1	CC	5A14	6	M	ms
1	CC	5A15	6	M	ms
1	DC	4B13	6	M	d
1	SC	3A16	6	D	vs
1	SC	9B10	5	F	d
1	SC	9B15	5	F	d
1	SC	3B14	6	F	d
1	SC	9B9	6	F	d
1	SC	9B12	8	F	d
1	SC	9B13	14	F	d
1	SC	9B1	5	F	ms
1	SC	9B4	14	F	ms
2	CC	7A1	19	D	vs
2	CC	7A4	19	D	vs
2	CC	1B12	19	M	d
2	CC	5A5	31	M	ms
2	CC	7A7	19	M	vs
2	CC	7A5	20	M	vs
2	CC	7A6	31	M	vs
2	CC	7A9	35	M	vs
2	CC	7A12	35	M	vs
2	CC	7A11	37	M	vs
2	CC	5A8	35	W	mp
2	DC	6A1	19	D	vs
2	DC	6A3	19	D	vs
2	DC	6A2	20	D	vs
2	DC	4A7	16	M	vs
2	DC	4A20	19	M	vs
2	DC	6A8	20	W	mp
2	DC	6A6	33	W	mp
2	DC	6A4	34	W	mp
2	DC	6A9	34	W	mp
2	DC	6A5	35	W	mp
2	HP	2B15	20	D	es
2	HP	10B10	15	F	d
2	HP	10B13	14	M	d
2	HP	10B14	16	M	d
2	HP	10B11	19	M	d
2	HP	8A2	19	M	vs
2	HP	8A1	20	M	vs
2	SC	3B10	33	D	es
2	SC	3A11	19	D	vs
2	SC	3A18	19	D	vs
2	SC	7B8	16	F	d
2	SC	7B1	20	F	d
2	SC	3A6	19	M	vs
2	SC	3A4	31	M	vs
3	CC	5B6	21	M	es
3	CC	5B15	21	M	es
3	CC	5B2	21	M	ms
3	CC	5B4	21	M	ms
3	CC	5B7	21	M	ms
3	CC	5B9	21	M	ms
3	CC	5B11	21	M	ms
3	CC	5B12	21	M	ms
3	CC	5B13	21	M	ms
3	CC	5B8	22	M	ms
3	DC	4B1	21	F	ms
3	DC	4B2	21	F	ms
3	HP	2B12	21	D	es
3	HP	2B13	21	D	es
3	HP	2B14	21	D	es
3	HP	10B3	21	F	d
3	HP	2B10	21	M	d
3	HP	2B11	21	M	d
3	SC	3B6	21	D	es
3	SC	3B17	14	F	ms
3	SC	3B12	4	M	d
4	CC	7A3	16	D	es
4	CC	7A2	20	D	vs
4	CC	1B9	6	F	d
4	CC	1B11	1	M	d
4	CC	1B15	1	M	d
4	CC	5B14	1	M	ms
4	CC	5A12	2	M	ms
4	CC	5A13	2	M	ms
4	CC	5A2	4	M	ms
4	CC	5A6	16	M	ms
4	CC	7A13	24	M	ms
4	CC	7A15	24	M	ms
4	CC	7A10	30	M	vs
4	CC	5A10	2	W	mp
4	CC	1B1	14	W	mp
4	CC	5A1	24	W	mp
4	CC	5A7	30	W	mp
4	CC	5A4	35	W	mp
4	CC	5A9	35	W	mp
4	DC	6B2	1	D	vs
4	DC	4A2	4	D	vs
4	DC	6B12	6	D	vs
4	DC	4B4	15	F	ms
4	DC	4B19	24	M	d
4	DC	4B8	4	M	es
4	DC	4A14	4	M	ms
4	DC	4A16	4	M	ms
4	DC	6A11	4	M	ms
4	DC	6A12	4	M	ms
4	DC	6A13	4	M	ms
4	DC	6B13	14	M	ms
4	DC	4A8	14	M	vs
4	DC	5A14	2	W	mp
4	DC	4A3	14	W	mp
4	DC	6A7	24	W	mp
4	DC	6A10	34	W	mp
4	HP	10B1	14	F	d
4	HP	2B4	14	F	d
4	HP	2B7	14	F	d
4	HP	8A14	8	F	ms

