INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

SPRUCE BUDWORM (*Choristoneura fumiferana* Clem.) LATE-INSTAR DISPERSAL AND IMPACT ON HOST-SPECIES NATURAL REGENERATION IN A BOREAL MIXEDWOOD FOREST OF ONTARIO

by

Ryan T. Bichon ©

A thesis submitted in partial fulfillment

of the requirements for the degree of

Master of Science in Forestry

Faculty of Forestry

Lakehead University

May 1996

Dr. Y.H. Prévost
_____

Major Advisor

Dr. T.J. Lysyk
_____

External Reviewer

ABSTRACT

Bichon, R.T. 1996. Spruce budworm (*Choristoneura fumiferana* Clem.) late-instar dispersal and impact on host-species natural regeneration in a boreal mixedwood forest of Ontario. 204 pp. Advisor: Y.H. Prévost

Key Words: *Abies balsamea*, balsam fir, black spruce, boreal mixedwood, *Choristoneura fumiferana*, dispersal, *Picea glauca*, *Picea mariana*, regeneration, spruce budworm, white spruce.

Understory feeding by the spruce budworm (*Choristoneura fumiferana* Clem.) has potential to alter the species composition of established regeneration and therefore the value of the future forest. This study sets out to test the hypothesis that the spruce budworm kills more balsam fir (*Abies balsamea* (L.) Mill.) than spruce (*Picea spp.*) seedlings, thereby increasing the spruce component of the future forest. Four 10-ha study plots were established in a boreal mixedwood forest near Black Sturgeon Lake Ontario in 1993. A spruce budworm outbreak had been underway in this area for more than 10 years and was expected to collapse at any time. Branch samples were collected from mature balsam fir, white spruce (*Picea glauca* [Moench] Voss), and black spruce (*Picea mariana* [Mill.] B.S.P.) trees to compare foliage defoliation and budworm densities. Water traps were set beneath host trees to capture late-instar larvae as they dispersed to the understory. Stand characteristics were documented through stem tallies of trees and seedlings. All host seedlings (diameter < 3 cm) were assessed for budworm feeding damage.

Stem tallies indicated that the spruce budworm had increased the relative importance of spruce by killing more balsam fir in the overstory. This influence became progressively more pronounced among smaller diameter classes. However, mortality ceased abruptly at the seedling level. Despite fairly high dispersal numbers under host trees (40-160 larvae per m^2), budworm damage to regeneration was minimal and evidence of a selective influence on species composition could not be shown. The reason for a lack of damage to regeneration remains unknown, but a number of possible reasons are provided. Over 90% of all seedlings in the understory were less than 30 cm tall. Almost 97% of all regeneration was balsam fir. Possible reasons for the lack of spruce regeneration are provided and possible changes to the species composition of the forest in the future are considered. It is concluded that a harvesting system other than clearcutting may be necessary to insure adequate spruce regeneration in the boreal mixedwood forest.

CONTENTS

TABLES

FIGURES

ACKNOWLEDGEMENTS

INTRODUCTION

The eastern spruce budworm (*Choristoneura fumiferana* Clem.) is a major outbreak defoliator of balsam fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea* spp.) throughout the boreal forests of North America. Severe outbreaks occur periodically and leave behind great expanses of dead and dying host trees. This large-scale devastation of the forest results in substantial economic losses as humans compete with the spruce budworm for the privilege of harvesting budworm-susceptible stands (Baskerville 1975). The spruce budworm is considered to be the most important insect pest problem currently facing the pulp and paper industry in forests of the northeast.

Unlike many insect pests, the spruce budworm is native to North America and outbreaks probably have been associated with fir-spruce forests at least since the last period of glaciation some 10,000 years ago (Gordon 1985). Outbreaks therefore are a natural phenomenon, but historically they probably occurred in small, localized patches of forest where fire had been absent for longer than the normal fire cycle and succession had progressed toward a dominance of balsam fir and spruce. In recent times, however, it seems that outbreaks of the spruce budworm may be occurring with greater severity and over greater areas than ever before, largely due to the activities of human beings (Blais 1983). Fire suppression, road construction, urbanization, insecticide applications, herbicide applications, harvesting practices, and the establishment of parks all have increased the land area occupied by budworm-susceptible forests with a high fir-spruce component. All indications are that such forests will continue to be an increasingly important part of the landscape.

A better understanding of budworm / forest interrelationships is necessary to ensure effective management of budworm-susceptible forests in the future.

Budworm-caused mortality of host trees brings about changes to the structure and species composition of a forest. These changes may be superficially obvious where host trees are removed from among non-host trees, but become far more subtle if one looks at interactions involving host-tree species only. The budworm feeds on both fir and spruce, but the possibility exists that differential feeding damage to host trees may favour the presence of one species over another in the long term (Ghent et al. 1957). Regeneration is influenced by the spruce budworm when it destroys reproductive structures as well as foliage. At epidemic levels, the spruce budworm also disperses to the understory and feeds on fir and spruce regeneration already established on the forest floor (Ghent 1958a). The effects of differential feeding damage therefore extend to future generations of trees as well as those in the present forest. The long-standing question is: do spruce budworm outbreaks favour the existence of balsam fir or spruce over the long term?

It has been argued that spruce budworm outbreaks favour the existence of balsam fir rather than spruce and thus facilitate the conversion of forests to pure balsam fir (Swaine 1933; De Gryse 1944). It also has also been argued that budworm outbreaks favour the existence of spruce, thereby increasing the spruce component of a forest over the long term (Craighead 1924; Gordon 1985). These hypotheses, mostly based on observations, are in conflict with each other and present observers remain polarized in their viewpoints. A few studies specific to the question at hand have been conducted, but none have provided a definitive answer (Ghent et al. 1957; Fye and Thomas 1963).

Forest harvesting operations often rely on established natural regeneration to reforest an area. Spruce is much more desirable than balsam

fir because it is longer lived, less susceptible to early rot, and less susceptible to the spruce budworm (Binotto and Locke 1981; Gordon 1985). Understory feeding by budworm larvae may influence the species composition of regeneration and thus the value of the next stand. Parks set aside to 'preserve' an early-successional forest may, over time, be converted to late-successional fir-spruce forests that are highly susceptible to budworm attack. It would be very beneficial to know if the spruce budworm is more likely to convert these forests to pure balsam fir or promote a higher spruce component.

The practice of spraying an insecticide to kill the spruce budworm is called into question by the uncertainty of budworm influences on the forest. Generally, it is accepted that the spruce budworm kills more mature balsam fir than spruce trees during an outbreak (MacLean 1980). Understory feeding by the spruce budworm might also kill more balsam fir than spruce at the regeneration level. If this is the case, then one would expect the next stand to have a higher component of spruce. A higher spruce component results in a stand with greater value and greater resistance to budworm outbreaks. The spruce budworm thus becomes a beneficial influence on the forest. It even has been argued that spraying insecticides to kill the spruce budworm may serve only to protect balsam fir regeneration, which would have been eaten had the outbreak been left to run its course (Gordon 1985; Appendix I). The controversy over this issue can be settled only by a better understanding of the budworm's role as an understory defoliator.

This study sets out to test the hypothesis that understory feeding by the spruce budworm kills more balsam fir regeneration than spruce regeneration, thereby exerting a selective influence in favour of spruce. The broad objectives of the study are 1) to explore changes to host-tree species composition of a boreal mixedwood forest during the later stages of a spruce budworm outbreak,

2) to contribute to a better understanding of late-instar dispersal activity, and 3) to assess the impact of understory feeding damage on the species composition of host regeneration. The difficulties of exploring long-term influences of the spruce budworm using a study conducted at a specific point in time are recognized, but it is hoped that the findings of this study will provide some information about the processes taking place and contribute to a better understanding of budworm / forest interrelationships.

LITERATURE REVIEW

THE SPRUCE BUDWORM

Range

The spruce budworm is a coniferophagous (conifer-eating) insect that occurs across northeastern North America from Newfoundland west to northern British Columbia, the Yukon, and Northwest Territories. A native to North America, the budworm is associated with fir-spruce forests in the Boreal, Great Lakes - St. Lawrence, and Acadian forest regions described by Rowe (1972) (Harvey 1985). The most extensive and most destructive outbreaks of the spruce budworm have occurred in the Atlantic Provinces (New Brunswick, Nova Scotia, Newfoundland), Quebec, and Ontario in Canada and in Maine and the Great Lake states of the northeastern United States (Talerico 1983; Mattson *et al.* 1988).

Host-Tree Species

Spruce budworm larvae can feed on the new growth of a number of conifers in the family *Pinaceae*, but balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* [Moench] Voss), red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* [Mill.] B.S.P.) are the primary hosts. The budworm is present over most areas where balsam fir and spruce occur, but its range most closely matches that of balsam fir. Occasional hosts of the spruce budworm are tamarack (*Larix laricina* [Du Roi] K. Koch), eastern hemlock (*Tsuga canadensis* [L.] Carr.), Engelmann spruce (*Picea engelmannii* Parry ex

Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and eastern white pine (*Pinus strobus* L.) (Harvey 1985; Mattson *et al.* 1988). Red spruce is an important host in Nova Scotia, New Brunswick, southern Quebec, southeastern Ontario, and Maine, but is not found in northern Ontario (Blum 1990). Black spruce is common throughout the range of the spruce budworm (Viereck and Johnston 1990) and is an important host at times, especially in Newfoundland (Schooley 1980; Blais 1981c). However, black spruce most often escapes serious defoliation because budworm development is not synchronized with the bud phenology of black spruce (Blais 1957; Prévost and Laing 1986). Bud phenology of red spruce is somewhat similar to that of black spruce, but is more closely matched to the budworm life cycle (Hudes and Shoemaker 1984; Blum and MacLean 1984). The spruce budworm therefore is specialized to attack just two primary host plants over most of its range: balsam fir and white spruce.

Balsam fir is described as the "preferred host" of the spruce budworm in an overwhelming majority of the literature. This long-standing practice continues despite some evidence that white spruce may be preferred by egg-laying females (Jaynes and Speers 1949; Wilson 1963; Renwick and Radke 1982) and a preferred food source for larvae (Koller and Leonard 1981; Lysyk 1989; Albert 1991). However, there also is evidence to support the claim that balsam fir is most preferred (Kimmins 1971; Durzan and Lepushanski 1968).

Both species are very suitable hosts. Their bud phenologies are similar and well matched to the life cycle of the budworm. Both balsam fir and white spruce provide acceptable nutrition and the total amount of foliage consumed per budworm is identical for both hosts (Koller and Leonard 1981). Given the existence of conflicting opinions regarding host preference, one may conclude that any real differences are subtle. However, it is well known that outbreaks of the spruce budworm are associated almost exclusively with extensive stands of

mature balsam fir (Swaine and Craighead 1924; Mott 1963; Baskerville 1975; Blais 1952, 1958b, 1981c; and many others). White spruce is found in association with balsam fir, but often as a less important component of the forest. Commonly abundant balsam fir undoubtedly is the "most important" host of the spruce budworm, despite some uncertainty about it being preferred.

Life Cycle

The spruce budworm is univoltine, completing its life cycle over a period of one year. Adults emerge from pupae as moths in late June to late July (Mattson *et al.* 1988). Newly-emerged virgin females remain at their site of emergence and at dusk begin "calling" to males through release of an airborne chemical attractant known as a sex pheromone (Sanders 1969; Sanders and Lucuik 1972). Mating takes place during the first photoperiod after emergence and oviposition begins within 24 hours of mating (Sanders and Lucuik 1975; Sanders 1991).

A female generally lays 5-10 egg masses, with each mass containing 5-50 (mean =20) eggs (Mattson *et al.* 1988). Eggs usually are deposited on the undersides of needles, with each female laying a total of about 200 eggs (Miller 1975; Talerico 1983). Females generally do not fly until mating and some oviposition has occurred (Wellington and Henson 1947; Blais 1953; Miller 1975). As a result, the first egg mass is laid very near the site of emergence (Sanders 1991). Subsequent egg masses are laid in nearby trees as females become increasingly capable of flight. After laying about half of their total egg complement, females become vigorous fliers and often undertake long-range dispersal flights (Henson 1951; Greenbank 1973). When population densities are high and stands heavily defoliated, mass dispersal of moths may be a regular, nightly occurrence (Morris and Mott 1963; Greenbank *et al.* 1980). A

large proportion of dispersing moths is made up of egg-carrying females that lay the remainder of their eggs upon landing, sometimes hundreds of kilometres away from the point of adult emergence (Greenbank *et al.* 1980; Dobesberger *et al.* 1983).

Eggs hatch in 10-14 days after being laid (Mattson *et al.* 1988). Newly-hatched larvae (first larval instars or L1's) are tiny caterpillars measuring only about two millimetres in length (Swaine and Craighead 1924). Spruce budworm larvae undergo successive moults as they develop, progressing through a series of six larval instars. Successive instars are reached as the budworm sheds its skin and a hardened head capsule, allowing it to expand to a larger size. Head capsules grow larger at each successive moult, but remain at a constant size throughout the period of each larval instar. Identification of developmental stages can be made on the basis of head capsule width, which falls within a specific range of values for each instar (McGugan 1954; Bean and Batzer 1957).

Upon emergence from eggs, L1's react photopositively, moving toward bright light at the tips of branches. The larvae do not feed at this stage of development, but disperse in search of sites at which to spin cocoon-like overwintering shelters called hibernacula (Talerico 1983; Mattson *et al.* 1988). Turbulent winds or crowded conditions on branch tips cause the larvae to drop on silken threads rather than spinning hibernacula immediately. These threads commonly break off and the tiny larvae, buoyed by strands of silk, disperse on air currents in a process known as ballooning (Mattson *et al.* 1988).

Hibernacula can occur on both host and non-host trees between bark scales, bark fissures, staminate flower bracts, or in lichens. After spinning hibernacula, larvae moult to the second-instar and overwinter in a form of hibernation known as diapause (Talerico 1983; Mattson *et al.* 1988).

Second-instar larvae (L2's) emerge from hibernacula in late April to mid-May of the following spring and seek out a food source. Like first-instar larvae, L2's react photopositively, moving toward the branch tips. The larvae disperse again through ballooning, often being carried over distances of several kilometres (Mattson *et al.* 1988).

Emergence of second-instar larvae occurs coincident with or a few days before vegetative budbreak of balsam fir and white spruce (Swaine and Craighead 1924). Larvae that emerge before vegetative buds open must find a source of food that will carry them through until budbreak, when new foliage becomes readily available. They find such a food source by mining unopened vegetative buds (Swaine and Craighead 1924), old needles of balsam fir and spruce (Atwood 1944), or staminate (pollen) flowers that are swollen and soft two weeks prior to vegetative budbreak (Blais 1952).

After an initial mining phase, larvae move to the branch tips in search of new foliage. The moult to third instar occurs during the late mining stage or early bud-feeding stage (Sanders 1991). It is at this point in the budworm life cycle that synchrony with bud phenology of host trees is thought to be critical. If vegetative buds still are tightly closed and unavailable as food, young larvae will either starve to death or abandon the tree in search of other food (Blais 1957).

Vegetative buds of balsam fir are the first to open and therefore the first available to waiting larvae. White spruce buds open a few days later and thus are available at about the same time as those of balsam fir. Red spruce buds open a few days later and black spruce buds do not open until about ten days later than buds of balsam fir, by which time larvae have starved or have found some other place to feed. It is this asynchrony with the budworm life cycle that

makes black spruce relatively immune to severe damage by the budworm (Craighead 1924; Blais 1957).

Once vegetative buds begin to flush, larvae settle at the expanding shoots, construct small feeding shelters out of silk, and begin to feed on succulent new foliage. Larvae prefer foliage of the current year's shoots and will feed on it exclusively as long as it is available. When population densities are high and defoliation is severe, larvae may be forced to consume older foliage, a habit referred to as "back-feeding" (Talerico 1983; Mattson *et al.* 1988). Budworm larvae usually are in the larger L5 and L6 stages at this time and are more capable of consuming foliage from previous years. Rather than back-feeding, many larvae disperse to the understory and feed on young host-trees and seedlings (Talerico 1983).

Pupation occurs during mid-June to early July within feeding shelters or in other protected sites. Moths emerge from pupae 10-14 days later (Mattson *et al.* 1988) and the cycle repeats itself.

Late-Instar Dispersal

A key factor to success of the spruce budworm as a major outbreak defoliator lies in its dispersal strategies. Some dispersal occurs during most life stages, but major population dispersal occurs at four annual life-cycle stages: 1) adult; 2) first-instar; 3) second-instar; and 4) late-instar. These dispersal activities have been reviewed in brief, but dispersal of late instars deserves more detailed discussion because it is a main focus of field work to be described later.

Dispersal of late-instar larvae is governed largely by reactions to light (Wellington 1948). Late-instar larvae react photopositively, moving toward the source of direct light (i.e. the sun). This behaviour keeps budworm larvae in the

outer peripheries of the crowns of host trees where suitable food in the form of new buds is most likely to be found.

High temperatures have been shown to play a role in the initiation of late-instar dispersal by inducing a photonegative reaction to direct light (Wellington 1948). The mean threshold temperature at which photic responses are reversed varies with larval developmental stage. Later instars require progressively higher temperatures to induce a photonegative response, a trend probably related to the fact that later instars are more likely to encounter higher temperatures during mid-summer.

In laboratory tests, Wellington (1948) determined that sixth-instar larvae became photonegative at a mean temperature of about 38°C. There was some question how often larvae might experience such temperatures under natural conditions, so Wellington (1948) also collected data from temperature measurements in the field. It was shown that the temperature of air in feeding tunnels of sixth-instar larvae was as much as 5°C above free air temperature. The internal body temperature of sixth-instar larvae also was found to be as much as 3-4°C higher than the air surrounding them. Thus, an outside air temperature of 30°C is sufficient to raise the internal body temperatures of larvae in feeding tunnels above 38°C. Wellington concluded that late-instar larvae under natural conditions stand an excellent chance of experiencing temperatures high enough to induce a photonegative reaction to direct light.

Shepherd (1958) measured internal body temperatures of sixth-instar larvae under field conditions and found that body temperature varied with degree of shading. Larvae that were shaded by foliage or the silk webbing of feeding shelters had a body temperature of only 1.1°C in excess of outside air temperature. Internal temperatures of larvae in direct sunlight were an average of 7°C higher than outside air and as much as 10°C in some cases. Late-instar

larvae feeding on host trees shaded by an overstory are less likely to experience threshold dispersal temperatures than larvae feeding on open-grown or exposed trees.

Sanders (1991) states that an air temperature of about 20°C in full sunshine is sufficient to raise the temperatures of larvae to about 32°C, at which point they may leave their feeding tunnels and orient themselves in the shadows of twigs. If heated further or somehow disturbed, larvae readily drop on silken threads. Temperature thus plays an important role in the initiation of late-instar dispersal, which probably occurs to some extent on an annual basis.

Wellington (1948) found that the normally photopositive behaviour of late-instar larvae also was reversed by progressive starvation. Under conditions of severe defoliation larvae must wander in search of additional food. Budworm larvae are not at all sure-footed while in motion, so wind and sudden rain may knock some of them out of the trees as they wander. The larvae move about in search of food, but are reluctant to leave the extremities of branches where they have been feeding, even at unrealistically high densities created under experimental conditions (Morris and Mott 1963). Progressive starvation induces a strong photonegative reaction to direct sunlight and leads to a mass exodus of larvae from the branch tips (Wellington 1948; Morris and Mott 1963).

During photonegative dispersal some larvae move inward towards the trunk of the tree, but many disperse from the branch by dropping on silken threads (Wellington 1948). Larvae that drop may land on lower branches, on understory vegetation, or on the ground. Photonegative larvae ignore any food they may encounter as they disperse. Once out of direct sunlight, late-instar larvae remain photopositive to diffuse light, which lacks a discrete point of origin. This reaction causes larvae to move toward brightness once again, increasing their chances of finding suitable food. Larvae that remain in the

crowns of trees return to the peripheries, often on branches located lower in the tree than those fed upon earlier. Larvae in the shaded understory move upward toward the brightness of the sky before feeding. Some larvae climb back up the larger trees from which they dispersed, while others remain in the understory and feed at the tops of seedlings (Wellington 1948).

Dispersal of late-instar larvae can occur over a wide range of stand conditions and defoliation levels. Some dispersal may occur every year due to the influence of temperature, but mass dispersal of late-instar larvae is more likely to occur in severely infested stands where both food supply and shade are scarce (Wellington 1948; Morris and Mott 1963). Mass dispersal of late-instar larvae also is more likely to occur during the later stages of an outbreak when successive years of heavy defoliation have left only bare twigs at the peripheries of crowns (Wellington and Henson 1947).

Wellington (1948) reasoned that acquired photonegative reactions to direct light are a survival strategy for the spruce budworm. Without mechanisms to reverse photopositive behaviour, budworm larvae would be confined to the top portions of trees where lethal temperatures or starvation could lead to large-scale mortality. Dispersal leads to redistribution of the larvae throughout lower levels of the forest where temperatures are more favourable and/or food more abundant.

Very few studies have explored dispersal by late-instar larvae and it is necessary to look at early-instar dispersal for information. In a study of early-instar dispersal of the western spruce budworm (*Choristoneura occidentalis* Freeman), Beckwith and Burnell (1982) found that larvae were increasingly filtered out at lower levels by adjacent or lower foliage. In a similar study of early-instar dispersal by the eastern spruce budworm, Régnière and Fletcher (1983) found that only a small proportion of larvae actually reached the ground.

Sticky traps located beneath dead and poorly-foliated lower branches of trees and under non-host vegetation caught more larvae than those beneath host trees with healthy lower foliage. It was concluded that larvae were forced to disperse again when they encountered unsuitable feeding sites, thus ending up at progressively lower levels in the stand. Larvae that encountered suitable foliage remained at a higher level.

Jennings *et al.* (1983) used sticky traps at ground level to monitor early-instar dispersal in Maine. More larvae were caught in partial cut treatment areas (strip clearcuts) than in undisturbed forest. Higher catches in the strip clearcut areas were attributed to a reduction in the number of host trees to intercept dispersing larvae and an abundance of non-host vegetation that had developed.

Fellin (1985) used sticky traps at ground level to determine how many early-instar larvae of the western spruce budworm reached the forest floor in stands that had received various silvicultural treatments. Trap catches were higher in partial cut treatments (shelterwood, seed tree, and understory cleaning) than in undisturbed forest. Fellin (1985) attributed higher catches in partial cut areas to the fact that nonmerchantable understory trees had been removed. Without an understory layer to intercept dispersing larvae, there was a clear path of travel between overstory trees and ground level.

Interception or filtering effects of mid-layer foliage on dispersing late-intars has not been studied, but one would expect a similar trend. Evidence of such a trend may be found in examples of understory feeding provided by Gordon (1985). Stand structure data from two typical fir-spruce stands in Ontario showed a dense middle layer of suppressed trees situated beneath the main canopy and above understory seedlings. Following budworm outbreaks, the dense middle layers of both stands suffered high mortality and almost

complete elimination. In contrast, seedlings located beneath these middle layers generally suffered low mortality, although some feeding damage did occur. These findings suggest that large numbers of dispersing late-instar larvae may have been intercepted by the dense middle layers of host foliage.

Although late-instar dispersal often has been observed in the past, very few studies have attempted to quantify the number of larvae that reach the understory. Morris and Mott (1963) explored late-instar dispersal experimentally by placing a known number of larvae on suspended branch samples at different densities and later counting the number of larvae that remained. Few larvae were found to have left the branches, even at unrealistically high budworm densities. Morris and Mott concluded that late-instar dispersal was likely to be important only in heavily defoliated stands where the food supply had been depleted.

A study by Kelly and Régnière (1985) represents the only known published account of late-instar dispersal numbers. The study was conducted in a boreal mixedwood in Lake Superior Park, Ontario that had suffered moderate to severe defoliation for more than ten years. The main focus of this study was number of pupae that fell to the ground, but sticky traps near ground level captured late-instar larvae as well. Trap catches were similar over two years of the study and indicated that about 20 larvae per m^2 and about 4.5 pupae per m^2 fell to the ground under mature balsam fir and white spruce trees (catches under each species were not shown separately).

Population Dynamics

Despite many years of scientific research, population dynamics of the spruce budworm still are not well understood. Comprehensive accounts of budworm outbreaks and the factors influencing them, such as those developed

by Swaine *et al.* (1924), had an important influence on the shaping of early theories. Many years of intensive investigations culminated in a series of related papers being published as a monograph by Morris (1963). This publication established a paradigm on which the majority of scientific research has been based.

The following is a brief summary of the more important concepts of budworm population dynamics as established by Morris (1963). Budworm populations normally exist at endemic levels and are held in check by various controlling factors, including predators, parasitoids, and diseases. The existence of large, contiguous areas of mature or overmature balsam fir is a necessary precondition for an outbreak to develop. The occurrence of consecutive years of warm, dry summers favours survival of budworm larvae. High survival rates, combined with an extensive food supply, allow the budworm population to escape natural control factors and explode to epidemic levels. Outbreaks occur sporadically through time, appearing whenever favourable conditions are present. Epidemic levels are reached first in localized areas known as epicentres. Outbreaks then spread from these epicentres to surrounding areas through moth dispersal. Clouds of moths arriving in a new location augment the local population and allow it to escape natural controls as well. The outbreak continues to grow unchecked until host-tree mortality increases and the food supply is depleted. The population crashes and is held in check once again by natural control factors.

The concepts put forth by Morris (1963) seemed sound and were mostly supported by subsequent research. As a result, they remained largely unchallenged for many years. Over 20 years passed before a monograph by Royama (1984) suddenly called into question almost every long-standing fundamental concept related to budworm population dynamics.

The following is a brief summary of new ideas expounded by Royama (1984). Budworm populations oscillate continuously between endemic and epidemic levels; they do not suddenly jump from one condition to the other. Populations oscillate in unison over wide areas, increasing everywhere at the same time, but reaching epidemic levels in some areas sooner than others. Perceived epicentres are simply the locations at which budworm populations first reach epidemic levels. The population densities in surrounding areas soon catch up, giving the appearance that the epicentre is spreading. Furthermore, populations oscillate independently of food supply or weather conditions, with a fixed periodicity of about 35 years between epidemic levels. Oscillations are driven by several density-dependent mortality factors, including parasitoids, diseases, and an intriguing complex of unknown causes referred to as the "fifth agent". Predation, food supply, weather, moth dispersal, and survival of early-instar larvae during dispersal are not causes of the basic oscillation, but rather factors that contribute to secondary fluctuations about the basic oscillation. Higher or lower than normal peaks and troughs in the oscillation cycle are responsible for perceived irregularities in outbreak periodicity over time.

The theories put forth by Morris (1963) and Royama (1984) are compared and contrasted in far more detail by Mattson *et al.* (1988), Sanders (1991), and Miller and Rusnock (1993). Neither set of theories is accepted as being more correct at present and both have strong evidence to support them. Generally, it is believed that these issues cannot be resolved given the current level of understanding.

Despite controversy surrounding the forces that drive population dynamics of the spruce budworm, the general pattern of rapid population increase at the start of an outbreak remains unchanged. When budworm populations are at endemic levels, it often is difficult to find a budworm even

after intensive sampling over a wide area (Greenbank 1963; Royama 1984).
Miller (1975) states that the population density of late instars is often less than
five larvae per host tree during endemic periods, growing from five larvae per
tree to 2000 larvae per tree in just four years at the start of an outbreak. By the
fifth or sixth year of an outbreak, population densities can reach 20,000 larvae
per tree or higher.

Feeding Damage

The spruce budworm consumes large amounts of foliage during feeding
stages and grows rapidly. Mature larvae are 20-30 mm long and weigh about
100 mg fresh weight, representing at least a 1500-fold increase in mass since
first feeding (Mattson et al. 1988). The large amount of food needed to attain
this growth rate results in severe defoliation of host trees when budworm
densities are high. Defoliation removes a portion of the tree's photosynthetic
factory, leading to reduced radial growth and volume increment (Blais 1958a;
MacLean 1984). Radial growth loss in the crown portion of the stem can occur
during the first year of severe defoliation, but growth loss in the lower portions
of the stem may lag behind by two to five years (Raske 1981; MacLean 1985).

Height growth is reduced or prevented when terminal shoots (leaders)
are destroyed. Top killing of trees is common following consecutive years of
severe defoliation and may drastically reduce overall height (Blais 1958a;
Raske 1981; MacLean 1985). Tree vigour is reduced, resulting in rootlet
mortality and increased susceptibility to decay organisms (Craighead 1924;
Raske 1981). Continued defoliation leads to eventual death of the tree
(MacLean 1985).

MacLean (1980) synthesized data from a number of outbreaks in
different regions and found that timing of mortality is quite consistent. Trees

begin to die after four or five years of severe defoliation in mature stands. Outbreaks usually last for about ten years, but mortality continues for a few years after the outbreak has subsided (MacLean 1980; Batzer and Popp 1985). An additional 12% of host trees may die during the 11th and 12th years and a further 5% may die over the following four years (MacLean 1980). Mortality may be accelerated where back-feeding is extensive (Blais 1981a). Final mortality reaches an average of 85% in mature balsam fir (MacLean 1980).

Spatial variability of mortality seems to be more pronounced than temporal variability. Baskerville and MacLean (1979) found that mortality in what appeared to be a uniform balsam fir stand varied considerably between plots. Mortality ranged from 34-80%, with the lowest and highest levels of mortality found in plots located only 50 m apart. Irregularities in the distribution of mortality created "holes" in the forest as mortality progressed.

Mortality may be even more variable in mixedwood stands where host trees growing in the shade of non-host trees tend to suffer less defoliation than those growing in pure stands or full light (Turner 1952; Blais 1958b; Lawrence and Houseweart 1981). In general, percentage mortality of host trees tends to decrease as basal area of non-host trees increases (Witter *et al.* 1984; Batzer and Popp 1985; Solomon and Brann 1992).

The spruce budworm is considered to be a foliage feeder, but it has been shown that reproductive structures of host trees are preferred whenever they are available (Blais 1952; Greenbank 1963; Tripp 1950; Powell 1973; Schooley 1980; Prévost and Laing 1986). Both pollen-producing microstrobili (Blais 1952; Blais 1957) and seed-producing megastrobili (Powell 1973; Prévost and Laing 1986) burst one to two weeks prior to vegetative buds. Sexual structures provide second-instar larvae with a nutritious food source to carry them over

until vegetative buds burst and new foliage becomes available. This feeding can have a profound effect on the reproductive abilities of host trees.

Defoliation by the spruce budworm lowers reproductive vigour of host trees and limits the number and length of shoots upon which reproductive buds may develop (Schooley 1978). Budworm larvae are known to feed extensively on developing male reproductive structures while they are available (Bess 1946; Blais 1952, Greenbank 1963), with the result that pollen available for dissemination and ultimately seed production is drastically reduced (Powell 1973).

In addition to reducing pollen production, the budworm directly affects seed production through feeding on cone flowers and immature cones. Some cones are destroyed, while others are only partially eaten. Partially eaten cones become gnarled or curved and damaged areas become coated with an exuded gum. These deformities prevent damaged cones from opening normally to release seed (Schooley 1980). Such damage is common on balsam fir (Powell 1973; Schooley 1978), white spruce (Tripp 1950; Tripp and Hedlin 1956), and black spruce (Schooley 1980). Direct feeding on seed cones is a major factor limiting seed production and the establishment of natural regeneration. Under conditions of severe budworm infestation, seed production by host trees often is eliminated altogether. Destruction of seed supplies can delay regeneration and affect the species composition of regenerating stands (Schooley 1980).

Balsam fir normally is a prolific seed producer and an adequate number of seedlings usually is established in the understory before budworm-caused mortality occurs (Schooley 1978). Destruction of seed crops is a far more serious problem for black spruce, beneath which few seedlings may be established prior to mortality (Schooley 1980).

THE BOREAL MIXEDWOOD FOREST

Range, Species Composition, and Importance

While discussion in this report is focused on boreal mixedwood forests of Ontario, it should be noted that mixedwood forests and the spruce budworm occur over a wide range of sites in the Boreal, Great Lakes - St. Lawrence, and Acadian Forest Regions of Canada and similar forests of the northeastern United States. Studies of the spruce budworm in forests of all regions will be called upon to shed light on the Ontario boreal mixedwood situation and it is worthwhile to provide at least a superficial introduction to them, based on the classification of Rowe (1972).

The Boreal Forest Region comprises the greater part of forested land in Canada, stretching from Newfoundland west to the Rocky Mountains of British Columbia and northwest to Alaska. This continuous belt of forest is primarily made up of coniferous trees, but contains a general admixture of broad-leaved trees. Characteristic conifers of the central and eastern portions of the Boreal Forest Region are balsam fir, white spruce, black spruce, jack pine (*Pinus banksiana* Lamb.), and tamarack. White birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and balsam poplar (*Populus balsamifera* L.) are important and widespread broad-leaved tree species. Mixedwood forests containing various proportions of both softwoods and hardwoods are common throughout the southern portions and especially the south-central portions of the Boreal Forest Region (Rowe 1972).

Mixedwood forests become less common northward where conifers dominate and finally give way to subarctic tundra. Conifers also dominate the western extremes of the Boreal Forest Region in high elevation areas of the Rockies. The Atlantic portions of the boreal forest again are dominated by

conifers, with balsam fir, black spruce, and white spruce being the characteristic species in order of abundance. White birch, trembling aspen, and balsam poplar are not as abundant in the Atlantic provinces as they are farther west, but their presence does result in occasional mixedwood stands (Rowe 1972).

The Great Lakes - St. Lawrence Forest Region is found along the Great Lakes in Ontario and along the St. Lawrence River valley of southern Quebec into northern New Brunswick. This region is characterized by white pine, red pine (*Pinus resinosa* Ait.), eastern hemlock, and yellow birch (*Betula alleghaniensis* Britton). The forests are of a very mixed nature and contain all species commonly found throughout the central and eastern portions of the boreal forest (Rowe 1972).

The Acadian Forest Region is found over most of the Maritime Provinces and is closely related to the Great Lakes - St. Lawrence Forest Region. This region also is of a very mixed nature and again contains all species found in the central and eastern portions of the boreal forest, although jack pine is less common. Red spruce is an important component of the forest in this region (Rowe 1972).

The boreal mixedwood forest escapes exact definition because it is so extremely variable and complex in terms of species composition and occupation of sites (McClain 1981). In Ontario, a working definition of boreal mixedwood forest, based on site and species composition, has been proposed by the Spruce-Fir-Aspen Forest Research Committee (Weingartner and Basham 1979). Under the proposed definition, boreal mixedwood forest includes any sites that support or could support any of the five main component species: balsam fir, white spruce, black spruce, white birch, and trembling aspen. Poorly drained lowlands that commonly support pure black spruce, dry sandy uplands that commonly support pure jack pine, and excessively drained shallow soils on

rocky ridges that commonly support jack pine and/or black spruce are excluded. It is expected that this broad definition of boreal mixedwood forest will be further refined over time (Weingartner and Basham 1979).

The actual composition of a boreal mixedwood forest at any point in time will vary with a number of influencing factors. All five tree species specified in the definition of boreal mixedwood need not be present and species not included in the definition may be present at any time. Jack pine, white pine, red pine, eastern white cedar (*Thuja occidentalis* L.), and tamarack are examples of atypical species commonly found in the boreal mixedwood forests of Ontario (McClain 1981).

The area of Ontario broadly classified as boreal mixedwood forest covers the southern portion of Rowe's (1972) Boreal Forest Region and the northernmost portion of the Great Lakes - St. Lawrence Forest Region. About 45-50% (some 21.3 million ha) of this area is actually mixedwood in that it contains some mixture of softwoods and hardwoods where neither softwoods nor hardwoods comprise greater than 75% of the stems present in a stand. The remainder is primarily coniferous, with only a small proportion being classified as hardwood (McClain 1981).

Mixedwoods generally occupy the most fertile sites in Ontario, which tend to be located close to mills and established communities. The high productivity of these sites, together with low harvesting and transportation costs, make boreal mixedwoods some of the most economically important forests in Ontario (Ketcheson 1981).

Boreal Forest Succession and Climax

The concepts of boreal forest succession and climax have long been controversial. For purpose of discussion, forest succession is defined here as

the process of directional change in structure and species composition leading to a stable community of plants that can reproduce successfully beneath their own shade and, in theory, maintain the community indefinitely (Kimmins 1987). Shade-intolerant pioneer species that occupy a site following disturbance (early succession) are replaced over time by shade-tolerant species (late succession), leading to a stable community that is known as a climax (Kimmins 1987; Bergeron and Dubuc 1989).

Frequent natural disturbances by fire, insects, disease, and wind have led many to conclude that the concept of a climax does not apply to the boreal forest (Swaine 1933; Graham 1941; Maycock and Curtis 1960; Rowe 1961; Dix and Swan 1971; Sprugel 1976; Heinselman 1981; Wein and El-Bayoumi 1983; Kimmins 1987; Bergeron and Dubuc 1989; and many others). Nonetheless, the concept of forest succession remains a central theme of forest ecology despite the fact that a true climax may never occur under natural conditions (Sprugel 1976; McIntosh 1981; Kimmins 1987). Climax may be viewed more appropriately at the scale of the landscape, wherein all stages of succession exist and are constantly shifting, but the overall effect is one of long-term stability. Climax becomes the maintenance of a dynamic equilibrium rather than predictable dominance by a single species or vegetation type, although it is well recognized that directional succession between disturbances is towards an increase in shade-tolerant species (Rowe 1961; Sprugel 1976; Carleton and Maycock 1978; McIntosh 1981).

Fire always has been the most important factor controlling succession in the boreal forest. Many tree species have developed strategies for coping with the frequent occurrence of fire and even depend on fire for their existence. Balsam fir and white spruce are peculiar in that they seem to have no definite strategy for coping with fire and are easily killed when it occurs (Heinselman

1981). Even white spruce has some relation to fire, however, because a reduction of the litter layer is needed before white spruce seeds from adjacent stands can become established in abundance (Rowe 1961; Kayll 1968). Late-successional balsam fir and white spruce exist as scattered individuals where fire occurs regularly and are found in abundance only where fire has been absent for a period of time longer than the normal fire cycle (Heinselman 1981). In the absence of fire, directional succession is toward forests dominated by shade-tolerant balsam fir and spruce. In the continued absence of fire, balsam fir is considered the only species readily capable of continued establishment (Bergeron and Dubuc 1989).

Given the irregular occurrence of fire over the short term, it is likely that stands containing an abundance of balsam fir and spruce have always existed to some extent since the last period of glaciation. It also is likely that the spruce budworm has been associated with these species over the same period of time (Baskerville 1975). Outbreaks of the spruce budworm leave behind large areas of dead and dying host trees, thus increasing the probability that fire will occur. Historical records indicate that severe fires generally have followed spruce budworm outbreaks by five to ten years (Stocks 1985). The spruce budworm might be considered a part of the fire cycle as it promotes the occurrence of fire where fire has been absent for an abnormally long period of time (Alexander and Euler 1981).

However, the occurrence of fire after a spruce budworm outbreak is not guaranteed. Fire potential of a site peaks in five to eight years following budworm-caused mortality of balsam fir, then gradually decreases over time. Spring fires that occur before the flushing of broad-leaved species can be severe and explosive in nature. Summer fires that occur after the flushing of understory vegetation may spread slowly or not at all (Stocks 1985, 1987). The

occurrence and behaviour of fire in budworm-devastated stands depend of a number of factors, including general climate, current weather conditions, stand composition, time since tree mortality, and time of year to name a few. Thus, there have always been opportunities for stand renewal without fire following a spruce budworm outbreak (Blais 1954).

Fire is common in Ontario and northern Quebec, with the spruce budworm becoming a more important force of disturbance further east where fire is not as prevalent (Blais 1983). Where both fire and spruce budworm are absent, wind may become the major force of disturbance (Sprugel 1976; White *et al.* 1985). The point to be made is that some force of disturbance always is present, reflecting the fact that disturbance is an integral part of forest ecosystems (Loucks 1970; Baldwin 1991). Such disturbances insure that stagnant, overmature and decadent forests do not accumulate over large areas and that healthy forests of young, vigorous trees always are present (Rowe 1961). In addition, periodic disturbances insure the recycling of nutrients and the maintenance of a diversity of plant species (Loucks 1970; Cogbill 1985).

Silvics of Important Tree Species

A brief review of silvics for the five main tree species found in a boreal mixedwood forest is provided here as a starting point in understanding the complex dynamics in this forest type. Information for each tree species has been condensed from silvical summaries compiled by other authors (Burns and Honkala 1990a, b).

Balsam Fir

Balsam fir is considered to be a late-successional tree species of small to medium size (Frank 1990). It is classified as very tolerant of shade and more

so than associated spruces, except perhaps red spruce. High tolerance of shade allows balsam fir to become established and to grow under a canopy of larger trees. Trees suppressed by heavy shade do not flower and physiological maturity is brought about by increased exposure to light. Dominant trees growing in full light flower prolifically and regularly. Some seed is produced every year by dominant trees and good seed crops occur at intervals of every 2-4 years.

Seeds ripen and are dispersed in late summer of the same year in which flowering occurred. Dehiscent cones break apart and fall to the ground, with the result that most seeds fall close to the base of the parent tree. Wind may disperse seed over an effective distance of 25-60 m. Germination of seeds takes place in the following spring or summer, with seedbed moisture content being the main influencing factor. Almost any seedbed type is satisfactory as long as sufficient moisture is available and remains available until seedling establishment. Shaded sites are best and light intensities of only 10% of full sunlight have no detrimental effect on germination success.

Newly-germinated seedlings quickly develop a heavy central root that penetrates to the bottom of the humus layer and then splits into several laterals. Small seedlings may be smothered by hardwood leaves or crushed by ice or snow, but losses after the first winter usually are minor. Seedlings can be considered established once they reach a height of about 15 cm, especially if secondary branching has occurred. Competition from shrubs and hardwood sprouts can be severe and long-term where basal area of the original stand is reduced by 50% or more. Severe intraspecific competition also occurs where abundant balsam fir seedlings develop into dense thickets. Established seedlings require light intensities of at least 50% of full sunlight for optimum growth, but can survive many years of suppression and still respond to release.