LEGEND

Harvest treatments	CC	clear cut
	DC	deferred cut
	HP	hardwoods poisoned
	SC	softwoods cut
FEC V-types	1	Balsam poplar hardwood and mixedwood
	2	Black ash hardwood and mixedwood
	4	White birch hardwood and mixedwood
	5	Aspen hardwood
	6	Trembling aspen(white birch)–balsam fir/mountain maple
	7	Trembling aspen–balsam fir/balsam fir shrub
	8	Trembling aspen(white birch)–mountain maple
	14	Balsam fir mixedwood
	15	White spruce mixedwood
	16	Balsam fir–white spruce mwd/feathermoss
	19	Black spruce mwd/herb rich
	20	Black spruce mwd/feathermoss
	21	Cedar/mountain maple
	22	Cedar/speckled alder/labrador tea
	24	White spruce–balsam fir/shrub rich
	25	White spruce–balsam fir/feathermoss
	30	Jack pine–black spruce/blueberry/lichen
	31	Black spruce–jack pine/tall shrub/feathermoss
	33	Black spruce/feathermoss
	34	Black spruce/labrador tea/feathermoss(sphagnum)
	35	Black spruce/speckled alder/sphagnum
	37	Black spruce/ericaceous shrub/sphagnum
Soil moisture	D	dry
	F	fresh
	M	moist
	W	wet
Soil depth	es	extremely shallow
	vs	very shallow
	ms	medium shallow
	d	deep
	mp	mucky peat
	Q	within cluster dispersion (variance) of newly formed cluster

Appendix 13b (cont.).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
4	HP	10B2	1	M	d
4	HP	8A12	4	M	ms
4	HP	8A9	14	M	ms
4	HP	8A10	14	M	ms
4	HP	8A4	4	M	vs
4	SC	3B1	14	D	es
4	SC	3B5	14	D	es
4	SC	3B9	14	D	es
4	SC	7B2	1	D	vs
4	SC	3A13	4	D	vs
4	SC	3A14	4	D	vs
4	SC	7B12	1	F	d
4	SC	9B7	1	F	d
4	SC	9B14	1	F	d
4	SC	7B7	4	F	d
4	SC	9B5	4	F	d
4	SC	7B11	16	F	d
4	SC	9B11	1	M	d
4	SC	3B11	4	M	es
4	SC	3A8	1	M	vs
4	SC	3A5	14	M	vs
4	SC	3A19	14	M	vs
4	SC	3A7		M	vs
4	SC	3A1	2	W	mp
4	SC	3B18	2	W	mp
4	SC	3A2	4	W	mp
4	SC	3B20	14	W	mp
4	SC	3B19	24	W	mp
5	CC	5B3	4	M	ms
5	DC	6B4	14	D	vs
5	DC	6B8	16	D	vs
5	DC	6B10	16	D	vs
5	DC	6B11	16	D	vs
5	DC	4B9	8	M	d
5	DC	4B10	14	M	d
5	DC	6B17	14	M	ms
5	DC	6B16	15	M	ms
5	DC	4A5	24	M	ms
5	DC	4A10	24	M	ms
5	DC	6B15	24	M	ms
5	DC	6A15	25	M	ms
5	HP	10B4	6	F	d
5	HP	2B2	14	F	d
5	HP	2B5	14	F	d
5	HP	10B7	15	F	d
5	HP	10B6	16	F	d
5	HP	10B15	15	M	d
5	HP	10B5	16	M	d
5	HP	10B9	16	M	d
5	HP	10B12	24	M	d
5	HP	8A7	14	M	ms
5	HP	8A3	24	M	vs
5	SC	3B2	4	D	es
5	SC	7B5	8	D	vs
5	SC	3A17	14	D	vs
5	SC	7B9	16	D	vs
5	SC	7B3	24	D	vs
5	SC	3A9	25	D	vs
5	SC	9B8	8	F	d
5	SC	7B10	14	F	d
5	SC	3B16	15	F	d
5	SC	7B6	15	F	d
5	SC	7B13	14	F	ms
5	SC	7B14	24	F	ms
5	SC	9B3	24	F	ms
5	SC	9B6	24	M	d
5	SC	3A3	15	M	vs
6	CC	1B10	14	F	d
6	CC	1B8	14	M	d
6	CC	5B10	14	M	es
6	CC	5A3	14	M	ms
6	CC	5B5	14	M	ms
6	CC	7A14	24	M	ms
6	CC	7A8	16	M	vs
6	DC	6B3	6	D	vs
6	DC	4A1	14	D	vs
6	DC	6B1	14	D	vs
6	DC	6B6	14	D	vs
6	DC	6B9	14	D	vs
6	DC	6B5	16	D	vs
6	DC	6B7	16	D	vs
6	DC	4A4	14	F	ms
6	DC	4B3	14	F	ms
6	DC	4B12	14	M	d
6	DC	4B15	14	M	d
6	DC	4B16	14	M	d
6	DC	4B18	16	M	d
6	DC	4B20	6	M	es
6	DC	4B7	16	M	es
6	DC	4A15	14	M	ms
6	DC	4A17	14	M	ms
6	DC	6B14	14	M	ms
6	DC	4A6	14	M	vs
6	DC	4A19	14	M	vs
6	HP	2B9	4	F	d
6	HP	10B8	14	F	d
6	HP	2B1	14	F	d
6	HP	2B3	14	F	d
6	HP	2B6	14	F	d
6	HP	2B8	14	F	d
6	HP	8A15	4	F	ms
6	HP	8A13	14	F	ms
6	HP	8A11	14	M	ms
6	HP	8A5	16	M	ms
6	HP	8A6	16	M	ms
6	HP	8A8	14	M	vs
6	SC	3B4	14	D	es
6	SC	3B7	14	D	es
6	SC	3B3	16	D	es
6	SC	3B8	16	D	es
6	SC	3A15	6	D	vs
6	SC	3A10	14	D	vs
6	SC	3A12	14	D	vs
6	SC	7B4	16	D	vs
6	SC	3B15	4	F	d
6	SC	3B13	24	F	d
6	SC	9B2	14	F	ms
6	SC	7B15	14	M	ms
6	SC	3A20	25	M	vs

Appendix 13c. Condensed dendrogram for cluster analysis of shrub cover measured for sample units on the RC-17 project (sample units within clusters ordered by harvest treatment, soil moisture, soil depth and FEC V-type, in that order).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
1	CC	1B6	5	F	d
1	CC	1B9	5	F	d
1	CC	1B10	14	F	d
1	CC	1B14	1	M	d
1	CC	1B15	1	M	d
1	CC	1B13	8	M	d
1	CC	1B12	19	M	d
1	CC	5A11	2	M	ms
1	CC	5A13	2	M	ms
1	CC	5A15	6	M	ms
1	CC	5A6	16	M	ms
1	CC	7A14	24	M	ms
1	DC	6B2	1	D	vs
1	DC	4A2	4	D	vs
1	DC	6B3	6	D	vs
1	DC	6B12	6	D	vs
1	DC	6B1	14	D	vs
1	DC	6B9	14	D	vs
1	DC	6B8	16	D	vs
1	DC	4B4	15	F	ms
1	DC	4B13	6	M	d
1	DC	4B9	8	M	d
1	DC	4B12	14	M	d
1	DC	4B15	14	M	d
1	DC	4B18	16	M	d
1	DC	4A14	4	M	ms
1	DC	4A16	4	M	ms
1	DC	4A15	14	M	ms
1	DC	6B14	14	M	ms
1	DC	6B17	14	M	ms
1	DC	4A5	24	M	ms
1	DC	4A10	24	M	ms
1	DC	6B15	24	M	ms
1	DC	4A6	14	M	vs
1	DC	4A7	16	M	vs
1	DC	4A3	14	W	mp
1	HP	10B4	6	F	d
1	HP	2B6	14	F	d
1	HP	2B8	14	F	d
1	HP	10B7	15	F	d
1	HP	10B6	16	F	d
1	HP	10B9	16	M	d
1	HP	8A7	14	M	ms
1	HP	8A11	14	M	ms
1	HP	8A6	16	M	ms
1	HP	8A4	4	M	vs
1	HP	8A3	24	M	vs
1	SC	3B5	14	D	es
1	SC	3B8	16	D	es
1	SC	3A15	6	D	vs
1	SC	3A17	14	D	vs
1	SC	7B4	16	D	vs
1	SC	7B3	24	D	vs
1	SC	3A9	25	D	vs
1	SC	9B7	1	F	d
1	SC	9B14	1	F	d
1	SC	7B7	4	F	d
1	SC	9B5	4	F	d
1	SC	9B10	5	F	d
1	SC	3B14	6	F	d
1	SC	9B9	6	F	d
1	SC	9B13	14	F	d
1	SC	7B11	16	F	d
1	SC	9B1	5	F	ms
1	SC	3B17	14	F	ms
1	SC	7B13	14	F	ms
1	SC	9B3	24	F	ms
1	SC	3B11	4	M	es
1	SC	7B15	14	M	ms
1	SC	3A19	14	M	vs
1	SC	3A20	25	M	vs
1	SC	3A7		M	vs
2	CC	5A14	6	M	ms
2	DC	4B16	14	M	d
2	DC	6B13	14	M	ms
2	DC	6B16	15	M	ms
2	DC	6A15	25	M	ms
2	HP	2B4	14	F	d
2	HP	8A15	4	F	ms
2	SC	3A16	6	D	vs
2	SC	7B5	8	D	vs
2	SC	3B15	4	F	d
2	SC	9B15	5	F	d
2	SC	9B12	8	F	d
2	SC	3B16	15	F	d
2	SC	3B13	24	F	d
2	SC	9B2	14	F	ms
2	SC	9B4	14	F	ms
3	CC	1B7	6	F	d
3	CC	1B11	1	M	d
3	CC	5B14	1	M	ms
3	CC	5A12	2	M	ms
3	CC	5B2	21	M	ms
3	CC	5B4	21	M	ms
3	CC	5B12	21	M	ms
3	CC	7A15	24	M	ms
3	CC	7A9	35	M	vs
3	CC	7A12	35	M	vs
3	CC	5A10	2	W	mp
3	CC	1B1	14	W	mp
3	CC	5A1	24	W	mp
3	CC	5A4	35	W	mp
3	CC	5A8	35	W	mp
3	CC	5A9	35	W	mp
3	DC	6B7	16	D	vs
3	DC	6A1	19	D	vs
3	DC	4A4	14	F	ms
3	DC	4B1	21	F	ms
3	DC	4B8	4	M	es
3	DC	4B7	16	M	es
3	DC	6A11	4	M	ms
3	DC	6A12	4	M	ms
3	DC	6A13	4	M	ms
3	DC	6A14	2	W	mp
3	DC	6A7	24	W	mp
3	DC	6A10	34	W	mp
3	HP	10B8	14	F	d
3	HP	10B10	15	F	d