White Spruce

White spruce often is an important component of late-successional forests (Nienstaedt and Zasada 1990). It is classified as intermediate in its tolerance of shade, being equally or less tolerant than balsam fir. Like balsam fir, white spruce is able to become established under shade from a canopy of larger trees. Flowering and seed production are primarily functions of dominant and co-dominant trees. Flowering takes place in spring and seed ripens by late summer of the same year. Good seed crops may be produced every 2-6 years on the best sites, but may occur as infrequently as every 10-12 years on poorer sites. Seed production is considered to be sporadic, with good seed years always followed by poor ones.

The seed of white spruce is primarily wind-dispersed, but most falls within a distance of about 50 m from the parent tree. Germination occurs in the following spring or summer. A variety of seedbeds are suitable for germination as long as sufficient moisture is available. Root penetration of newly-germinated white spruce seedlings is not as aggressive as that of balsam fir. Litter and fermentation layers greater than 5-8 cm can greatly restrict the establishment of white spruce seedlings. Germination commonly occurs on rotted logs, which form an important seedbed for white spruce regeneration. Patches of mineral soil exposed by the roots of windthrown trees are considered to be the best seedbeds available under mature stands.

Initial growth of established white spruce seedlings is slow. As a result, seedlings often are over-topped by faster-growing species and may remain suppressed in the understory for 50-70 years. White spruce shows excellent response to release at almost any age. Trees commonly live to be 250 years or older on good sites where stand-destroying fires do not occur.

Black Spruce

Black spruce is a broadly distributed tree with a successional status that is difficult to characterize (Viereck and Johnston 1990). It has the smallest seeds of any spruce in North America and holds a portion of these seeds in semi-serotinous cones at the tops of trees. The occurrence of fire causes cones to open and accelerates seed fall so that black spruce may immediately re-colonize the site. These factors suggest that black spruce is an early-successional species. Trees commonly live to be 200 years or more in the absence of fire, allowing black spruce to succeed most early-successional species. Black spruce is classified as tolerant of shade and seedlings may become established in as little as 10% of full light intensity. Black spruce grows in pure stands on organic soils and along the northern limit of its range, but throughout the main part of its range it is commonly found in mixedwood associations. Thus, black spruce is a generalist of sorts, possessing characteristics of both early- and late-successional species.

Seed production increases with age, reaching a maximum between 100 and 200 years, but continuing to 250 years. Seeds ripen by late summer of the same year in which flowering occurred. Some seed is released throughout each year, with dispersal numbers being highest in spring and lowest in fall. Despite their small size, seeds are dispersed by wind over an effective distance of only about 80 m. Good seedbeds are provided by the occurrence of fires that remove the surface organic layer. Feathermoss, which commonly is associated with black spruce, provides a suitable seedbed during wet years, but often dries out before the seedling root can grow through it and into the soil. Exposed mineral soil usually is the most suitable seedbed.

Established seedlings are less tolerant of shade than balsam fir or white cedar. Black spruce is considered to be tolerant, but survival and growth

improve with increasing light intensity. The relatively slow growth rate of black spruce often results in it becoming over-topped by faster growing species when in mixedwood stands. Suppressed seedlings respond well to release. Black spruce cannot compete successfully with balsam fir over the long term and usually is succeeded by the more shade-tolerant fir.

Vegetative reproduction through layering sometimes is an important method of reproduction. Layering occurs when a lower branch touches the ground and becomes overgrown by moss. The branch develops its own root system and becomes a separate (though genetically identical) tree. This method of reproduction is far more common in poorer, more open-grown stands than it is in dense, highly productive stands.

White Birch

White birch (or paper birch) is a medium-sized, fast-growing but short-lived tree that is common in mixedwood forests (Safford *et al.* 1990). It is classified as intolerant of shade, but is more tolerant than trembling aspen. Flowering occurs in spring and seed is ripe by late summer. Seed dispersal is heaviest in the fall, but may continue throughout the winter. The seeds of white birch are very small and may be dispersed by wind over great distances, but most seeds fall within the stand where they were produced. Some seeds remain dormant, but viable, for a year or more after being shed.

Germination is best on exposed mineral soil. In comparison to that on exposed mineral soil, germination is about 50% on humus and only about 10% on litter. Rotting logs and mineral soil exposed by fallen trees are important seedbeds in wind-thrown conifer stands. Newly-germinated seedlings are very fragile and successful establishment is much better on shaded sites than in full sunlight.

White birch also reproduces by sprouts that grow from stumps. Stump sprouts seldom are abundant enough to regenerate stands after disturbance, but play an important role in maintaining the presence of white birch. Stump sprouts later may contribute to seed production as they become mature trees.

Established seedlings and stump sprouts grow well in light intensities as low as 50% of full sun, but higher light intensities are necessary for improved growth and vigour. Moderately suppressed trees may struggle for many years at low growth rates, but most eventually die. Severely suppressed trees succumb readily unless released. White birch is an early-successional species that is normally replaced by more shade-tolerant species in the absence of site disturbance, often after only one generation of dominance by birch. The fact that white birch has some tolerance to shade allows it to maintain a position among fir and spruce in mixedwood stands.

Trembling Aspen

Trembling aspen (or quaking aspen) is classified as very intolerant of shade throughout its life (Perala 1990). It is an aggressive pioneer species that readily colonizes sites following disturbance and holds its position through subsequent disturbances. Colonization of new sites is accomplished through seed dispersal. Good seed crops are produced every 4 or 5 years, with lighter crops in between. Flowering occurs in spring and ripe seeds are dispersed soon afterwards over a period of 3-5 weeks. The seeds of trembling aspen are extremely small and may be carried by wind for several kilometres. Germination occurs within a day or two after dispersal if a suitable moist seedbed is encountered. Exposed mineral soil is the best seedbed and litter is the poorest. Seeds remain viable only for 2-4 weeks and very few seeds actually produce an established seedling after germination.

Once an area has been successfully colonized, trembling aspen holds its position by reproducing vegetatively. Root suckers are produced from meristems on lateral roots that run close to the soil surface. Trembling aspen reproduces vigorously by this means after any type of disturbance. The number of suckers appearing on a given site increases with stocking density of aspen in the parent stand and basal area removed from the stand during disturbance. Clearcutting aspen-dominated stands may lead to invasion by as many as 75,000 suckers per hectare.

Established seedlings and especially root suckers grow rapidly. Their extreme intolerance of shade requires that they remain above competing vegetation and they quickly over-top conifer seedlings. Natural thinning of aspen is rapid in densely regenerated stands and any trees that fall below the canopy soon die. Trembling aspen is a fast-growing, but short-lived tree. In the east, it is most often succeeded by longer-lived, shade-tolerant species such as balsam fir. In the absence of disturbance, aspen becomes a transient species. It exists here and there as scattered individuals, but cannot compete successfully with longer-lived, late-successional species. Replacement by more shade-tolerant conifers may occur after only a single generation of aspen dominance.

BUDWORM / FOREST INTERRELATIONS

The Budworm / Forest Problem

Swaine (1933) states that the forests of northeastern North America encountered by the earliest European arrivals had reached a relatively stable equilibrium in the presence of periodic natural disturbances. These forests probably would have been able to maintain their general characteristics

indefinitely if left alone. As Kimmins (1987) points out, however, forested ecosystems will remain in their natural condition only if the frequency and intensity of disturbances remain unchanged. There is overwhelming evidence to suggest that human activities recently have altered disturbance patterns and upset the natural balance once present in these forests.

Large-scale human-caused changes to the forest began around the year 1800 when the British navy turned to its colonies in northeastern North America for ship masts and construction timber. A new industry to supply such materials grew quickly and by 1810 wood became Canada's major export. White pine, the only species considered to be of value at that time, was in great demand and the tallest, straightest trees soon were eliminated from accessible shoreline areas of Nova Scotia, New Brunswick, and Quebec, especially along the St. Lawrence River. Operations then moved inland in search of more large pines, spreading up tributaries of the St. Lawrence River and through the Great Lakes, reaching Lake Superior near Thunder Bay by about 1880 (MacKay 1978).

A second wave of human influences soon followed the white pine timber industry. Sawmills were established to supply white pine lumber for rapidly expanding towns. Operators of these sawmills were willing to accept shorter logs and smaller trees – the rejects left behind by earlier white pine timber operations. The white pine timber trade, along with the tree itself, declined during the late 1800's and had all but disappeared by about 1900. In contrast, the sawmill industry continued to flourish throughout the early 1900's. Even smaller white pines were becoming scarce by this time, however, and the industry turned to selective harvesting of large white spruce trees to supply its sawmills (MacKay 1978).

Yet another wave of human influences on the forest followed, spreading again from east to west. With the supply of white pines largely depleted and

with stocks of large white spruce dwindling, industry turned its attention to the remaining forests of smaller, previously undesirable tree species. The first pulp mill in northeastern North America was established in southwestern Quebec in 1866. More pulp mills were added over time, slowly at first, then very rapidly during the 1920's as Canada became the world's greatest exporter of newsprint. Harvesting to supply pulp mills remained selective at first, with large white spruce trees favoured, but clearcutting of smaller black spruce soon was adopted as the standard cutting practice (MacKay 1978). New technology enabled pulp mills to utilize species other than spruce and the pulp and paper industry flourished through clearcutting of smaller and more common black spruce, jack pine, and even balsam fir that had been overlooked completely in the past (Turner 1952; MacKay 1978).

Clearcutting, which involves the removal of all merchantable trees from a given site, was the only harvesting method considered economically feasible for pulpwood forests. All mature conifers were removed, but undesirable hardwoods often were left standing. Logs were cut and piled manually and hauled away by oxen or horses (MacKay 1978). After being clearcut, forests were left to regenerate on their own. Site disturbance was minimal on areas that were "horse-logged" and established natural regeneration of balsam fir and spruce, left largely intact, grew to reforest the site. It is well known, however, that early clearcutting practices favoured balsam fir at the expense of spruce (Westveld 1953; Swift 1983; Blais 1983; MacKay 1985).

The pulp and paper industry soon grew to the point where it could no longer tolerate large-scale destruction of potential wood supplies by fire. Fire came to be known as an inherently destructive agent in the forest, bringing with it tremendous economic and social losses. As a result, aggressive fire suppression policies were put in place in all of the eastern provinces by the

early 1900's (MacKay 1985). Early fire suppression efforts were not effective enough to eliminate fire altogether, but suppression did lead to a general increase in the time between fires, allowing more and more forests to accumulate in late-successional stages dominated by balsam fir (Wein and Moore 1979).

Early selective harvesting, early clearcutting, and fire suppression have resulted in a general degradation of the forests over much of eastern North America, a preponderance of balsam fir, and increased susceptibility to the spruce budworm (Swaine and Craighead 1924; Turner 1952; Baskerville 1975; Blais 1981c; Blais 1983; Swift 1983; MacKay 1985; and others). Swaine (1933) states that human activities resulted in an enormous increase in the balsam fir component in almost all forests south of the black spruce belt of northern Quebec. Gordon (1985) states that pure balsam fir stands growing in Quebec and northern New Brunswick might give one the impression this is what the area has always produced, but records indicate that enormous volumes of spruce have been harvested from these sites in the past.

In Ontario, the conversion of forests to balsam fir has not been as pronounced. Humans have exerted a lesser influence on the forests of northern Ontario for a shorter time (Blais 1985); the warm, dry climate of Ontario is less well-suited to balsam fir than the cool, moist climate further east (Halliday and Brown 1943); and fire remains a more important force of disturbance in Ontario (Baskerville 1975; Blais 1983). Modern clearcutting involves heavy equipment and generally results in far greater site disturbance than did horse-logging in the past (Yang and Fry 1981). Cutovers in Ontario tend to be dominated by trembling aspen suckers rather than balsam fir (Yang and Fry 1981; Hearnden et al. 1992), but these sites most often develop into vertically stratified mixedwoods with an understory dominated by balsam fir (Day and Harvey

1981). Fire suppression has drastically increased the time between fires in Ontario (Alexander 1980) and forests have been allowed to accumulate in late-successional stages. As a result, balsam fir has become more abundant in Ontario than ever before and has the potential to become even more abundant in the future (Klein 1985).

Economically, an abundance of balsam fir may not be a problem in itself. Although less desirable than spruce, balsam fir has come to be regarded as an acceptable species for pulp production and is even the mainstay of the industry in areas east of Ontario. Balsam fir is a fast-growing tree that naturally regenerates quite well after clearcutting, thus eliminating the need for costly silvicultural treatment of harvested sites. An increase in balsam fir becomes a serious problem only because it leads to increased susceptibility to the spruce budworm (Swaine and Craighead 1924; Baskerville 1975; Marshall 1975; Blais 1981c).

Periodic outbreaks of the spruce budworm generally cover millions of hectares of forested land and result in the loss of many millions of cubic metres of wood (Blais 1981c; Blais 1985). Pulp mills want, and in many cases need, this wood that is lost to the budworm. Long-term sustainable yield calculations are upset by changes in growing stock and economic stability may be difficult to maintain in the presence of budworm outbreaks (Baskerville 1975; Irland and Runyon 1984).

Like losses due to fire, losses of wood to the spruce budworm can no longer be tolerated by an industry moving ever-closer to full utilization of forests just to sustain itself. While fire suppression efforts have been unsuccessful in eliminating fire, control efforts directed at the spruce budworm have been even less successful. Millions of dollars per year may be spent on insecticidal spray operations during an outbreak, with the goal of keeping trees alive for a couple

of years until they can be harvested (Blais 1974, 1979, 1981c). The major cause of outbreak collapse is depletion of the food supply through mortality of fir and spruce (Blais 1981c) or the end of a natural cycle that is brought about by forces not well understood (Royama 1984).

Humans and the spruce budworm are in direct competition with each other for the privilege of harvesting forests of fir and spruce. Humans harvest the forest at a rate that is more or less constant, taking one small bite at a time, while the spruce budworm tends to harvest the entire forest all at once (Baskerville 1975). Salvage (harvesting trees after death) or presalvage (harvesting trees before they die) often is carried out in an attempt to reduce losses, but recovery of all wood from millions of hectares of forest is not possible over a short period of time. Secondary insects and decay fungi quickly degrade the quality of wood in dead trees. As a result, budworm-killed forests can be salvaged economically for only two to three years before decay renders the trees useless (Binotto and Locke 1981).

Neither salvage nor silvicultural treatment to insure satisfactory regeneration is possible over all areas given the large scale at which an outbreak occurs. As a result, many areas are left to regenerate on their own. Successional changes that take place in these forests following a spruce budworm outbreak remain the topic of some debate and many fear that white spruce may go the way of the white pine (De Gryse 1944; Sprugel 1976; Gordon 1985; MacKay 1985; Bergeron and Dubuc 1989; and many others). What is the fate of the spruce component in these forests?

The Budworm / Forest System

Throughout the literature, an underlying concept related to forest succession is that of each tree species having a different strategy for survival in

the midst of periodic disturbances. Thousands of years of repeated recoveries from disturbances have led to specialized relationships between tree species and disturbance regimes. It often has been proposed that balsam fir and the spruce budworm may work together as components of a highly-evolved forest renewal system (Blais 1959, 1981c; Dix and Swan 1971; Grigal and Ohmann 1973; Baskerville 1975; Sprugel 1976; Cogbill 1985; Gordon 1985; MacLean 1988; Bergeron and Dubuc 1989; Zoladeski and Maycock 1990; Mattson *et al.* 1991b; and others). Upon reaching sexual maturity balsam fir immediately begins to seed prolifically and store propagules as seedlings in the understory. A budworm outbreak passes through the stand, killing all or most of the mature trees. Seedlings already established on the forest floor insure that balsam fir is the first species to gain a dominant position in the stand following budworm attack. Released by removal of the canopy, seedlings grow quickly in the increased light, dominate the site, and upon reaching maturity begin to store seedlings in preparation for the next budworm outbreak.

In the absence of budworm attack, balsam fir stands become overmature and decadent, possibly being replaced by other species over time (Grigal and Ohmann 1973; Bergeron and Dubuc 1989). Periodic disturbances by the spruce budworm therefore are essential for continued dominance of balsam fir. The prolific flowering habit of balsam fir, which provides the budworm with massive quantities of high quality food, may be a mechanism to promote the occurrence of a budworm attack. Thus, mature individuals are sacrificed to insure the continued dominance of the species. A budworm outbreak also insures that nutrients are recycled and that the presence of healthy, vigorous stands is maintained. Balsam fir prepares for the inevitable arrival of the spruce budworm and the spruce budworm, upon arrival, insures the continued dominance of balsam fir.

A generalization of the balsam fir / spruce budworm system, such as that just provided, does not fit every situation in every forest. There are many variations of the general relationship, each associated with a specific situation and dependent upon a number of variable influences. However, it is believed that a variation of such a relationship probably could be adapted for almost any host forest within the range of the budworm (Baskerville 1975).

The concept of a budworm / forest system seems to be quite well accepted. Relationships between balsam fir and the spruce budworm have been described as a self-rejuvenating dynamic climax (Blais 1959), a pulse-system of rejuvenation (Dix and Swan 1971), a self-regulating system (Baskerville 1975), a "*raison d'être*", which is stand rejuvenation (Blais 1981c), crucial instability that prevents stagnation (Cogbill 1985), the result of co-evolution of the budworm and the forest (Gordon 1985), a cyclic ecological system (MacLean 1988), a self-perpetuating system (Zoladeski and Maycock 1990), and a "*coup-de-grâce*" grazing system based on highly evolved interaction (Mattson *et al*. 1991b). The concept seems plausible when one considers that the spruce budworm and balsam fir probably have co-existed at least since the end of the last ice age, some 10,000 years ago (Baskerville 1975; Gordon 1985; Anderson *et al*. 1986).

It seems that succession following a spruce budworm outbreak is simply a return to forests dominated by balsam fir (Baskerville 1975; MacLean 1984). Since budworm outbreaks do not in any way threaten the continued existence of balsam fir, the long-term food supply of the budworm also is not threatened (Mattson *et al*. 1988). By maintaining balsam fir, outbreaks may even insure the continued existence of the spruce budworm, albeit only periodically in abundance. The question remains: what is the fate of the spruce component in these forests?

Budworm Damage to Established Regeneration

Blais (1954, 1958b), working in northwestern Ontario, found that suppressed balsam fir trees with stem diameters less than 7.6 cm were severely defoliated as larvae dropped from the overstory. These suppressed trees were among the first to die during a budworm outbreak and mortality in the understory was widespread. Understory balsam fir located in the immediate vicinity of large balsam fir and white spruce suffered the highest mortality because of the large numbers of larvae dropping from the overstory at these locations. Despite widespread mortality in the understory, it was among the smallest individuals, the seedlings, that the greatest number of survivors was found after the outbreak had subsided (Blais 1954). Only understory balsam fir was considered in this study, however, and it is not known if spruce regeneration suffered similar damage.

Vincent (1956) undertook a study of budworm damage to understory regeneration in New Brunswick. Damage to regeneration was found to increase with degree of infestation in the overstory. Mortality of seedlings (height < 3 m) was high (near 50%) in the most heavily infested stands. However, mortality of small seedlings (height < 30 cm) was only about 1.5% or less in all cases, regardless of infestation level.

In a study of budworm damage to regeneration that remains the most comprehensive to date, Ghent (1958a) collected balsam fir seedlings in 1951 from 42 sites over 11 plots established near Black Sturgeon Lake in northern Ontario. Plots had been established as part of an earlier study (Ghent et al. 1957). Ghent (1958a) collected seedlings from five height classes between ground level and 107 cm. The selected top height of 107 cm included over 97% of the seedlings found in the Black Sturgeon Lake area, with increasingly higher percentages found in the lower height classes. Altogether, over 1500 seedlings

were collected, aged, and assessed for feeding damage caused by late-instar budworm that had dropped from the defoliated overstory. The results indicated that damage was almost exclusive to the terminal and terminal-lateral buds of the leader. Ghent (1958a) attributed this leader damage to the photopositive movements of budworm larvae, causing them to move to the highest point before feeding.

It was observed that most seedlings had at least one or two larvae feeding on them where budworm densities were high (Ghent 1958a). This observation suggests the number of late-instar larvae that disperse to the understory can be substantial during outbreaks. Feeding damage resulted in reduced height growth of seedlings as the terminal buds were destroyed. Deformities in the stems of seedlings resulted as lower buds or branches became new leaders. These deformities occurred annually, especially in the later stages of the outbreak when food supply in the overstory became limited and more budworm larvae dispersed to the understory in search of new foliage. Leader damage was so consistent that Ghent (1958a) even developed a method of tracking the history of budworm outbreaks through observations of seedling stem deformities.

Leader damage over consecutive years had reduced many seedlings to low-sprawling shrubs, testament to what Ghent (1958a) referred to as the tenacious survival of balsam fir seedlings. It was observed that, even after being reduced to the status of a low-sprawling shrub, seedlings soon developed dominant leaders and attained excellent height growth once the budworm outbreak had subsided. Ghent provided an example of one seedling that attained a height of only 38 cm over 14 years prior to the end of the outbreak, but then more than doubled its height over the next three years. Casual observation of the understory at this time gave the impression that seedlings

were fast-growing and of recent origin. It was only upon closer inspection that the many years of severely suppressed growth were revealed. Ghent (1958a) concluded that this deceptive appearance might be responsible for the earlier belief that seedlings became established after a budworm outbreak rather than before it.

Mortality of seedlings due to budworm damage was not mentioned by Ghent (1958a), but the reported findings suggest that mortality of seedlings due to feeding by late-instar larvae was low. A selective thinning of balsam fir seedlings in favour of spruce seedlings therefore seems unlikely. Only balsam fir seedlings were analyzed in this study, however, and the impact of dispersing late-instar larvae on spruce regeneration was not explored.

Wile (1979), on the Cape Breton Highlands of Nova Scotia, conducted an assessment of budworm damage to natural regeneration under 15 mature and overmature balsam fir stands that had been heavily defoliated by the spruce budworm. This outbreak began in 1974. Regeneration was surveyed in 1978, at a time when 32% of the overstory trees had died and defoliation of the remaining live trees was severe. Five 4 m^2 plots were established in each of the 15 stands that were surveyed. Over 80% of the stands were at least 80% stocked with balsam fir seedlings. Over 90% of these seedlings were less than 15 cm in height and in good condition. It was observed that only seedlings over 15 cm in height showed signs of budworm defoliation, but damage to these seedlings often was severe.

Moulton (1982), working in Newfoundland, surveyed budworm damage to balsam fir regeneration under 35 stands of balsam fir, black spruce, or mixed fir-spruce that had been severely defoliated. This outbreak began in 1971. Data were collected in 1980 and only stands greater than 30 years of age were sampled. A survey of 782 plots (4-m^2) showed that balsam fir was the

predominant regeneration species in all stands. Defoliation of seedlings was classified on a one to five scale, with over 80% of all seedlings assigned a score of five (= little or no defoliation damage). Regeneration was only slightly, if at all, damaged by the spruce budworm despite severe defoliation of the overstory. There was a weak trend for older (= taller, with caution) seedlings to be more heavily damaged.

Gordon (1985) documented budworm damage to regeneration in two typical fir-spruce forest types in Ontario. In one case, damage to seedlings was minimal (< 10%). In the other case, damage approached 100% on some seedlings and it was expected that these seedlings would die. In both cases, mortality was widespread among trees in the 2 cm diameter class and greater.

Ruel and Huot (1993) undertook a study of advanced regeneration in over 100 balsam fir stands in Quebec. Density, height, and budworm damage were documented for host-species regeneration in 98 sub-plots (4-m^2) in each stand. Assessments were conducted prior to harvest of the stands and repeated five years after harvest. Cutovers with low stocking of softwood regeneration were found to exist where stands had been most severely defoliated by the spruce budworm. Decreases in stocking were most prevalent among stems greater than 50 cm in height. Regeneration losses were attributed to budworm-caused mortality of the taller balsam fir advanced regeneration.

In recognition of the fact that small balsam fir seedlings rarely suffer high mortality during a spruce budworm outbreak, Mattson (1985) has proposed that these seedlings may have chemical defenses that make them practically immune to budworm damage. High levels of allelochemicals (such as terpenes) act as feeding deterrents and inducible defenses may exist to make seedlings

even less suitable when feeding damage occurs. These defensive abilities are reduced at the sapling stage and lost altogether upon reaching maturity.

However, in a study of budworm larvae feeding on trees of different ages in Minnesota, Mattson *et al.* (1991a) found no significant differences in survival of larvae on trees 1-2 m tall and those on trees 15 m tall. Budworm growth was 10% lower on the smaller trees, but this difference may have been related to influences of microclimate.

Despite a lack of evidence, there is a strong logical argument for the existence of chemical defenses. Mattson *et al.* (1991b) suggest that if the spruce budworm and balsam fir are partners in a highly evolved ecological system, then there should be some mechanism in place to insure continuity. Balsam fir may compete with other species through fast turn-over of the population, aided by the spruce budworm. Mature trees are easily killed during a budworm outbreak, but it is extremely important that seedlings survive to re-establish balsam fir as the dominant species. Chemical defense mechanisms are a logical strategy to insure this happens.

Clearly, defoliation of regeneration by late-instar larvae is not a simple, predictable event. Large numbers of larvae may disperse to the understory during heavy infestations, but seedling mortality appears most often to be low. However, Witter *et al.* (1984) state that 100% seedling mortality has been known to occur occasionally.

Budworm Influences on Host-Tree Species Composition

It is now a well-accepted fact that mature spruce trees are less vulnerable to budworm outbreaks than mature balsam fir trees (Swaine and Craighead 1924; Belyea 1952; Turner 1952; Hatcher 1964; Bergeron and Dubuc 1989; MacLean 1980; Blais 1981a; Solomon and Brann 1992; and many

others). Asynchrony of budworm development and bud phenology is an important factor related to higher survival of black spruce and red spruce. However, even white spruce, with a bud phenology similar to balsam fir, is less vulnerable to budworm outbreaks. MacLean (1980) has shown that mature balsam fir generally suffers about 85% mortality following a spruce budworm outbreak, while mature spruce suffers only about 36% mortality. Researchers often have taken advantage of this better survival of spruce, using patterns of growth-ring suppression in large white spruce trees to trace the occurrence of budworm outbreaks back in time over hundreds of years (Turner 1952; Elliott 1960; Blais 1954, 1962, 1965, 1981b, 1983).

The reason for better survival of white spruce is not fully understood, but many years of research suggest that it is due to physical rather than chemical factors. Foliage of white spruce is more dense than that of balsam fir and in excess of what is needed. The budworm can consume this excess foliage without adversely affecting the health and vigour of mature trees (Mattson 1985; Lysyk 1990). White spruce produces more buds than balsam fir and these buds grow into longer shoots with larger needles. Because each white spruce bud produces more food, fewer buds need to be consumed per budworm (Greenbank 1963; Batzer 1969; Koller and Leonard 1981). Larvae remain at a single white spruce bud for a longer time, allowing buds not under attack to develop more completely. Also, the growth rate of white spruce is rapid enough that shoot development is able to outpace defoliation (Greenbank 1963; Koller and Leonard 1981; Régnière and You 1991). In contrast, balsam fir buds suffer heavy damage because they are smaller, less abundant, and slower growing. It also has been shown that early-season needles of balsam fir are consumed more easily because they are softer than white spruce needles (Vescio 1995).

Regardless of the reason, it remains an accepted fact that budworm-caused mortality is lower for mature spruce trees than for mature balsam fir trees. The influence of such differential mortality on long-term successional trends is not well understood and it is not known if mortality of spruce also is lower at the regeneration level.

Craighead (1924) observed that the balsam fir component of fir-spruce stands regularly was more damaged by spruce budworm outbreaks than the spruce component. He proposed that the destruction of a much higher percentage of balsam fir logically must lead to a decrease in balsam fir relative to spruce. The superior recuperative powers of spruce, both from natural suppression and budworm defoliation, facilitated this increase in the spruce component.

Craighead (1924) further stated that the trend toward purer stands of spruce was a natural progression that occurred even in the absence of any major disturbance. The shorter-lived balsam fir would drop out of the stand over time, allowing the longer-lived spruce component to increase. A budworm outbreak simply accelerated this process by administering a thinning of the balsam fir. The older the stand, the more severe is the thinning. The surviving spruce occupy a greater percentage of the post-budworm stand and an even greater percentage of the next stand as spruce regeneration becomes established on sites previously occupied by balsam fir. It was concluded that the spruce budworm plays an important role in the conversion of fir-spruce stands to pure spruce.

In the next decade the opposite theory began to emerge. Swaine (1933) stated that one effect of an earlier spruce budworm outbreak in New Brunswick was to increase the balsam fir component from 50% in the previous stands to 85% in the young, new stands.

De Gryse (1944) further advanced the development of this theory, stating it had been expressed repeatedly that the balsam fir component of a stand increases following a spruce budworm outbreak. He observed that accumulated debris on the soil surface hampered spruce regeneration, but was not an obstacle to the rooting of balsam fir seedlings. Balsam fir also was a more aggressive competitor for both light and root space. It was concluded that the aggressiveness of balsam fir regeneration reduces the possibility of replacement by spruce for several generations, if not forever. Succession following a spruce budworm outbreak clearly was toward a balsam fir climax.

Ghent *et al.* (1957) reviewed the earlier theories of forest succession following a spruce budworm outbreak and concluded that the issue had not been resolved adequately. Many theories were based on casual observations rather than scientific study. Craighead (1924) had considered spruce to have superior recuperative powers from natural suppression while De Gryse (1944) had considered balsam fir to have superior shade tolerance and competitive abilities. Changes to species composition as a result of a budworm thinning were not well understood. Surveys conducted in the past had determined only the presence or absence of sufficient regeneration in post-budworm stands and provided little information on changes to species composition at the seedling level.

To take the discussion of such events out of the realm of speculation and place it in a more scientific arena, the Forest Insect Laboratory in Sault Ste. Marie, Ontario initiated a series of intensive investigations of budworm-devastated stands (Ghent *et al.* 1957). Twenty six permanent sample plots averaging 0.4 ha in size were established between 1948 and 1950 in three areas where the Forest Insect Laboratory maintained field stations: seven plots near Laniel Quebec, thirteen plots near Black Sturgeon Lake in north-central

Ontario, and six plots near Cedar Lake in northwestern Ontario. Stand attributes were tallied in 1950 at which time all areas had been or were being destroyed by the spruce budworm, but overstory mortality had not altered understory conditions appreciably. A re-tally of plots was conducted in 1955, at which time overstory mortality was more or less complete and seedlings had benefited from release. The goals of the 1955 re-measurement were to provide a check on any short-term successional trends that might have developed and to determine if a budworm disturbance influenced succession in favour of balsam fir or spruce (Ghent *et al.* 1957).

Investigations of regeneration at Laniel, Black Sturgeon Lake, and Cedar Lake revealed that black spruce constituted only about 10% of all spruce seedlings tallied in the plots. It was felt that this small number of seedlings did not provide satisfactory data for separate analysis. Ghent *et al.* (1957) therefore adopted the common practice of combining white spruce seedlings and black spruce seedlings, referring to both species collectively as "spruce".

The findings of Ghent *et al.* (1957) answered many questions regarding succession in budworm-devastated stands. Age determinations of seedlings by ring counts at ground level clearly showed that the overwhelming majority of balsam fir and spruce seedlings already were established in the understory prior to budworm outbreak. Given that seedlings in the chosen study areas were established already, the authors were concerned primarily with comparing relative growth rates of the species as a measure of their competitive abilities.

Height class distributions of fir and spruce seedlings in 1950 were identical, except that there were fewer spruce than fir in each height class (Ghent *et al.* 1957). The re-tally of 1955 showed exactly the same results. Fir and spruce seedlings had identical height distributions, except for fewer spruce in each class. Mean heights of balsam fir and spruce seedlings were found to

be not significantly different in 1950 or in 1955. Distributions for both species simply had shifted together into upper height classes over the five-year period. There was no evidence of a consistent difference in rate of height growth for these species while suppressed or immediately following release. It was concluded that rate of height growth is not a factor in interspecific competition at the seedling level. Both species competed equally well.

Seedling counts were conducted in all plots using 4-m^2 sub-plots at a 10% sample intensity (Ghent *et al.* 1957). Results of this sampling showed that both balsam fir and spruce seedlings decreased in number by 20-65% over the five-year period. This decrease was equivalent to over 13,000 balsam fir seedlings per hectare in some plots at Black Sturgeon Lake. Dead seedlings encountered during the 1955 re-tally made up only 0.9 and 1.4 per cent of the reduction in seedlings for balsam fir and spruce respectively, leaving a large number of seedlings unaccounted for. Further investigations revealed that many seedlings had been covered by fallen logs as budworm-killed trees deteriorated and fell to the ground. Coverage by fallen logs accounted for 72% of the decrease in balsam fir seedlings. Intense shrub competition, which developed as the overstory opened up and more light was allowed to reach the forest floor, accounted for an additional 16% of the decrease in balsam fir seedlings. Together, fallen logs and shrub competition accounted for between 75% and 90% of seedling mortality.

Despite appreciable decreases in seedling numbers for both balsam fir and spruce, the ratios of balsam fir to spruce seedlings remained relatively unchanged over the five-year period (Ghent *et al.* 1957). Trends of both increasing and decreasing balsam fir were shown by the data, but most changes were minor and attributed to the random destruction of seedlings by fallen trees. When data from all plots were considered together, the ratio of

increasing to decreasing trends was 11:12. No inherent difference between survival of balsam fir and spruce seedlings could be shown.

The ratio of balsam fir to spruce for the tree stratum in 1950 was compared to the same ratio for seedlings in 1950 and in 1955 (Ghent *et al.* 1957). Trends of both increasing and decreasing balsam fir were found once again, with an apparent overall effect of increasing balsam fir relative to spruce. These trends varied according to region of study, however, and the overall trend toward more balsam fir may have been influenced by the unequal number of plots established in each region. Regional differences in trends were considered to be an important finding. Different trends in different regions could explain the existence of theories both for and against an increase of balsam fir following a budworm outbreak. Both theories may be correct, with each being applicable only under a specific set of circumstances or in a specific region.

Ghent *et al.* (1957) stated that questions of seed supply, germinative ability, and survival during early years of growth clearly are important in better understanding relative numbers of balsam fir and spruce seedlings. They found there was no recruitment of new seedlings for a period of time following overstory defoliation, but noted that in some plots where defoliation was less severe there was a slight increase in the number of spruce seedlings from 1950 to 1955. This finding suggested the possibility of differential establishment of new seedlings following a spruce budworm outbreak. Mortality of spruce trees was known to be lower and more patchy than that of balsam fir trees, allowing a continued supply of seeds from recovered spruce trees after the balsam fir overstory had been eliminated. A lack of understanding of such processes prevented any reliable prediction of the pattern of forest succession following a spruce budworm outbreak.

Ghent *et al.* (1957) concluded that established balsam fir and spruce seedlings share a remarkable ecological equivalence. They found no evidence that either species enjoys a consistent competitive advantage over the other. It was reasoned that if some selective advantage had been operating uniformly after every major forest disturbance, it surely would have eliminated the less favoured species. Both balsam fir and spruce were found to be capable of disproportionate reproduction, but the overall relationship was one of ecologically similar species commonly found in competitive association.

The plots at Laniel, Black Sturgeon Lake, and Cedar Lake were visited again in mid-summer of 1961 to track the development of regeneration and assess new seedling recruitment from possible seed sources (Fye and Thomas 1963). Results of the seedling re-tallies showed that there had been no new recruitment of seedlings on any of the five remaining plots at Cedar Lake. In contrast, new seedlings were found in all plots at Laniel and in 11 of 13 plots at Black Sturgeon Lake. Some plots showed a higher recruitment of balsam fir, while others showed a higher recruitment of spruce. Overall, new balsam fir seedlings greatly outnumbered new spruce seedlings. Seed sources from which new seedlings originated were determined to be residual trees that had survived the budworm outbreak.

In 1962, a sub-sample of regeneration from four plots at Black Sturgeon Lake was analyzed to determine height growth characteristics over the previous ten years (Fye and Thomas 1963). For both fir and spruce, average height increments over the ten-year period were greatest for taller regeneration and smallest for shorter regeneration. Thus, the taller regeneration already had established dominance and was enjoying rapid height growth. Shorter regeneration was becoming suppressed and much of it had been reduced to low-vigour survival status, similar to that of regeneration under the mature stand

before the budworm outbreak. It was concluded that the larger, faster-growing seedlings likely would go on to form the next merchantable stand. Average annual increments in height growth for balsam fir and spruce were found to be very similar over all height and diameter classes, providing a further example of the competitive equality of the two species. Continued competition, continued loss of suppressed seedlings, and continued recruitment of new seedlings as dominant regeneration reached seed-bearing age likely would bring about more changes in the future (Fye and Thomas 1963).

Many years passed without much research on budworm-caused changes to the species composition of the forest. It became generally accepted that spruce species fit quite well into the budworm / forest system. White, red, and black spruce all were fed upon by the spruce budworm to an equal or lesser extent than balsam fir. These spruces also were quite tolerant of shade, being equally or slightly less tolerant than balsam fir. It had been shown that balsam fir and the spruces were ecologically similar in many respects. Fir-spruce forests generally were replaced by fir-spruce forests following budworm outbreaks and it appeared that the continued existence of this forest type was in no way threatened by the spruce budworm (Witter et al. 1984; Mattson et al. 1988). Following a spruce budworm outbreak, proportions of spruce could increase or decrease on any particular site, but changes were dependent on many variables. Over an entire region, however, the proportion of spruce appeared to remain stable (Witter et al. 1984; Blais 1985; Mattson et al. 1988).

It may be that the spruce budworm is responsible for maintenance of the spruce component in mixed forests. Balsam fir, because of its superior shade tolerance and highly aggressive regeneration, is the only boreal species considered to be readily capable of continual establishment beneath a closed canopy (Rowe 1961; Dix and Swan 1971; Zoladeski and Maycock 1990). In the

absence of disturbance, the balsam fir component of a forest increases and may even assume complete dominance (Grigal and Ohmann 1973; Mattson *et al.* 1991b). The spruce budworm provides a periodic disturbance that not only maintains the dominance of balsam fir, but also "rescues" less shade-tolerant and less aggressive species, including hardwoods as well as spruce (Baskerville 1975; Gordon 1985). Without such a disturbance, it is possible that species other than balsam fir might be doomed to eventual exclusion.

Gordon (1985) undertook long-term monitoring of plots (established 1959-1960) in balsam fir / white spruce and balsam fir / red spruce forests in Ontario. Monitoring continued over a period of time in which the spruce budworm reached epidemic proportions in both stand types, with similar consequences. Spruce budworm outbreaks were found to exert an influence on species composition of host trees that clearly is in favour of spruce.

Gordon (1985) has proposed that an increase in the spruce component of a stand may be brought about by the spruce budworm in two ways. First, the budworm causes severe mortality of mature balsam fir in the overstory. This high mortality results in almost complete elimination of the balsam fir seed source. Immature, suppressed balsam fir trees also are eliminated, insuring that a balsam fir seed source is absent for many years to come. Mortality of spruce trees, both mature and suppressed, is lower than that suffered by balsam fir. Surviving spruce trees recover and continue to produce seed during the absence of mature balsam fir. This continued production of seed by spruce trees leads to a higher number of spruce seedlings becoming established in the understory.

The second way in which the budworm may increase the spruce component of a stand is through direct feeding on established regeneration (Gordon 1985). Balsam fir seedlings growing in the understory are more

heavily damaged than spruce seedlings. The budworm administers a thinning of established regeneration, removing more balsam fir than spruce and thereby increasing the spruce component of future stands. On the basis of these findings, Gordon (1985) proposed that the spruce budworm is an essential factor in maintaining the spruce component of fir-spruce forests through time.

In an earlier study, Vincent (1956) documented budworm-caused mortality to understory regeneration in New Brunswick. While the published results of the study treated fir and spruce seedlings collectively rather than separately, Vincent considered it worthwhile to note that only a single dead spruce seedling was encountered, despite the fact that seedling mortality was almost 50% in some areas.

Even if budworm-caused mortality among seedlings is not widespread, the higher levels of damage suffered by balsam fir seedlings may allow spruce seedlings to gain a height advantage (A.G. Gordon, personal communication, 1994). This early height advantage enables spruce seedlings to become established as dominant individuals in the understory. Once taller, spruce seedlings are able to maintain their advantage and eventually out-compete the more abundant fir seedlings that surround them.

HISTORY OF THE BLACK STURGEON LAKE STUDY AREA

The study to be described in this report was conducted in a boreal mixedwood forest in Ontario, located southwest of Lake Nipigon near Black Sturgeon Lake. This area falls within Rowe's (1972) B.10 - Nipigon Forest Section of the Boreal Forest Region, which encompasses the Lake Nipigon basin. The entire basin once was under water as part of post-glacial Lake Warren or Lake Algonquin. As a result, soils in this area consist of bedded

lacustrine sands and clay deposits laid down on the floor of an ancient lake. The best forests occur to the south and west of present Lake Nipigon where the deep, better drained soils support mixed stands of trembling aspen, white birch, black spruce, white spruce, and balsam fir. Balsam fir and white spruce are prominent on sites where fire has not occurred for an extended time (Rowe 1972). Halliday and Brown (1943) state that the area immediately southwest of Lake Nipigon is one of two areas in northwestern Ontario with an exceptionally high concentration of balsam fir; the other area is located further west near Lac Seul.

Some of the most comprehensive studies of regeneration in budworm devastated stands have been conducted in the Black Sturgeon Lake area by the Forest Insect Laboratory in Sault Ste. Marie (Ghent *et al.* 1957; Ghent 1958a, b; Ghent 1963; Fye and Thomas 1963). The early history of the area is quite well known and includes trial applications of DDT in the 1940's (Elliott 1960). The Canadian Forest Service in Sault Ste. Marie still monitors budworm populations in this area on an annual basis.