Q=209904

Q=340410

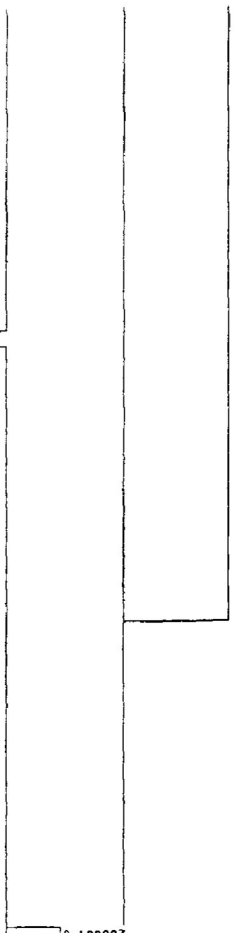
Q=254358

LEGEND

Harvest treatments	CC	clear cut
	DC	deferred cut
	HP	hardwoods poisoned
	SC	softwoods cut
FEC V-types	1	Balsam poplar hardwood and mixedwood
	2	Black ash hardwood and mixedwood
	4	White birch hardwood and mixedwood
	5	Aspen hardwood
	6	Trembling aspen(white birch)–balsam fir/mountain maple
	7	Trembling aspen–balsam fir/balsam fir shrub
	8	Trembling aspen(white birch)–mountain maple
	14	Balsam fir mixedwood
	15	White spruce mixedwood
	16	Balsam fir–white spruce mwd/feathermoss
	19	Black spruce mwd/herb rich
	20	Black spruce mwd/feathermoss
	21	Cedar/mountain maple
	22	Cedar/speckled alder/labrador tea
	24	White spruce–balsam fir/shrub rich
	25	White spruce–balsam fir/feathermoss
	30	Jack pine–black spruce/blueberry/lichen
	31	Black spruce–jack pine/tall shrub/feathermoss
	33	Black spruce/feathermoss
	34	Black spruce/labrador tea/feathermoss(sphagnum)
	35	Black spruce/speckled alder/sphagnum
	37	Black spruce/ericaceous shrub/sphagnum
Soil moisture	D	dry
	F	fresh
	M	moist
	W	wet
Soil depth	es	extremely shallow
	vs	very shallow
	ms	medium shallow
	d	deep
	mp	mucky peat
	Q	within cluster dispersion (variance) of newly formed cluster