It seems likely that the area southwest of Lake Nipigon has been subjected to periodic outbreaks of the spruce budworm for a very long time. The earliest evidence of a spruce budworm outbreak in northwestern Ontario comes from the Lake Nipigon area. Patterns of radial growth in a 300-year old white spruce showed characteristic ring suppression of a spruce budworm outbreak beginning in 1702 and lasting for ten years. Little is known about this outbreak because no other trees this old could be found (Blais 1985).

Patterns of growth-ring suppression in old white spruce trees indicate that a spruce budworm outbreak occurred over the entire Lake Nipigon basin between 1800 and 1810. Another outbreak occurred between 1880 and 1890,

but this outbreak was more restricted to the area southwest of Lake Nipigon. The exact boundaries of these outbreaks remain uncertain (Elliott 1960).

Direct observations of spruce budworm outbreaks in the 20th century have provided a recent history with somewhat better detail. A well-developed spruce budworm outbreak was discovered in 1943 in an area southwest of Lake Nipigon and just north of Black Sturgeon Lake (Elliott 1960). The exact time of origin of this outbreak is not known because it already was underway when discovered, but studies conducted in the area suggest that severe defoliation first occurred in 1937 or 1938 (Fettes 1950; Belyea 1952; Ghent 1958b; Elliott 1960). The area of infestation grew rapidly over the next few years and was widespread by 1942 (Elliott 1960).

As the area of interest for the present study is located quite close to the "epicentre" of this outbreak, it seems likely that the infestation had spread to the study area by about 1940. As it turns out, however, the Great Lakes Forest Products Company was given cutting rights for the Black Sturgeon Lake area at the same time that this outbreak was developing. The company established its first cutting camp in the area in 1937 and two of the four plots used in this study were harvested shortly thereafter (R. Klein, personal communication, 1995). Government of Ontario Forest Resources Inventory (FRI) maps suggest that the other two plots used in this study were harvested about ten years later, by which time they likely had suffered from heavy defoliation by the spruce budworm. The spruce budworm outbreak that began in the Black Sturgeon Lake area in the late 1930's was extremely severe and continued until 1949 when budworm populations dropped sharply. The study area fell within a zone of severe defoliation where 100% of the balsam fir trees were killed (Elliott 1960).

In accordance with standard harvesting practices of the time, all plots in the study area were clearcut and wood was removed from the sites using horses (R. Klein, personal communication, 1995). Most white birch and trembling aspen were left standing as they were not merchantable species at that time. Site disturbance was minimal and a thick layer of fir and spruce regeneration was left largely intact. Klein conducted a survey of the study area in 1960, at which time regeneration was so thick that one had great difficulty walking through it. Over 80% of the stems in the area at this time were young balsam fir.

Another outbreak of the spruce budworm was detected in the Lake Nipigon area in 1980. Once again, the outbreak began in the area immediately southwest of Lake Nipigon near Black Sturgeon Lake (Sanders, personal communication, 1993; Blais 1985). At initiation of the current study in 1993, the 1980 outbreak still had not collapsed. Mortality among host trees was high and salvage/presalvage operations were underway. There has been much discussion about how to manage the complex and problematic mixedwood forest type in the Black Sturgeon area. Given the large size of the current budworm infestation, it will not be possible to carry out salvage operations in all stands. Many areas will have to be left to regenerate naturally. What will be the fate of the spruce component of these forests? Do late-instar budworm larvae that disperse to the understory eat more balsam fir than spruce regeneration, thereby favouring a higher component of spruce in the next stand? Is the highly desirable spruce component in this forest type likely to increase, or is the area destined to become even more dominated by balsam fir and even more susceptible to future outbreaks of the spruce budworm?

PROJECT OVERVIEW

LOCATION AND LAYOUT OF STUDY PLOTS

A portion of boreal mixedwood forest located about 120 km northeast of Thunder Bay, Ontario, near Black Sturgeon Lake, was selected as a study area in early spring of 1993 (Fig. 1). The forest in this area contained a high percentage of balsam fir and good representation of all other tree species commonly found in a boreal mixedwood. An outbreak of the spruce budworm had begun in the area about 1980 and was still underway at the time of this study in 1993. The outbreak already had persisted for longer than most and was expected to collapse at any time (C.J. Sanders, personal communication, 1993). These conditions provided an excellent opportunity to study dispersal of late-instar budworm larvae and to assess the impact of these larvae on host-tree natural regeneration.

Four 10-ha (320 m by 320 m) study plots were established in conjunction with a large, multi-disciplinary, multi-agency project known as the Black Sturgeon Boreal Mixedwood Research Project. Locations for these plots were selected in early June of 1993 with the assistance of Dr. C.J. Sanders of the Canadian Forestry Service (CFS) in Sault Ste. Marie and Dr. Y.H. Prévost of Lakehead University in Thunder Bay. The four plots used in this study were integrated with a number of other 10-ha plots being established by Dr. J.B. Scarratt, CFS coordinator for the larger Boreal Mixedwood Project.

The area selected for study was located near the intersection of the Black Sturgeon Road and an airstrip for small planes (49°14' N, 80°45' W).
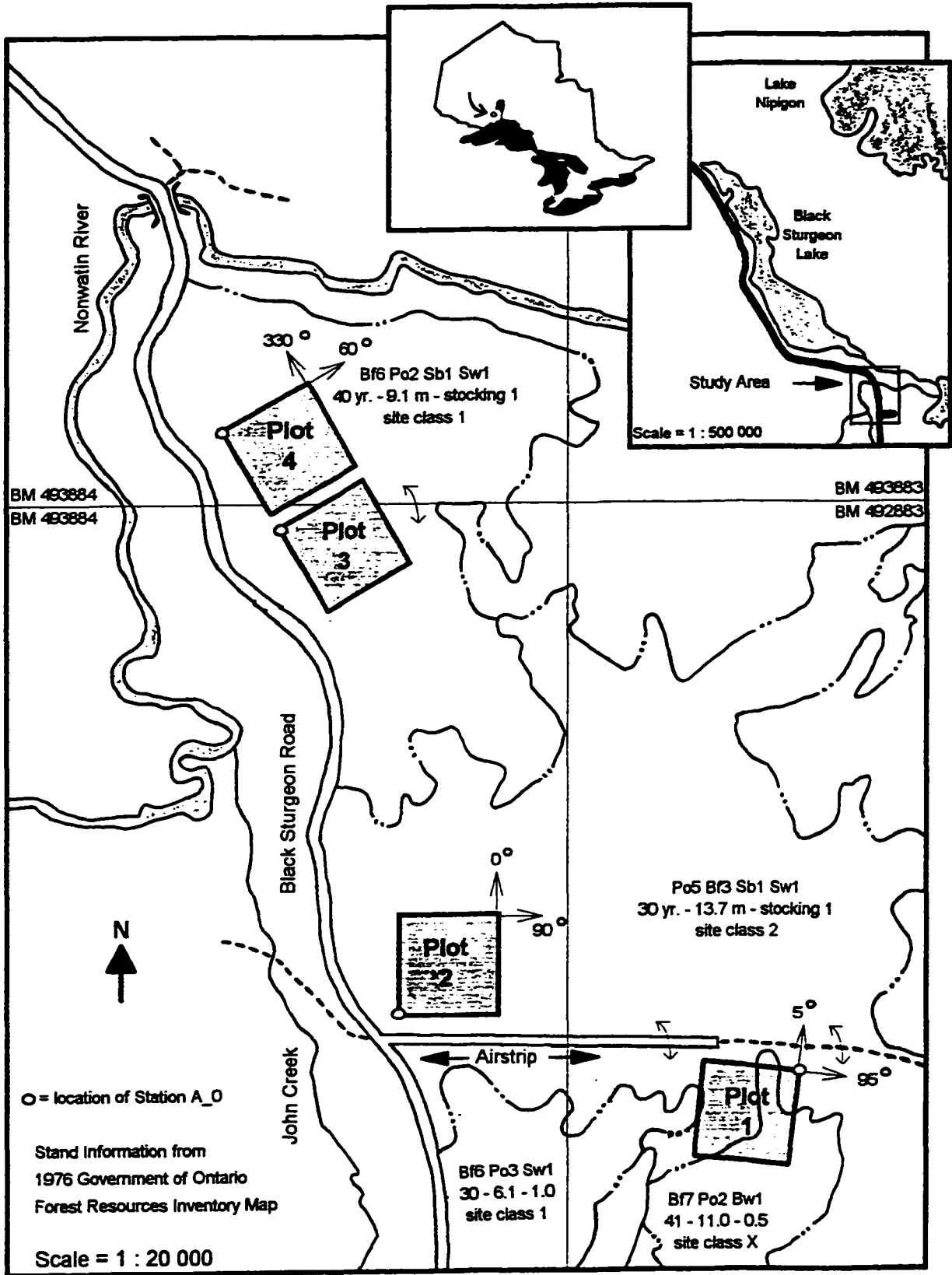
Figure 1. Map of study area and plot locations.

Stand information from 1976 Government of Ontario Forest Resource Inventory (FRI) maps indicated that stands in the area were 30 and 40 years old, putting 1993 ages at 47 and 57 years (Fig. 1).

Perimeters of the four study plots were established by compassing and chaining. Plot boundaries were marked clearly using paint and flagging tape. A series of parallel lines was marked through each plot at a 40 m spacing and stations were established along each line at 40 m intervals, resulting in a system of major grid-lines running in two directions. The nine lines running in one direction were assigned the letters A to I. The nine lines running perpendicular to these were assigned the numbers 0 to 8. Grid-line intersection points were deemed "stations" that could be chosen as random locations for sampling. Each station was identified by grid-line coordinates consisting of a letter-number combination (e.g. B_2) (Fig. 2). Station coordinates were painted on the tree nearest each grid-line intersection point.

A system of minor grid-lines, running midway between all major grid-lines, was assumed to exist but was not physically marked. These invisible lines were named according to major grid-lines running along either side of them (e.g. B-C or 2-3). Together, major and minor grid-lines resulted in a system of grid-lines spaced at 20 m intervals. Intersection points of all grid-lines, major and minor, were considered to be stations, thus increasing the total number of stations available without having to spend an excessive amount of time on layout. Stations lying on minor grid-lines were located where necessary by compassing and measuring from well-marked stations on major grid-lines. Stations on minor grid-lines were named by assigning the appropriate letter-number combination (e.g. BC_23 or CD_3) (Fig. 2).

GENERAL PLOT LAYOUT
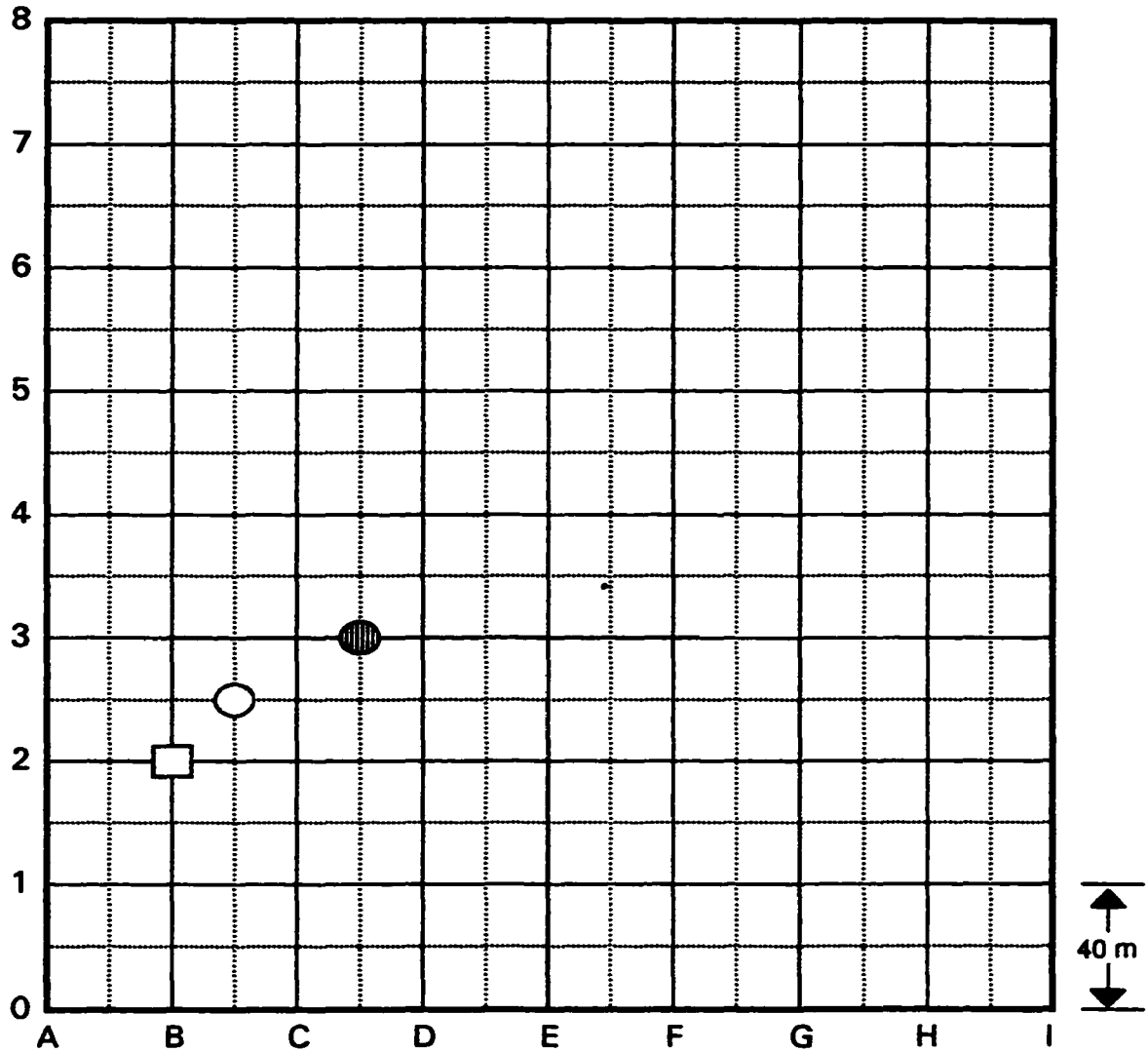
Examples of using co-ordinate system to name stations.

▨ Station B_2

◯ Station BC_23

⬤ Station CD_3

Figure 2. Layout and naming convention for system of grid-lines used in study plots.

SAMPLING ACTIVITIES

Field work for this study consisted of four main parts: 1) sampling at selected tree species, 2) sampling at random locations, 3) sampling at selected white spruce regeneration sites, and 4) destructive sampling of seedlings. Random selection of sampling sites was achieved through the assignment of a three-digit number to each station (on a map similar to that shown in Fig. 2) and the selection of a subset of stations using a random number table (McClave and Dietrich 1988).

Sampling at selected tree species involved the collection of 45-cm branch tips from the upper mid-crown level of mature host trees. At 20 randomly selected stations in each 10-ha plot, one branch sample was collected from the nearest dominant or co-dominant balsam fir, white spruce, and black spruce tree using pole pruners. Because all samples could not be collected at one time, branch samples were collected from a random sub-sample of the twenty stations in each plot on three different dates. Branch samples were used to compare foliage characteristics between host trees and to determine canopy-level budworm densities. Water traps (consisting of plastic trays filled with water) were placed on the ground beneath each of the same trees from which a branch sample was collected. All traps were checked every few days during the late-instar dispersal period to determine how many larvae dispersed to the understory from each host-tree species. Regeneration assessments were conducted in 4-m^2 sub-plots around each water trap to determine the amount of damage caused by budworm larvae feeding in the understory.

Sampling at random locations involved the establishment of vegetation sub-plots to gain an unbiased estimate of stand structure and species composition at the overstory and understory levels. Overstory conditions were

documented through stem tallies of trees in 1/100-ha sub-plots. Smaller 4-m^2 sub-plots were used to document non-host understory vegetation and host seedling densities. Initially, sub-plots were established at 30 locations per 10-ha plot. An additional 20 sub-plots in each 10-ha plot later were established to increase sampling intensities.

Sampling at selected white spruce regeneration sites involved assessments of budworm damage to regeneration at ten locations per plot. This part of the study was necessitated by a lack of spruce regeneration encountered in earlier sampling. Higher numbers of spruce seedlings were required for comparison of budworm damage between host-regeneration species. Sites at which white spruce regeneration was most abundant were sought out and 4-m^2 sub-plots were established at these locations.

Destructive sampling of seedlings involved the collection of seedlings from outside the boundaries around two study plots. Annual growth rings on a stem cross-section at ground level were counted to determine the age of each seedling. Data were used to establish height-age relationships for balsam fir and white spruce seedlings in the study area.

The locations of all sampling sites are summarized in plot maps in Appendix II. All sampling was conducted during the summer of 1993 (Fig. 3). Budworm damage was determined using a variation of the Fettes method of spruce budworm defoliation assessment (Fig. 4). This method is used commonly by forest entomologists to document budworm damage to foliage (Sanders 1980). For both branch samples and seedlings, the 25 most distal buds were observed and a Fettes score was assigned to each bud. All scores then were averaged to produce a representative score for the branch sample or seedling. Defoliation scores were based on total number of buds where seedlings had less than 25 buds.
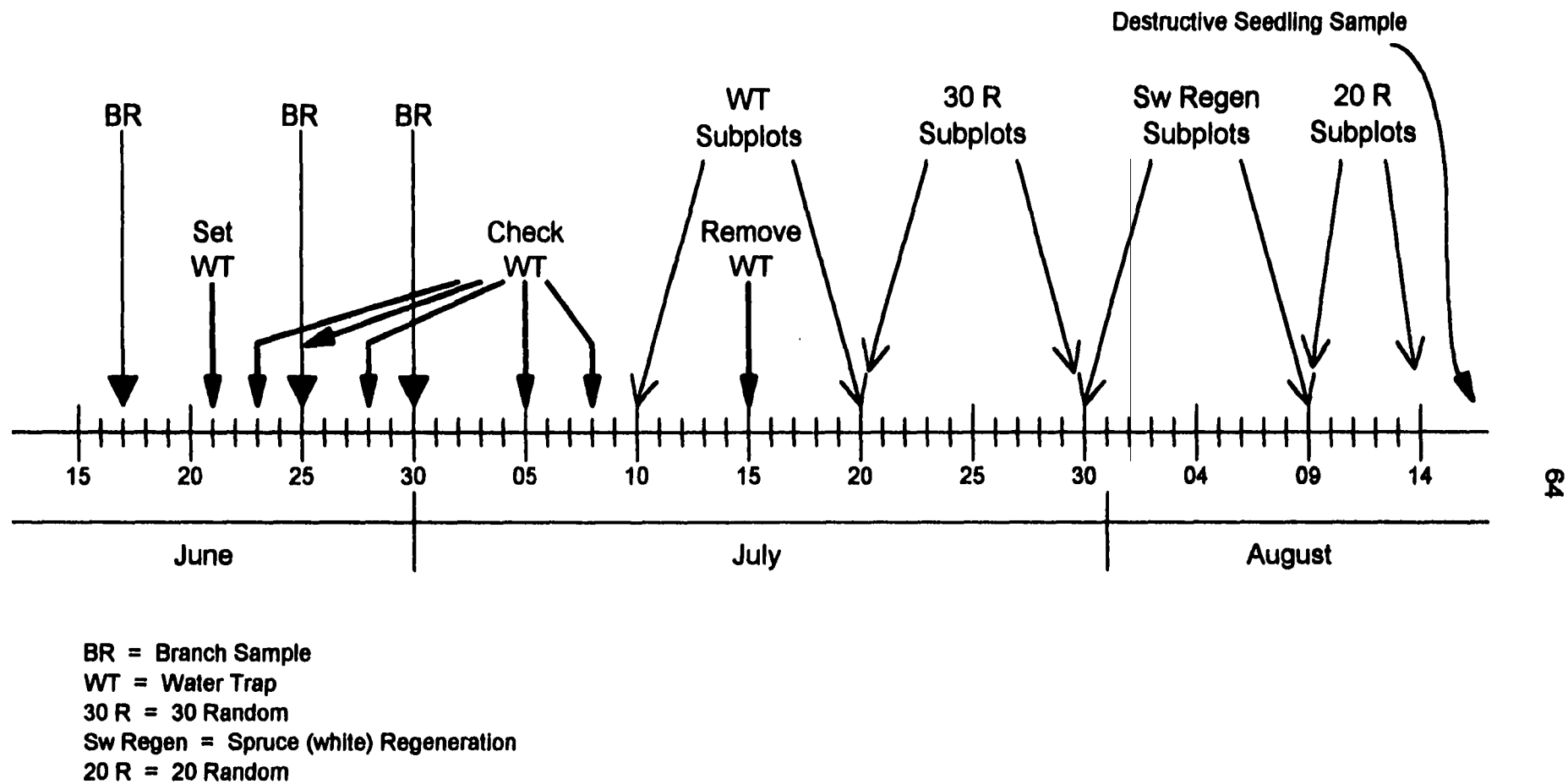
Figure 3. Schedule of sampling activities in 1993.

BR = Branch Sample
WT = Water Trap
30 R = 30 Random
Sw Regen = Spruce (white) Regeneration
20 R = 20 Random

Fettes Method
of SBW Defoliation Assessment
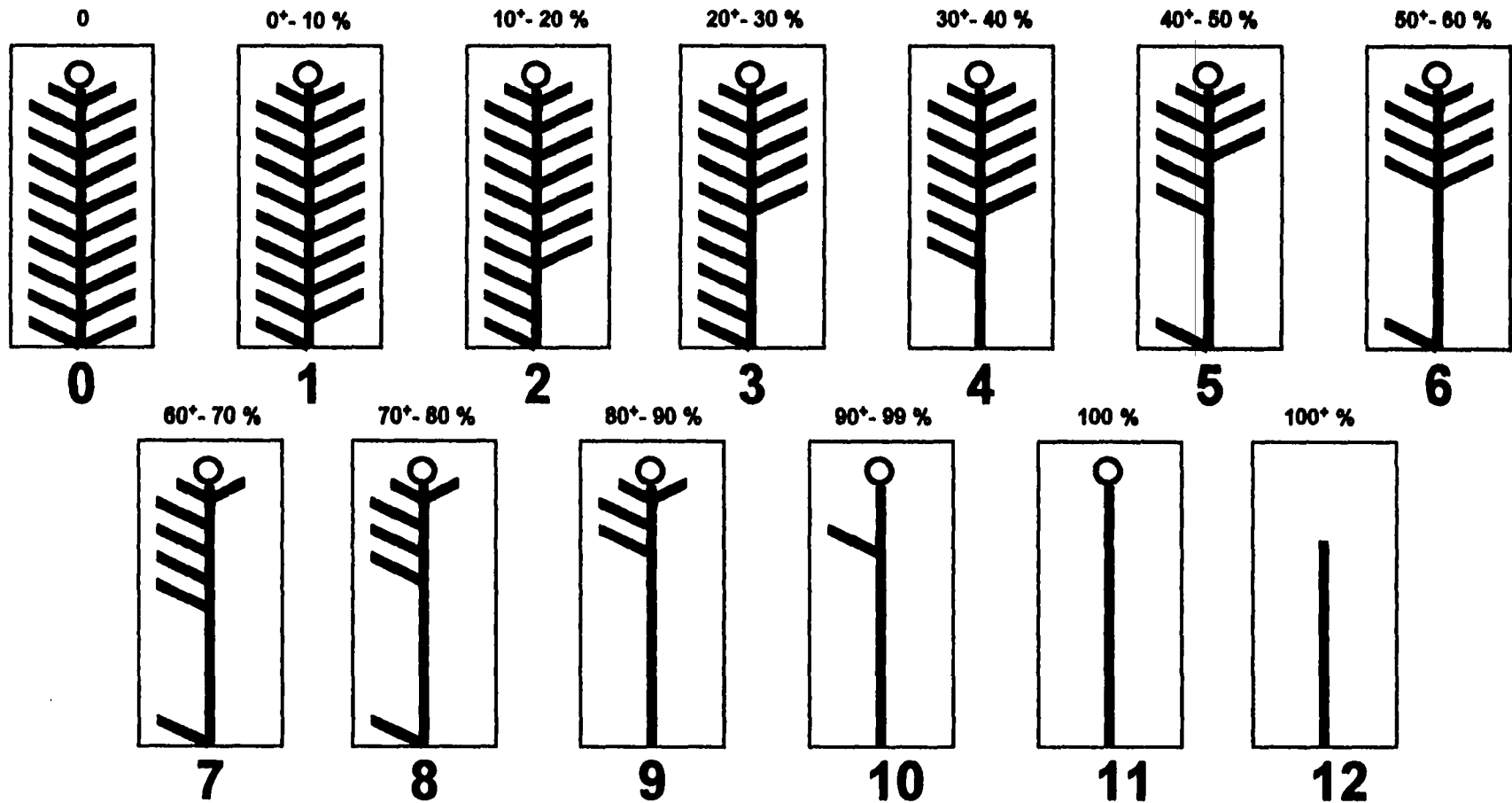
Figure 4. Fettes Method of spruce budworm defoliation assessment. (After Sanders 1980 and Allen *et al.* 1984)

ANALYSES OF DATA

All data were recorded on tally sheets while in the field and later entered into Microsoft Excel spreadsheets. Prior to analysis, variables in each data set were verified and examined for outliers. Summary statistics and various analyses were generated using SPSS for Windows, Release 6.1, 1994.

Analysis of variance (ANOVA) was employed wherever possible to explore differences between groups of data (cells) for each response variable. Prior to analysis of data for each variable, a spread-versus-level test between cells was used to determine an appropriate data transformation. Transformations were applied to the data where necessary to ensure that ANOVA assumptions of normal distribution and homogeneity of variances among all cells were met (Norusis 1992, SPSS 1994). Where raw data for a variable included zeros the data were "started" by adding "1" to each value, thus avoiding undefined values for transformed data (Brown 1993). If ANOVA indicated that statistically significant differences existed, then a multiple range test was used to determine where these differences occurred. A fairly conservative Tukey's Honest Significant Difference (Tukey-HSD) test was employed for all multiple range tests.

Nonparametric statistical tests were used where ANOVA assumptions could not be met through transformation of the data. A Kruskal-Wallis oneway test was used to determine whether significant differences existed between cells. If significant differences were found to exist, a series of Mann-Whitney tests between pairs of cells was used to determine where. Both the Kruskal-Wallis oneway and the Mann-Whitney test between pairs of cells are nonparametric procedures that make no underlying assumptions about the distribution of the data (Norusis 1992).

PART I – RANDOM SAMPLING

PURPOSE

Although carried out later than some other sampling activities, random sampling is discussed first to provide a further introduction to the forest type under consideration. Sub-plots were established at random locations to obtain unbiased estimates of stand structure and species composition within study plots. Overstory trees, understory vegetation, and host regeneration are described.

METHODS

Sub-plot centres were established by driving wooden stakes into the ground at 30 randomly selected stations per 10-ha plot. A nail was set in the top of each stake to serve as an anchor for plots cords, which formed radii for two sizes of circular sub-plots at each location. A 5.64 m cord was used to form the radius of a 1/100-ha sub-plot, within which all trees were tallied by species and diameter at breast height (DBH = 1.3 m). Stem calipers were used to classify stems into 2-cm diameter classes. All stems within a DBH class of 4 cm (3.0 - 4.9 cm) and greater were considered to be trees. Stems with a DBH of 3.0 cm or less were considered to be regeneration. The division between trees and regeneration was somewhat arbitrary, but there appeared to be a natural gap between larger and smaller stems at this point.

A 1.128 m cord was used to form the radius of a 4-m^2 sub-plot, within which characteristics of lesser vegetation were documented. Percentage cover of understory vegetation was estimated for all species, except host seedlings which were tallied by stem. Heights of high shrub species were measured, while low shrub and herbaceous species were assigned a typical height value. Percentage of ground cover occupied by leaf litter and feathermoss also was recorded for each sub-plot.

All host seedlings contained within 4-m^2 sub-plot boundaries were tallied by species. Height, maximum crown width, and crown width perpendicular to the maximum were measured to the nearest centimetre using rulers. Number of buds was counted to a maximum of 25. Seedlings with more than 25 buds were assigned a bud count value of 26. Based on assessment of the 25 most distal buds, a mean defoliation score was generated for each seedling using the Fettes method (Fig. 4). The leader of each seedling was examined and classified as: 1) no damage, 2) <50% damage, or 3) >50% damage. The substrate that anchored each seedling was examined and classified as: 1) mineral soil exposed by a fallen tree, 2) undisturbed leaf litter and/or feathermoss, or 3) rotting woody debris.

Sub-plots later were established at an additional 20 random locations in each 10-ha plot to increase sampling intensities. Trees and understory vegetation were tallied as described above. Seedlings in the additional sub-plots were tallied by species, but were not measured or assessed for defoliation and microsite. Thus, descriptives for trees, understory vegetation, and seedling densities are based on data from 50 sub-plots per 10-ha plot, while descriptives for physical characteristics of seedlings (height, defoliation, etc.) are based on data from 30 sub-plots per 10-ha plot.

RESULTS

Tree Stratum

Stem tallies of trees in all plots were combined and used to calculate basal area per hectare as a simple measure of importance of each tree species in the study area (Fig. 5). It is clear that the forest once was heavily dominated by balsam fir, but mortality has reduced the importance of this species substantially. In contrast, mortality of white spruce and black spruce appears to be less pronounced.
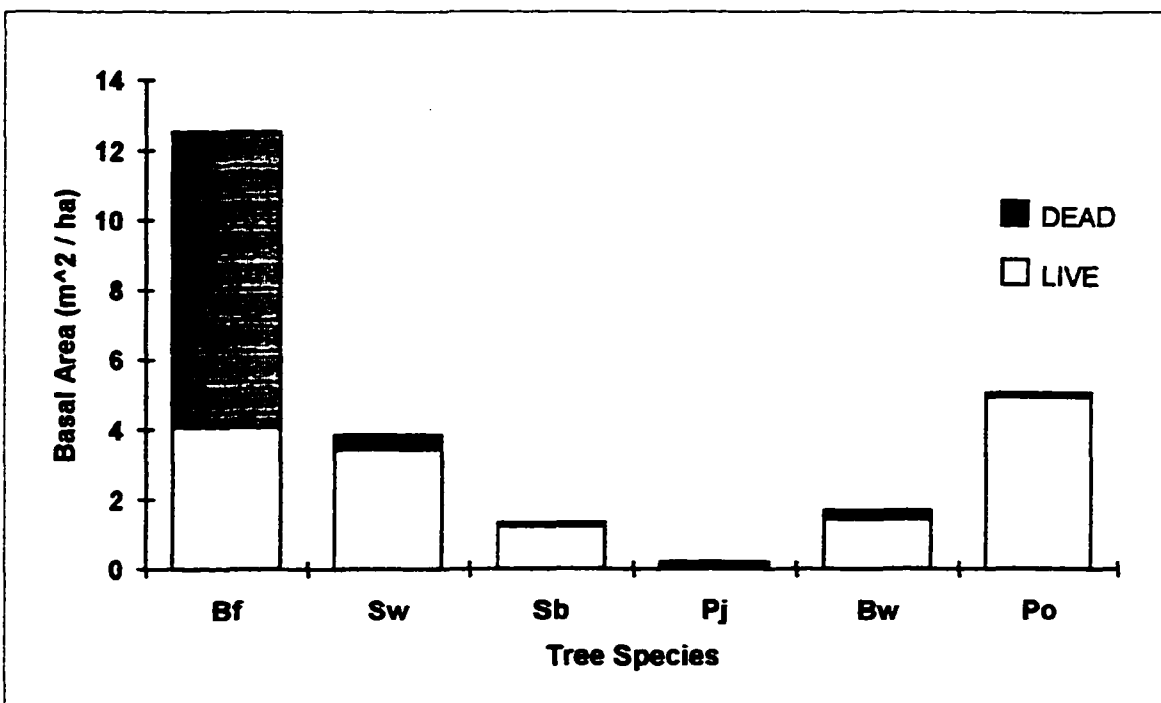
Bf = balsam fir   Sb = black spruce   Bw = white birch
Sw = white spruce   Pj = jack pine   Po = trembling aspen (poplar)

Based on all trees in DBH classes of 4 cm and greater in 200 random sub-plots (1/100 ha).

Figure 5. Basal area per hectare by tree species.

Jack pine is a minor component of the forest in the study area. A few mature trees were found growing on or beside old skid trails, probably as a result of increased site disturbance at these locations when the forest was last harvested. A single live white pine (14 cm DBH class) was tallied in plot 3. Although extremely rare in the study area at this time, white pine appears to have been far more abundant in the past. Stumps of large white pine trees, some with diameters in the 75 cm range, were encountered occasionally, but no stumps of this size fell within the sub-plots that were established. In general, all stumps encountered in the study area were larger than those of trees in the present forest. Most stumps appeared to be from large white spruce trees, although positive identification was difficult given the advanced stage of decay.

The structure of the present tree stratum can be seen in more detail when data are broken down by diameter class for each species in each plot (Appendix III). Diameter class distributions for the five main tree species are shown graphically for Plots 1, 2, 3, and 4 in Figures 6, 7, 8, and 9 respectively. All five species of trees common to a boreal mixedwood are found in all plots, but there is some variation in species composition. Trembling aspen is an important overstory species in all plots. White birch is more prominent in Plots 1 & 2 than it is in Plots 3 & 4. Despite the high mortality it has suffered, balsam fir remains the most abundant species in all plots, especially among the middle and lower diameter classes. White spruce is never found in abundance, but its presence is fairly consistent in all plots and over all diameters, including the largest classes. Black spruce is more abundant in Plot 1 than it is in any of the other plots. The general structure of budworm host-trees can be seen when stem tallies for these species in all plots are combined (Fig. 10).

Mortality of balsam fir in all plots clearly increases as diameter class decreases (Figures 6-10). White spruce and black spruce also have suffered

Plot 1
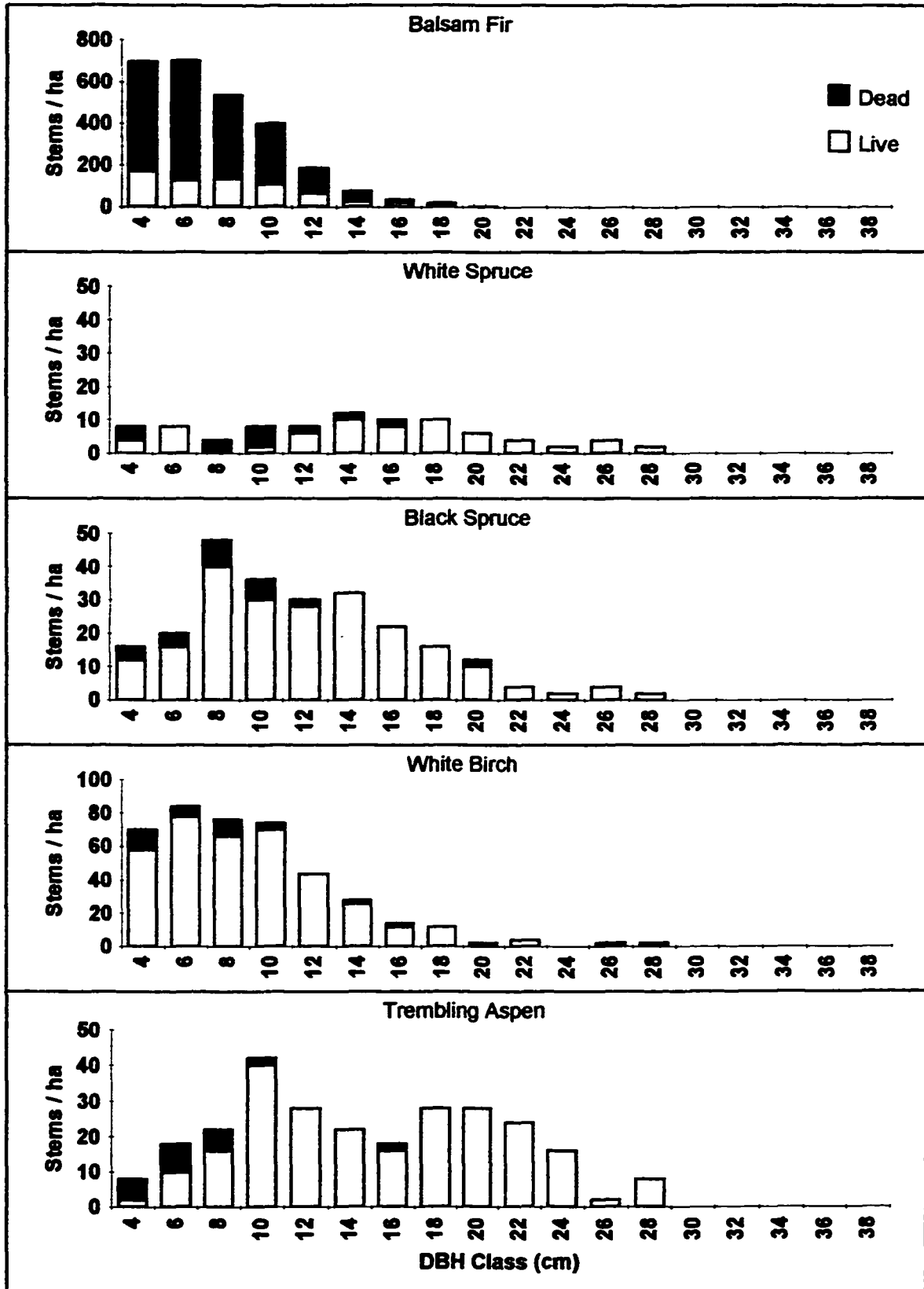
Figure 6. Live and dead stems per hectare by tree species in Plot 1.

Plot 2
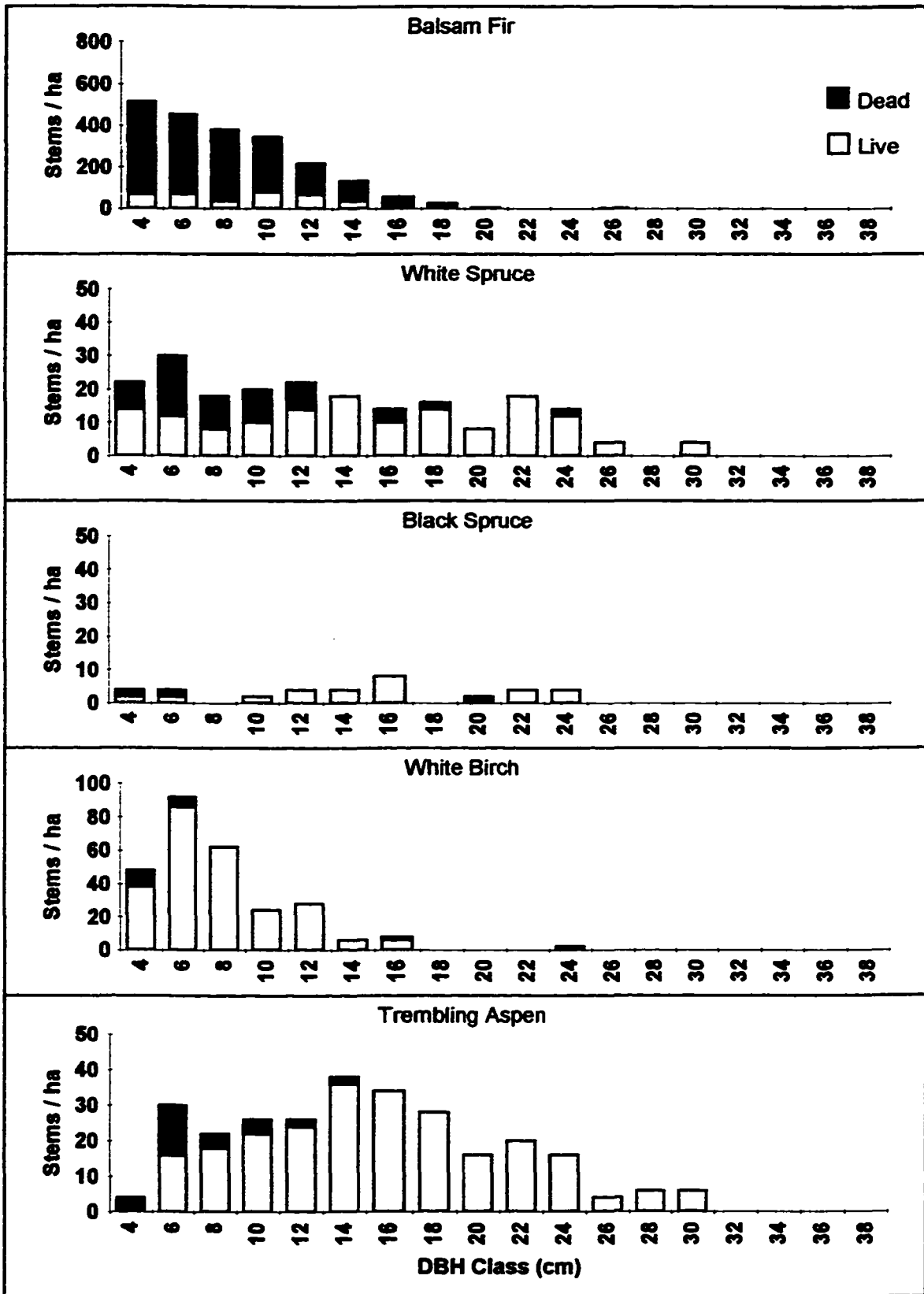
Note changes in vertical scale.   Based on fifty 1/00 ha sub-plots.

Figure 7. Live and dead stems per hectare by tree species in Plot 2.

73

Plot 3

Balsam Fir

■ Dead
☐ Live

White Spruce

Black Spruce

White Birch

Trembling Aspen

DBH Class (cm)

Note changes in vertical scale.