Appendix 13c (cont.).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
3	HP	8A14	8	F	ms
3	HP	10B2	1	M	d
3	HP	10B13	14	M	d
3	HP	10B5	16	M	d
3	HP	10B14	16	M	d
3	HP	10B11	19	M	d
3	HP	10B12	24	M	d
3	HP	8A12	4	M	ms
3	HP	8A9	14	M	ms
3	HP	8A10	14	M	ms
3	HP	8A8	14	M	vs
3	HP	8A2	19	M	vs
3	SC	7B2	1	D	vs
3	SC	7B12	1	F	d
3	SC	7B14	24	F	ms
3	SC	9B11	1	M	d
3	SC	3A1	2	W	mp
3	SC	3B18	2	W	mp
3	SC	3A2	4	W	mp
3	SC	3B20	14	W	mp
3	SC	3B19	24	W	mp
4	CC	7A3	16	D	es
4	CC	7A1	19	D	vs
4	CC	7A4	19	D	vs
4	CC	1B2	6	F	d
4	CC	1B3	6	F	d
4	CC	1B4	6	F	d
4	CC	1B5	16	F	d
4	CC	1B8	14	M	d
4	CC	5B10	14	M	es
4	CC	5A2	4	M	ms
4	CC	5B3	4	M	ms
4	CC	5A3	14	M	ms
4	CC	5B5	14	M	ms
4	CC	7A13	24	M	ms
4	CC	5A5	31	M	ms
4	CC	7A8	16	M	vs
4	CC	7A7	19	M	vs
4	CC	7A5	20	M	vs
4	CC	7A10	30	M	vs
4	CC	7A6	31	M	vs
4	DC	4A1	14	D	vs
4	DC	6B4	14	D	vs
4	DC	6B6	14	D	vs
4	DC	6B5	16	D	vs
4	DC	6B10	16	D	vs
4	DC	6B11	16	D	vs
4	DC	6A3	19	D	vs
4	DC	6A2	20	D	vs
4	DC	4B3	14	F	ms
4	DC	4B10	14	M	d
4	DC	4B19	24	M	d
4	DC	4B20	6	M	es
4	DC	4A17	14	M	ms
4	DC	4A8	14	M	vs
4	DC	4A19	14	M	vs
4	DC	4A20	19	M	vs
4	HP	2B15	20	D	es
4	HP	2B9	4	F	d
4	HP	10B1	14	F	d
4	HP	2B1	14	F	d
4	HP	2B2	14	F	d
4	HP	2B3	14	F	d
4	HP	2B5	14	F	d
4	HP	2B7	14	F	d
4	HP	10B3	21	F	d
4	HP	8A13	14	F	ms
4	HP	10B15	15	M	d
4	HP	8A5	16	M	ms
4	HP	8A1	20	M	vs
4	SC	3B2	4	D	es
4	SC	3B1	14	D	es
4	SC	3B4	14	D	es
4	SC	3B7	14	D	es
4	SC	3B9	14	D	es
4	SC	3B3	16	D	es
4	SC	3B10	33	D	es
4	SC	3A13	4	D	vs
4	SC	3A14	4	D	vs
4	SC	3A10	14	D	vs
4	SC	3A12	14	D	vs
4	SC	7B9	16	D	vs
4	SC	3A11	19	D	vs
4	SC	3A18	19	D	vs
4	SC	9B8	8	F	d
4	SC	7B10	14	F	d
4	SC	7B6	15	F	d
4	SC	7B8	16	F	d
4	SC	7B1	20	F	d
4	SC	3B12	4	M	d
4	SC	9B6	24	M	d
4	SC	3A8	1	M	vs
4	SC	3A5	14	M	vs
4	SC	3A3	15	M	vs
4	SC	3A6	19	M	vs
4	SC	3A4	31	M	vs
5	CC	7A2	20	D	vs
5	CC	5B6	21	M	es
5	CC	5B15	21	M	es
5	CC	5B7	21	M	ms
5	CC	5B9	21	M	ms
5	CC	5B11	21	M	ms
5	CC	5B13	21	M	ms
5	CC	5B8	22	M	ms
5	CC	7A11	37	M	vs
5	CC	5A7	30	W	mp
5	DC	4B2	21	F	ms
5	DC	6A8	20	W	mp
5	DC	6A6	33	W	mp
5	DC	6A4	34	W	mp
5	DC	6A9	34	W	mp
5	DC	6A5	35	W	mp
5	HP	2B12	21	D	es
5	HP	2B13	21	D	es
5	HP	2B14	21	D	es
5	HP	2B10	21	M	d
5	HP	2B11	21	M	d
5	SC	3B6	21	D	es