Based on fifty 1/100 ha sub-plots.
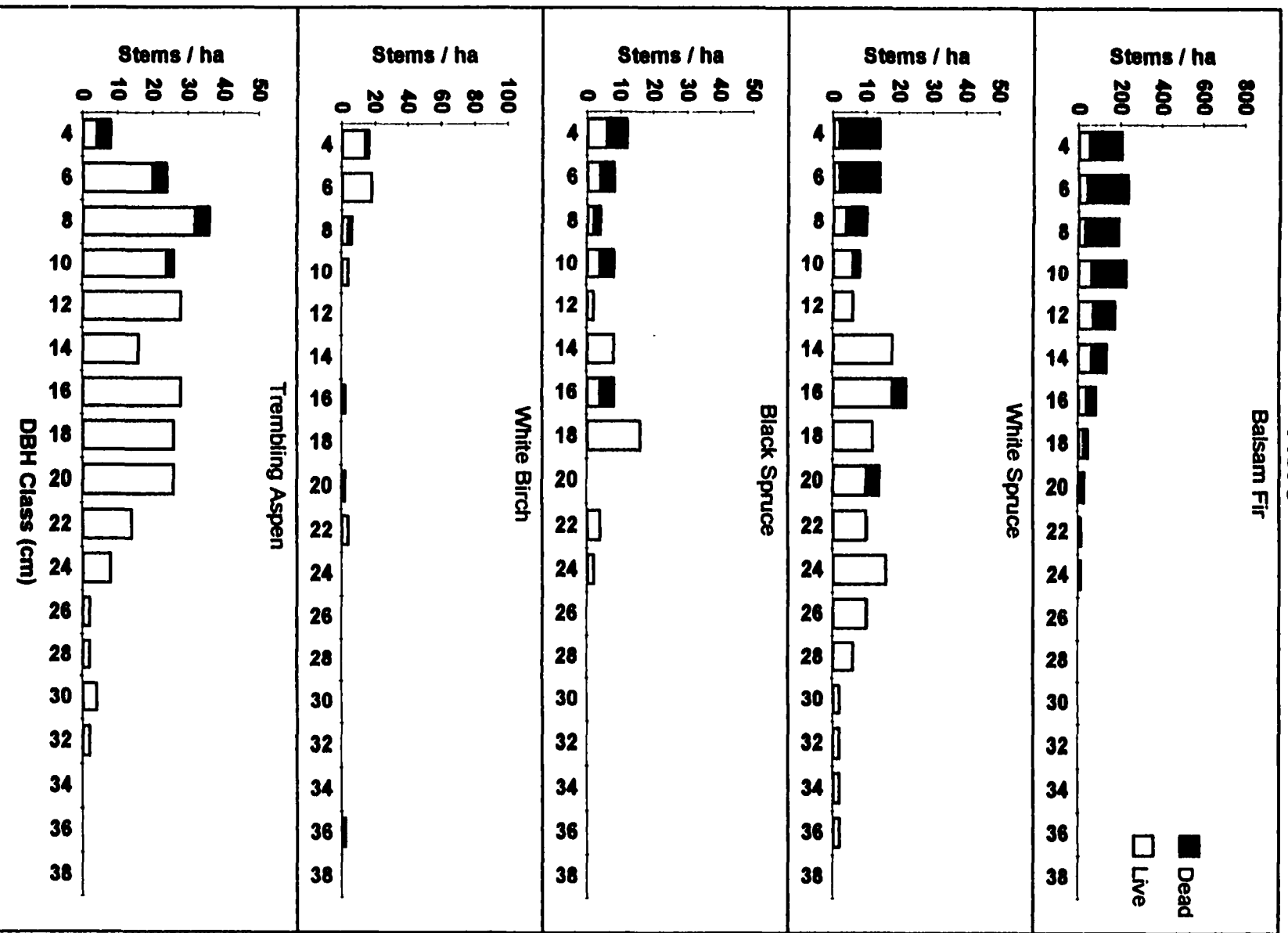
Figure 8. Live and dead stems per hectare by tree species in Plot 3.
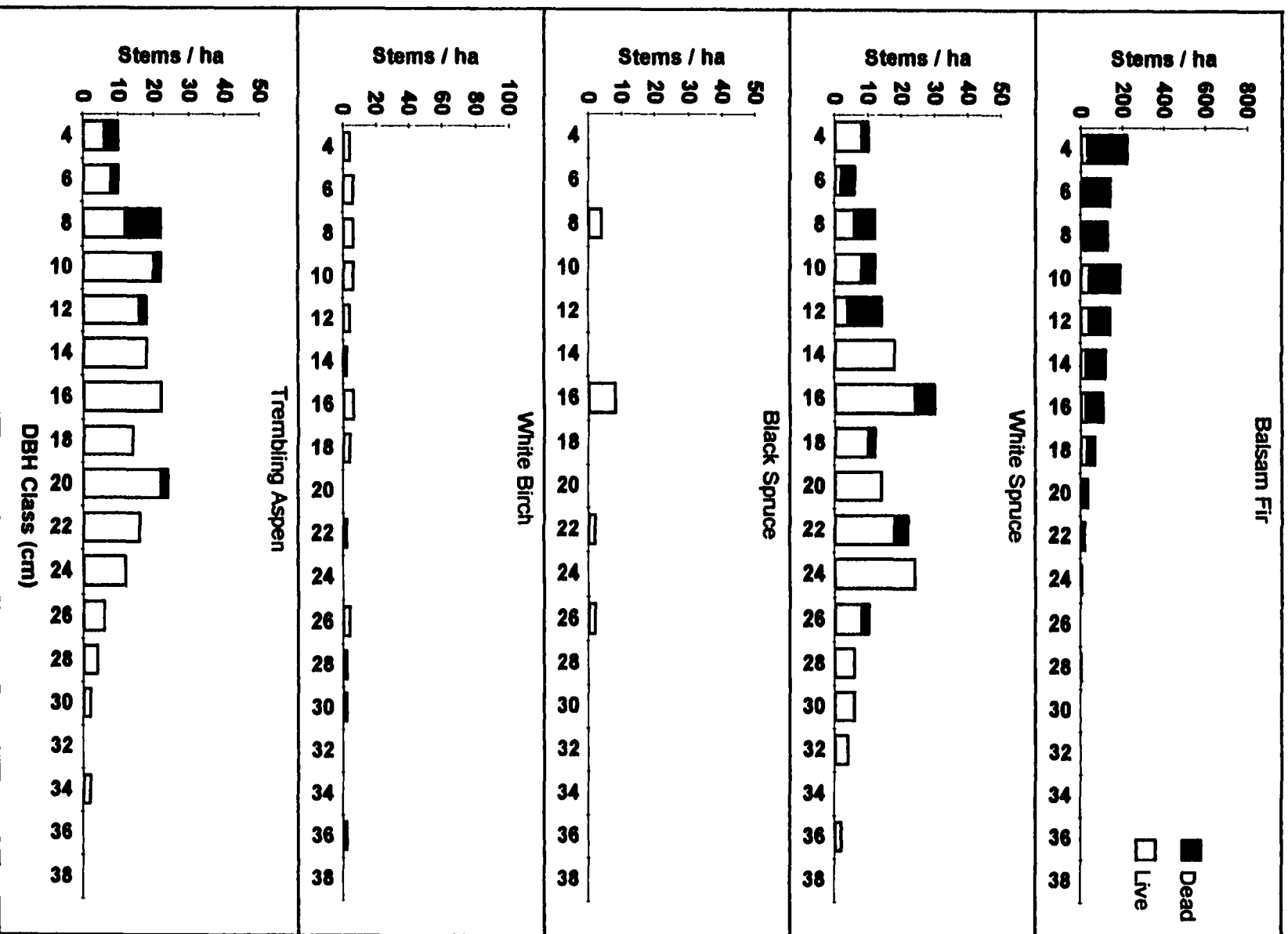
Plot 4

Figure 9. Live and dead stems per hectare by tree species in Plot 4.

Note changes in vertical scale.　　　Based on fifty 1/100 ha sub-plots.

All Plots Combined
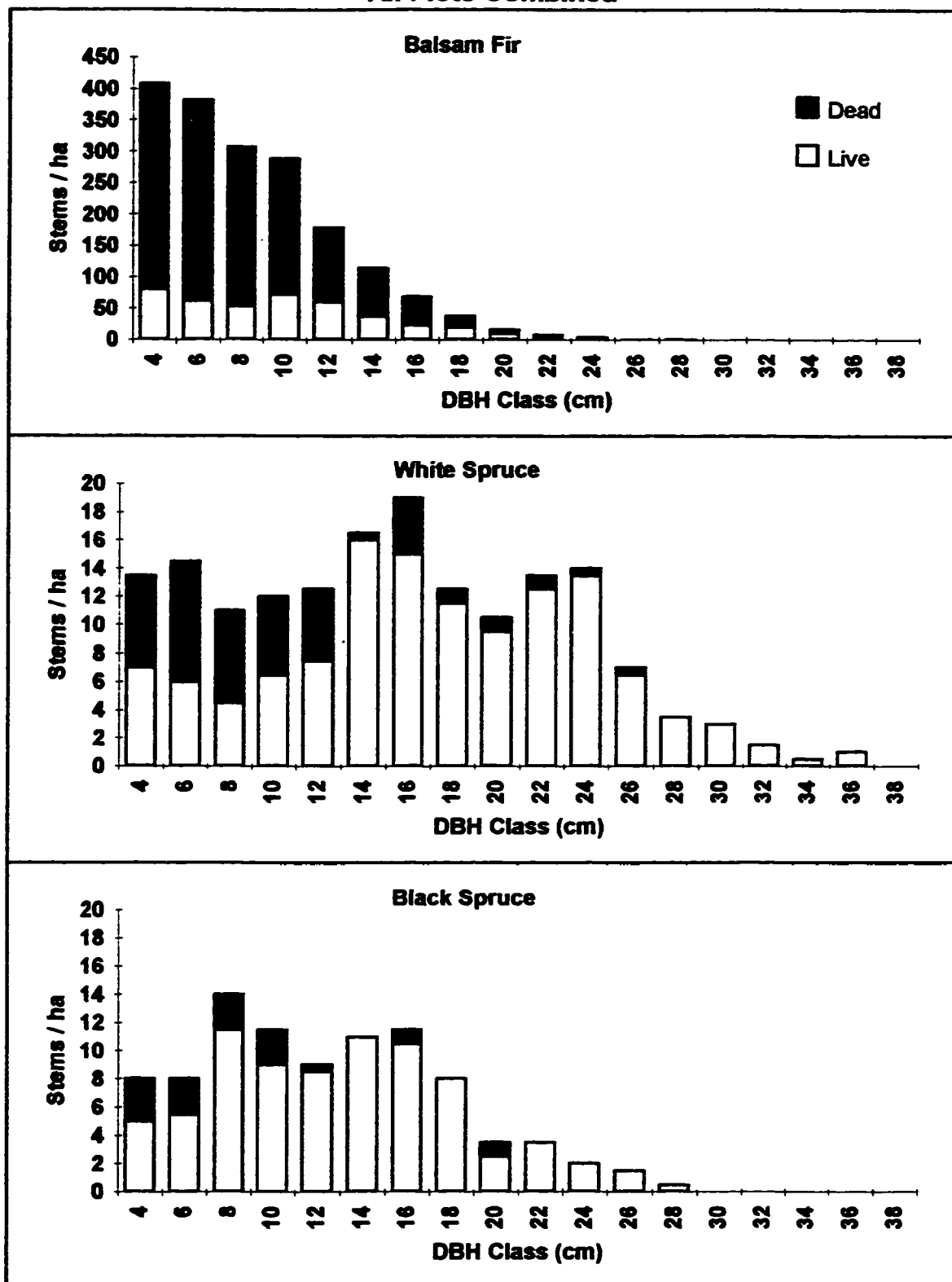
Note changes in vertical scale.   Based on 200 random 1/100 ha sub-plots over four 10-ha plots.

Figure 10. Live and dead stems per hectare for host trees in all plots.

the highest mortality in the smaller diameter classes, but to a lesser extent than balsam fir. Recent changes to the host-tree species composition of the forest were explored by comparing ratios of balsam fir to spruce trees (Table 1). Living and dead trees together were considered to be representative of species composition in the past. Live trees were used to represent species composition at present. When all diameter classes are considered, the ratio of balsam fir trees to spruce trees is seen to have fallen from 7.0:1 at some time in the past to 2.1:1 at the time of this study. Changes in species ratios are most pronounced among nonmerchantable stems in diameter classes lower than 10 cm. It is likely that the current spruce budworm outbreak has been the major force driving these changes in species ratios.

Table 1. Stems per hectare ratios for balsam fir to spruce trees.

DBH Classes	Condition	Stems per ha Bf	Stems per ha Spruce	Ratio Bf : Spruce
4 cm +	Live & Dead	1,814	258	**7.0 : 1**
	Live Only	430	205	**2.1 : 1**
10 cm +	Live & Dead	717	233	**3.1 : 1**
	Live Only	189	165	**1.1 : 1**
4 - 8 cm	Live & Dead	1,097	25	**43.9 : 1**
	Live Only	241	40	**6.0 : 1**

Spruce = white spruce and black spruce combined.

Understory Vegetation

To reflect the relative importance of understory vegetation in study plots, a simple vegetation index (Towill and Archibald 1991) was generated for each species by multiplying mean percentage cover and height. Total importance values then were generated for high shrub and low shrub layers in each plot by adding importance values for all species. The results are shown for Plots 1, 2, 3, and 4 in Tables 2, 3, 4, and 5 respectively. All plots contain a rich diversity of understory species. The most noticeable differences between plots occur at the high shrub level, where a layer of beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.) is more prominent in Plots 3 & 4 than in Plots 1 & 2. Plot 1 has less understory vegetation than the other plots and a slightly higher proportion of feathermoss as ground cover.

Regeneration

Seedling Densities

A total of 1819 host seedlings was tallied over all two hundred 4-m^2 sub-plots. Only eight (0.4 %) of these seedlings were dead: all balsam fir with heights between 8 cm and 195 cm. The tally of 1811 live seedlings included 1753 (96.8%) balsam fir, 36 (2.0%) white spruce, and 22 (1.2%) black spruce. Mean density was 9.1 seedlings per 4-m^2 sub-plot or about 22,500 seedlings per hectare. Seedling density was lowest in Plot 2 and highest in Plot 3 (Table 6). The ratio of balsam fir to spruce seedlings was lowest in Plot 2 and highest in Plot 4. When data from all plots are considered together, balsam fir seedlings outnumbered spruce seedlings by more than 30:1 (Table 7).

Table 2. Relative importance of non-host understory vegetation in Plot 1.

High Shrub

Importance Value
(mean % cover x wt'd mean height)

	Freq. %	Bar chart (T 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42)
Mountain Maple	14	1.8 % x 1.5 m
Beaked Hazel	18	3.3 % x 1.1 m
White Birch	18	0.6 % x 0.7 m
Trembling Aspen	12	0.2 % x 0.4 m
Speckled Alder	0	
Willow	2	0.2 % x 0.5 m
Saskatoon	4	0.1 % x 0.3 m
Mountain Ash	8	0.1 % x 0.4 m

Total Importance

7.0

Low Shrub, Herbaceous, and Others

(mean % cover x assigned height x 10)

	%	Bar chart (T 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42)
Honeysuckle	44	2.5 % x 0.5 m
Squashberry	2	0.1 % x 0.5 m
Red Baneberry	0	
Sarsaparilla	78	7.5 % x 0.3 m
Twisted Stalk	20	0.5 % x 0.3 m
Prickly Wild Rose	18	0.5 % x 0.3 m
Red Raspberry	6	0.3 % x 0.3 m
Ribes	14	0.3 % x 0.3 m
Lady Fern	6	0.2 % x 0.3 m
Bracken Fern	0	
Labrador Tea	2	0.4 % x 0.3 m
Blueberry	52	2.5 % x 0.2 m
Blue Bead Lily	30	1.3 % x 0.2 m
Large-Leaved Aster	6	0.08 % x 0.2 m
Clematis	2	0.04 % x 0.2 m
Bunchberry	90	10.7 % x 0.1 m
Twinflower	72	11.0 % x 0.1 m
Dwarf Raspberry	34	1.6 % x 0.1 m
Running Club Moss	52	4.5 % x 0.1 m
Misc. Lily	80	2.7 % x 0.1 m
Ground Pine	4	0.1 % x 0.1 m
Ground Cedar	8	0.4 % x 0.1 m
Starflower	38	1.0 % x 0.1 m
Strawberry	12	0.6 % x 0.1 m
Fragrant Bedstraw	4	0.04 % x 0.1 m
Round-Leaved Orchid	2	0.02 % x 0.1 m
Dwarf Rattlesnake Plantain	4	0.04 % x 0.1 m
Sweet Coltsfoot	0	
Violets & Mitreworts	8	0.1 % x 0.05 m
Pyrola	42	0.5 % x 0.05 m
Goldthread	4	0.1 % x 0.05 m
Creeping Snowberry	26	2.1 % x 0.05 m
Wood Anemone	4	0.08 % x 0.05 m
Grass	10	0.2 % x 0.1 m

Total Importance

8.4

Ground Cover

Feather Moss	100	57.2 % cover
Leaf Litter	88	42.8 % cover

T = Trace
Based on data from fifty random sub-plots (4 m^2 circular).
See Appendix IV for scientific names of species.

Table 3. Relative importance of non-host understory vegetation in Plot 2.

High Shrub

Importance Value (mean % cover x wt'd mean height)

Species	Freq. %	Importance Value
Mountain Maple	18	2.5 % x 1.4 m
Beaked Hazel	36	5.9 % x 1.1 m
White Birch	8	0.9 % x 1.8 m
Trembling Aspen	6	0.1 % x 1.0 m
Speckled Alder	2	1.0 % x 2.5 m
Willow	8	0.7 % x 1.0 m
Saskatoon	24	1.0 % x 0.75 m
Mountain Ash	2	0.1 % x 0.8 m

Total Importance 15.7

Low Shrub, Herbaceous, and Others

(mean % cover x assigned height x 10)

Species	%	Value
Honeysuckle	80	20.0 % x 0.5 m
Squashberry	2	0.1 % x 0.5 m
Red Baneberry	2	0.06 % x 0.5 m
Sarsaparilla	78	7.3 % x 0.3 m
Twisted Stalk	60	2.4 % x 0.3 m
Prickly Wild Rose	30	1.7 % x 0.3 m
Red Raspberry	6	0.4 % x 0.3 m
Ribes	6	0.5 % x 0.3 m
Lady Fern	2	0.04 % x 0.4 m
Bracken Fern	2	0.06 % x 0.4 m
Labrador Tea	2	0.04 % x 0.3 m
Blueberry	62	2.0 % x 0.2 m
Blue Bead Lily	88	4.8 % x 0.2 m
Large-Leaved Aster	20	1.1 % x 0.2 m
Clematis	2	0.02 % x 0.2 m
Bunchberry	98	16.9 % x 0.1 m
Twinflower	92	12.0 % x 0.1 m
Dwarf Raspberry	52	2.1 % x 0.1 m
Running Club Moss	24	1.2 % x 0.1 m
Misc. Lily	78	2.3 % x 0.1 m
Ground Pine	16	0.6 % x 0.1 m
Ground Cedar	0	
Starflower	40	1.2 % x 0.1 m
Strawberry	22	1.1 % x 0.1 m
Fragrant Bedstraw	26	0.7 % x 0.1 m
Round-Leaved Orchid	0	
Dwarf Rattlesnake Plantain	2	0.06 % x 0.1 m
Sweet Coltsfoot	2	0.02 % x 0.1 m
Violets & Mitreworts	20	1.2 % x 0.05
Pyrola	84	1.4 % x 0.05 m
Goldthread	50	1.9 % x 0.05 m
Creeping Snowberry	4	0.08 % x 0.05 m
Wood Anemone	14	0.2 % x 0.05 m
Grass	58	1.5 % x 0.1 m

Total Importance 19.6

Ground Cover

Species	%	
Feather Moss	98	49.7 % cover
Leaf Litter	98	48.3 % cover

T = Trace

Based on data from fifty random sub-plots (4 m^2 circular).

See Appendix IV for scientific names of species.

Table 4. Relative importance of non-host understory vegetation in Plot 3.

High Shrub — Importance Value (mean % cover x wt'd mean height)

Species	Freq. %	Importance Value
Mountain Maple	42	14.3 % x 1.8 m
Beaked Hazel	78	22.4 % x 1.3 m
White Birch	12	0.3 % x 0.9 m
Trembling Aspen	2	0.1 % x 2.0 m
Speckled Alder	0	
Willow	6	0.8 % x 1.6 m
Saskatoon	36	2.5 % x 1.0 m
Mountain Ash	4	0.1 % x 0.3 m

Total Importance 59.1

Low Shrub, Herbaceous, and Others (mean % cover x assigned height x 10)

Species	%	Value
Honeysuckle	88	27.2 % x 0.5 m
Squashberry	0	
Red Baneberry	0	
Sarsaparilla	82	6.5 % x 0.3 m
Twisted Stalk	60	2.1 % x 0.3 m
Prickly Wild Rose	26	1.2 % x 0.3 m
Red Raspberry	8	1.1 % x 0.3 m
Ribes	0	
Lady Fern	0	
Bracken Fern	0	
Labrador Tea	0	
Blueberry	68	3.5 % x 0.2 m
Blue Bead Lily	88	5.0 % x 0.2 m
Large-Leaved Aster	66	8.4 % x 0.2 m
Clematis	0	
Bunchberry	68	5.1 % x 0.1 m
Twinflower	48	5.8 % x 0.1 m
Dwarf Raspberry	60	3.5 % x 0.1 m
Running Club Moss	18	0.5 % x 0.1 m
Misc. Lily	72	2.2 % x 0.1 m
Ground Pine	30	1.1 % x 0.1 m
Ground Cedar	2	0.1 % x 0.1 m
Starflower	30	0.8 % x 0.1 m
Strawberry	10	0.3 % x 0.1 m
Fragrant Bedstraw	16	0.3 % x 0.1 m
Round-Leaved Orchid	2	0.06 % x 0.1 m
Dwarf Rattlesnake Plantain	2	0.02 % x 0.1 m
Sweet Coltsfoot	0	
Violets & Mitreworts	6	1.1 % x 0.05 m
Pyrola	62	1.0 % x 0.05 m
Goldthread	10	0.3 % x 0.05 m
Creeping Snowberry	0	
Wood Anemone	18	0.3 % x 0.05 m
Grass	64	1.4 % x 0.1 m

Total Importance 22.5

Ground Cover

Species	%	cover
Feather Moss	100	50.5 % cover
Leaf Litter	98	49.5 % cover

T = Trace

Based on data from fifty random sub-plots (4 m^2 circular).

See Appendix IV for scientific names of species.

Table 5. Relative importance of non-host understory vegetation in Plot 4.

High Shrub

Importance Value

(mean % cover x wt'd mean height)

	Freq. %	T 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Mountain Maple	32	9.8 % x 1.9 m
Beaked Hazel	80	29.2 % x 1.5 m
White Birch	10	0.8 % x 1.5 m
Trembling Aspen	16	0.3 % x 1.2 m
Speckled Alder	2	0.6 % x 1.5 m
Willow	2	0.2 % x 1.5 m
Saskatoon	26	2.4 % x 0.8 m
Mountain Ash	0	

Total Importance

67.1

Low Shrub, Herbaceous, and Others

(mean % cover x assigned height x 10)

	%	T 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Honeysuckle	88	24.9 % x 0.5 m
Squashberry	2	0.1 % x 0.5 m
Red Baneberry	0	
Sarsaparilla	78	10.5 % x 0.3 m
Twisted Stalk	68	1.6 % x 0.3 m
Prickly Wild Rose	22	0.8 % x 0.3 m
Red Raspberry	18	0.8 % x 0.3 m
Ribes	0	
Lady Fern	0	
Bracken Fern	0	
Labrador Tea	0	
Blueberry	52	1.5 % x 0.2 m
Blue Bead Lily	86	6.0 % x 0.2 m
Large-Leaved Aster	52	4.1 % x 0.2 m
Clematis	0	
Bunchberry	54	6.5 % x 0.1 m
Twinflower	40	8.3 % x 0.1 m
Dwarf Raspberry	78	3.6 % x 0.1 m
Running Club Moss	26	0.8 % x 0.1 m
Misc. Lily	60	2.1 % x 0.1 m
Ground Pine	52	1.7 % x 0.1 m
Ground Cedar	0	
Starflower	16	0.3 % x 0.1 m
Strawberry	2	0.04 % x 0.1 m
Fragrant Bedstraw	18	0.4 % x 0.1 m
Round-Leaved Orchid	0	
Dwarf Rattlesnake Plantain	2	0.06 % x 0.1 m
Sweet Coltsfoot	0	
Violets & Mitreworts	10	0.7 % x 0.05 m
Pyrola	70	1.1 % x 0.05 m
Goldthread	8	0.2 % x 0.05 m
Creeping Snowberry	0	
Wood Anemone	28	0.5 % x 0.05 m
Grass	58	1.5 % x 0.1 m

Total Importance

21.6

Ground Cover

Feather Moss	100	46.8 % cover
Leaf Litter	100	53.2 % cover

T = Trace

Based on data from fifty random sub-plots (4 m^2 circular).

See Appendix IV for scientific names of species.

Table 6. Seedling densities in random sub-plots.

		Balsam Fir		White Spruce		Black Spruce		All Species	
		per sub-plot	per ha	per sub-plot	per ha	per sub-plot	per ha	per sub-plot	per ha
Plot 1	mean	4.92	12300	0.12	300	0.14	350	5.18	12950
	S.D.	7.56	18904	0.39	964	0.53	1337	7.86	19651
Plot 2	mean	3.58	8950	0.22	550	0.04	100	3.84	9600
	S.D.	6.32	15804	0.68	1697	0.28	707	6.80	17011
Plot 3	mean	15.94	39850	0.26	650	0.26	650	16.46	41150
	S.D.	19.16	47909	0.72	1808	1.19	2980	19.63	49063
Plot 4	mean	10.62	26550	0.12	300	0.00	0	10.74	26850
	S.D.	18.62	46544	0.39	964	0.00	0	18.74	46844
All Plots	mean	8.77	21913	0.18	450	0.11	275	9.06	22638
	S.D.	14.97	37413	0.57	1413	0.67	1677	15.26	38161

Based on data from 50 random sub-plots (4 m^2) in each of four 10-ha plots.

Table 7. Stems per hectare ratios for balsam fir to spruce seedlings in random sub-plots.

	Stems per ha Bf	Stems per ha Spruce	Ratio Bf : Spruce
Plot 1	12,300	650	18.9 : 1
Plot 2	8,950	650	13.8 : 1
Plot 3	39,850	1,300	30.6 : 1
Plot 4	26,550	300	88.5 : 1
All Plots	21,913	725	30.2 : 1

Spruce = white spruce and black spruce combined.

Height Distributions

Height distributions for seedlings in Plots 1, 2, 3, and 4 are shown in Figures 11, 12, 13, and 14, respectively. Balsam fir seedlings clearly are most abundant in the shorter height classes in all plots. Little can be concluded about the height distributions of spruce because sample sizes are too small. However, it appears that white spruce seedlings may have a height distribution similar to that for balsam fir. The similarities between balsam fir and white spruce are more apparent when data from all plots are combined (Fig. 15).

Overall mean height of seedlings in the study area was 17.3 cm, but this value is influenced by a small number of very tall seedlings. Using a top height of 53 cm to eliminate outliers and still include 98% of the seedlings tallied, overall mean height drops to 15.5 cm (Table 8).

Height comparisons between species within plots are prohibited by low numbers of spruce seedlings. However, an analysis of height data for seedlings in all plots combined was undertaken as an exploratory step. A series of nonparametric Mann-Whitney tests for height differences between pairs of species was used to compare seedlings of all heights as well as seedlings with a top height of 53 cm (Table 9). Both spruce species were significantly taller than balsam fir when seedlings of all heights were considered, but height differences between species were not statistically significant at a top height of 53 cm. It appears that seedling heights in general were similar for all species, but the spruces, while far less abundant than balsam fir, tended to carry a larger proportion of individuals in the taller height classes.

Plot 1
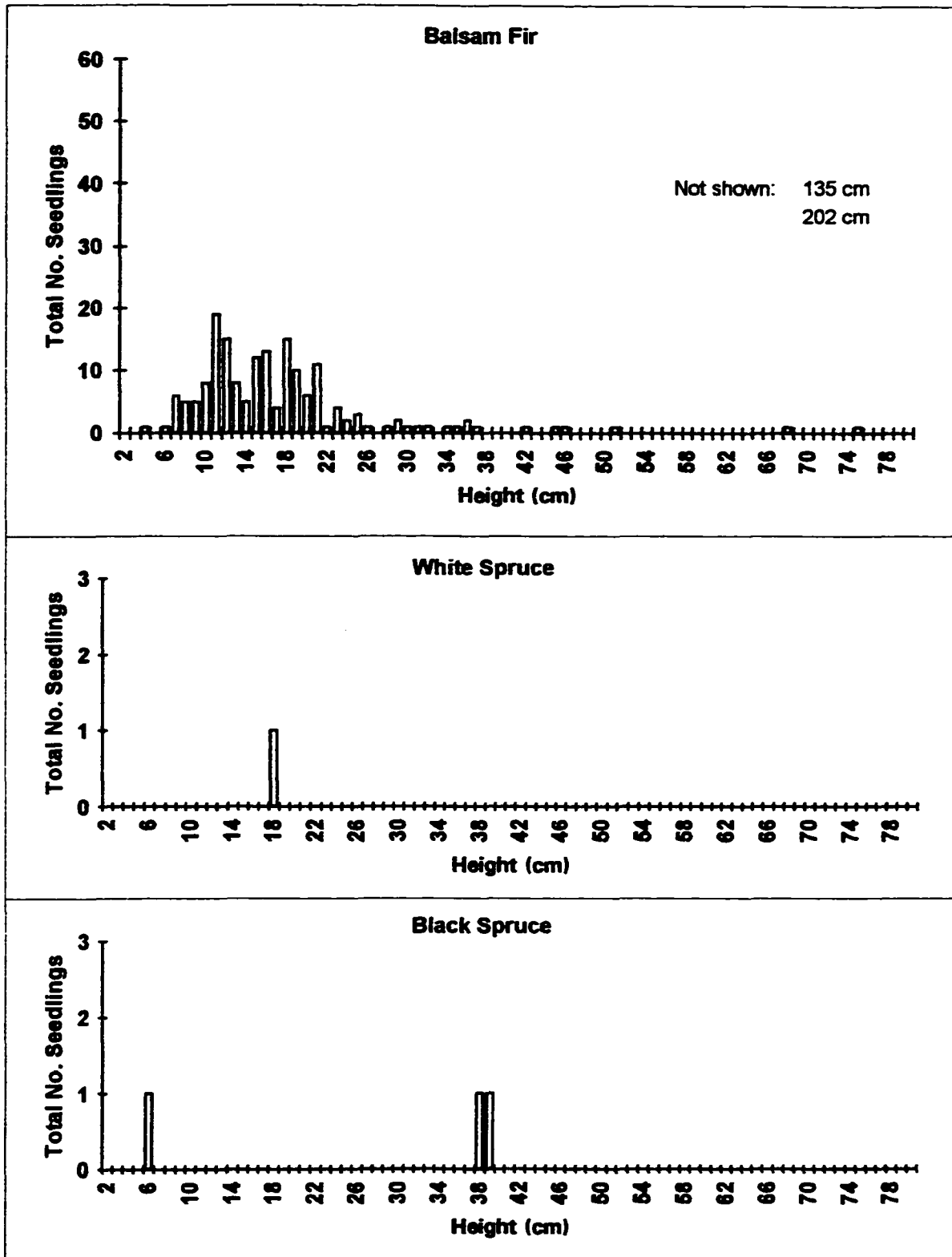
Based on data from 30 sub-plots (4 m^2).
Note changes in vertical scale.

Figure 11. Height distributions for host-species regeneration in Plot 1.

Plot 2

Balsam Fir

White Spruce

Black Spruce
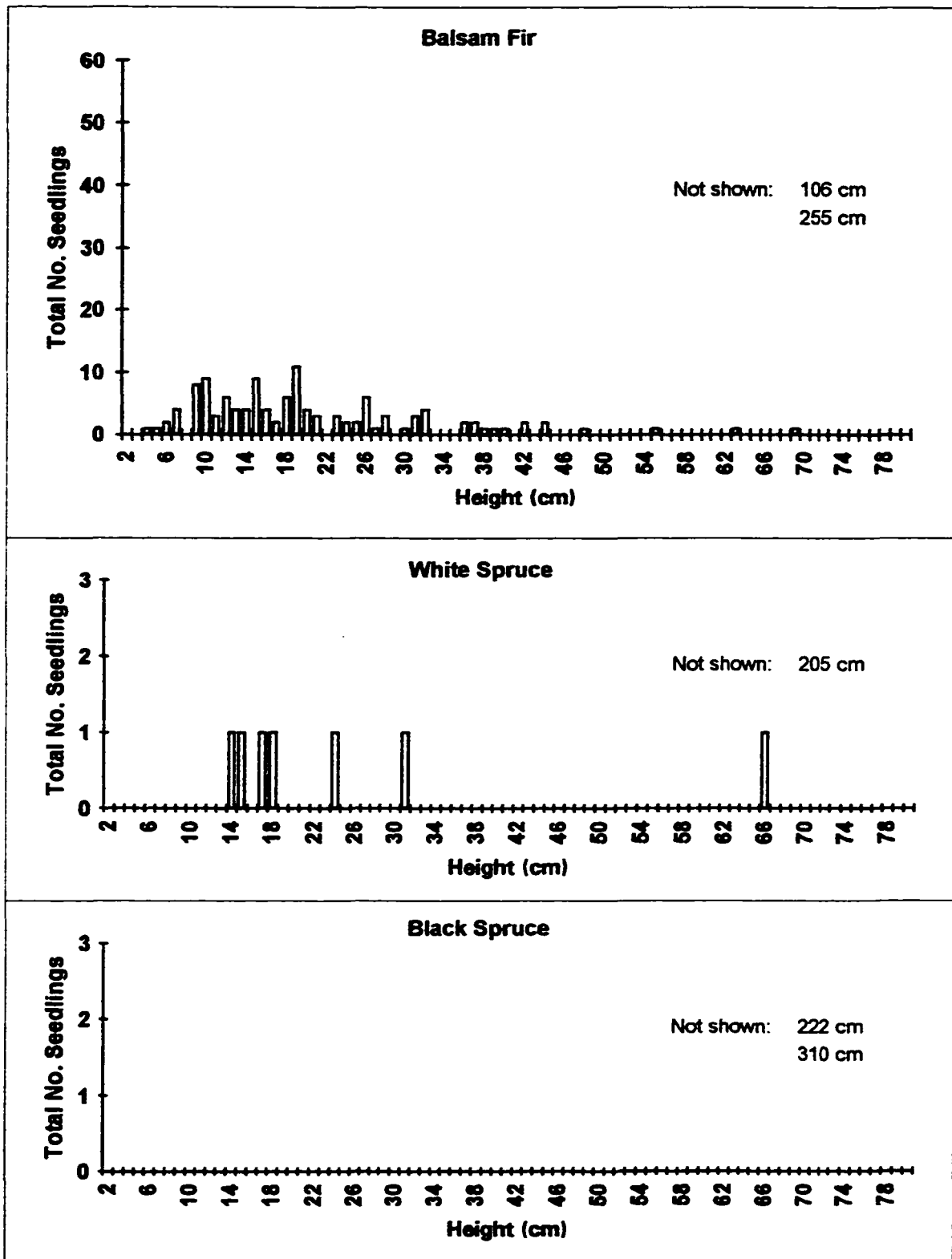
Based on data from 30 sub-plots (4 m^2).
Note changes in vertical scale.

Figure 12. Height distributions for host-species regeneration in Plot 2.

Plot 3

Balsam Fir

White Spruce

Black Spruce
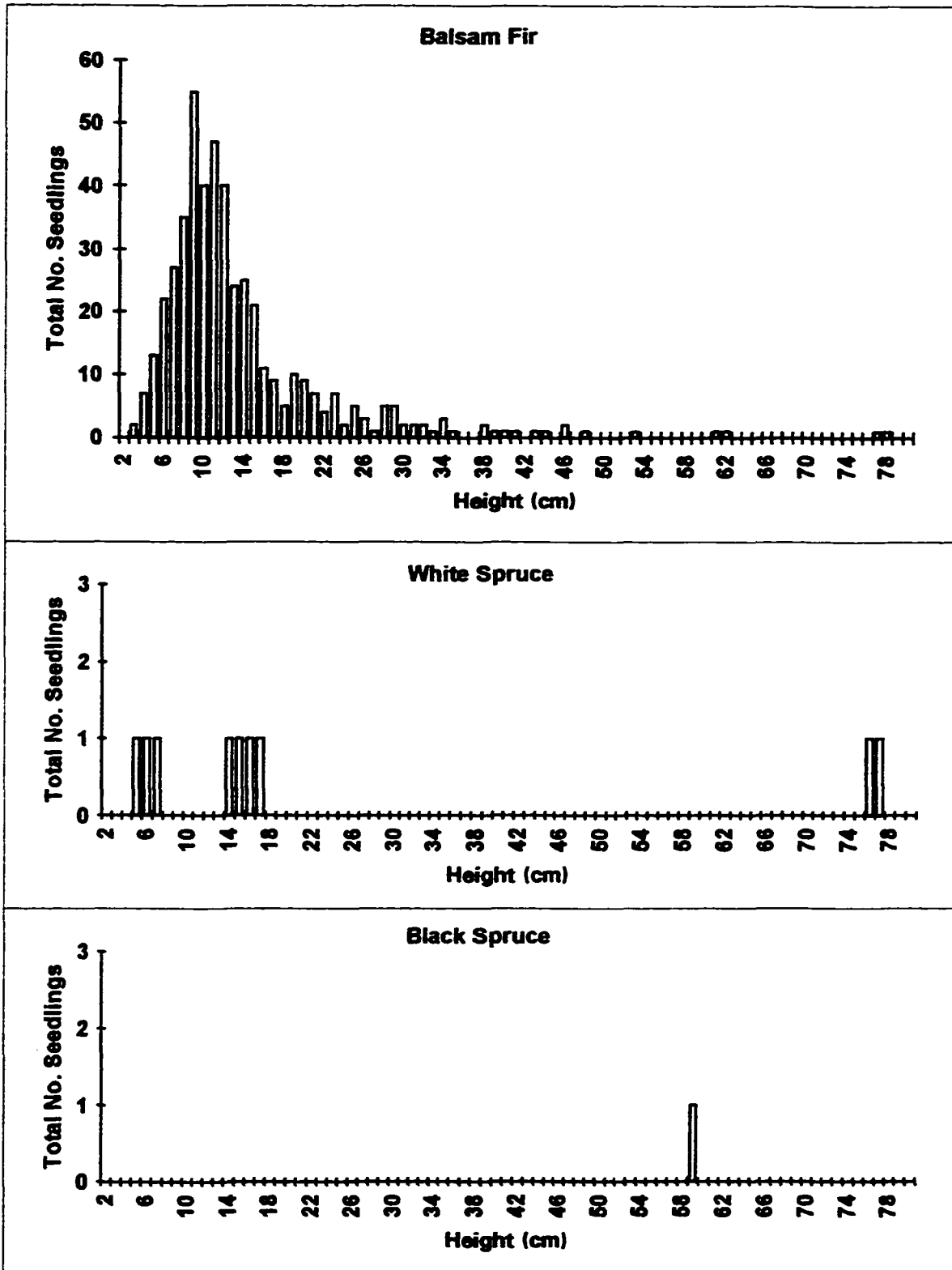
Based on data from 30 sub-plots (4 m^2).
Note changes in vertical scale.

Figure 13. Height distributions for host-species regeneration in Plot 3.

Plot 4
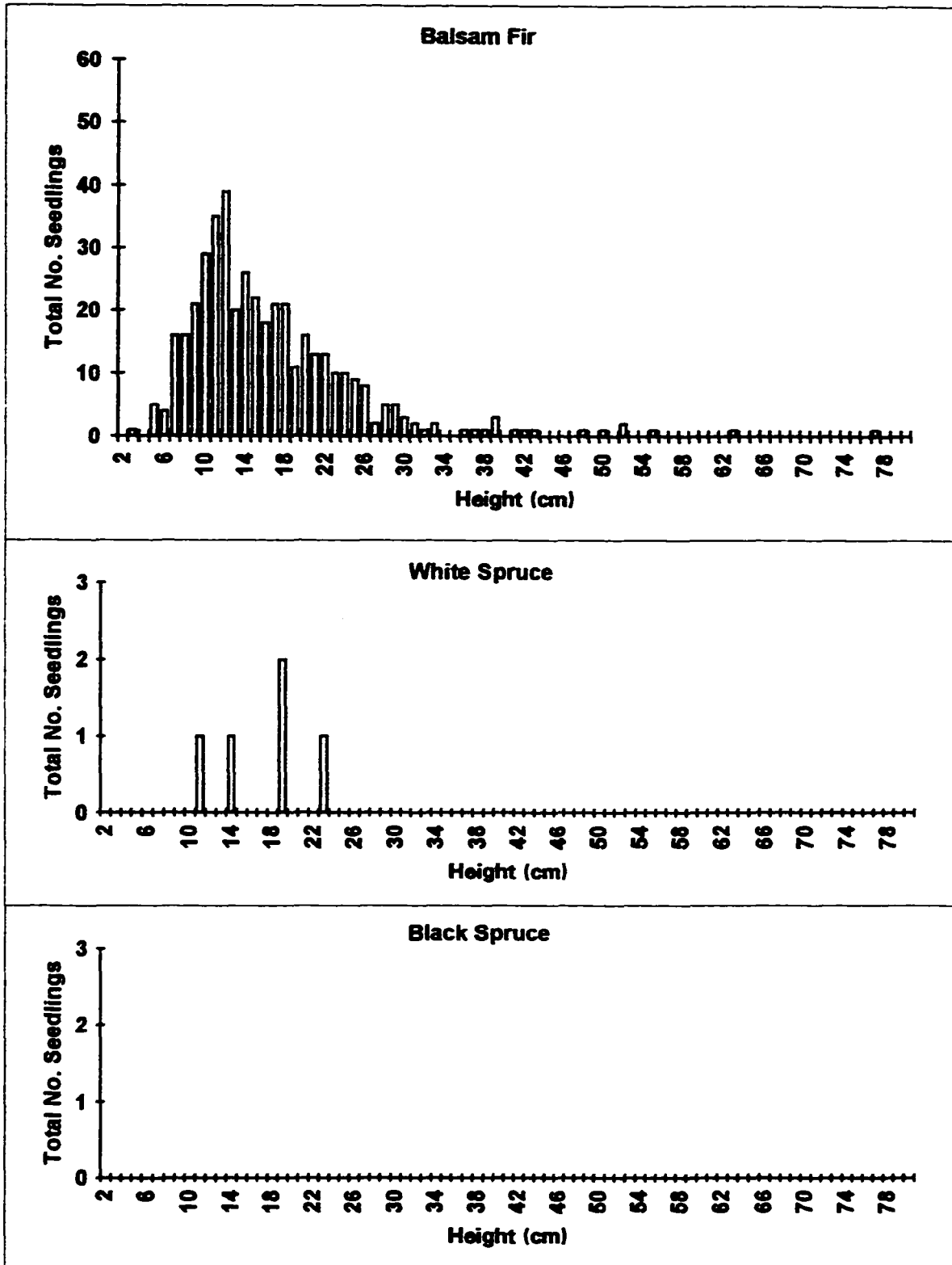
Based on data from 30 sub-plots (4 m^2).
Note changes in vertical scale.