Appendix 13d. Condensed dendrogram for cluster analysis of herb cover measured for sample units on the RC-17 project (sample units within clusters ordered by harvest treatment, soil moisture, soil depth and FEC V-type, in that order).

Cluster	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
1	CC	7A1	19	D	vs
1	CC	1B3	6	F	d
1	CC	1B9	6	F	d
1	CC	1B14	1	M	d
1	CC	1B12	19	M	d
1	CC	5B6	21	M	es
1	CC	5B15	21	M	es
1	CC	5A14	6	M	ms
1	CC	5A15	6	M	ms
1	CC	5B5	14	M	ms
1	CC	5B11	21	M	ms
1	CC	5B13	21	M	ms
1	CC	7A14	24	M	ms
1	CC	7A12	35	M	vs
1	CC	5A9	35	W	mp
1	DC	6B2	1	D	vs
1	DC	6B3	6	D	vs
1	DC	4B3	14	F	ms
1	DC	4B4	15	F	ms
1	DC	4B1	21	F	ms
1	DC	4B13	6	M	d
1	DC	4B9	8	M	d
1	DC	4B10	14	M	d
1	DC	4B12	14	M	d
1	DC	4B15	14	M	d
1	DC	4B16	14	M	d
1	DC	4A16	4	M	ms
1	DC	6A11	4	M	ms
1	DC	6A12	4	M	ms
1	DC	4A15	14	M	ms
1	DC	4A8	14	M	vs
1	HP	2B13	21	D	es
1	HP	10B4	6	F	d
1	HP	2B2	14	F	d
1	HP	2B5	14	F	d
1	HP	10B10	15	F	d
1	HP	2B10	21	M	d
1	HP	8A8	14	M	vs
1	HP	8A3	24	M	vs
1	SC	3B2	4	D	es
1	SC	3B1	14	D	es
1	SC	3B4	14	D	es
1	SC	3B5	14	D	es
1	SC	3B7	14	D	es
1	SC	3B8	16	D	es
1	SC	7B2	1	D	vs
1	SC	3A10	14	D	vs
1	SC	3A17	14	D	vs
1	SC	7B4	16	D	vs
1	SC	7B3	24	D	vs
1	SC	3B15	4	F	d
1	SC	7B7	4	F	d
1	SC	9B10	5	F	d
1	SC	9B9	6	F	d
1	SC	3B16	15	F	d
1	SC	7B6	15	F	d
1	SC	3B13	24	F	d
1	SC	3B17	14	F	ms
1	SC	9B4	14	F	ms
1	SC	3B12	4	M	d
1	SC	3B11	4	M	es
1	SC	3A5	14	M	vs
1	SC	3A19	14	M	vs
1	SC	3A3	15	M	vs
1	SC	3A6	19	M	vs
1	SC	3A2	4	W	mp
2	CC	7A3	16	D	es
2	CC	5B4	21	M	ms
2	CC	5B7	21	M	ms
2	CC	5B9	21	M	ms
2	CC	5B12	21	M	ms
2	CC	5B8	22	M	ms
2	CC	5A4	35	W	mp
2	DC	6B6	14	D	vs
2	DC	6B5	16	D	vs
2	DC	6B7	16	D	vs
2	DC	6A3	19	D	vs
2	DC	4B2	21	F	ms
2	DC	4B18	16	M	d
2	DC	4B7	16	M	es
2	DC	4A7	16	M	vs
2	DC	4A20	19	M	vs
2	HP	2B12	21	D	es
2	HP	2B14	21	D	es
2	HP	10B6	16	F	d
2	HP	10B5	16	M	d
2	HP	10B9	16	M	d
2	HP	10B14	16	M	d
2	HP	10B11	19	M	d
2	HP	2B11	21	M	d
2	SC	3B3	16	D	es
2	SC	3B6	21	D	es
2	SC	3A15	6	D	vs
2	SC	7B9	16	D	vs
2	SC	3A11	19	D	vs
2	SC	3A7		M	vs
3	CC	1B7	6	F	d
3	CC	1B11	1	M	d
3	CC	1B13	8	M	d
3	CC	5A11	2	M	ms
3	CC	5A12	2	M	ms
3	CC	5A13	2	M	ms
3	CC	5B2	21	M	ms
3	CC	7A15	24	M	ms
3	CC	5A10	2	W	mp
3	CC	5A8	35	W	mp
3	DC	4A2	4	D	vs
3	DC	6B1	14	D	vs
3	DC	6B8	16	D	vs
3	DC	4B8	4	M	es
3	DC	6B17	14	M	ms
3	DC	4A5	24	M	ms
3	DC	4A10	24	M	ms
3	DC	6B15	24	M	ms
3	DC	6A14	2	W	mp
3	DC	4A3	14	W	mp
3	DC	6A7	24	W	mp

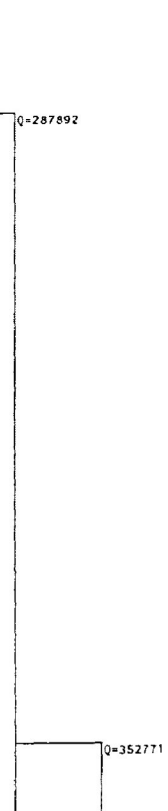
Q=226151

Q=258177

Q=310483

LEGEND

Harvest treatments	CC	clear cut
	DC	deferred cut
	HP	hardwoods poisoned
	SC	softwoods cut
FEC V-types	1	Balsam poplar hardwood and mixedwood
	2	Black ash hardwood and mixedwood
	4	White birch hardwood and mixedwood
	5	Aspen hardwood
	6	Trembling aspen(white birch)–balsam fir/mountain maple
	7	Trembling aspen–balsam fir/balsam fir shrub
	8	Trembling aspen(white birch)–mountain maple
	14	Balsam fir mixedwood
	15	White spruce mixedwood
	16	Balsam fir–white spruce mwd/feathermoss
	19	Black spruce mwd/herb rich
	20	Black spruce mwd/feathermoss
	21	Cedar/mountain maple
	22	Cedar/speckled alder/labrador tea
	24	White spruce–balsam fir/shrub rich
	25	White spruce–balsam fir/feathermoss
	30	Jack pine–black spruce/blueberry/lichen
	31	Black spruce–jack pine/tall shrub/feathermoss
	33	Black spruce/feathermoss
	34	Black spruce/labrador tea/feathermoss(sphagnum)
	35	Black spruce/speckled alder/sphagnum
	37	Black spruce/ericaceous shrub/sphagnum
Soil moisture	D	dry
	F	fresh
	M	moist
	W	wet
Soil depth	es	extremely shallow
	vs	very shallow
	ms	medium shallow
	d	deep
	mp	mucky peat
	Q	within cluster dispersion (variance) of newly formed cluster

Appendix 13d (cont.).