Figure 14. Height distributions for host-species regeneration in Plot 4.

All Plots

Figure 15. Height distributions for host-species regeneration in all plots.
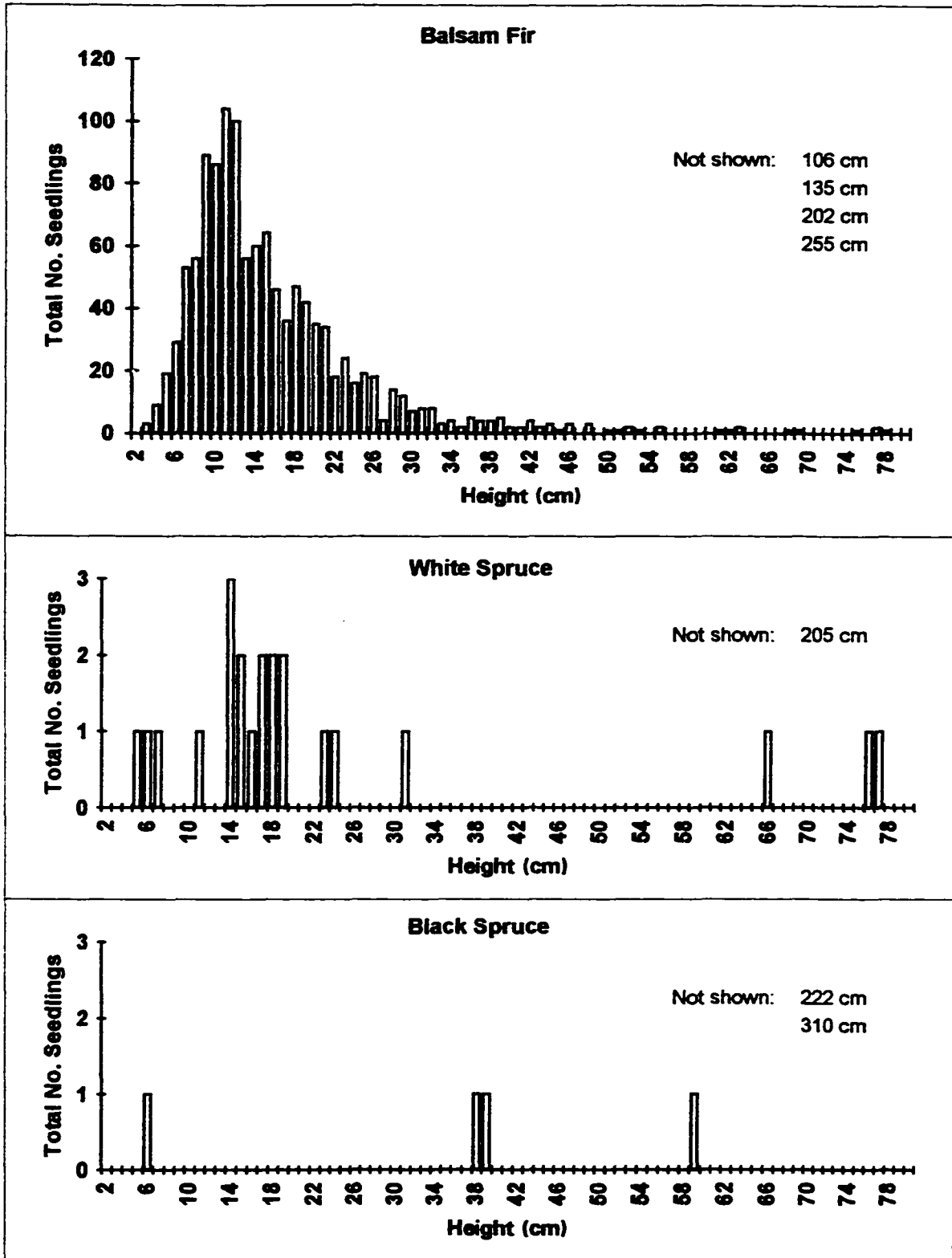
Based on data from 120 sub-plots (4 m^2) over all 10 ha plots.
Note changes in vertical scale.

Table 8. Summary of mean heights of seedlings in random sub-plots.

		Balsam Fir		White Spruce		Black Spruce		All Species	
		All Seedlings	53 cm Top Ht.	All Seedlings	53 cm Top Ht.	All Seedlings	53 cm Top Ht.	All Seedlings	53 cm Top Ht.
Plot 1	n	174	170	1	1	3	3	178	174
	mean	19.1	16.8	18	18	27.7	27.7	19.3	17
	S.D.	19.2	7.8	- - -	- - -	18.8	18.8	19.1	8.1
Plot 2	n	123	118	8	6	2	0	133	124
	mean	23	19.4	48.8	19.8	266	- - -	28.2	19.4
	S.D.	25.3	9.9	65.4	6.5	62.2	- - -	41.9	9.7
Plot 3	n	468	463	9	7	1	0	478	470
	mean	13.9	13.3	25.9	11.4	59	- - -	14.2	13.3
	S.D.	9.8	7.7	29	5.2	- - -	- - -	10.7	7.6
Plot 4	n	420	417	5	5	0	0	425	422
	mean	16.5	16.2	17.2	17.2	- - -	- - -	16.5	16.2
	S.D.	8.7	7.7	4.7	4.7	- - -	- - -	8.7	7.7
All Plots	n	1185	1168	23	19	6	3	1214	1190
	mean	16.5	15.4	31.6	15.9	112.3	27.7	17.3	15.5
	S.D.	13.9	8.2	43	6.3	123.4	18.8	18.3	8.2

Based on data from 30 sub-plots (4 m^2) in each of four 10-ha plots.
Top height of 53 cm includes 98% of all seedlings tallied.

89

Table 9. Summary of Mann-Whitney tests for height differences between seedling species.

Seedling Height		Mann-Whitney Test Results		
		Bf < **Sw** = **Sb**		
All Seedlings	n	1185	23	6
(max. ht. 310 cm)	mean	16.5	31.6	112.3
	S.D.	13.9	43	123.4
		Bf = **Sw** = **Sb**		
53 cm	n	1168	19	3
Top Height	mean	15.4	15.9	27.7
	S.D.	8.2	6.3	18.8

Based on data from 120 sub-plots (4 m^2) over four 10-ha plots.

<   - significantly less than
=   - not significantly different
     (alpha = 0.05)

Defoliation

Mean defoliation scores for seedlings were low in all plots, with a mean Fettes score of only 2.2 for seedlings in all plots combined (Table 10). Defoliation scores between species within each plot are not readily comparable due to a lack of spruce seedlings. Despite higher than average defoliation scores for spruce seedlings in some plots, a Kruskal-Wallis oneway test suggests that differences in defoliation between species are not statistically significant (p = 0.354) when data from all plots are combined. The high defoliation scores assigned to black spruce may be related to the fact that these seedlings tended to be among the tallest of all seedlings encountered.

Frequency distributions for defoliation scores were similar in all plots and therefore were combined before presentation (Fig. 16). More than 75% of all seedlings tallied in random sub-plots received a defoliation score of three or

Table 10. Summary of mean defoliation scores for seedlings in random sub-plots.

		Bf	Sw	Sb	All
Plot 1	n	174	1	3	178
	mean	2.0	6.0	1.3	2.0
	S.D.	2.8	- - -	1.2	2.8
Plot 2	n	123	8	2	133
	mean	2.8	3.1	10.0	2.9
	S.D.	3.6	4.4	- - -	3.7
Plot 3	n	468	9	1	478
	mean	2.1	1.4	1.0	2.1
	S.D.	2.8	2.4	- - -	2.8
Plot 4	n	420	5	0	425
	mean	2.2	1.8	- - -	2.1
	S.D.	2.6	1.8	- - -	2.6
All Plots	n	1185	23	6	1214
	mean	2.2	2.3	4.2	2.2
	S.D.	2.8	3.2	4.6	2.9

Based on data from 30 sub-plots (4 m^2) in each of four 10-ha plots.

less. However, more than 50% of all seedlings were damaged to some extent (Table 11). Over 80% of all seedlings that were damaged suffered defoliation of the leader, suggesting a strong tendency for larvae to feed in the tops of seedlings. Almost half of the seedlings that were damaged suffered greater than 50% defoliation of the leader. It was observed in the field that many seedlings suffered damage to the leader only and that defoliation was limited to the terminal and terminal-lateral shoots of seedlings almost exclusively.

Relation Between Height and Defoliation

Working in the study plots, one got the distinct impression that taller seedlings were more defoliated than shorter ones. This relation is of interest because seedling height may have confounded defoliation scores. A Pearson correlation coefficient (r) was generated to explore the relationship between
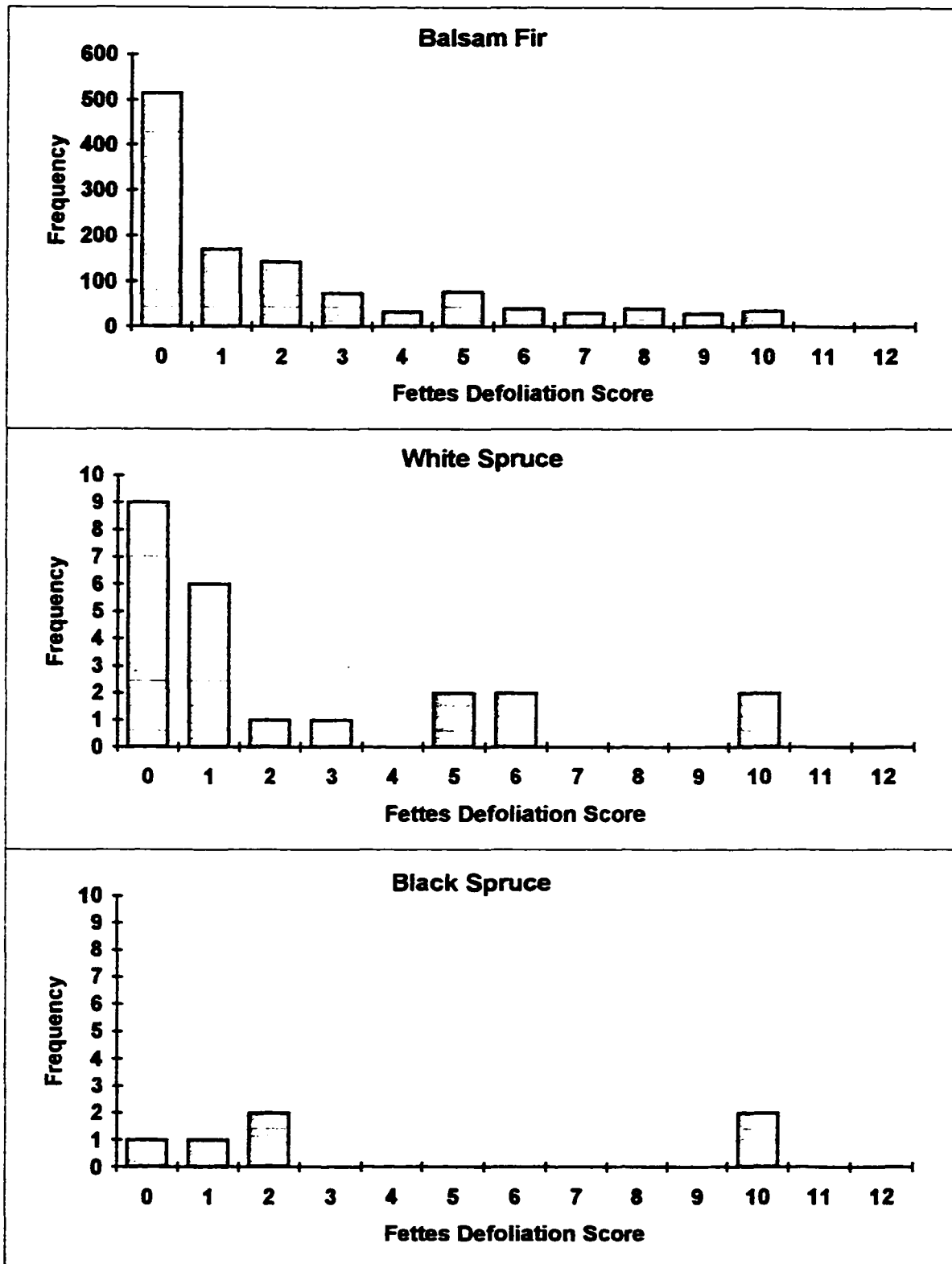
Figure 16. Defoliation score frequencies for seedlings in random sub-plots.

Based on data from 120 sub-plots (4 m^2) over four 10-ha plots.
Note changes in vertical scale.

Table 11. Summary of leader damage to host seedlings in random sub-plots.

Seedling Species	Total No. Live	Seedlings Damaged to any Degree		Severity of Leader Damage								
				No Damage			< 50 % Damage			> 50 % Damage		
		No.	% of Total	No.	% of Total	% of Damaged	No.	% of Total	% of Damaged	No.	% of Total	% of Damaged
Bf	1185	669	56.5	90	7.6	13.5	256	21.6	38.3	323	27.3	48.3
Sw	23	14	60.9	2	8.7	14.3	4	17.4	28.6	8	34.8	57.1
Sb	6	5	83.3	2	33.3	40.0	1	16.7	20.0	2	33.3	40.0
All	1214	688	56.7	94	7.7	13.7	261	21.5	37.9	333	27.4	48.4

Based on data from 120 random sub-plots (4 m^2) over four 10 ha plots.

93

height and defoliation. Although a strong relation was perceived, the two variables were found to be not highly correlated ($r = 0.250$, $n = 1214$).

To explore this relationship further, the number of buds counted on each seedling was multiplied by the assigned Fettes score (expressed as a percentage). The resulting variable provided an estimate of the number of buds consumed on each seedling. The correlation coefficient for height and number of buds consumed was quite high ($r = 0.630$, $n = 1214$). Thus, the perception that taller seedlings were more defoliated may be related to the fact that more buds were consumed on taller seedlings, but not necessarily a greater percentage of buds. This concept is best conveyed through a simple diagram (Fig. 17). The greater number of buds consumed on a taller seedling gives the impression that defoliation is greater. Based on percentage of total buds consumed, however, both tall and short seedlings are equally defoliated.

Despite a lack of correlation between height and defoliation, defoliation scores still may be confounded by height to some extent, at least for very tall seedlings. This is because a tall seedling may have had hundreds of buds throughout the crown, but only the top 25 buds were considered during defoliation assessments. For example, assume that a tall seedling has a total of 100 buds, but only the top 25 buds have been defoliated by the budworm. The other 75 buds are undamaged. An assessment of this seedling might result in a mean defoliation of 100% if only the top 25 buds are considered. However, if all buds are considered, defoliation would be 25%. This influence has important consequences only where seedlings have more than 25 buds, but becomes more important as the total number of buds increases. Of the seedlings tallied in random sub-plots for this study, over 93% had 25 buds or less. The upward bias of defoliation scores for taller seedlings should be kept

| Fettes Score: | 4 | 4 |
| Buds Consumed: | 1 | 3 |
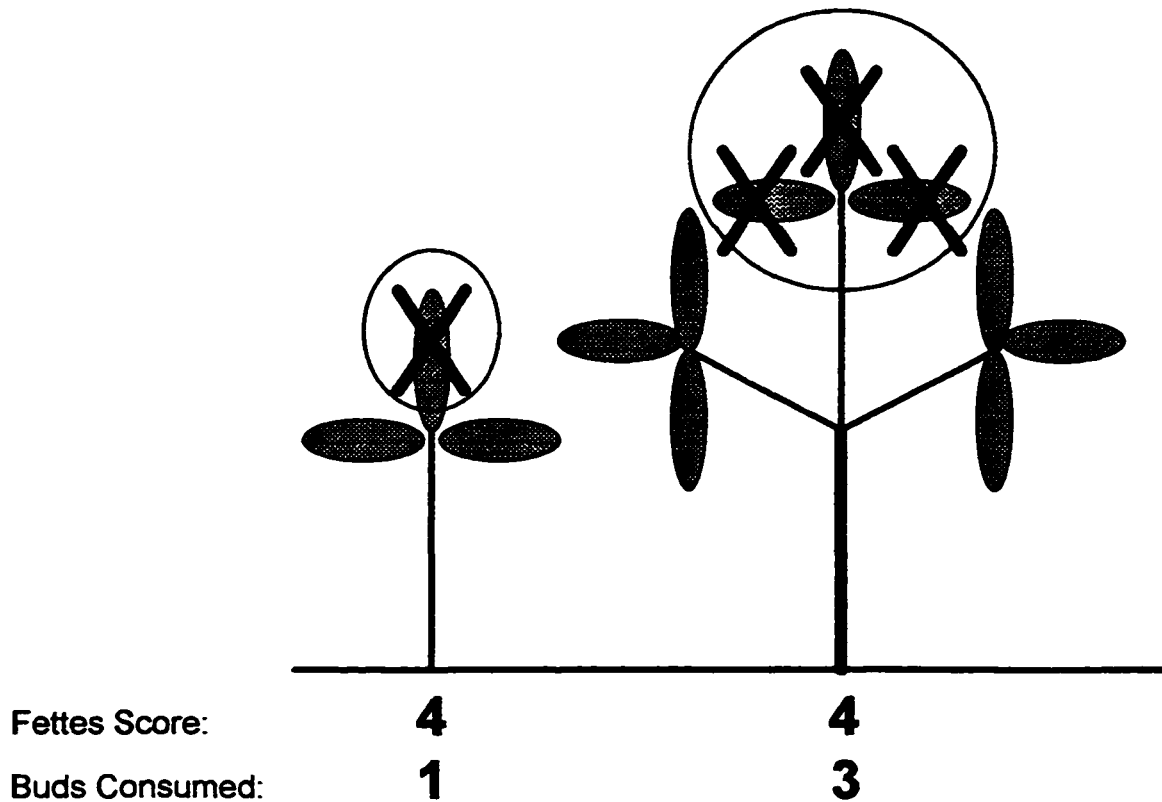
Figure 17. Relation between Fettes defoliation scores and number of buds consumed.

in mind, but the small number of exceptionally large seedlings does not invalidate overall defoliation scores.

The greater number of buds consumed on taller seedlings also may be related to seedling crown width, which was found to be highly correlated with height ($r = 0.824$, $n = 1214$). Because taller seedlings are wider, they occupy a larger surface area when viewed from above. Taller seedlings also are more likely to have foliage located above surrounding non-host vegetation. Thus, there would be a greater chance of late-instar larvae landing on taller seedlings. A greater number of larvae landing on taller seedlings would result in damage to a greater number of buds.

Microsites

Over 75% of all balsam fir seedlings were found on undisturbed leaf litter or feathermoss, suggesting that the organic layer on the forest floor does not prohibit the establishment of this species (Table 12). Little can be concluded about the importance of microsite types for white spruce and black spruce because of small sample sizes. However, it appears that rotting wood may be an important microsite for white spruce. Black spruce was found most often on undisturbed litter, but the large size of these seedlings suggests they also might be very old. Evidence of site disturbance or rotting wood may have disappeared since the time at which these seedlings became established.

Patches of mineral soil exposed by windthrown trees did occur in some sub-plots, but only occasionally. Very few of these sites had seedlings growing on them, possibly because there has been little or no seed rain for many years during the budworm outbreak. A search for and examination of exposed mineral soil microsites confirmed that almost no seedlings were established on such sites throughout the study plots.

Table 12. Summary of microsites for seedlings in random sub-plots.

Seedling Species	Total Seedlings	Microsite					
		Exposed Mineral Soil		Leaf Litter or Moss		Rotting Wood	
		No. of Seedlings	% of Total	No. of Seedlings	% of Total	No. of Seedlings	% of Total
Bf	1185	6	0.5	892	75.3	287	24.2
Sw	23	0	0.0	6	26.1	17	73.9
Sb	6	0	0.0	5	83.3	1	16.7
All	1214	6	0.5	903	74.4	305	25.1

Based on data from 120 random sub-plots (4 m^2) over four 10 ha plots.

PART II -- SAMPLING AT MATURE HOST TREES

PURPOSE

Sampling was carried out at mature balsam fir, white spruce, and black spruce trees to compare budworm densities, dispersal numbers, and understory feeding damage between host-tree species. Branch tips were collected from the crowns of mature trees to determine budworm densities. Traps placed beneath each tree were used to monitor late-instar dispersal. Assessments of regeneration were conducted to explore budworm damage to seedling species under different tree species.

METHODS

Canopy-Level Branch Samples

Branch sampling began with the random selection of 20 stations per 10-ha plot. At each selected station the nearest dominant or co-dominant balsam fir, white spruce, and black spruce were marked as trees to be sampled. Unfortunately, not all tree species could be found at every location. Balsam fir and white spruce trees were found at all selected stations. Less common black spruce trees were sought out within a 20 m radius of each station, but if a suitable tree could not be found in this area then only balsam fir and white spruce were sampled. All three species were found at all selected stations in Plots 1 & 2, but black spruce trees could not be found at four stations in Plot 3 and at five stations in Plot 4.

Altogether, 231 trees were marked to be sampled. Age, height, and diameter were recorded for each of these trees. Age was determined by counting annual growth increments on a core taken at stump height (30 cm). Tree height was measured to the nearest decimetre using a Suunto clinometer. Diameter at breast height was measured to the nearest millimetre using a standard diameter tape.

Collection and processing of branch samples from three trees (where possible) at each of 20 stations in each of four 10-ha plots could not be carried out all at once due to the amount of time required. Branch samples therefore were collected in stages. During the first stage, branches were collected from trees at five stations in each plot. These stations were selected at random from among the total of 20 stations previously selected. Similarly, five stations in each plot were selected at random during the second sampling stage. Members of the field team had become more proficient at sampling by this time and the remaining ten stations in each plot were sampled during the third stage.

Branch samples were collected using pole pruners outfitted with catch-baskets. Catch-baskets were necessary to ensure that budworm larvae, which readily drop from the branch when disturbed at late-instar stages, were not lost during sample collection (Sanders 1980). Great care was taken not to disturb foliage surrounding a targeted branch, thus reducing the chance of additional larvae falling into the basket from neighbouring branches. With a little practice, members of the field team were able to collect branch samples efficiently and with the required finesse.

One 45-cm branch tip, a unit commonly used for budworm studies (Sanders 1980, Régnière and Sanders 1983), was collected from the upper mid-crown of each selected tree. Following collection with pole pruners, each branch tip was trimmed to approximately 45 cm, cut in half, and placed in a

paper bag for transporting. Bags were sealed by folding over the tops and stapling them closed. Station coordinates and tree species for all samples were recorded on the bag at time of collection. Samples were transported back to the base camp and stored in a cool place until they could be processed.

Processing of branch samples involved measuring and recording various attributes for each branch tip. The bag and branch sample first were weighed on a triple beam, balance-type scale. A predetermined bag weight of 43 g was subtracted from the scale reading and the result was recorded as branch sample mass to the nearest gramme. The branch tip then was removed from the bag. Its length and width at the widest point were measured to the nearest centimetre using rulers.

For branches collected at the first stage, the total number of buds on each sample was counted to document food availability on each host-tree species. Bud counts for the second and third sample stages could not be determined with sufficient confidence due to heavy defoliation of some samples. Defoliation was assessed for branches collected at all stages by observing the 25 most distal buds on each sample and employing the Fettes method (Fig. 4) to generate a mean defoliation score.

Each branch sample was examined thoroughly to extract all budworm larvae. Abundance and developmental stages (instars) of all spruce budworm larvae were recorded. Instar identification was based on head capsule width (McGugan 1954). Pupae were recorded as L7's. Phytophagous larvae of other insects, mostly the spruce coneworm (*Dioryctria reniculelloides* Matuura and Munroe), were encountered occasionally, but were not recorded. All branch samples were examined for evidence of flowering to determine if one tree species might have a reproductive advantage over another. The presence or

absence of pollen-producing "flowers" or flower scars on current (1993) and previous (1992) year's growth was noted.

Branch sample collection and processing generally required four days of work at each of the three stages. Samples were collected over two days and stored separately. Samples then were processed over the next two days, with those collected on the first day processed first. The date of the third day of work was assigned as a representative date for each sampling stage: Stage 1 = 17-June; Stage 2 = 25-June; Stage 3 = 30-June.

Late-Instar Dispersal

Late-instar dispersal was monitored by setting water traps beneath each of the same trees selected for branch sampling. Water traps consisted of plastic trays that measured 50 cm long, 25 cm wide, and 6 cm deep. One trap was placed on level ground under the drip-line of the crown of each tree. Traps always were positioned on the south side of the tree for consistency. Disturbance to each site was kept to a minimum, but shrubs and herbs immediately above each trap were cleared away to provide a clear path of travel between canopy and ground level. Water was carried in backpacks designed for fire-fighting and used to fill all traps. A few drops of Kodak Photo-Flo 200 Solution were added to the water in each trap to break the surface tension, thus ensuring that larvae landing in a trap would sink to the bottom rather than float to the side and escape.

Once in place, all traps were checked on the same day at periodic intervals of a few days. The number and instar development of all spruce budworm larvae found in each water trap were recorded. The water in each trap was strained, topped with fresh water, and replenished with additional Photo-Flo at each visit.

Regeneration Beneath Host Trees

One circular sub-plot covering an area of 4-m^2 was established around each of the 231 water traps set under selected host trees. A wooden stake was pounded into the ground at the centre of one side of each water trap. A nail then was set in the top of each stake to serve as an anchor point for a plot cord. Although referred to as 4-m^2 sub-plots, it should be noted that water traps occupied 0.125 m^2 (= 1/8 m^2) of each sub-plot, making the actual area containing regeneration equal to 3.875 m^2.

Species and height to the nearest centimetre were recorded for each host-tree seedling contained within sub-plot boundaries. Seedling defoliation was estimated by observation of the 25 most distal buds and employment of the Fettes method (Fig. 4) to generate a mean defoliation score. Where seedlings had less than 25 buds, defoliation estimates were based on all buds.

RESULTS

Description of Selected Trees

A summary of ages, heights, and diameters for selected trees (Table 13) confirms that Plots 3 & 4 contained trees that were older and larger than trees in Plots 1 & 2, but this difference is not extreme. FRI maps suggest the 1993 ages of the two stands in the study area to be 47 and 57 years. Age data obtained from extracted cores generally support these stand ages, with balsam fir ages being quite close. White spruce and black spruce trees appear to be slightly older than balsam fir in all study plots, with white spruce consistently the oldest. Actual ages remain somewhat uncertain because many trees may have started out as advanced regeneration that was suppressed below a height of 30 cm for many years.

Table 13. Summary of ages, heights, and diameters for selected trees.

Plot	Species	Age			Height (m)			DBH (cm)		
		n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
1	Bf	18	45	6	20	12.6	2.3	20	14.3	2.9
	Sw	19	59	19	20	14.9	3.6	20	20.2	6.4
	Sb	20	51	12	20	13.6	2.0	20	16.1	3.1
	All	57	52	14	60	13.7	2.9	60	16.9	5.0
2	Bf	18	44	6	20	13.4	2.0	20	14.7	3.1
	Sw	19	59	16	20	16.6	2.5	20	22.6	5.5
	Sb	20	47	9	20	14.5	2.2	20	16.6	2.3
	All	57	50	13	60	14.8	2.6	60	18.0	5.1
3	Bf	19	52	6	20	14.3	1.9	20	16.8	3.7
	Sw	19	60	11	20	16.2	2.0	20	23.1	5.1
	Sb	15	54	14	16	13.5	2.7	16	16.7	4.7
	All	53	55	11	56	14.7	2.4	56	19.0	5.4
4	Bf	14	58	7	20	16.3	2.2	20	19.5	4.8
	Sw	19	61	12	20	16.6	2.6	20	24.6	5.9
	Sb	15	60	19	15	15.6	2.5	15	19.2	6.1
	All	48	59	13	55	16.2	2.4	55	21.3	6.0
All	All	215	54	13	231	14.8	2.7	231	18.7	5.6

Ages were taken at a stump height of 30 cm.
Corrections for growth below this height have not been applied.

Canopy-Level Branch Samples

Physical Characteristics of Branch Samples

Because branch samples were weighed while budworm larvae were still on them, it was necessary to subtract the weights of these larvae before using data for branch sample mass. Since numbers and instars of all larvae were recorded at time of branch sample processing, this weight adjustment initially was looked upon as a simple task. Mean fresh weight values for each larval instar were to be obtained from the literature and used to adjust branch sample weights accordingly.

However, an extensive search of the literature later failed to produce the necessary fresh weight values for larvae of all instars. Approximate weights therefore had to be calculated. Mean dry weight values for instar stages L2 to L6 were obtained from Régnière and You (1991). Regression equations relating dry weights to fresh weights (Eidt and Cameron 1972) were used to convert these mean dry weight values to mean fresh weight values. This process resulted in mean fresh weight values per budworm for L2 to L6 stages: L2 = 0.43 mg; L3 = 1.72 mg; L4 = 6.82 mg; L5 = 26.76 mg; L6 = 81.21 mg. Mean fresh weight per pupa was calculated to be 76.33 mg using data from Eidt and Cameron (1972). Data for branch sample mass were adjusted for the presence of budworm larvae and pupae by subtracting the above values as necessary. Adjustments to branch sample mass were of minor importance in most cases. Maximum reduction in mass was 5.52 g (or 2.3% of total mass), with a mean reduction of 0.56 g (0.33%). Nonetheless, adjustments were applied to data for all branch samples and any references to branch sample mass or density hereafter relate to adjusted values.

A series of ANOVA oneway tests indicated that branch sample length, width, area, mass, and density were not significantly different between dates.

Mean values therefore were summarized by plot and tree species only (Table 14). ANOVA oneway tests between species showed no significant differences for length or width. Branch sample surface area was found not to be significantly different between species, but this was expected because area was calculated using length and width. Branch sample mass for both spruce species was significantly greater than that for balsam fir. Branch sample density was found to be significantly different between all three species, with white spruce the most dense and balsam fir the least dense.

Bud counts for 17-June branch samples were lowest on balsam fir and highest on black spruce (Table 15). White spruce had almost three times as many buds as balsam fir when densities were expressed per branch sample. When bud densities were expressed as number per kg of branch sample to compensate for differences in mass between species, white spruce still had more than twice as many buds as balsam fir. Black spruce had significantly more buds per kg than balsam fir and white spruce.

During selection of trees to be sampled, the nearest dominant or co-dominant tree of each species was selected at each station -- with the condition that all selected trees be in relatively good health. This condition was imposed to avoid sampling from the many dead and moribund balsam fir trees in the area. Despite selection of apparently healthy trees, many branch samples from balsam fir trees carried few buds. The buds that were present often were small and not very vigorous during shoot elongation. On some balsam fir samples, many buds had not opened by 17-June. Unopened balsam fir buds also were encountered frequently on the second and third sample dates, indicative of the generally poor health of this species throughout the study area. In contrast, the majority of buds on black spruce samples appeared healthy and white spruce buds flushed long, full shoots where they were not destroyed by the budworm.

Table 14. Physical characteristics of branch samples by plot and tree species.

Character	Tree	Plot 1			Plot 2			Plot 3			Plot 4			All Plots			ANOVA
		Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	(All Plots)
	n	20	20	20	20	20	20	20	20	16	20	20	15	80	80	71	
Length (cm)	mean	46.4	45.5	45.7	45.8	46.7	45.5	45.4	45.4	45.3	45.0	45.5	45.5	45.6	45.8	45.5	ns
	S.D.	1.9	2.2	1.9	1.6	2.0	1.5	1.3	2.0	1.1	1.3	1.6	1.7	1.6	2.0	1.5	
Width (cm)	mean	40.2	36.9	36.2	37.7	36.2	38.6	37.3	36.5	35.6	37.5	38.0	41.3	38.2	36.9	37.8	ns
	S.D.	7.4	9.4	8.4	7.0	7.2	8.2	6.5	10.1	6.8	6.5	10.2	12.3	6.8	9.1	9.1	
Area (dm^2)	mean	9.3	8.4	8.2	8.6	8.5	8.8	8.5	8.3	8.1	8.4	8.6	9.4	8.7	8.4	8.6	ns
	S.D.	1.8	2.3	1.9	1.8	1.8	1.8	1.5	2.4	1.7	1.5	2.4	3.0	1.7	2.2	2.1	
Mass (g)	mean	113.9	131.2	143.7	131.8	180.1	164.8	138.5	186.1	176.7	156.5	222.8	158.6	135.2	180.1	160.2	Bf < Sb = Sw
	S.D.	33.7	22.1	38.2	32.9	56.3	51.5	25.9	38.5	51.5	47.8	89.6	43.6	38.5	65.1	47.0	
Density (g/dm^2)	mean	12.3	16.5	18.3	15.8	21.5	18.9	16.7	23.8	22.9	18.8	26.4	17.6	15.9	22.0	19.4	Bf < Sb < Sw
	S.D.	2.9	4.1	6.2	4.7	5.3	4.7	3.7	6.2	8.7	5.4	9.5	5.0	4.8	7.4	6.4	

ANOVA refers to a oneway test between species, followed by a Tukey-HSD multiple range test (alpha = 0.05).

ns	no significant differences
<	significantly less than
=	not significantly different

Table 15. Bud densities by plot and tree species for 17-June branch samples.

| Character | Tree | Plot 1 | | | Plot 2 | | | Plot 3 | | | Plot 4 | | | All Plots | | | ANOVA |
		Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	(All Plots)
Buds	n	5	5	5	5	5	5	5	5	4	5	5	4	20	20	18	
per	mean	28	99	197	38	39	106	35	113	84	34	139	104	34	98	126	Bf < Sw = Sb
Sample	S.D.	24	56	80	16	40	36	19	58	25	38	47	73	24	60	70	
Buds	n	5	5	5	5	5	5	5	5	4	5	5	4	20	20	18	
per	mean	222	806	1217	363	279	768	239	575	526	236	547	663	265	552	815	Bf < Sw < Sb
kg	S.D.	168	539	198	202	193	116	114	245	192	202	126	279	171	349	325	

ANOVA refers to a oneway test between species, followed by a Tukey-HSD multiple range test (alpha = 0.05).

< significantly less than
= not significantly different

Budworm Population Densities

When budworm counts per branch sample from the four study plots are considered together, mean number of larvae per 45-cm branch tip is highest for white spruce on all three sample dates (Fig. 18). This difference is most pronounced on 17-June, when white spruce had more than three times as many larvae as balsam fir or black spruce. Budworm numbers for all species decreased between 17-June and 25-June, especially for white spruce. There was a further, although less pronounced, decrease in budworm numbers between 25-June and 30-June. Black spruce is the exception here, with budworm numbers for this species actually increasing slightly by 30-June.

Instar development appears to have been slower on black spruce than on balsam fir or white spruce. This difference can be seen more clearly when instar stages are expressed as a percentage of total budworm counts (Fig. 19) Budworm development on balsam fir and white spruce appears to have been similar, although slightly more advanced on white spruce for all dates. In addition to larvae, a total of 23 budworm pupae were tallied during branch sample processing. All of these pupae were recorded on 30-June and all but one were found on white spruce.

Budworm densities expressed on a per branch sample basis may not reflect true relations between host-tree species because of differences in branch structure. Number of larvae per kg of branch sample has been suggested as the best expression of budworm density for comparisons between host species (Régnière et al. 1989). Number of budworm larvae per square metre of surface area has been used commonly in the past. Budworm densities are summarized by plot, tree species, and date using all three density measures (Table 16). White spruce is shown to have had significantly more budworm larvae on the first two sample dates, regardless of how densities are expressed.

Figure 18. Mean number of budworm larvae per branch sample by date, tree species, and larval instar.
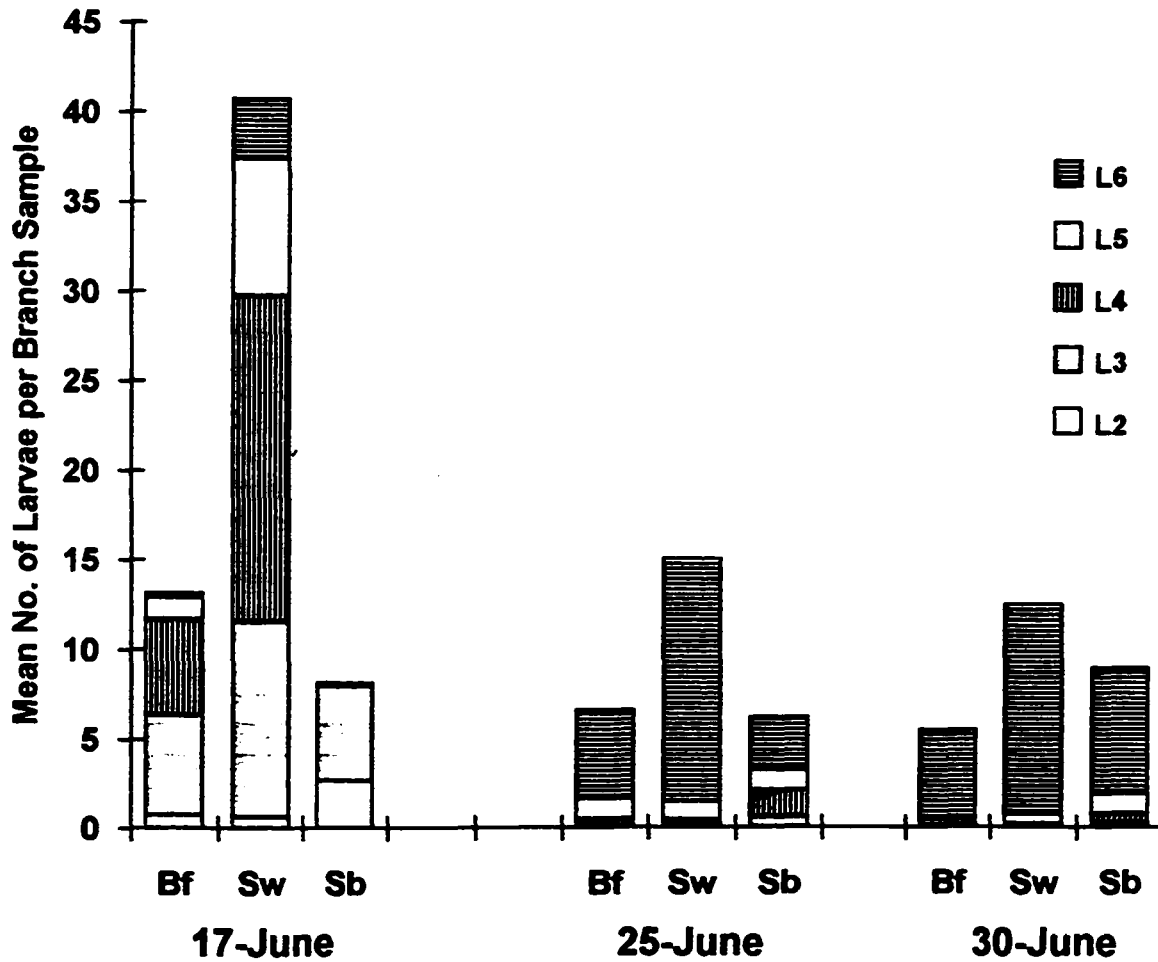
Sample sizes and standard deviations are shown in Table 16.
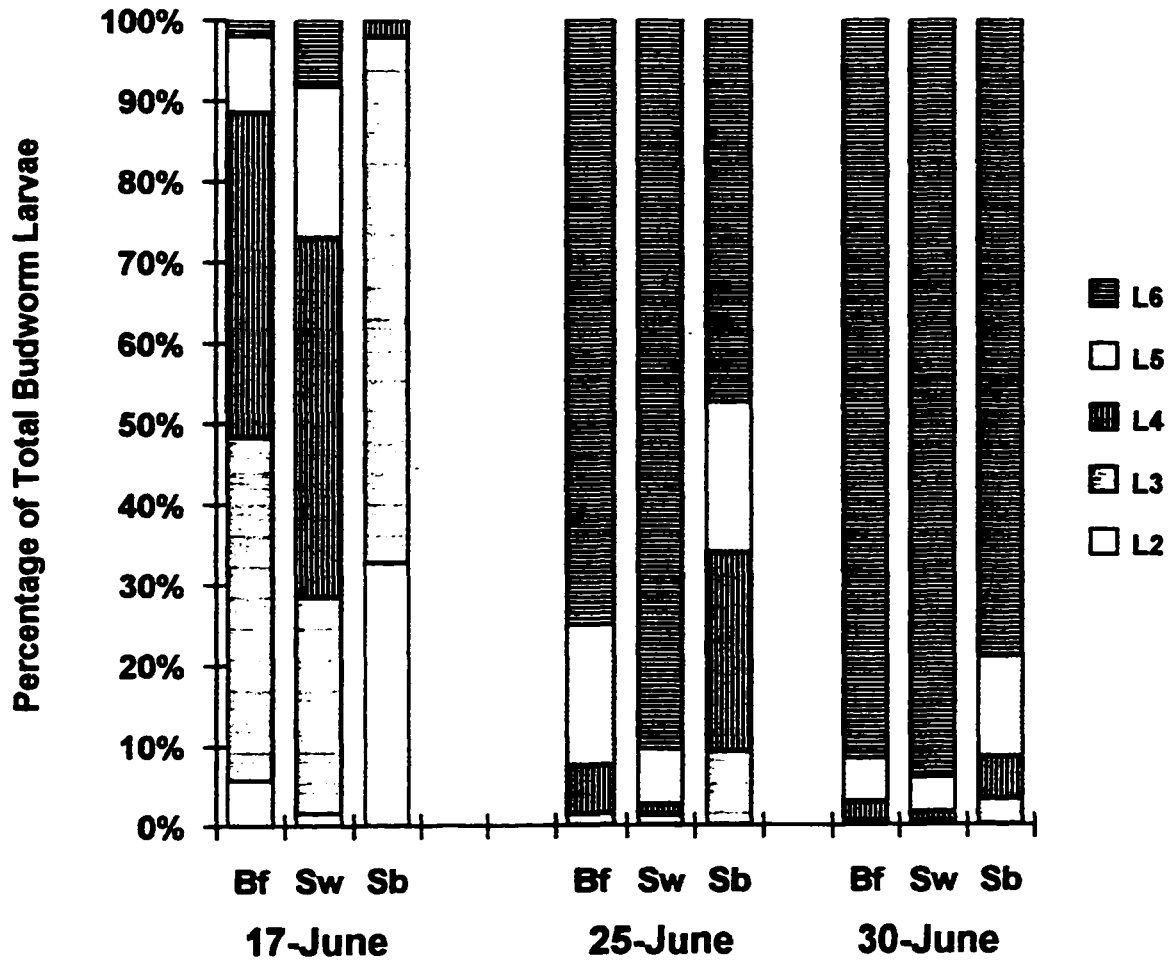
Figure 19. **Percentage of total budworm larvae per branch sample by date, tree species, and larval instar.**

Table 16. Mean number of budworm larvae by plot, tree species, and date: a) per branch sample, b) per kg of branch sample, c) per m^2 of branch sample.

a. Budworm larvae per branch sample

Date	Tree	Plot 1 Bf	Sw	Sb	Plot 2 Bf	Sw	Sb	Plot 3 Bf	Sw	Sb	Plot 4 Bf	Sw	Sb	All Plots Bf	Sw	Sb	ANOVA (All Plots)
17-June	n	5	5	5	5	5	5	5	5	4	5	5	4	20	20	18	Sb = Bf < Sw
	mean	8.0	35.6	10.8	12.0	14.8	12.4	17.8	48.2	4.3	14.8	64.4	3.5	13.2	40.8	8.2	
	S.D.	1.2	17.7	11.4	8.1	12.3	7.8	15.8	27.3	6.0	23.6	20.6	3.1	14.1	26.3	8.3	
25-June	n	5	5	5	5	5	5	5	5	5	5	5	4	20	20	19	Sb = Bf < Sw
	mean	6.8	12.6	3.4	4.6	23.6	7.2	10.4	14.0	8.2	4.6	10.0	6.0	6.6	15.1	6.2	
	S.D.	4.5	6.7	1.5	2.4	9.9	9.0	9.6	7.8	2.8	4.6	8.5	7.0	5.9	9.3	5.6	
30-June	n	10	10	10	10	10	10	10	10	7	10	10	7	40	40	34	Bf < Sw
	mean	2.0	2.6	7.1	12.1	21.1	17.5	2.8	10.6	3.0	5.0	15.4	5.3	5.5	12.4	8.9	Sb = Bf
	S.D.	2.2	2.5	6.6	10.9	17.5	14.7	4.4	6.9	2.2	6.2	16.3	3.9	7.6	13.8	10.4	Sb = Sw

b. Budworm larvae per kg of branch sample

Date	Tree	Plot 1 Bf	Sw	Sb	Plot 2 Bf	Sw	Sb	Plot 3 Bf	Sw	Sb	Plot 4 Bf	Sw	Sb	All Plots Bf	Sw	Sb	ANOVA (All Plots)
17-June	n	5	5	5	5	5	5	5	5	4	5	5	4	20	20	18	Sb = Bf < Sw
	mean	69	296	70	120	115	94	122	245	27	79	255	22	98	228	57	
	S.D.	21	190	70	112	81	51	101	127	38	102	58	20	88	134	55	
25-June	n	5	5	5	5	5	5	5	5	5	5	5	4	20	20	19	Sb = Bf < Sw
	mean	64	104	25	33	127	44	77	78	50	31	73	39	51	95	40	
	S.D.	45	66	12	18	50	52	76	33	15	24	63	44	47	55	33	
30-June	n	10	10	10	10	10	10	10	10	7	10	10	7	40	40	34	
	mean	18	20	52	85	105	101	18	58	16	28	56	34	37	60	55	ns
	S.D.	20	19	47	62	74	89	27	37	11	37	42	22	47	55	63	

. . . continued

110

Table 16. (Continued)

c. Budworm larvae per m^2 of branch sample

Date	Tree	Plot 1			Plot 2			Plot 3			Plot 4			All Plots			ANOVA
		Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	(All Plots)
17-June	n	5	5	5	5	5	5	5	5	4	5	5	4	20	20	18	Sb = Bf < Sw
	mean	89	453	186	117	185	144	185	569	46	141	593	41	133	450	111	
	S.D.	32	345	203	71	134	93	138	403	67	204	62	37	124	302	130	
25-June	n	5	5	5	5	5	5	5	5	5	5	5	4	20	20	19	Sb = Bf < Sw
	mean	76	159	39	55	269	72	145	197	108	59	164	71	84	197	72	
	S.D.	56	91	19	25	75	88	154	57	31	52	175	81	88	110	61	
30-June	n	10	10	10	10	10	10	10	10	7	10	10	7	40	40	34	Bf < Sb = Sw
	mean	21	37	95	147	228	227	33	135	43	57	188	66	65	147	117	
	S.D.	22	39	113	108	156	225	55	107	31	71	200	44	85	152	153	

ANOVA refers to a oneway test between species, followed by a Tukey-HSD multiple range test where significant differences exist. (alpha = 0.05)

ns   no significant differences
<   significantly less than
=   not significantly different

111

Results are less consistent among density measures for the third sample date, but expression of density on a per kg basis suggests that differences between tree species were no longer significant by this date.

Budworm densities also can be expressed as number of larvae per bud to provide some measure of food supply (Sanders 1980). Buds were counted in this study only for 17-June branch samples. Black spruce had the greatest number of buds per branch sample and the lowest number of larvae, resulting in a density of 0.07 larvae per bud or, conversely, about 14 buds per budworm. The numbers of larvae per bud for balsam fir and white spruce were 0.42 and 0.43, respectively, or about 2.4 buds per budworm for both species. Thus, white spruce branch tips had three times as many larvae as balsam fir on 17-June, but also three times as many buds.

Branch Defoliation

Mean defoliation was lower for black spruce branch samples than for balsam fir or white spruce on all sample dates (Fig. 20; Table 17). Balsam fir and white spruce suffered similar defoliation damage on all dates, with mean defoliation for both species approaching 100% by 25-June. In contrast, mean defoliation of black spruce never exceeded 30%.

Flowering History

None of the branch samples examined for this study showed any evidence of pollen production on 1993 or 1992 growth segments. It is highly unlikely that flowering occurred during these two years. Only two branch samples showed any signs of reproductive activity on earlier growth. Both samples were from balsam fir trees and both had only a few persistent, cup-like flower scars located near the 45-cm cut off point. No attempt was made to
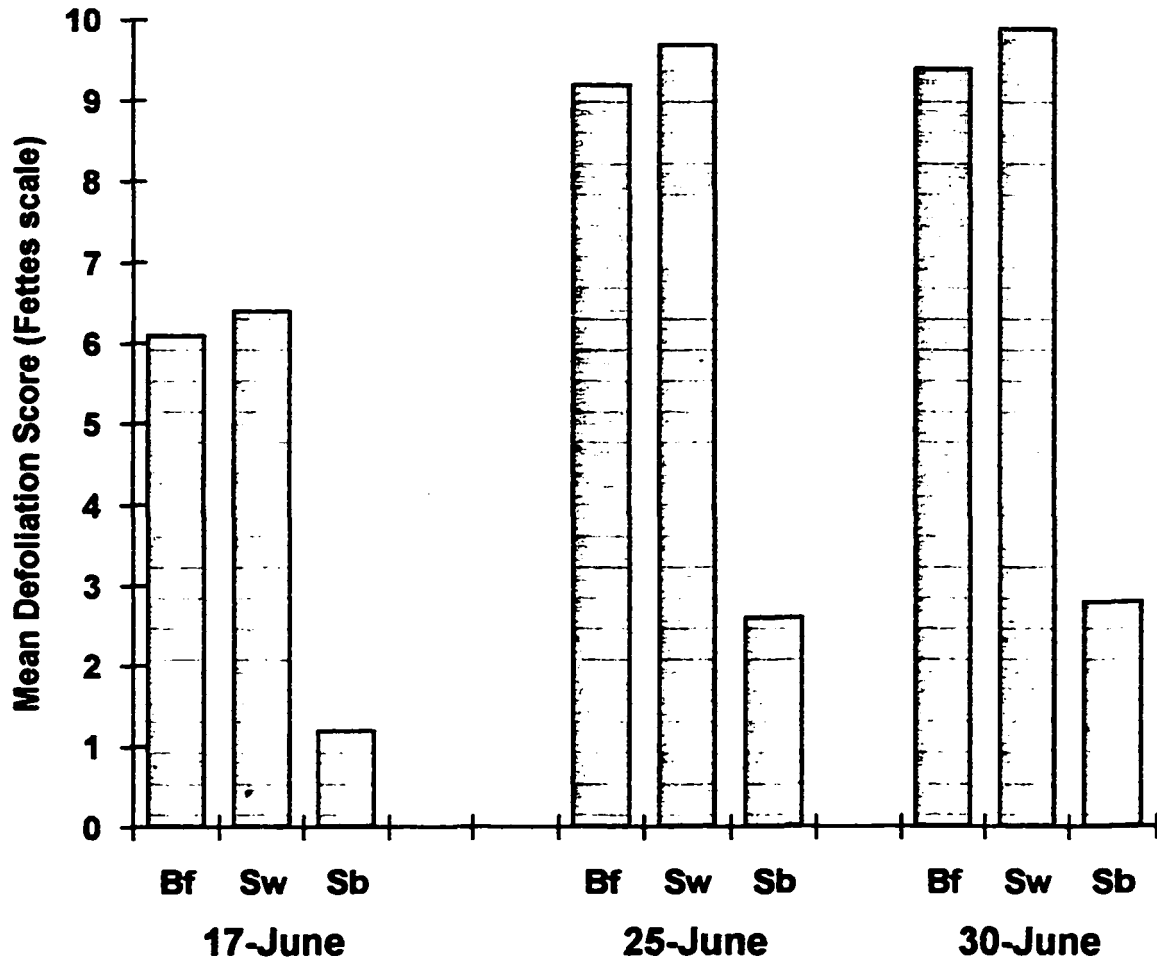
Figure 20. Mean Fettes scores for branch defoliation by date and tree species.

Table 17. Mean defoliation scores (Fettes) for branch samples by plot, tree species, and date.

Date	Tree	Plot 1			Plot 2			Plot 3			Plot 4			All Plots			NPAR
		Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	Bf	Sw	Sb	(All Plots)
17-June	n	5	5	5	5	5	5	4	5	4	5	5	4	19	20	18	
	mean	9.4	8.8	1.6	6.8	7.8	1.0	2.3	4.0	1.3	5.2	5.0	0.8	6.1	6.4	1.2	Sb < Bf = Sw
	S.D.	2.1	2.2	0.9	3.3	3.0	0.7	1.3	3.2	1.0	4.0	3.2	0.5	3.7	3.4	3.4	
25-June	n	5	5	5	5	5	5	5	5	5	5	5	4	20	20	19	
	mean	8.4	8.2	2.8	10.0	10.0	1.4	8.6	10.0	4.2	9.8	10.4	1.8	9.2	9.7	2.6	Sb < Bf = Sw
	S.D.	2.1	3.1	4.0	2.1	1.9	0.9	2.6	1.0	1.8	1.6	0.5	1.7	2.1	2.0	2.5	
30-June	n	10	10	10	10	10	10	10	10	7	10	10	7	40	40	34	
	mean	9.4	9.4	3.3	10.4	10.9	3.8	7.6	8.9	1.9	10.2	10.3	1.4	9.4	9.9	2.8	Sb < Bf = Sw
	S.D.	2.5	3.5	3.6	1.1	0.6	2.1	3.6	3.0	1.2	1.9	0.7	1.3	2.6	2.6	2.5	

NPAR refers to a nonparametric Kruskal-Wallis oneway test between species, followed by a series of Mann-Whitney tests between pairs of species (alpha = 0.05).

<   significantly less than
=   not significantly different

114

determine how long ago these flowers were produced, but it appears that pollen production has not occurred for many years.

Late-Instar Dispersal

Water Trap Catches

All water traps were checked on six dates during the late-instar dispersal period (Fig. 21). Total catches, based on all 231 traps, were highest on the first date (23-June) and then decreased rapidly over the next few days. On 23-June, about 1% of the captured larvae were in the L4 stage, about 3% were in the L5 stage, and the remainder (96%) were in the L6 stage. On all subsequent dates, captured larvae were in the L6 stage almost exclusively.

Because water traps were set over two days, collection periods were not equal for all traps at time of the first check. Traps in Plots 1 & 2 had been collecting for two days, while those in Plots 3 & 4 had been collecting for only one day. The count on 23-June (Fig. 21) reflects total number of budworm larvae, without regard for different lengths of collection periods in different plots. Total trap counts from Plots 1 & 2 were divided by two before calculating mean catches per trap on 23-June (Fig. 22). This adjustment served to make data from all plots comparable on the basis of a one-day collection period.

Mean water trap catches were summarized by plot, tree species, and date (Table 18). Nonparametric tests were used to compare catches between species for all plots combined. Mean catches under white spruce trees were found to be significantly higher than those under balsam fir or black spruce trees on all dates, except 15-July on which no significant differences existed. Mean catches for traps under balsam fir and black spruce trees were not significantly different on any of the check dates.

Figure 21. Total water trap catches by date and larval instar.
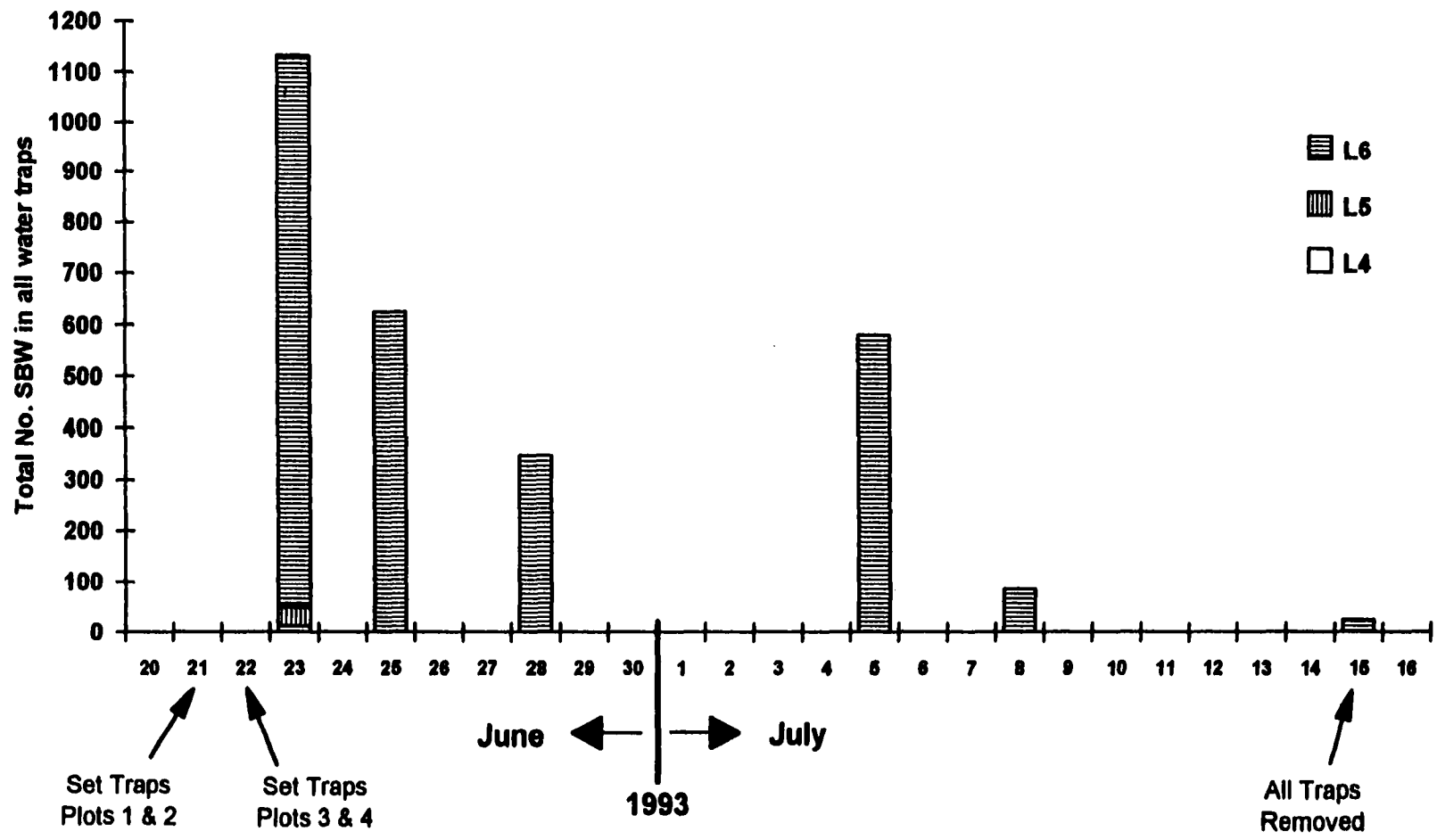
A total of 231 traps were checked on each date (Bf n=80; Sw n=80; Sb n=71).
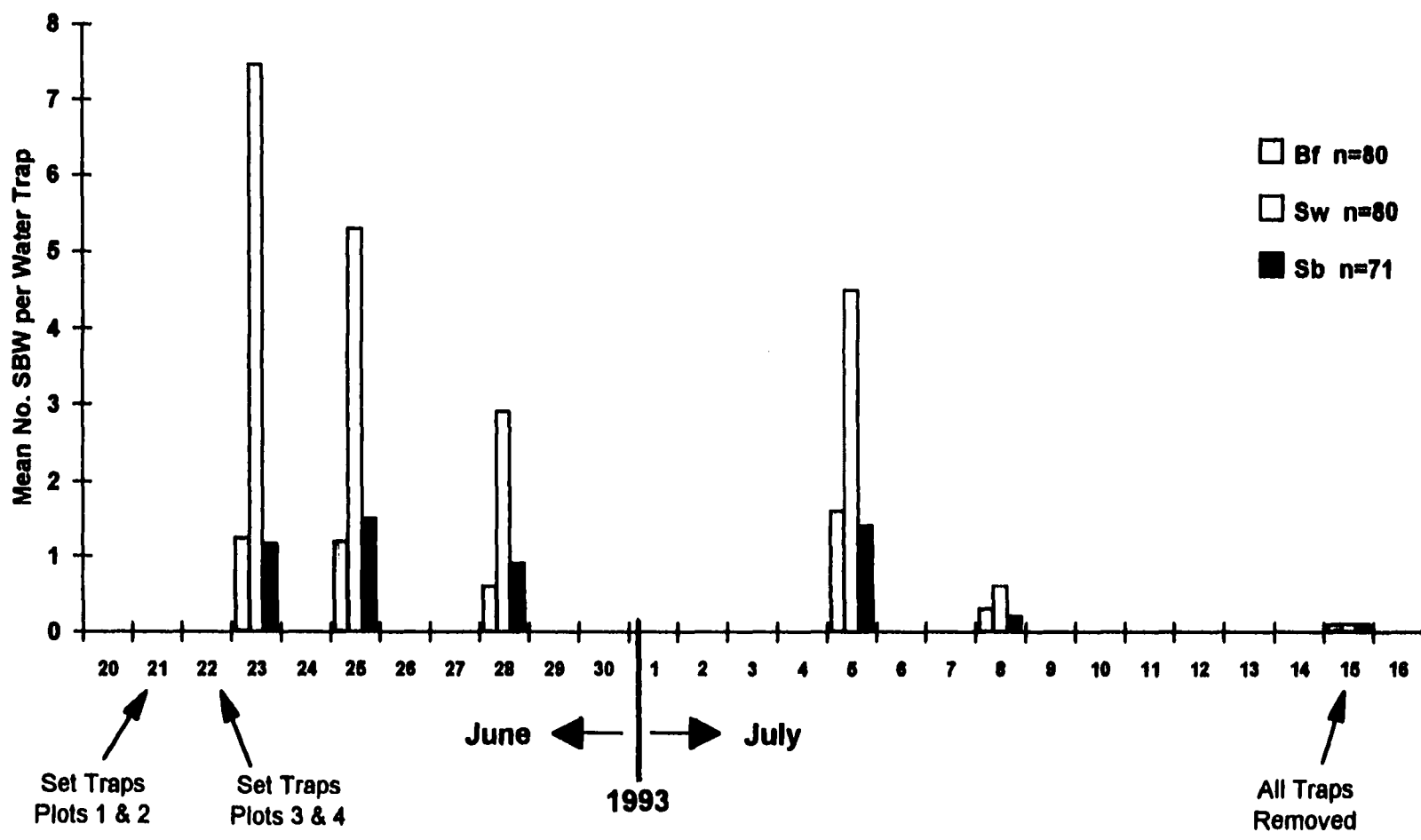
Figure 22. Mean water trap catches by date and tree species.

Standard deviations are shown in Table 18.

117

Table 18. Mean number of budworm larvae per water trap by plot, tree species, and check date.

Check Date	Tree n	Plot 1 Bf 20	Sw 20	Sb 20	Plot 2 Bf 20	Sw 20	Sb 20	Plot 3 Bf 20	Sw 20	Sb 16	Plot 4 Bf 20	Sw 20	Sb 15	All Plots Bf 80	Sw 80	Sb 71	NPAR (All Plots)
23-June mean		0.80	6.07	0.68	1.32	9.23	0.85	1.80	8.90	0.94	1.35	6.65	2.53	1.24	7.46	1.17	Sb = Bf < Sw
S.D.		0.92	7.64	1.78	1.89	9.85	1.50	2.69	15.94	2.49	2.23	9.19	6.67	2.05	11.03	3.50	
25-June mean		0.45	4.15	0.45	1.40	9.15	2.10	1.70	2.70	1.00	1.10	5.30	2.60	1.16	5.33	1.49	Bf = Sb < Sw
S.D.		1.39	6.75	1.00	2.19	8.52	3.70	3.16	3.84	1.59	1.55	6.71	7.13	2.20	6.97	3.93	
28-June mean		0.60	2.30	0.55	0.60	4.50	1.10	0.65	2.55	0.75	0.65	2.35	1.20	0.63	2.93	0.89	Bf = Sb < Sw
S.D.		1.05	2.36	1.15	0.88	3.91	1.97	0.93	3.49	1.39	1.04	2.16	2.37	0.96	3.15	1.74	
05-July mean		1.10	2.90	1.25	2.60	5.65	1.80	0.85	4.55	0.56	1.75	4.75	1.73	1.58	4.46	1.35	Sb = Bf < Sw
S.D.		1.86	3.21	2.51	3.22	4.68	2.17	1.69	3.58	1.09	2.15	4.71	3.26	2.36	4.14	2.37	
08-July mean		0.25	0.75	0.25	0.45	0.65	0.30	0.35	0.55	0.19	0.05	0.45	0.13	0.28	0.60	0.23	Sb = Bf < Sw
S.D.		0.44	1.16	0.44	0.76	0.75	0.47	0.67	0.89	0.40	0.22	1.00	0.52	0.57	0.95	0.45	
15-July mean		0.15	0.30	0.10	0.05	0.00	0.10	0.05	0.20	0.00	0.20	0.00	0.07	0.11	0.13	0.07	ns
S.D.		0.37	1.13	0.45	0.22	0.00	0.31	0.22	0.52	0.00	0.70	0.00	0.26	0.42	0.62	0.31	
Total Catches mean		3.05	16.48	3.25	6.43	29.18	6.25	5.40	19.45	3.44	5.10	19.50	8.27	4.99	20.90	5.20	Bf = Sb < Sw
(all dates) S.D.		3.71	16.58	5.63	6.50	22.86	8.25	6.15	23.24	4.41	4.46	19.86	19.68	5.37	21.03	10.62	

Water traps were set in Plots 1 & 2 on 21-June and in Plots 3 & 4 on 22-June.
Trap catches for Plots 1 & 2 on 23-June (shaded area) have been divided by two so that
all trap catches on 23-June are comparable on the basis of a one day collection period.

NPAR refers to a nonparametric Kruskal-Wallis oneway test between species, followed by
a series of Mann-Whitney tests between pairs of species (alpha = 0.05).

ns   no significant differences
<   significantly less than
=   not significantly different

118

Mean total catches of about five larvae per water trap under balsam fir and black spruce and about 20 larvae per trap under white spruce do not seem exceptionally high when one considers that these catches occurred over a dispersal period of about three weeks. However, it should be kept in mind that each water trap covered an area of only 1/8 m^2. Estimates of dispersal numbers per square metre of ground perhaps put things in better perspective. A mean total catch of five larvae per trap is equivalent to 40 larvae for every square metre of ground under the dripline of every mature balsam fir and black spruce tree in the study area. Under white spruce trees, dispersal numbers are equivalent to more than 160 larvae per square metre.

Trap catches were highly variable for all species on all dates. While mean catch numbers serve to reflect general tendencies, it is of interest to note some outstanding catch numbers as well. Data for all water traps that collected 40 or more larvae over a collection period of one day are summarized in Table 19, together with total catches for these traps and equivalent dispersal numbers per square metre of ground. All outstanding catches occurred under white spruce trees, with equivalent total dispersal numbers as high as 840 larvae per square metre. It also is noteworthy that 15 traps under white spruce trees caught zero larvae on 23-June and two traps under white spruce trees caught zero larvae over the entire dispersal period.

Dispersal Activity in Relation to Time and Temperature

The generally high trap catches recorded for 23-June suggest that dispersal already was underway at the time when traps were set. This is an unfortunate reality. For reasons beyond control, 21-June was the earliest date on which traps could be set. Initially, it appeared that setting traps on this date would present no major problems. Branch samples processed on 17-June

Table 19. Some noteworthy water trap catches.

Plot	Tree	Date of Trap Set	23-June Trap Check		Total Catch Over All Dates	
			Trap Catch	Equivalent No./m^2/day	Trap Catch	Equivalent No./m^2
1	Sw	21-June	24	96	65	520
1	Sw	21-June	36	144	73	584
1	Sw	21-June	63	252	78	624
2	Sw	21-June	18	72	63	504
2	Sw	21-June	21	84	38	304
2	Sw	21-June	25	100	66	528
2	Sw	21-June	32	128	57	456
2	Sw	21-June	41	164	65	520
2	Sw	21-June	45	180	76	608
2	Sw	21-June	45	180	100	800
2	Sw	21-June	73	292	105	840
3	Sw	22-June	10	80	30	240
3	Sw	22-June	26	208	67	536
3	Sw	22-June	38	304	60	480
3	Sw	22-June	63	504	81	648
4	Sw	22-June	11	88	42	336
4	Sw	22-June	30	240	45	360
4	Sw	22-June	34	272	87	696

Selected data are for all water traps that caught 40 or more larvae over a collection period of one day.

indicated that few larvae (only 5.9%) had reached the L6 stage. Most larvae (38.6%) were in the L4 stage and some larvae (6.2%) were still in the L2 stage. With larval development still in relatively early stages at this time, dispersal did not seem imminent.

The forest was watched closely every day, but no sign of dispersal activity was observed up to and including 19-June. On 20-June, silken strands could be seen occasionally in the tops of some trees, suggesting that dispersal was about to begin. It was expected that dispersal would follow a normal distribution curve, beginning slowly and increasing over time before entering a decline phase.

Rather than increasing gradually, however, budworm dispersal suddenly exploded on 21-June. Late-instar larvae could be seen raining down to the understory everywhere. This unexpected and sudden mass-dispersal is believed to have been triggered by extreme temperature (Fig. 23). The wind on 21-June was light and heat from the sun was intense. The temperature on 21-June reached 30.7°C in Thunder Bay, the highest temperature recorded for any date in 1993 (Environment Canada 1993). Summer temperatures in Thunder Bay generally are cooler than those in surrounding inland areas because of the moderating influences of Lake Superior. It is likely that the temperature on 21-June was somewhat higher in the Black Sturgeon area than it was in Thunder Bay.

Because dispersal began before most water traps were set, the data do not cover the entire dispersal period. The beginning and possibly the most important part of the dispersal period were missed. Dispersal numbers already were declining by the time all traps were set and checked for the first time.

With the above-described limitations in mind, an attempt was made to interpolate daily dispersal activity at Black Sturgeon during the summer of 1993 (Fig. 23). Total trap counts for each of the six dates were converted to a mean count per trap per day (black squares in Fig. 23). These means then were moved to mid-points between check dates and connected with a smooth line to represent daily dispersal activity (solid line). Since dispersal already was occurring before traps were set, the start of activity must be surmised on the basis of observations (dashed line). Unfortunately, there is no way of knowing how high trap catches might have been at peak dispersal.
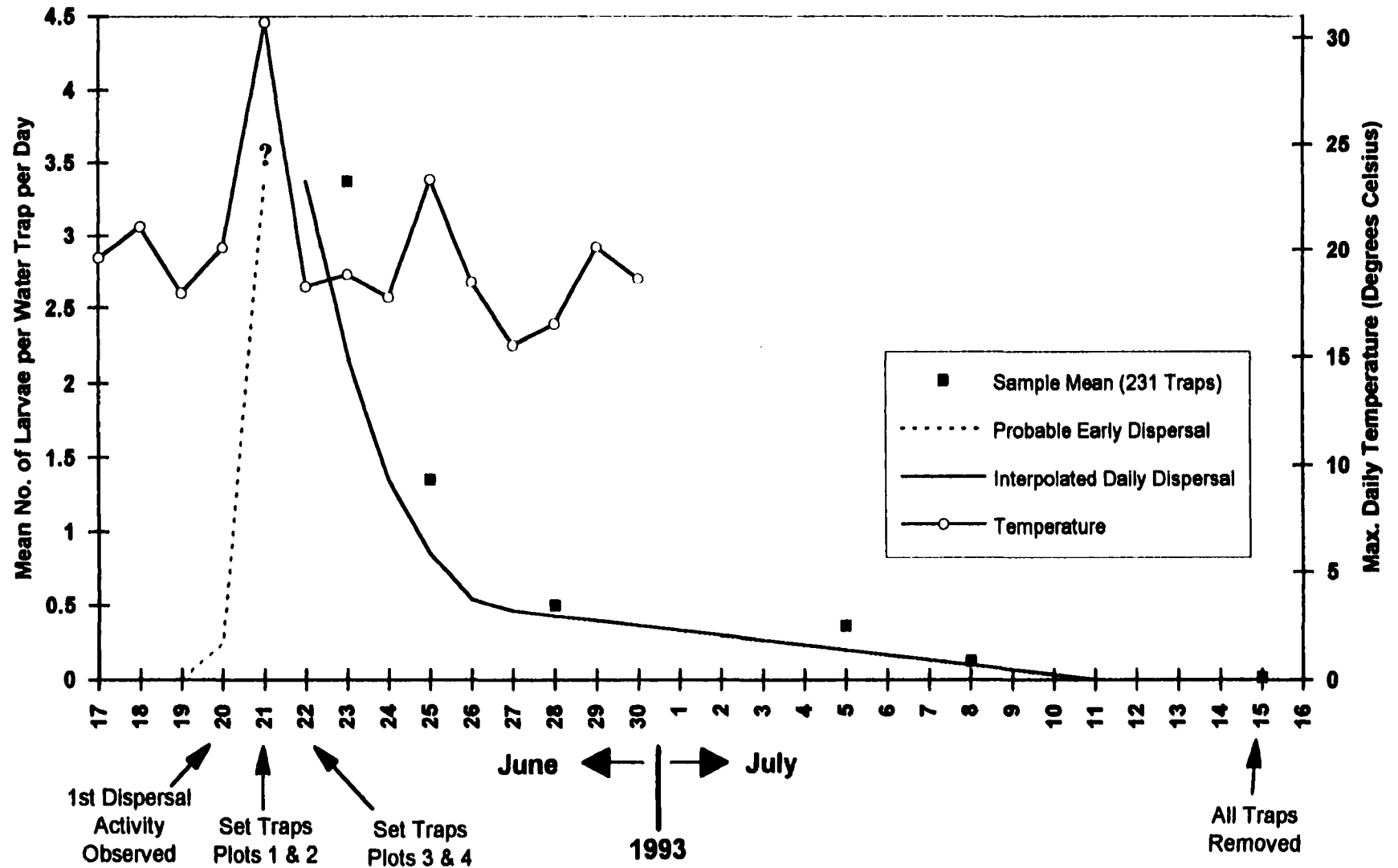
Temperatures were obtained from Environment Canada (1993) weather records for Thunder Bay, Ontario.

Figure 23. Mean water trap catches in relation to time and temperature.

122

Regeneration Beneath Host Trees

Seedling Densities

A total of 1566 seedlings was tallied in 4-m^2 sub-plots around all 231 water traps. No dead seedlings were encountered. Of the seedlings tallied, 1503 (96%) were balsam fir, 38 (2.4%) were white spruce, and 25 (1.6%) were black spruce. Balsam fir seedlings outnumbered spruce seedlings by a ratio of 24:1, slightly less than the 30:1 ratio suggested by data from random sub-plots.

Overall mean density was 6.8 seedlings per sub-plot, but water traps occupied 1/8 m^2 of each sub-plot. Before presentation of the data (Table 20), seedling counts were adjusted to reflect densities that might have been found in standard 4-m^2 sub-plots. Overall mean density increased to 7.0 seedlings per sub-plot after adjustment, a lower number than the density of 9.1 seedlings per sub-plot suggested by random sub-plots.

An ANOVA oneway test was used to compare seedling densities (all seedling species combined) under different tree species (all plots combined). Results indicated that seedling densities were not significantly different under balsam fir, white spruce, and black spruce trees (p = 0.455).

Height Distributions

Height distributions for regeneration are summarized by plot, tree species, and seedling species in Table 21. Overall mean height was 15.4 cm, but dropped to 14.7 cm (S.D. = 7.3, n = 1551) after imposition of a 53 cm top height that included 99% of all seedlings. Random sub-plots earlier suggested an overall mean height of 17.3 cm for all seedlings and 15.5 cm using a top height of 53 cm. Thus, seedlings under host trees were shorter than those in random sub-plots, but only by less than one centimetre.

Table 20. Seedling densities in sub-plots under host trees.

Seedling	Tree n	Plot 1 Bf 20	Sw 20	Sb 20	All 60	Plot 2 Bf 20	Sw 20	Sb 20	All 60	Plot 3 Bf 20	Sw 20	Sb 16	All 56	Plot 4 Bf 20	Sw 20	Sb 15	All 55	All Plots Bf 80	Sw 80	Sb 71	All 231
Bf	mean	5.42	2.89	1.86	3.39	3.61	3.77	2.79	3.39	9.60	16.10	10.90	12.29	8.62	8.21	7.98	8.30	6.81	7.74	5.45	6.72
	S.D.	8.18	3.72	2.45	5.50	3.17	8.64	3.72	5.65	11.43	18.51	17.53	15.99	13.61	9.03	8.61	10.63	10.02	12.29	9.99	10.84
Sw	mean	0.88	0.05	0.00	0.31	0.26	0.00	0.00	0.09	0.26	0.00	0.00	0.09	0.15	0.36	0.00	0.19	0.39	0.10	0.00	0.17
	S.D.	3.45	0.23	---	2.01	0.74	---	---	0.44	0.57	---	---	0.36	0.51	1.62	---	1.01	1.79	0.81	---	1.17
Sb	mean	0.21	0.05	0.26	0.17	0.10	0.15	0.46	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.02	0.08	0.05	0.22	0.11
	S.D.	0.64	0.23	0.81	0.61	0.32	0.69	1.85	1.15	---	---	---	---	---	---	0.27	0.14	0.36	0.36	1.07	0.67
All	mean	6.50	2.99	2.12	3.87	3.97	3.92	3.25	3.72	9.86	16.10	10.90	12.39	8.77	8.57	8.05	8.50	7.28	7.90	5.67	7.00
	S.D.	11.17	3.77	2.67	7.12	3.56	9.31	4.48	6.21	11.35	18.51	17.53	15.96	13.56	9.26	8.79	10.72	10.65	12.43	10.07	11.13

Because sub-plots were partially occupied by water traps, all data have been adjusted to reflect seedling numbers in full 4 m^2 sub-plots.

124

Table 21. Seedling heights under host trees.

Seedling	Tree	Plot 1 Bf	Sw	Sb	All	Plot 2 Bf	Sw	Sb	All	Plot 3 Bf	Sw	Sb	All	Plot 4 Bf	Sw	Sb	All	All Plots Bf	Sw	Sb	All
	n	20	20	20	60	20	20	20	60	20	20	16	56	20	20	15	55	80	80	71	231
Bf	n	105	56	36	197	70	73	54	197	186	312	169	667	167	159	116	442	528	600	375	1503
	mean	19.6	17.2	21.3	19.2	16.5	17.0	17.1	16.8	14.4	13.3	12.7	13.4	14.1	14.8	15.4	14.7	15.6	14.5	15.0	15.0
	S.D.	11.2	19.2	25.3	16.9	8.4	8.0	7.1	7.9	6.8	6.4	10.0	7.6	7.0	10.7	7.3	8.6	8.4	9.8	11.6	9.8
Sw	n	17	1	0	18	5	0	0	5	5	0	0	5	3	7	0	10	30	8	0	38
	mean	19.6	17.0	---	19.5	19.6	---	---	19.6	12.4	---	---	12.4	16.3	15.0	---	15.4	18.1	15.3	---	17.5
	S.D.	7.4	0.0	---	7.2	10.3	---	---	10.3	11.5	---	---	11.5	6.7	5.0	---	5.2	8.6	4.7	---	8.0
Sb	n	4	1	5	10	2	3	9	14	0	0	0	0	0	0	1	1	6	4	15	25
	mean	19.0	45.0	24.4	24.3	87.5	19.3	37.0	40.4	---	---	---	---	---	---	8.0	8.0	41.8	25.8	30.9	32.7
	S.D.	9.1	0.0	12.4	12.5	88.4	9.7	17.0	35.3	---	---	---	---	---	---	0.0	0.0	53.5	15.1	16.9	28.7
All	n	126	58	41	225	77	76	63	216	191	312	169	672	170	166	117	453	564	612	390	1566
	mean	19.6	17.6	21.7	19.5	18.5	17.1	20.0	18.4	14.3	13.3	12.7	13.4	14.2	14.8	15.4	14.7	16.0	14.6	15.6	15.4
	S.D.	10.7	19.2	24.0	16.2	17.4	8.0	11.4	13.0	6.9	6.4	10.0	7.6	7.0	10.5	7.3	8.5	10.1	9.8	12.2	10.6

Height data for all plots and all seedling species were combined and analyzed for differences between overstory tree species. An ANOVA oneway test indicated the presence of significant differences among heights of seedlings beneath host-tree species (p = 0.012). A Tukey-HSD multiple range test between pairs of tree species showed that seedlings under white spruce trees were significantly shorter than seedlings under balsam fir trees. Seedlings under black spruce trees were intermediate in height and not significantly different from seedlings under balsam fir or white spruce.
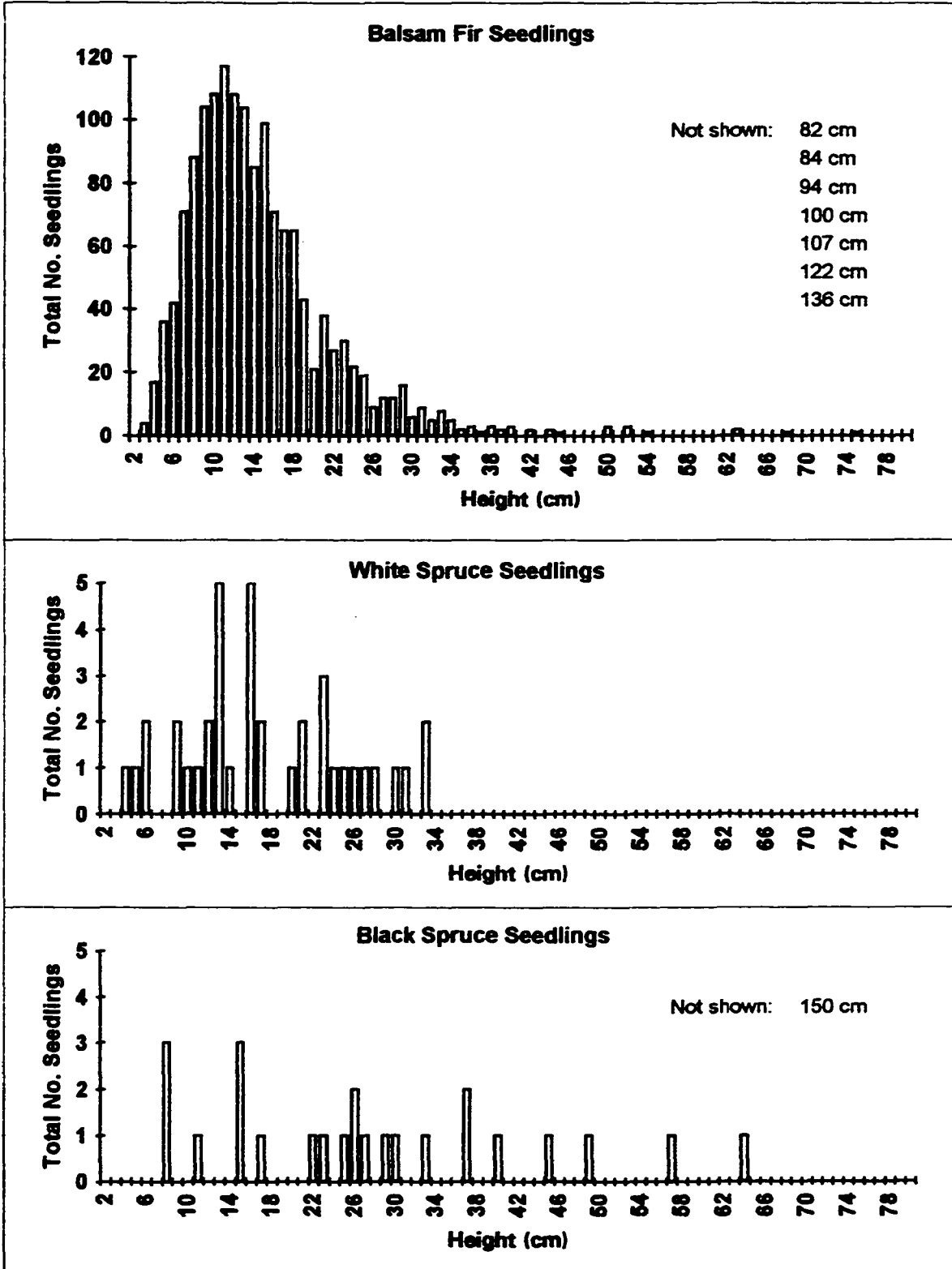
Height data for seedlings under all host trees in all plots were analyzed for differences between seedling species using an ANOVA oneway test. Significant height differences between seedling species were found to exist (p < 0.001). A Tukey-HSD test indicated that black spruce seedlings were significantly taller than balsam fir or white spruce seedlings.