CLUSTER	Harvest treatment	Sample unit	FEC V-type	Soil moisture	Soil depth
3	DC	6A10	34	W	mp
3	HF	2B7	14	F	d
3	HP	2B8	14	F	d
3	HF	10B13	14	M	d
3	HF	10B15	15	M	d
3	HP	8A7	14	M	ms
3	HF	8A10	14	M	ms
3	HP	8A6	16	M	ms
3	HF	8A2	19	M	vs
3	SC	3A16	6	D	vs
3	SC	7B12	1	F	d
3	SC	9B7	1	F	d
3	SC	9B14	1	F	d
3	SC	9B8	3	F	d
3	SC	9B13	14	F	d
3	SC	7B14	24	F	ms
3	SC	9B6	24	M	d
3	SC	3A1	2	W	mp
3	SC	3B18	2	W	mp
3	SC	3B20	14	W	mp
3	SC	3B19	24	W	mp
4	CC	7A2	20	D	vs
4	CC	1B2	6	F	d
4	CC	1B4	6	F	d
4	CC	1B10	14	F	d
4	CC	5A2	4	M	ms
4	CC	5A3	14	M	ms
4	CC	5A6	16	M	ms
4	CC	7A13	24	M	ms
4	CC	5A5	31	M	ms
4	CC	7A7	19	M	vs
4	CC	7A6	31	M	vs
4	CC	7A9	35	M	vs
4	CC	7A11	37	M	vs
4	CC	1B1	14	W	mp
4	CC	5A1	24	W	mp
4	DC	6B12	6	D	vs
4	DC	4A1	14	D	vs
4	DC	6A1	19	D	vs
4	DC	6A2	20	D	vs
4	DC	4A4	14	F	ms
4	DC	4B19	24	M	d
4	DC	6A13	4	M	ms
4	DC	4A17	14	M	ms
4	DC	6B14	14	M	ms
4	DC	6A15	25	M	ms
4	DC	4A6	14	M	vs
4	DC	4A19	14	M	vs
4	DC	6A9	34	W	mp
4	DC	6A5	35	W	mp
4	HF	2B9	4	F	d
4	HP	10B8	14	F	d
4	HP	2B6	14	F	d
4	HP	8A12	4	M	ms
4	HP	8A9	14	M	ms
4	HF	8A11	14	M	ms
4	HP	8A5	16	M	ms
4	HP	8A4	4	M	vs
4	SC	3A13	4	D	vs
4	SC	3A14	4	D	vs
4	SC	7B5	8	D	vs
4	SC	3A12	14	D	vs
4	SC	3A9	25	D	vs
4	SC	9B15	5	F	d
4	SC	3B14	6	F	d
4	SC	9B12	8	F	d
4	SC	7B10	14	F	d
4	SC	9B1	5	F	ms
4	SC	7B13	14	F	ms
4	SC	9B3	24	F	ms
4	SC	9B11	1	M	d
4	SC	7B15	14	M	ms
4	SC	3A4	31	M	vs
5	CC	1B6	5	F	d
5	CC	1B15	1	M	d
5	CC	1B8	14	M	d
5	CC	5B10	14	M	es
5	CC	5B14	1	M	ms
5	CC	5B3	4	M	ms
5	DC	6B4	14	D	vs
5	DC	6B9	14	D	vs
5	DC	4B20	6	M	es
5	DC	4A14	4	M	ms
5	DC	6B13	14	M	ms
5	DC	6B16	15	M	ms
5	HP	10B1	14	F	d
5	HP	2B1	14	F	d
5	HP	2B3	14	F	d
5	HP	2B4	14	F	d
5	HP	10B7	15	F	d
5	HP	10B3	21	F	d
5	HP	8A15	4	F	ms
5	HP	8A14	8	F	ms
5	HP	8A13	14	F	ms
5	HP	10B2	1	M	d
5	HP	10B12	24	M	d
5	SC	3B9	14	D	es
5	SC	9B5	4	F	d
5	SC	9B2	14	F	ms
5	SC	3A8	1	M	vs
6	CC	7A4	19	D	vs
6	CC	1B5	16	F	d
6	CC	7A8	16	M	vs
6	CC	7A5	20	M	vs
6	CC	7A10	30	M	vs
6	CC	5A7	30	W	mp
6	DC	6B10	16	D	vs
6	DC	6B11	16	D	vs
6	DC	6A8	20	W	mp
6	DC	6A6	33	W	mp
6	DC	6A4	34	W	mp
6	HP	2B15	20	D	es
6	HF	8A1	20	M	vs
6	SC	3B10	33	D	es
6	SC	3A18	19	D	vs
6	SC	7B8	16	F	d
6	SC	7B11	16	F	d
6	SC	7B1	20	F	d
6	SC	3A20	25	M	vs