Frequency distributions for height were compared between seedling species (Fig. 24). Balsam fir and white spruce seedlings appear to have similar height distributions, a trend also shown by data from random sub-plots. Black spruce seedlings are less common, but appear to be spread more evenly over a greater range of heights. The tendency for black spruce to carry a larger proportion of the population in taller height classes also was shown by data from random sub-plots.

Defoliation

Mean defoliation scores for seedlings were summarized by plot, overstory tree species, and seedling species (Table 22). The overall mean defoliation score for seedlings under all host trees was 2.6, only slightly higher than the overall mean score of 2.2 shown for random sub-plots. Nonparametric tests were used to compare defoliation scores for seedlings (all species in all

All Plots

Balsam Fir Seedlings

Not shown: 82 cm
84 cm
94 cm
100 cm
107 cm
122 cm
136 cm

White Spruce Seedlings

Black Spruce Seedlings

Not shown: 150 cm

Based on data from 231 sub-plots (4 m^2) under host trees in four 10 ha plots.
Note changes in vertical scale.

Figure 24. Height distributions for host-species regeneration under all host trees.

Table 22. Seedling defoliation under host trees.

Seedling	Tree n	Plot 1 Bf 20	Sw 20	Sb 20	All 60	Plot 2 Bf 20	Sw 20	Sb 20	All 60	Plot 3 Bf 20	Sw 20	Sb 16	All 56	Plot 4 Bf 20	Sw 20	Sb 15	All 55	All Plots Bf 80	Sw 80	Sb 71	All 231
Bf	n	105	56	36	197	70	73	54	197	186	312	169	667	167	159	116	442	528	600	375	1503
	mean	1.9	2.2	2.0	2.0	2.8	3.2	1.9	2.7	2.4	3.0	1.8	2.5	2.3	4.8	2.3	3.2	2.3	3.4	2.0	2.7
	S.D.	2.0	3.3	2.9	2.6	3.5	3.3	2.6	3.2	3.2	3.4	2.7	3.2	2.7	4.2	2.9	3.6	2.9	3.7	2.8	3.3
Sw	n	17	1	0	18	5	0	0	5	5	0	0	5	3	7	0	10	30	8	0	38
	mean	2.0	3.0	---	2.1	3.4	---	---	3.4	1.4	---	---	1.4	1.7	3.1	---	2.7	2.1	3.1	---	2.3
	S.D.	2.6	0.0	---	2.6	3.4	---	---	3.4	2.2	---	---	2.2	1.5	2.1	---	2.0	2.6	2.0	---	2.5
Sb	n	4	1	5	10	2	3	9	14	0	0	0	0	0	0	1	1	6	4	15	25
	mean	0.5	0.0	0.0	0.2	4.0	1.0	0.7	1.2	---	---	---	---	---	---	0.0	0.0	1.7	0.8	0.4	0.8
	S.D.	1.0	0.0	0.0	0.6	4.2	1.7	0.7	1.9	---	---	---	---	---	---	0.0	0.0	2.7	1.5	0.6	1.5
All	n	126	58	41	225	77	76	63	216	191	312	169	672	170	166	117	453	564	612	390	1566
	mean	1.8	2.2	1.8	1.9	2.9	3.1	1.7	2.6	2.4	3.0	1.8	2.5	2.3	4.7	2.2	3.2	2.3	3.4	1.9	2.6
	S.D.	2.1	3.2	2.8	2.6	3.5	3.3	2.4	3.2	3.2	3.4	2.7	3.2	2.7	4.2	2.8	3.6	2.9	3.7	2.7	3.2

128

plots) under different overstory tree species. A Kruskal-Wallis oneway test showed that significant differences existed (p < 0.001). A series of Mann-Whitney tests between pairs of tree species showed that seedling defoliation was significantly different under all tree species, with the highest defoliation scores found under white spruce trees and the lowest scores found under black spruce trees.

Nonparametric tests also were used to compare defoliation scores between seedling species. Black spruce seedlings were found to have significantly lower defoliation scores than balsam fir and white spruce seedlings, which were not significantly different from each other. As was the case for random sub-plots, correlation between height and defoliation was low for seedlings beneath host trees (r = 0.167, n = 1566).

The occurrence of feeding damage to seedling species under tree species was summarized (Table 23). Over 60% of all seedlings under host trees suffered budworm damage to some extent. This proportion is higher than the 48% of seedlings damaged in random sub-plots, but seems low given the number of budworm larvae that dispersed from overstory trees. However, a greater proportion of seedlings was damaged under white spruce trees, from which the greatest number of larvae dispersed.

An examination of frequencies for defoliation scores (Fig. 25) reveals that only balsam fir seedlings were assigned Fettes scores greater than 10. Black spruce seedlings, with the exception of one individual (ht = 150 cm), never were assigned a Fettes score greater than 3.

Table 23. Summary of damage occurrence to host seedlings under host trees.

Seedling Species	Balsam Fir (80 Trees)			White Spruce (80 Trees)			Black Spruce (71 Trees)			All (231 Trees)		
	Total Live Seedlings	Seedlings Damaged	% of Total	Total Live Seedlings	Seedlings Damaged	% of Total	Total Live Seedlings	Seedlings Damaged	% of Total	Total Live Seedlings	Seedlings Damaged	% of Total
Bf	528	331	62.7	600	400	66.7	375	198	52.8	1503	929	61.8
Sw	30	18	60.0	8	8	100.0	0	0	0.0	38	26	68.4
Sb	6	3	50.0	4	1	25.0	15	5	33.3	25	9	36.0
All	564	352	62.4	612	409	66.8	390	203	52.1	1566	964	61.6

Based on data from 231 sub-plots (4 m^2) over four 10-ha plots.
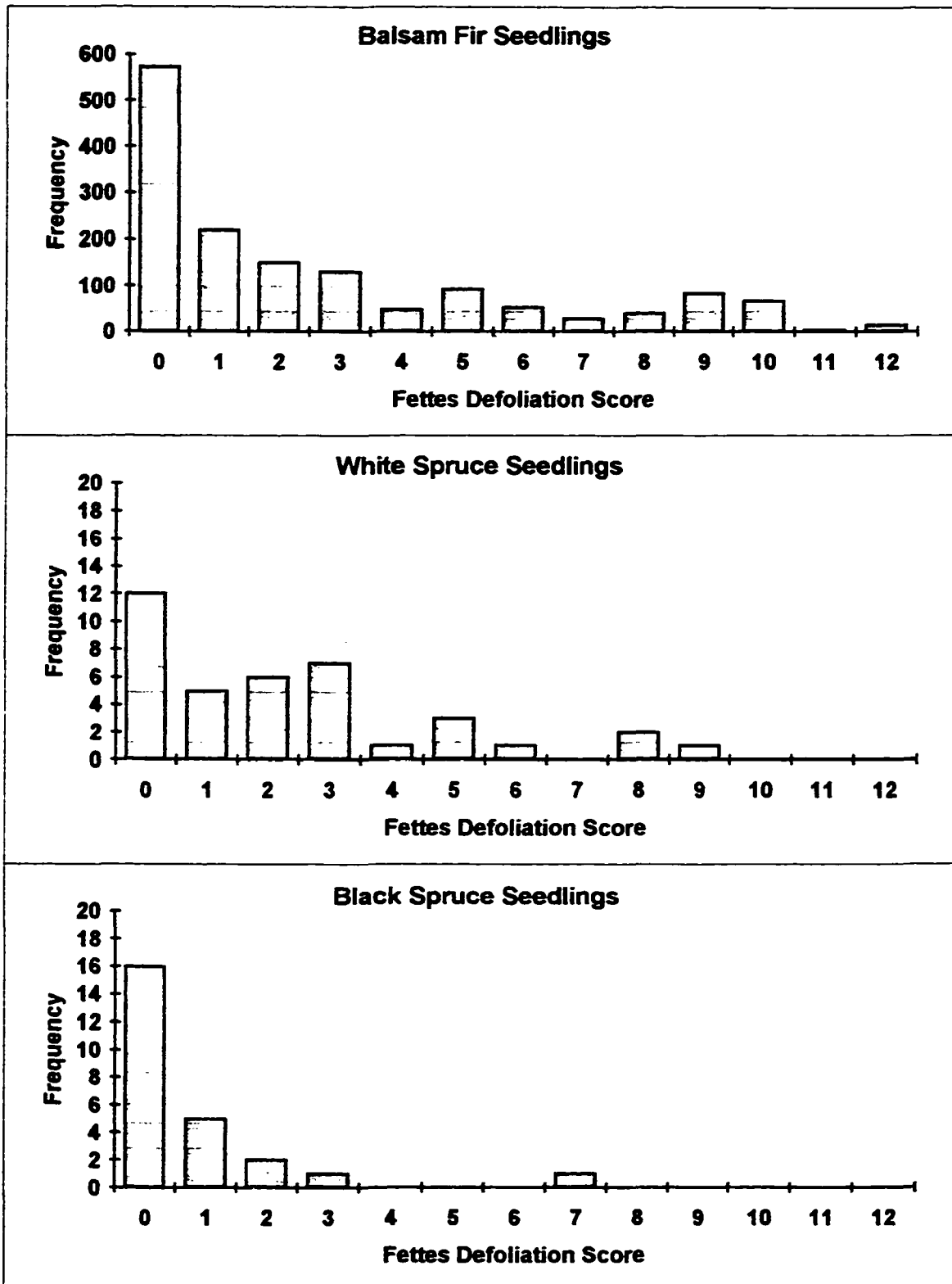
130

Balsam Fir Seedlings

White Spruce Seedlings

Black Spruce Seedlings

Based on data from 231 sub-plots (4 m^2) over four 10-ha plots.
Note changes in vertical scale.

Figure 25. Defoliation score frequencies for seedlings under all host trees.

PART III -- SAMPLING AT SELECTED
WHITE SPRUCE REGENERATION SITES

PURPOSE

The lack of spruce regeneration in random sub-plots and in sub-plots under host trees made comparisons between seedling species difficult. To increase the number of spruce seedlings, it was necessary to seek out locations where spruce regeneration was present and establish additional sub-plots at these locations. A higher number of spruce seedlings would permit better comparisons of height and defoliation between balsam fir and spruce seedlings.

METHODS

Rather than haphazardly searching for white spruce regeneration, which was chosen as the target species, ten squares of land bounded by major grid-lines were selected at random in each of the four 10-ha plots. Within each of these 40 areas, the forest was searched thoroughly and flags were tied to mark locations where white spruce was present in abundance. Each of the sites worthy of a flag was then re-visited and a sub-plot was established at the site where white spruce regeneration was most abundant. A wooden stake was driven into the ground at the location where a plot cord for a circular 4-m^2 sub-plot would encompass the maximum number of spruce seedlings possible. All host-tree seedlings contained within sub-plot boundaries were measured, assessed for budworm defoliation, and classified as to microsite location.

RESULTS

Seedling Densities

A total of 1666 seedlings was tallied in 40 sub-plots (4-m^2) over the four 10-ha plots. Only 23 (1.4%) of these seedlings were dead, but this proportion of dead seedlings was higher than 0.4% shown for random sub-plots and 0% beneath host trees. Dead seedlings were comprised of 15 balsam fir (14-32 cm height range), three white spruce (16-22 cm), and five black spruce (20-35 cm). All but one of these dead seedlings was growing on decaying logs. Mortality may have been due to desiccation of the substrate as overstory trees died and allowed more light to reach the forest floor.

Of the 1643 live seedlings tallied, 1191 (72.5%) were balsam fir, 324 (19.7%) were white spruce, and 128 (7.8%) were black spruce. Despite the fact that sites were selected because they had the most white spruce regeneration and the fact that sub-plots were positioned to encompass the maximum number of spruce seedlings possible, balsam fir seedlings still outnumbered spruce seedlings by a ratio of 2.6:1.

Overall mean density was 41.1 seedlings per sub-plot (Table 24), which is about five times as many seedlings as encountered in earlier sampling. This fact suggests that there is something about these locations that encourages not only white spruce regeneration, but regeneration of all host species. Even black spruce regeneration, which was extremely uncommon in earlier sub-plots, was present here at an overall density of 3.2 seedlings per sub-plot. However, it should be noted that black spruce regeneration was most abundant in Plot 1 and least abundant in Plot 4, a trend also shown in sub-plots established earlier.

Table 24. Seedling densities in white spruce regeneration sub-plots.

		Bf no. per sub-plot	Sw no. per sub-plot	Sb no. per sub-plot	All Species no. per sub-plot
Plot 1	mean	39.7	6.5	7.2	53.4
(n = 10)	S.D.	31.9	3.3	8.5	36.2
Plot 2	mean	29.9	9.9	4.4	44.2
(n = 10)	S.D.	26.4	10.2	7.0	36.1
Plot 3	mean	33.6	7.5	0.9	42.0
(n = 10)	S.D.	16.1	4.7	1.9	15.3
Plot 4	mean	15.9	8.5	0.3	24.7
(n = 10)	S.D.	20.2	4.7	0.9	22.1
All Plots	mean	29.8	8.1	3.2	41.1
(n = 40)	S.D.	25.0	6.2	6.1	29.7

Based on data from 10 sub-plots (4-m^2) in each of four 10-ha plots.

Height Distributions

Height data were summarized by plot and seedling species (Table 25). Mean heights appear to be similar for all seedling species over all plots, although ANOVA indicates that black spruce seedlings are significantly ($p = 0.010$) taller than balsam fir and white spruce seedlings when data from all plots are combined.

Height frequencies for seedlings in all plots combined (Fig. 26) confirm earlier indications that balsam fir and white spruce have similar distributions. The greater number of black spruce seedlings tallied in these sub-plots also permits a reliable comparison among all three species for the first time. The height distributions of all three seedling species appear to be similar, but black spruce once again is seen to carry a larger proportion of individuals in the taller height classes.

Table 25. Summary of mean heights of seedlings in white spruce regeneration sub-plots.

|		Bf	Sw	Sb	All Species
Plot 1	n	397	65	72	534
	mean	25.0	28.3	26.3	25.6
	S.D.	14.1	13.1	14.4	14.0
Plot 2	n	299	99	44	442
	mean	23.8	23.4	28.3	24.2
	S.D.	11.4	10.5	10.7	11.2
Plot 3	n	336	75	9	420
	mean	22.6	25.8	19.8	23.1
	S.D.	14.1	14.3	7.0	14.1
Plot 4	n	159	85	3	247
	mean	20.8	17.3	18.3	19.6
	S.D.	10.0	10.2	4.9	10.1
All Plots	n	1191	324	128	1643
	mean	23.5	23.3	26.3	23.7
	S.D.	13.0	12.5	12.8	12.9

Based on data from 10 sub-plots (4-m^2) in each of four 10-ha plots.

Defoliation

Mean defoliation scores for all seedling species in all plots were low, with an overall average defoliation score of 2.1 (Table 26). Defoliation is highest for balsam fir seedlings in Plot 2 (mean = 3.6), but even this maximum mean value is quite low. Black spruce seedlings appear to have suffered little defoliation in all plots. Nonparametric analyses of defoliation scores (all plots combined) confirm that black spruce seedlings were less defoliated than the other two species. Defoliation scores for balsam fir and white spruce were not significantly different.

Defoliation score frequencies (Fig. 27) also reveal similarities between balsam fir and white spruce. With the exception of one individual (ht = 42 cm), black spruce seedlings never were assigned a Fettes score greater than 3. Only two seedlings, both balsam fir (ht = 41 & 63 cm), received a defoliation

All Plots
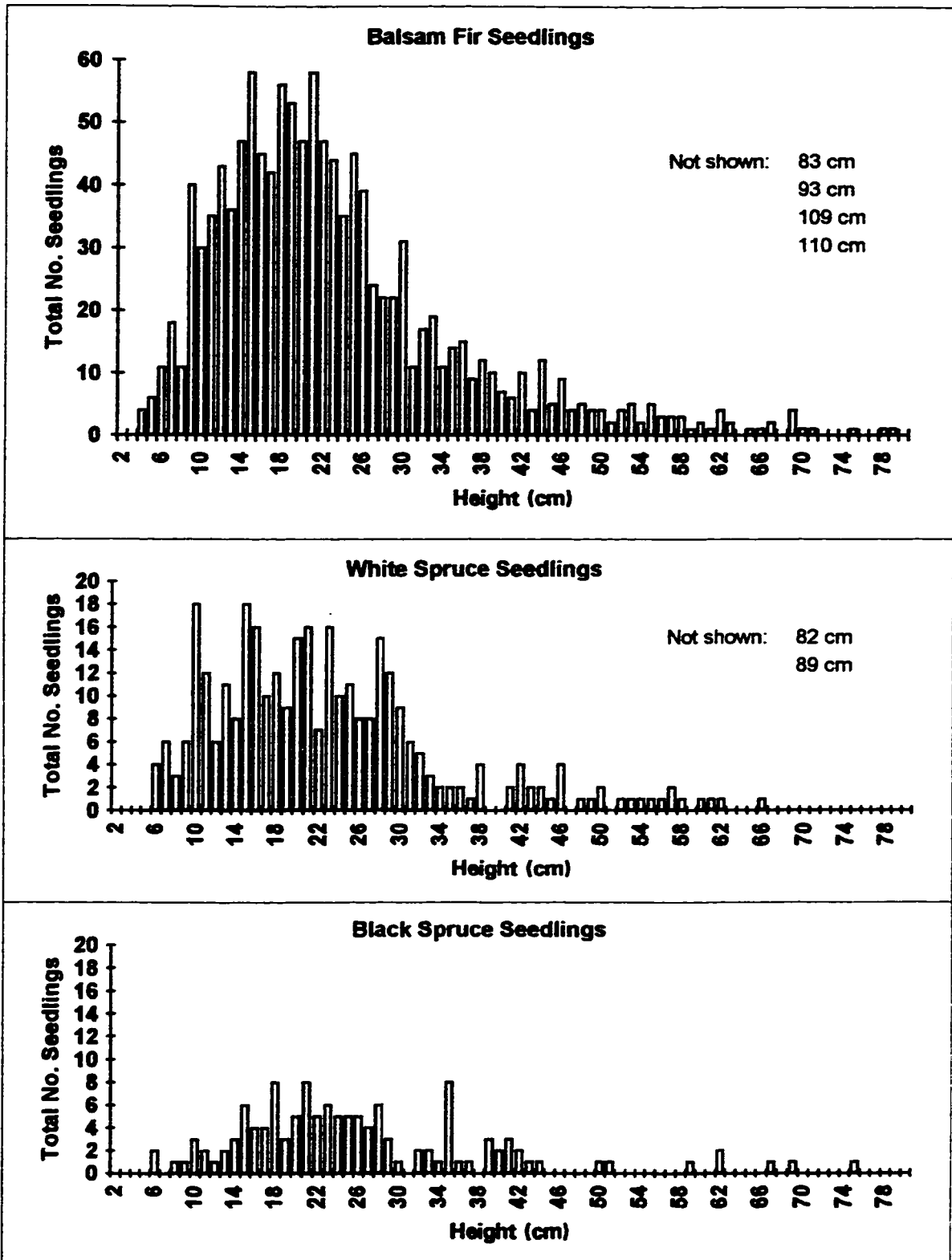
Based on data from 40 sub-plots (4-m^2) over four 10 ha plots.
Note changes in vertical scale.

Figure 26. Height distributions for host-species regeneration at selected white spruce regeneration sites.

score higher than 10. Correlation between height and defoliation was low (r = 0.287, n = 1643), but higher than that shown for earlier samples.

Over 60% of all seedlings suffered budworm damage to some extent (Table 27), representing a slightly higher proportion of damaged seedlings than under host trees. The high occurrence of damage in these sub-plots may be related to high seedling densities, which allow budworm larvae to move between seedlings more easily.

Over 88% of all seedlings that were attacked suffered damage to the leader (Table 27). Damage was high (>50%) in more than half of the cases where leader damage occurred, especially for white spruce seedlings. These results provide further evidence of a strong tendency for budworm larvae to feed at the tops of seedlings.

Table 26. Summary of mean defoliation scores for seedlings in white spruce regeneration sub-plots.

		Bf	Sw	Sb	All
Plot 1	n	397	65	72	534
	mean	1.7	1.9	0.3	1.5
	S.D.	2.2	2.1	0.5	2.1
Plot 2	n	299	99	44	442
	mean	3.6	2.5	0.5	3.0
	S.D.	3.2	2.1	1.3	3.0
Plot 3	n	336	75	9	420
	mean	2.0	2.1	0.1	1.9
	S.D.	2.3	2.5	0.3	2.3
Plot 4	n	159	85	3	247
	mean	2.1	1.9	0.0	2.0
	S.D.	2.6	2.0	0.0	2.4
All Plots	n	1191	324	128	1643
	mean	2.3	2.1	0.4	2.1
	S.D.	2.7	2.2	0.9	2.5

Based on data from 10 sub-plots (4-m^2) in each of four 10-ha plots.
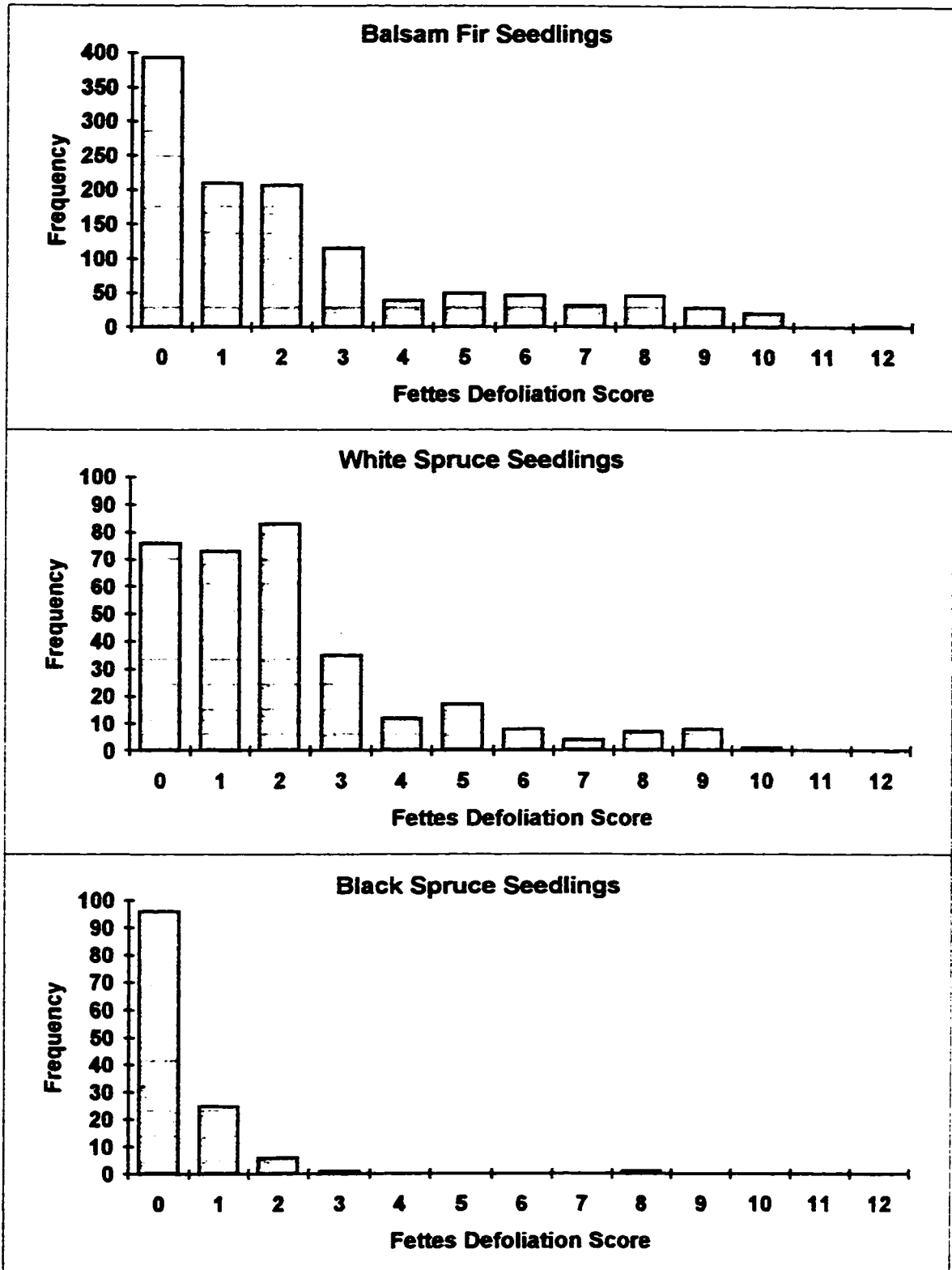
Balsam Fir Seedlings

White Spruce Seedlings

Black Spruce Seedlings

Based on data from 40 sub-plots (4-m^2) over four 10-ha plots.
Note changes in vertical scale.

Figure 27. Defoliation score frequencies for seedlings at selected white spruce regeneration sites.

Table 27. Summary of leader damage to host seedlings in white spruce regeneration sub-plots.

Seedling Species	Total No. Live	Seedlings Damaged to any Degree		Severity of Leader Damage								
				No Damage			< 50 % Damage			> 50 % Damage		
		No.	% of Total	No.	% of Total	% of Damaged	No.	% of Total	% of Damaged	No.	% of Total	% of Damaged
Bf	1191	798	67.0	96	8.1	12.0	297	24.9	37.2	405	34.0	50.8
Sw	324	248	76.5	22	6.8	8.9	31	9.6	12.5	195	60.2	78.6
Sb	128	32	25.0	6	4.7	18.8	11	8.6	34.4	15	11.7	46.9
All	1643	1078	65.6	124	7.5	11.5	339	20.6	31.4	615	37.4	57.1

Based on data from 10 sub-plots (4-m^2) in each of four 10-ha plots.

Microsites

Over 90% of all seedlings tallied in white spruce regeneration sub-plots were growing in rotting wood (Table 28), reflecting the fact that all sub-plots were established at locations centred around decaying logs. The high seedling densities at these locations suggest that rotting wood is a superior microsite for seedling establishment. All three species are able to establish seedlings at these sites, but rotting wood appears to be more important for both spruce species than for balsam fir. Almost 99% of all white spruce seedlings and over 96% of all black spruce seedlings in these sub-plots were found on rotting wood.

Table 28. Summary of seedling microsites in white spruce regeneration sub-plots.

Seedling Species	Total Seedlings	Microsite					
		Exposed Mineral Soil		Leaf Litter or Moss		Rotting Wood	
		No. of Seedlings	% of Total	No. of Seedlings	% of Total	No. of Seedlings	% of Total
Bf	1191	0	0.0	154	12.9	1037	87.1
Sw	324	0	0.0	4	1.2	320	98.8
Sb	128	0	0.0	5	3.9	123	96.1
All	1643	0	0.0	163	9.9	1480	90.1

Based on data from 10 sub-plots (4-m^2) in each of four 10-ha plots.

PART IV -- DESTRUCTIVE SAMPLING OF SEEDLINGS

PURPOSE

This part of the study was initiated out of curiosity and initially was not intended to be part of the final report. However, the results are quite interesting and are worthy of inclusion despite drawbacks associated with the sampling methodology. Seedlings were collected from within the study area and aged by ring counts to gain some idea of their age and when they became established. Probable establishment dates were related to development of the current outbreak to explore possible influences of the spruce budworm on seedling establishment patterns.

METHODS

While packing up the base camp in preparation to leave the Black Sturgeon area at the end of the 1993 field season, a sample of seedlings was uprooted and taken back to Thunder Bay. Time permitted the collection of seedlings from Plots 1 & 2 only. It was hoped that additional seedlings could be collected from Plots 3 & 4 at a later date, but there was no opportunity to do so.

Seedlings were collected from locations along three sides of both 10-ha plots, with the front (zero line) excluded in each case. The boundary lines of the plots were walked and seedlings were collected from a location centred at 10 m outside the plot at each station (40 m intervals). Sub-plot boundaries were not established. A few "representative" seedlings simply were pulled out

of the ground at each location and placed in a large paper bag. The majority of collected seedlings were balsam fir, but white spruce seedlings were collected whenever they were present near a sampling site. In all, 250 seedlings were collected: 110 balsam fir and 16 white spruce from Plot 1, and 93 balsam fir and 31 white spruce from Plot 2. All paper bags full of seedlings were wrapped in plastic and stored in a freezer at Lakehead University until they could be analyzed.

Height of each seedling was measured to the nearest centimetre and age was determined by counting growth rings on a cross-sectional slice of the stem taken at ground level. Stem slices were cut with a razor blade and examined under a dissecting microscope. However, an extremely high number of growth rings was observed on cross-sections of some small seedlings, resulting in some uncertainty as to whether the observed rings were in fact annual growth rings.

A sub-sample of ten seedlings was analyzed in greater detail using equipment in the wood technology laboratory at Lakehead University. Cross-sectional slices cut with a sledge microtome were made into slide mounts. A high-powered microscope was used to examine the cellular structure of stem cross-sections, confirming that the rings visible under the dissecting microscope were indeed annual growth rings. With greater confidence in what was and was not a growth ring, ages for the remaining seedlings were determined under a dissecting microscope, which was far less time-consuming than preparing slides.

RESULTS

Height over age data for all seedlings are summarized in a scatterplot (Fig. 28). Straight line and quadratic regression lines were fitted to explore general relationships between variables. Best fit regression lines naturally passed close to the origin, but not through it. The regression lines shown in Figure 28 (and all others to follow) have been forced through the origin to represent zero height at zero age. This adjustment insures that regression lines reflect biological reality and sets all seedlings at a common starting point.

The plotted data (Fig. 28) reveal that height becomes increasingly variable as age increases, testament to the plasticity of height growth for balsam fir and white spruce seedlings and their ability to tolerate suppression. An outstanding example is provided by a 32-year old balsam fir seedling from Plot 2 that is shorter than some 12-year old seedlings from the same plot. The overall relation between height and age is represented equally well by linear and quadratic regression lines over the majority of data, but the two lines diverge where height becomes extremely variable among the oldest seedlings. The quadratic regression line (Adjusted R^2 = 0.889) fits the data slightly better than the linear regression line (Adjusted R^2 = 0.881), suggesting that taller seedlings have enjoyed more rapid height growth than shorter seedlings. However, a disproportionately large number of tall and exceptionally old-looking seedlings was collected because of a personal interest in knowing their ages. Data for the tallest and oldest seedlings therefore represent extremes in variation among these individuals, but not necessarily the central tendency. It may be that neither regression line accurately reflects height-age relations among the tallest and oldest seedlings.
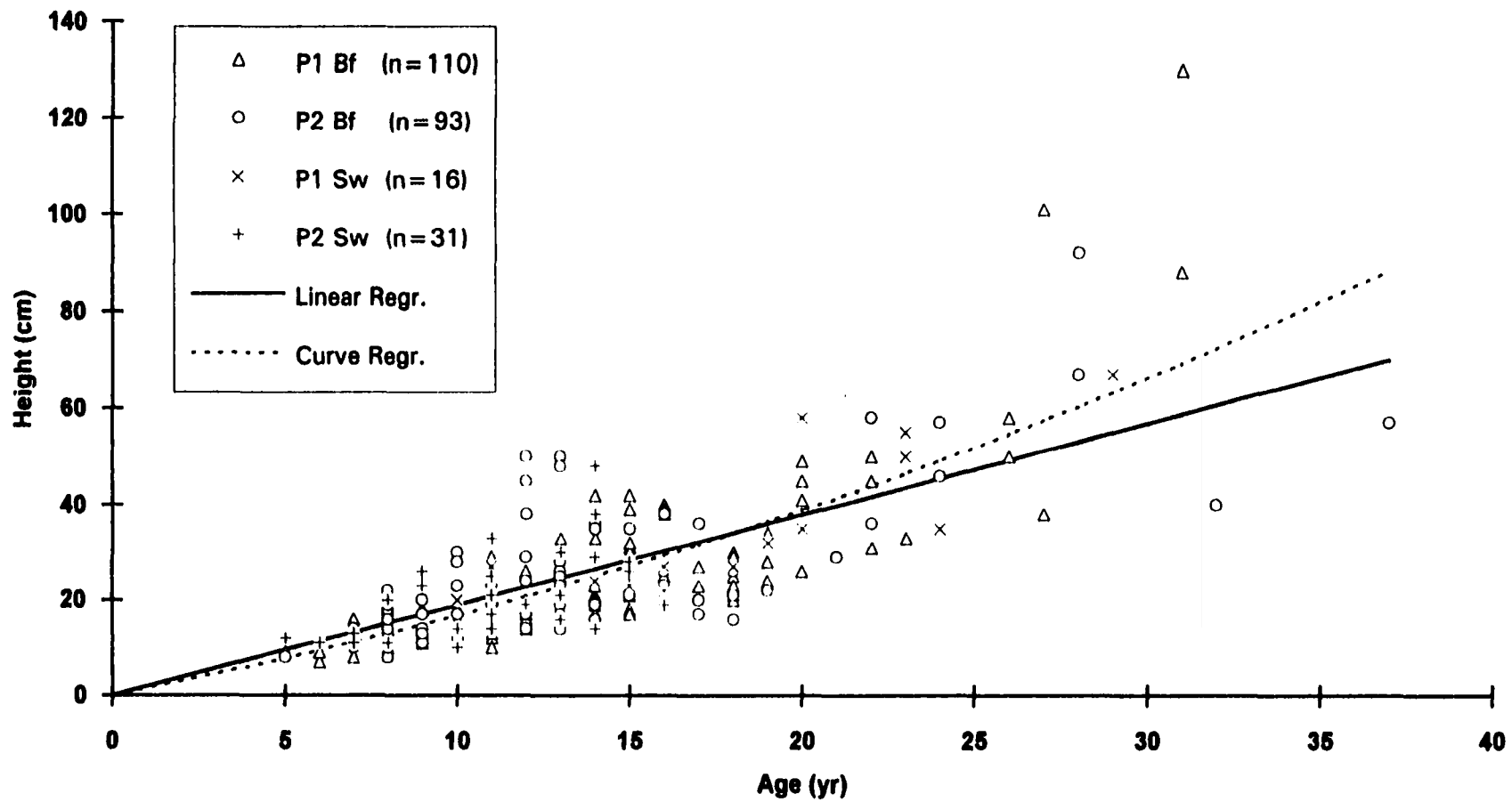
Regression	Equation	R^2	Adjusted R^2
Linear	ht = 1.893 * age	0.882	0.881
Quadratic	ht = (1.417 * age) + (0.026 * age^2)	0.890	0.889

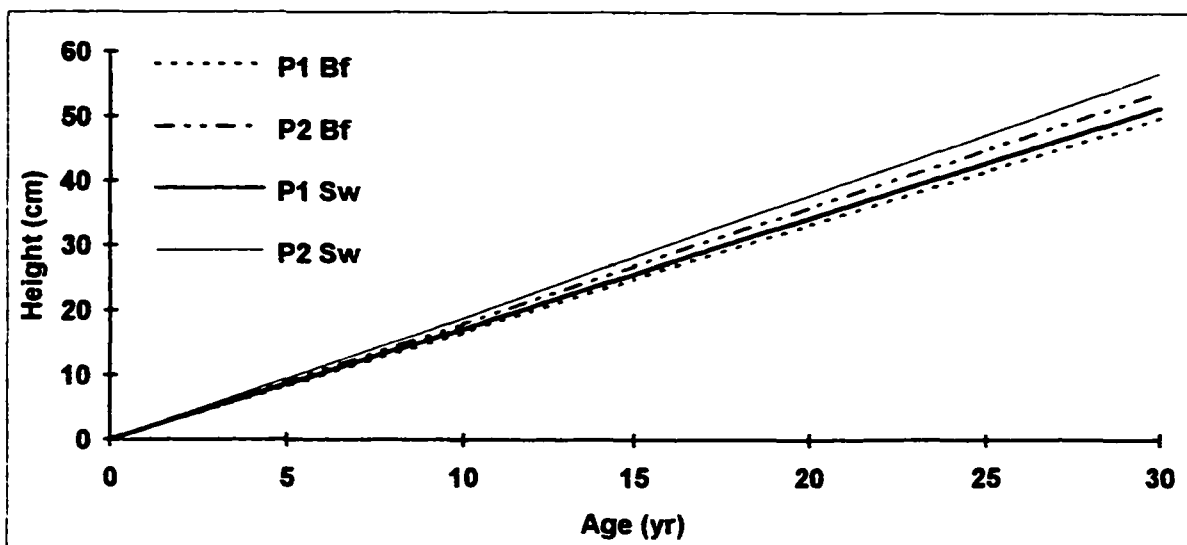Note: both regression lines have been forced through the origin.

Figure 28. Scatterplot and fitted regression lines for height over age of seedlings in destructive sample.

To overcome the fore-mentioned problems, a 53 cm top height was imposed before looking more closely at height-age relationships between species and plots. Recall that a top height of 53 cm was used for earlier samples and was shown to include over 98% of all seedlings in the study area. More specific to Plots 1 & 2, from which seedlings were collected, a 53 cm top height includes over 96% of all seedlings. With the tallest seedlings eliminated from the data set, exceptionally old seedlings with low heights became highly influential. Two seedlings with ages greater than 30 years were eliminated to overcome this problem.

The remaining data were divided by seedling species and plot, and separate regression equations were generated for each group. Straight and quadratic regression lines were almost identical in all cases, so further discussion is focused on the results of straight line regression only.

Regression lines for all species-by-plot groups were overlaid and found to be quite similar (Fig. 29a). White spruce seedlings appear to have grown at a slightly faster rate than balsam fir within each of the plots, but in both cases the differences in height growth were less than 1 mm per year. The difference in slopes between the highest and lowest regression lines represents only 2.3 mm per year, which is equivalent to less than 7 cm of height growth over 30 years.

Without delving into statistical test procedures, it seems reasonable to conclude that height over age for both seedling species in both plots can be represented by a single regression equation (Fig. 29b). Further tinkering with the equation through elimination of outliers (studentized residuals > 3) results in a slight improvement to the fit of the regression line (ht = 1.696 * age; Adjusted R^2 = 0.930). However, the relation shown (Fig. 29b) probably is adequate given the exploratory nature of the investigation.

a. Seedling species by plot.

Line	Equation	R^2	Adjusted R^2
P1 Bf	ht = 1.667 * age	0.933	0.932
P2 Bf	ht = 1.800 * age	0.883	0.881
P1 Sw	ht = 1.718 * age	0.975	0.973
P2 Sw	ht = 1.897 * age	0.898	0.894

All regression lines have been forced through the origin.
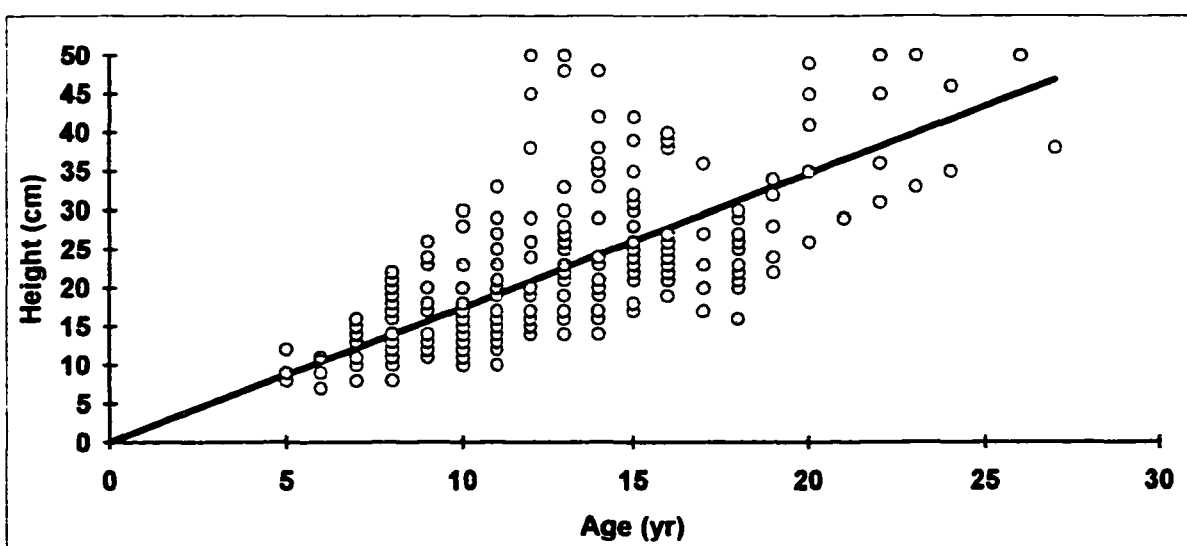
b. All seedling species and plots combined.

Line	Equation	R^2	Adjusted R^2
Both plots; Both species	ht = 1.736 * age	0.912	0.912

Regression line has been forced through the origin.

Figure 29. Linear regression lines for a) seedling species by plot and b) all seedling species and plots combined.

It appears that balsam fir and white spruce seedlings both have been growing in height at a mean rate of about 1.7 cm per year. Although based on relatively small sample sizes and quasi-random sampling, best fit regression lines through the origin suggest no clear differences in rate of height growth for balsam fir and white spruce seedlings.

Under the assumption that a growth rate of 1.7 cm per year is representative of height-age relations in general, it is possible to estimate ages of seedlings for which only height was measured. Using seedling height as an indicator of age, a probable year of establishment can be determined for each seedling. To this end, height data for all seedlings earlier tallied in random sub-plots were converted to age data. Ages were used to generate a probable year of establishment.

Black spruce seedlings were eliminated from the data set because height-age relations for this species were not explored. Taller than average seedlings were eliminated through imposition of a 53 cm top height. Data for balsam fir and white spruce were combined, but were divided into two groups based on plot. One group contained data for seedlings in Plots 1 & 2. The other group contained data for seedlings in Plots 3 & 4. The reason for grouping data into pairs of plots is two-fold. First, the height-age regression line was established using seedlings from Plots 1 & 2 only and it is not known if the same relation also can be used to represent seedlings in Plots 3 & 4. Second, characteristics of the forest in Plots 3 & 4 are sufficiently different that separate treatment of data for these plots seems appropriate even if the height-age relation is similar. The forest in Plots 3 & 4 is about 10 years older than that in Plots 1 & 2. Also, Plots 3 & 4 contain larger trees, a more prominent high-shrub layer, and a greater abundance of seedlings.

Distributions for probable establishment years are presented in Figure 30 for a) the destructive sample of seedlings that were aged, b) the random sample of seedlings tallied by height in Plots 1 & 2, and c) the random sample of seedlings tallied by height in Plots 3 & 4. The data shown in Figure 30a are not truly random because of the sampling methodology used. Seedlings were collected for no particular reason other than presence and therefore can be considered an essentially random sample. However, no strict conditions were imposed to insure random selection of seedlings and it appears that there was a tendency to collect a greater number of taller than average seedlings. The destructive sample probably was random enough to reflect relations between height and age accurately, but may not reflect the true distribution of heights (and therefore ages). The distribution of establishment years for these seedlings (Fig. 30a) should be accepted with caution. Data in Figure 30 b & c are from truly random samples, but ages of these seedlings have been estimated from relations among seedlings in Figure 30a. All data are approximations at best, but taken together they should represent seedling establishment patterns in general.

Upon examination of seedling establishment patterns (Fig. 30), a surprising trend is revealed. It was expected that seedling establishment would come to an abrupt end with the development of a budworm outbreak, which is generally considered to have started in 1980. However, the data suggest that the overwhelming majority of seedlings became established after 1980 rather than before.

From CFS budworm defoliation records held in Sault Ste. Marie, C.J. Sanders (personal communication) was able to provide a more detailed account of the 1980 outbreak in the Black Sturgeon Lake area. The outbreak first was detected in 1980, but was very patchy and not widespread at this time.

a. Destructive Sample

b. Plots 1 & 2

c. Plots 3 & 4

Defoliation : 50 % 80 % 100 %
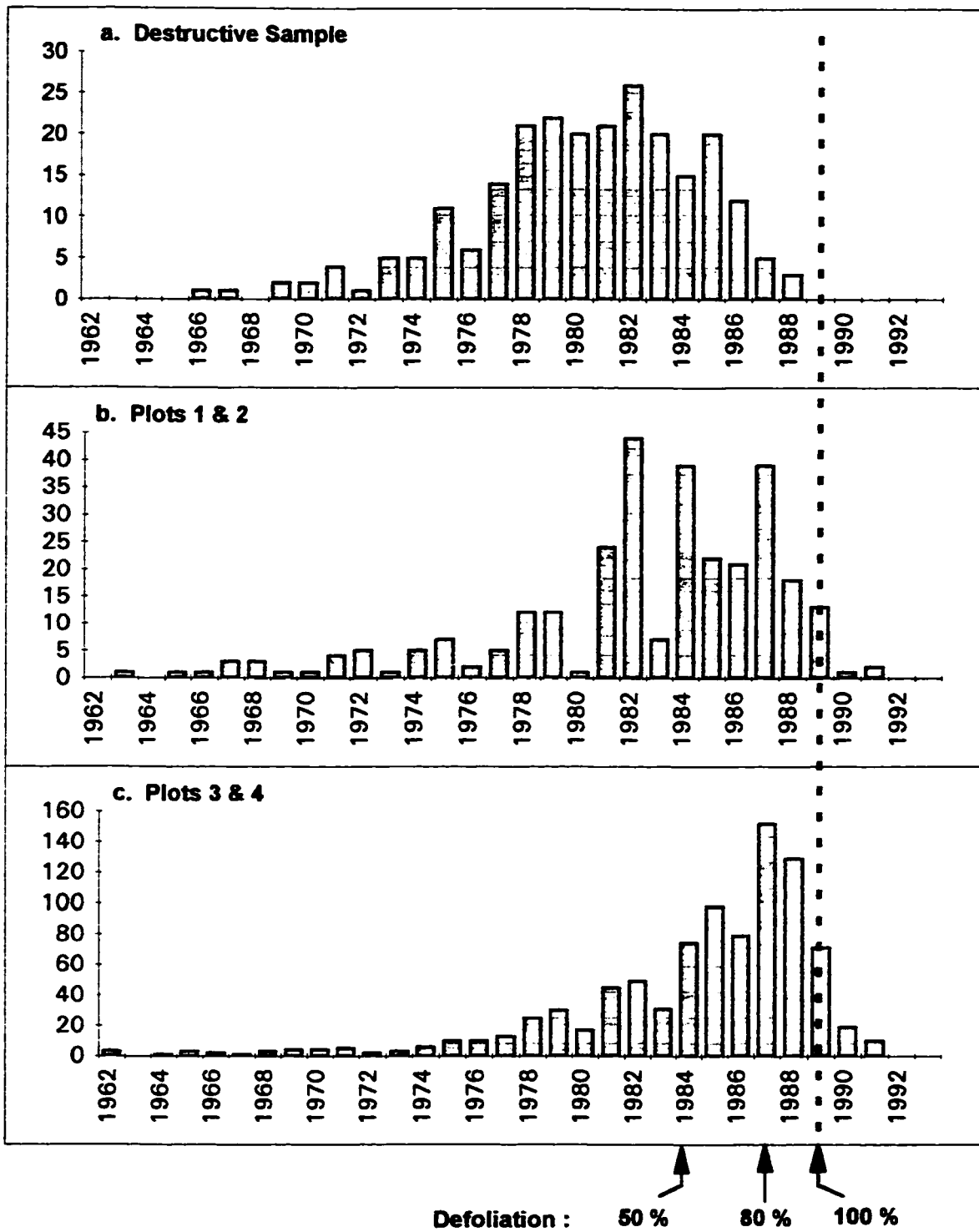
Defoliation levels were obtained by C.J. Sanders (pers. comm.) from CFS records for Black Sturgeon Lake.
Vertical axis represents number of seedlings in sample, but actual numbers are not important for interpretation.

Figure 30. Probable establishment years for seedlings in a) destructive sample, b) Plots 1 & 2, and c) Plots 3 & 4.

Budworm populations increased and the outbreak intensified over the years following 1980, with overall mean defoliation levels in the area reaching 50% by 1984. Defoliation levels reached 80% by 1987 and 100% by 1989. The data (Fig. 30) indicate that seedling establishment came to an abrupt end at about the same time that 100% defoliation was reached.

The graphs shown here (Fig. 30 b & c) are almost identical to those shown by Ghent (1958a) for an earlier budworm outbreak in the Black Sturgeon Lake area. In both cases, the majority of seedlings became established during the early stages of an outbreak, with recruitment of new seedlings ending abruptly as defoliation approached 100%.

Ghent (1958a) has suggested that the columns of a seedling establishment graph can be shifted to the left by 2-4 years when seedling ring counts are used to determine establishment dates. This is because ring counts at ground level tend to underestimate seedling age. Ghent (1958a) observed that some seedlings had branches below ground level and roots growing above them. This phenomenon also was observed during age determinations for the seedlings collected near Black Sturgeon Lake in 1993, especially among the oldest seedlings. Thus, seedling ages very likely are underestimated by a few years and shifting the columns of all graphs (Fig. 30) by two positions to the left seems warranted.

Ghent (1958a) also points out that budworm influences on seedling establishment occur before the year in which seedlings become established. Seedlings that germinate in any given year were developing as seeds during the previous year and were initiated in buds that were set in the year before seed development. Thus, if one is interested in when the budworm first had an impact on seedling establishment, the graph columns should be shifted an additional two positions to the left.

DISCUSSION

Characteristics of 45-cm branch tips provide a good indication of the health of mature host trees in the study area at 1993. Black spruce branch tips had high mass and an abundance of buds, but few budworm larvae. Defoliation for this species was low on all dates, confirming that black spruce is relatively immune to the spruce budworm (Craighead 1924). When viewed from the ground, mature black spruce trees generally appeared green and healthy, with full, dense foliage throughout their crowns.

White spruce and balsam fir trees had suffered heavy damage, with defoliation levels for both species approaching 100% by 25-June, 1993. The greater number of buds and the greater mass of white spruce branch samples suggest that this species has weathered the current budworm outbreak better than balsam fir. Mature white spruce trees generally showed bare branch tips over the entire crown and most trees had some dead branches in the lower crown. While obviously suffering as a result of the budworm outbreak, white spruce trees still held a good supply of foliage behind the bare branch tips. Most white spruce trees appeared healthy enough that they probably would survive if the outbreak was to end soon.

In contrast, balsam fir trees had suffered badly. Most branch samples showed heavy defoliation not only at the tips, but over their entire length and for foliage produced in past as well as recent years. Bud densities on balsam fir and white spruce trees usually are similar when expressed as number of buds per kg (Régnière *et al*. 1989) and balsam fir has even been known to develop more buds per kg than white spruce in response to budworm defoliation (Piene

and MacLean 1984). However, balsam fir branch samples examined for the current study had only half as many buds per kg as white spruce branch samples. Despite the fact that balsam fir branches were collected only from relatively healthy trees, some buds on some branch samples failed to open at all, suggestive of low vigour and poor health for this species. Dead balsam fir trees were common throughout the study area and many live trees had dead tops or a reddish cast, indicative of impending mortality.

In an earlier study of 45-cm branch tips, Régnière *et al.* (1989) found no difference in surface areas of branch samples from mature balsam fir and white spruce. Data from the current study confirm that surface areas for balsam fir and white spruce branch samples are similar. In addition, the data indicate that surface areas for black spruce branch samples are similar to those for balsam fir and white spruce.

Branch sample mass and density were found to be significantly higher for both spruce species than for balsam fir. Given that surface areas of branch samples were similar for all species, differences in branch sample mass and density must reflect structural differences between the genera. Data from the current study show that white spruce foliage (22.0 g/dm^2) was almost 40% more dense than balsam fir foliage (15.9 g/dm^2), a conclusion also reached by Régnière *et al.* (1989). Foliage mass was similar for white and black spruce branch samples, but white spruce foliage was more dense than that of black spruce (19.4 g/dm^2); this despite much higher defoliation levels for white spruce. The exceptional abundance of white spruce foliage may be an important factor related to the better survival of this species during a budworm outbreak, as suggested by others (Greenbank 1963; Mattson 1985).

Comparisons of budworm densities between host species certainly are influenced by differences in foliage density. Number of larvae per branch

sample or per unit of surface area may be adequate measures of budworm density when a single tree species is considered, but these measures are not readily comparable between species because they do not reflect differences in branch structure. Régnière *et al.* (1989) concluded that budworm densities are compared best between species when expressed as number of larvae per unit of branch sample mass. The current study supports this conclusion and makes a strong case for number of larvae per kg to be adopted as a standard measure of budworm density. Branch sample mass is relatively easy to measure, is less subjective than surface area calculations, and accounts for different foliage densities between host species. A standard measure of budworm density would make data from different studies more readily comparable.

Spruce budworm densities on balsam fir and white spruce generally are similar when expressed on a per kg basis (Régnière *et al.* 1989). Where budworm densities for these two tree species are different, as was the case for the current study, an alternative measure is needed to explain why. Bud density, which reflects food supply (Sanders 1980), seems to be a useful measure for this purpose. Expressed as number of larvae per kg of branch sample, 1993 data from Black Sturgeon Lake indicate that white spruce had more than twice as many larvae (228/kg) as balsam fir (98/kg). Taken alone, these figures suggest that white spruce is preferred by the spruce budworm. However, data from the current study show that number of larvae may be related to number of buds. Expressed as number per branch sample, white spruce had three times as many larvae as balsam fir and also three times as many buds. Expressed as number per unit mass, white spruce had twice as many larvae as balsam fir and also twice as many buds. Thus, it appears that bud density may be a good measure for explaining differences in larval densities. The downside to this measure is that bud counts are very time

consuming and may be difficult to determine under conditions of severe defoliation when many buds are partially or completely destroyed.

Mean defoliation scores for balsam fir and white spruce were found not to be significantly different on any of the three sample dates, despite consistently higher mean scores for white spruce. However, white spruce is rarely more defoliated than balsam fir (Régnière et al. 1989) and mean scores generated for the current study may be misleading due to the methodology employed. Sanders (1980) states that 25 buds usually are selected at random over the entire branch sample and assessed to generate a mean Fettes score. The current study diverges from standard methodology in that the 25 most distal buds on each sample were assessed rather than 25 random buds. It was felt that selection of 25 random buds would have underestimated defoliation on white spruce because this species had more buds and damage would be concentrated in the most distal buds due to photopositive tendencies of larvae (Wellington 1948). As it turns out, selection of the 25 most distal buds appears to have overestimated defoliation on white spruce because the most distal buds suffered heavy defoliation, while those near the base often suffered little or no defoliation. Had 25 random buds been assessed for defoliation in this study, mean scores would have been higher for balsam fir than for white spruce.

Either method of selecting buds for defoliation assessments probably is adequate for general comparisons between host species, but an alternative method would have to be developed where more accurate comparisons are desired. Such a method might involve counting all buds on a branch sample and then assessing a given percentage of the total buds at random. However, the additional time required for this method probably would not justify the increased accuracy in most cases.

It is clear that heavy defoliation, a lack of buds, and generally poor health of balsam fir trees are responsible for low budworm numbers on this species. Black spruce, with more than three times as many buds per kg as balsam fir, had about the same number of budworm larvae per kg as balsam fir on all three sample dates. The late flush of vegetative buds on black spruce (Blais 1957; Prévost and Laing 1986) probably is responsible for low initial numbers on this species. Once flushed, however, black spruce buds are considered to be a suitable food source for the budworm and therefore represent a large, available supply of new foliage (Blais 1957). It is noteworthy that budworm densities on black spruce were highest on the third sample date (30-June), suggesting that larvae somehow moved from heavily defoliated balsam fir and white spruce onto less defoliated black spruce trees. This phenomenon also was observed by Blais (1957), who concluded that late instars had drifted onto black spruce trees during dispersal. White spruce trees appeared to carry the bulk of the outbreak in 1993, with more than twice as many larvae per kg of branch sample on this species than others at 17-June. The abundance and early availability of new growth on white spruce likely are responsible for its apparent preference.

Budworm densities at the canopy level declined over time for all species (except black spruce on 30-June), indicating that many larvae left the terminal 45-cm segments of branches. However, declining budworm numbers on branch samples do not indicate where the larvae went. Budworm numbers declined more sharply on white spruce trees than on the other species. The reason for a more pronounced abandonment of white spruce branch tips is not clear. However, bud phenology may have been an important contributing factor. White spruce buds not only flush more foliage at a faster rate, but new growth also hardens off sooner than that of other hosts (Craighead 1924; Vescio 1995). Thus, new growth on white spruce becomes a less suitable food source earlier

than new growth on black spruce or balsam fir, with the result that larvae may abandon feeding sites on white spruce more readily.

Water trap catches confirm that many larvae left the branches of mature trees by dropping to the understory. Trap catches were consistently higher under white spruce trees, which is to be expected because of the higher budworm densities on this species. Mean catches over the entire dispersal period were about five larvae per water trap under balsam fir and black spruce trees, or about 40 larvae per m^2. More than four times as many larvae were captured under white spruce trees, with a mean catch of 20.9 larvae per trap, or 167.2 larvae per m^2, over the dispersal period. The number of larvae that reached the ground under some white spruce trees was surprisingly high, to a maximum of 840 larvae per m^2. All estimates of dispersal numbers should be considered conservative because traps were not put in place until after dispersal had begun. In addition, water traps set at ground level probably captured only a small proportion of the total number of larvae that dispersed. Many larvae likely would have been filtered our by mid-layer host foliage along the way (Beckwith and Burnell 1982).

Stem tallies of trees in random sub-plots confirm that a greater proportion of balsam fir than spruce trees had been killed by 1993. Among merchantable trees in the 10-cm DBH class and greater, the ratio of live balsam fir to spruce had dropped from about 3:1 to about 1:1. Additional mortality is expected to occur even if the budworm outbreak was to subside immediately (MacLean 1980). Given the exceptionally poor health of balsam fir trees in relation to spruce trees, it is likely that the species ratio will continue to develop towards a relative increase in spruce.

Changes to species ratios were greater among smaller, non-merchantable stems. Balsam fir once outnumbered spruce by a ratio of almost

44:1 at this level of the forest, but the ratio had been reduced to only 6:1 by 1993. The trend for higher mortality of balsam fir trees relative to spruce trees became more pronounced among progressively smaller diameter classes. If this trend was to continue into the smallest diameter classes, one would expect to see major changes in species ratios among seedlings. However, there was a clear break in the continuity of stem diameters between the 4 cm DBH class and the seedling level. Mortality ended abruptly at this break, with dead seedlings making up only 0.4% of the total seedling tally in random sub-plots. This sudden change in mortality rates at the seedling level is perhaps the most interesting finding of the current study.

Although a large number of larvae dispersed to the understory, the resulting damage to established regeneration was not severe. Overall mean defoliation of seedlings was highest beneath white spruce trees, which is to be expected given the higher number of larvae that dispersed from this species. However, even with more than 160 larvae per m^2 landing beneath white spruce trees and feeding on regeneration with a mean density of about two seedlings per m^2, mean defoliation was only about 34%. Mean defoliation of seedlings was even lower under balsam fir trees (23%) and black spruce trees (19%). Seedling damage was almost exclusive to the new growth of terminal and terminal-lateral buds of leaders, as observed by Ghent (1958a). Only about 60% of all seedlings in the understory were damaged to any extent, but over 85% of these seedlings had damage to the leader. Regrettably, the number of seedlings for which next year's terminal bud was completely destroyed (Fettes score of 12) was not recorded as a separate variable. However, this number is thought to have been quite low. All needles on the current year's growth of leaders often were consumed, but total destruction of next year's terminal bud was not common.

Pearson correlation coefficients for height and defoliation scores were low for all seedling samples (mean r = about 0.25). However, a greater number of buds was consumed on taller seedlings (r = 0.82). Because the majority of damage was inflicted to the terminal and terminal-lateral shoots of seedlings, the greater number of buds destroyed on larger seedlings resulted in the perception that they were much more defoliated than shorter seedlings (Fig. 16). Based on percentage of total buds, however, defoliation on taller seedlings was no more severe than that on shorter seedlings.

Few, if any, seedlings appeared to be near death. However, the large number of buds destroyed in the tops of taller seedlings almost certainly has reduced height growth to some extent over the past few years. Next year's terminal buds on heavily defoliated seedlings appeared smaller and weaker than those on seedlings with little or no defoliation. In addition, leader increments on tall seedlings often were extremely short for segments of growth added over the last couple of years, indicating that reduced height growth had occurred already.

Defoliation scores were difficult to compare between seedling species due to a lack of spruce regeneration in the study area. Black spruce seedlings most often appeared to suffer lower defoliation than balsam fir or white spruce seedlings. This trend suggests that black spruce seedlings are less preferred by the spruce budworm, especially among smaller seedlings. Exceptionally tall black spruce seedlings suffered high levels of defoliation in their tops, however, suggesting that any possible immunity of this species is not carried through to the sapling stage.

Defoliation of balsam fir and white spruce seedlings appears to have been similar in all respects. Both species were damaged more than the other in different samples, but only slightly. Fettes defoliation scores for balsam fir and

white spruce seedlings were not significantly different for all samples. The only possible difference between these species is shown by data for selected white spruce regeneration sub-plots, where damage to leaders was severe (>50%) more often for white spruce than for balsam fir.

Based on observations made while working in the field, there is one difference between seedling species that was noted. Balsam fir seedlings tended to carry all terminal buds in a cluster of three or four buds at the tip of the leader. Upon defoliating one of these shoots, budworm larvae could move easily to another shoot without having to leave the extremity of the previous year's leader. In contrast, once the terminal shoot of a spruce seedling is defoliated, budworm larvae must move down the previous year's leader before another new shoot is encountered. Given the budworm's strong photopositive tendencies and reluctance to leave the area with highest light intensity, it is possible that terminal-lateral shoots on spruce seedlings are less likely to be encountered and therefore less likely to suffer damage. The positions of terminal lateral shoots on spruce seedlings are such that they readily can take over as the leader where the original leader is destroyed.

The impression gained after analyzing a few thousand seedlings is that terminal shoots of white spruce seedlings may have had a higher incidence of budworm damage than terminal shoots of balsam fir seedlings, but terminal-lateral shoots were damaged less often on white spruce seedlings than on balsam fir seedlings. White spruce therefore may have a better ability to recover where budworm damage occurs. (Note: this phenomenon also may occur on canopy-level branch samples.) However, any differences are purely speculative at this point. The data suggest there is very little difference between defoliation levels for balsam fir and white spruce seedlings, and the

conclusion of no significant differences must be accepted. If differences do exist, they are subtle.

The lack of damage to seedlings is obvious, but one can only wonder what the reason might be. Mattson *et al.* (1991b) provide a strong argument for the existence of some mechanism to insure the survival of seedlings in a highly evolved system of renewal. It appears that such a mechanism may exist, but its nature remains unknown.

From a review of existing literature and data from the current study, five possible explanations were discovered that might explain why seedlings remain relatively undamaged by late-instar larvae. The first possible explanation involves filtering effects of mid-layer foliage. It has been shown that foliage of suppressed host-trees tends to filter out early-instar larvae as they disperse (Beckwith and Burnell 1982; Régnière and Fletcher 1983; Fellin 1985). It seems reasonable to expect that such filtering effects occur for late-instar larvae as well. Evidence is provided by the high mortality of suppressed trees growing above seedlings, as shown in this study and others (Blais 1954; Gordon 1985).

It is possible that seedlings are shielded from dispersing larvae by suppressed trees and lower branches of larger trees. This shield probably would be quite effective when late-instar dispersal occurs for the first time during an outbreak, but would become less effective over time as more suppressed trees die. The data collected for this study show that defoliation of seedlings remains low even when a large number of larvae reach the seedling level. A layer of suppressed host trees may play a role in reducing the number of larvae that reach the understory, but it seems unlikely that this is the primary mechanism that prevents heavy defoliation of seedlings. Of the five possible

explanations considered here, the filtering effects of mid-layer foliage seem least likely to be responsible for protection of seedlings.

The second possible reason for a lack of damage to seedlings is related to instar development. Kelly and Régnière (1985) found more than 50% of the larvae that dropped to the understory were pre-pupal and already had finished feeding. They concluded that most larvae likely would pupate near ground level. During the current study at Black Sturgeon Lake in 1993, many pre-pupal larvae were found in water traps during the later stages of the dispersal period. However, during the early stages of the dispersal period, when dispersal was most pronounced and trap catches were highest, very few larvae appeared to be at the stage where they had finished feeding. A much higher proportion of the budworm population might have been finished feeding at time of dispersal had high temperatures not forced them to leave the crowns of trees prematurely. Given that most larvae that dispersed to the understory were in the early L6 stage, it is unlikely that the majority of larvae would be prepared to stop feeding at time of dispersal.

The third possible explanation for a lack of damage to seedlings involves chemical defenses. As proposed by Mattson (1985), seedlings may possess an inherent immunity to spruce budworm damage. High levels of chemical feeding deterrents may act as a protection mechanism to insure that seedlings survive and re-claim dominance of the infested forest once the outbreak has subsided. Small seedlings lose their immunity as they grow, succumb readily to the next budworm outbreak upon reaching maturity, and thus insure rapid replacement by the next generation of seedlings that is established in the understory. Mattson *et al.* (1991b) make a good argument for the existence of such a system, but the presence or absence of seedling immunity has not been proven.

Mattson *et al.* (1991a) found no difference in budworm survival when larvae were placed on trees 1-2 m tall and on trees 15 m tall. The current study and many others (Ghent *et al.* 1957; Ghent 1958a; Wile 1979; Gordon 1985; MacLean 1988) have shown that the layer of regeneration established beneath mature stands at the time of a budworm outbreak usually is well below 1 m in height. Seedlings greater than 1 m in height may have lost much of their defense mechanism already.

The current study shows a high correlation between seedling height and number of buds consumed. The greater number of buds consumed on taller seedlings may be due to a weakening of the chemical defense mechanism as seedlings grow taller. However, the increase in number of buds consumed on taller seedlings also may be due to taller seedlings being larger targets or the fact that they provide an environment with a higher light intensity.

The only study known to have undertaken an examination of possible seedling immunity is that conducted by MacDonell (1994). Budworm larvae were reared in a laboratory and fed foliage from seedlings and mature trees to test the suitability of different food supplies. Unfortunately, the results of the MacDonell study were inconclusive due to budworm survival problems not related to foliage type used as a food supply. The existence of a chemical defense mechanism should be relatively easy to prove or disprove. A study similar to that conducted by MacDonell (1994) should establish whether such a mechanism exists. The nature of the mechanism then could be explored further if the results of an initial investigation were encouraging.

The fourth possible explanation for low seedling damage is related to predation. A large number of predatory vertebrates and invertebrates is known to feed on spruce budworm larvae and pupae. It is possible that predators in the understory are abundant enough or efficient enough to remove the majority

of larvae before they have an opportunity to cause serious damage to seedlings. Many species of birds are known to feed on budworm larvae and some species are capable of consuming large numbers (Crawford and Jennings 1985; Welsh 1985). However, it has been shown that birds most often feed in the canopy where budworm larvae are most plentiful. Thus, their influence may be greatly diminished in the understory (Torgersen 1985). Studies of the western spruce budworm have shown that ants also are important predators of larvae and pupae (Torgersen 1985; Youngs 1985).

Very little is known about the fate of larvae that disperse to the understory. Kelly and Régnière (1985) placed sentinel pupae on the forest floor and monitored their survival over the late-instar, pupation, and adult emergence stages of the budworm life cycle. They found that pupae disappeared at a mean rate of 72.5% per day (range 66% to 91% per day) due to predation by birds, small mammals, and insects. It was concluded that very few adults would emerge from the forest floor population. Chance of survival was estimated to be less than 0.001 after six days. Kelly and Régnière (1985) determined that mice were the major vertebrate predators of budworm pupae.

The fate of larvae between time of dispersal and pupation remains unknown, but there is a good chance that many are lost to the same organisms found to prey on pupae. The number of larvae seen feeding in the tops of seedlings at Black Sturgeon Lake during the 1993 late-instar dispersal period was not excessive given the number of larvae that dispersed. Very few pupae were encountered during seedling assessments conducted shortly after dispersal had ended. These observations suggest that larvae and pupae may have been reduced in number by predators. The only potential predators observed to be relatively abundant in the understory at 1993 were mice (species unknown), two bird species (ovenbird, *Seiurus aurocapillus*, and winter

wren, *Troglodytes troglodytes*) which perhaps were more visible and audible than abundant, and carrion beetles (*Nicrophorus sp.*) which were caught in abundance by water traps set for budworm larvae.

The fifth possible explanation for a lack of damage to seedlings involves micro-climatic conditions in the understory. It may be that the cool, shaded understory is not a suitable habitat for budworm larvae. Such an environment certainly is different from the upper canopy where budworm larvae thrive in full sunlight and high temperatures. Wellington (1948) has shown that budworm larvae are extremely photopositive. Régnière (1982) has shown that optimum temperature for budworm development is slightly below 30°C. It is possible that, upon reaching the understory, budworm larvae immediately begin their search for a high-light, high-temperature environment to which they are best suited. Many larvae may crawl back up to the crowns of mature trees (Morris and Mott 1963). Many larvae end up in the tops of seedlings (Wellington 1948; Ghent 1958a), which are the most light-intense environments in the understory. Larvae that end up in the tops of seedlings may disperse again if the seedling is heavily shaded or may proceed to feed on the leaders of seedlings if the environment is acceptable. This habit of dispersal and re-dispersal at the seedling level may lead to a higher concentration of larvae in the tops of the tallest seedlings. The result of this process would be a greater number of buds consumed in the tops of taller seedlings than shorter ones, as shown by the current study.

Of course, all or none of the previously described theories may be correct. The spruce budworm and the forest interact in many complex and subtle ways, as demonstrated by our lack of understanding of such interactions after more than 70 years of scientific research. There is no reason to expect that seedlings survive a budworm outbreak because of a single mechanism.

Seedling establishment dates generated from height and age data gathered for the current study are approximate because of the methods employed, but should accurately reflect the general pattern of seedling establishment over time. The data suggest the majority of seedlings in the understory became established after the start of the budworm outbreak rather than before it. Seedling establishment appears to have increased during the same time that budworm populations increased and then ended abruptly with the onset of heavy defoliation.

Given that the budworm prefers to feed on reproductive structures of host trees whenever they are available (Blais 1952; Schooley 1978; Prévost and Laing 1986), cessation of seedling establishment at time of heavy defoliation was expected. However, the coincidence of increased seedling establishment and increased budworm densities was rather unexpected. Authors in the past often have referred to the fact that seedlings became established "before" a budworm outbreak (Ghent *et al.* 1957; Ghent 1958a; Batzer and Popp 1985). The current study suggests that seedlings became established in abundance only "after" the outbreak began. More specifically, seedling establishment peaked "after" budworm populations began to increase, but "before" the onset of heavy defoliation.

This pattern of seedling establishment seems rather unusual at first glance. One would expect seedling establishment to end rather than begin with the development of an outbreak. However, it appears that the pattern of seedling establishment shown by the current study may be the norm rather than the exception. Seedling establishment dates shown by Ghent (1958a) for an earlier outbreak at Black Sturgeon Lake also indicate that the majority of seedlings became established during the build-up of a budworm outbreak rather

than before it. A similar trend also is shown by Batzer and Popp (1985) for a mixedwood forest in Minnesota.

The increased rate of seedling establishment during early stages of a budworm outbreak is not surprising when one considers all the processes taking place. Balsam fir begins to flower prolifically upon reaching maturity. Consecutive years of heavy flowering naturally lead to an increase in seed production and thus seedling establishment. Consecutive years of heavy flowering also provide the budworm with massive quantities of high quality food, insuring better budworm survival and the development of an outbreak (Blais 1952). Thus, the understory is stocked with new balsam fir seedlings immediately before the budworm reaches epidemic levels and causes widespread mortality among mature trees. The pattern certainly is suggestive of a specialized ecological system of stand renewal designed to insure the continued dominance of balsam fir.

Having established that the spruce budworm did not administer a selective thinning of balsam fir seedlings at Black Sturgeon Lake in 1993, interest can be shifted to the reasons why spruce regeneration is lacking. Data from the current study show that balsam fir seedlings outnumbered spruce seedlings by a ratio of more than 30:1 over all study plots. Mean seedling densities in the study area were 21,913 per ha for balsam fir, 450 per ha for white spruce, and 125 per ha for black spruce. These estimates are based on seedling tallies in 200 random sub-plots (fifty 4-m^2 sub-plots per 10-ha plot), but remain highly variable due to low sample intensities. It has been determined that a sample intensity as high as 10% may be needed to reduce standard errors to within 15% of the mean value (Ghent *et al.* 1957; Ghent 1963). However, a 10% sample intensity would have required about 10,000 sub-plots over 40 ha; a prohibitive number to say the least. The random nature of the 200

sub-plots used for the current study is relied upon to reflect mean tendencies in seedling densities.

Using live and dead stems per ha combined to represent pre-outbreak densities for trees, seedling survival rates needed to restore pre-outbreak stand conditions can be calculated. About 34% of the black spruce seedlings and about 37% of the white spruce seedlings in the understory at 1993 would have to survive to replace trees in the overstory (assuming 100% mortality of the present overstory). In contrast, only about 8% of the balsam fir seedlings would need to survive to insure dominance of balsam fir at levels equal to that in the pre-outbreak stand.

Given that balsam fir and white spruce have similar growth rates, at least as small seedlings (Ghent *et al.* 1957; Fye and Thomas 1963; current study), there is no reason to expect that a disproportionately larger number of spruce seedlings will survive. However, the current data show that spruce may have a slight advantage because they tend to carry a larger proportion of the seedling population in the taller height classes. This height advantage was shown to be somewhat more pronounced for black spruce than white spruce seedlings. Because the tallest seedlings in the understory are expected to maintain their dominance over time (Fye and Thomas 1963; Gordon 1985), a slightly greater percentage of spruce ultimately may survive. Other studies (Batzer and Popp 1985, Davis 1991) have shown that, in general, spruce regeneration tends to be larger and better established than balsam fir, despite lower densities for spruce. Even if a slightly greater proportion of spruce seedlings does survive in the study area at Black Sturgeon Lake, it does not seem likely that over 33% of spruce seedlings will survive, while only 8% of balsam fir seedlings survive. Based on seedling densities at 1993, it appears that the study area at Black

Sturgeon Lake will be dominated by balsam fir once again – perhaps even more so than at present.

There are two other ways in which the spruce component of the forest might increase over time. First, many of the mature spruce in the study area likely will survive the present budworm outbreak. Given the longevity of the spruce species, these mature trees should still be present when seedlings from the present understory rise up to become additional mature trees. Second, the future seed rain should contain a higher proportion of spruce seeds relative to balsam fir because the budworm has reduced the presence of balsam fir. A higher proportion of spruce seedlings should be established in the post-budworm stand than in the pre-budworm stand.

Other studies have shown that surviving mature trees resume seed production after the budworm outbreak has subsided and that many new seedlings may become established in the post-budworm forest (Fye and Thomas 1963; Batzer and Popp 1985). The survival of more mature spruce trees than balsam fir trees has potential to increase the spruce component in the understory, but it is difficult to predict if this potential will be realized. One can only speculate how a seemingly infinite number of variables may act together to shape the species composition of the future forest. The increased seed rain of spruce in the post-budworm stand may be of little consequence because the understory already is dominated by balsam fir seedlings. Even if a large number of spruce seedlings manage to become established in the near future, it seems unlikely that they would be able to out-compete the larger, better established balsam fir seedlings already present.

There appears to be only one way that spruce seedlings might make some gains on established balsam fir seedlings. Ghent *et al.* (1957) have documented the mass destruction of seedlings that occurs when budworm-

killed trees fall to the ground and crush established regeneration. This phenomenon is likely to occur in the present stands at Black Sturgeon Lake and was observed to be happening already to some extent in 1993. Because the destruction of seedlings by falling trees is essentially random, no changes to species composition should be expected. However, patches of mineral soil exposed by the roots of fallen trees should increase the number of suitable seedbeds available. As fallen trees begin to decay, they should create additional seedbeds suitable for new seedling establishment. The greater number of mature spruce trees left in the overstory following a budworm outbreak should insure that a greater proportion of the new seedlings are spruce. The extent to which this process occurs can only be determined through long-term monitoring of understory conditions. The sub-plots established for this study at Black Sturgeon Lake now have been permanently marked with aluminum stakes. It is hoped that periodic re-assessment of these sub-plots will provide valuable information related to further changes in species composition over time.

One might argue against the creation of additional seedbeds by fallen trees on the basis of current stand conditions. If fallen trees create more favourable seedbeds for spruce seedlings, then why are there so few spruce seedlings in the understory now? Would trees that fell after the previous outbreak not have created suitable seedbeds for spruce in the past? Answers to these questions may lie in the history of the study area. A.G. Gordon (personal communication, 1994) points out that the stands in the study area are not strictly the result of natural processes. Because the forest in the study plots was clearcut in the past, spruce would have lost any advantages that might have been gained through better survival of a budworm outbreak, continued

seed rain among fewer balsam fir trees, or enhanced seedbed conditions brought about by fallen trees.

In the natural sequence of events, mature spruce trees would have maintained a continuous presence and may have made some gains on the highly aggressive balsam fir over time. However, any advantage brought about by a spruce budworm outbreak is lost when the forest is clearcut during salvage operations. Without a presence of spruce in the overstory to insure the continued dispersal of seed, spruce is reduced to only a few scattered individuals that have managed to become established in a sea of balsam fir. Once diminished, it may take many generations for spruce to regain its former presence.

The fact that the study area (especially Plots 3 & 4) was cut soon after commercial operations began in the Black Sturgeon area suggests that these areas once had a high component of spruce, which was the most desirable species at the time. The relatively low component of spruce in the present stands suggests that spruce has been unable to re-establish its former presence. If these stands were to be clearcut again (which is happening now during salvage operations in the Black Sturgeon area), it is likely that the presence of spruce would be reduced even further for future stands. Thus, as suggested by Fowle (1983), the decline of spruce may be due to harvesting practices rather than the spruce budworm.

If harvesting companies wish to rely on natural regeneration of conifers in boreal mixedwood forests, they are limited by default to late successional species: balsam fir, white spruce, and black spruce. If a high component of spruce is desirable, then a continued presence of mature spruce may have to be maintained to emulate natural processes. If it turns out that a continued presence of mature spruce trees is needed to insure satisfactory spruce

regeneration, then it needs to be determined how many trees should be left and what type of seedbed conditions are most effective in encouraging more spruce regeneration. The experimental harvest blocks now established as part of the Black Sturgeon Boreal Mixedwood Research Project should provide answers to some very important questions. It will be extremely interesting to see what happens in the partial cut blocks where mature white spruce trees have been left standing.

In the meantime, the idea of leaving behind valuable white spruce trees may not be well accepted by forest products companies. Many budworm-devastated stands already are only marginally worthwhile to salvage. Without taking white spruce, it may not be economically feasible to salvage these stands at all. However, if maintenance of the spruce component over the long term is a primary objective, then it may be best to let some of these less feasible stands regenerate naturally. Maintenance of mature spruce trees in the stand may be the only hope of obtaining satisfactory spruce regeneration for the future.

Even in the absence of a budworm outbreak, maintenance of a spruce overstory may be the only hope of obtaining satisfactory natural regeneration of spruce. To achieve this condition, harvesting methods would have to be modified from the standard clearcut approach now used. This is not to say that clearcutting is an ecologically unsound forest management practice. Indeed, clearcutting is well suited for management of many early-successional tree species. However, the appropriateness of using a clearcut harvesting system to manage shade-tolerant, late-successional species is questionable. Rather than clearcutting the boreal mixedwood, some form of seed-tree or shelterwood treatment may have to be applied if emphasis is on natural regeneration. Such treatments would mimic a budworm disturbance more closely by cleaning out

the balsam fir and leaving behind a higher proportion of spruce. The valuable spruce left behind at time of first intervention need not be lost altogether. Once enough spruce seedlings are established, the large overstory spruce could be removed during a second intervention.

A complete review of silvicultural treatments applicable to budworm-susceptible forests is beyond the scope of this report. The literature dealing with this topic is voluminous and dates back to the early 1900's. However, it is worthwhile to mention that the harvesting scenario just described is not a new idea. Many authors have prescribed similar treatments in the past. A series of papers by Westveld (1946, 1953, 1954) provide a detailed account of partial cut treatments and their benefits in budworm-susceptible forests. Westveld argues that "higher-order silviculture" would result in higher value stands, enhanced site productivity, and increased budworm resistance all at the same time.

The question here is: if such promising methods have been known for so long, why are they not being used today? Miller and Rusnock (1993) discuss this question at length and provide a good explanation why silviculture-oriented approaches to the eastern spruce budworm problem have not gained acceptance. In short, there has been complacency with the status quo and a persistent unwillingness to try new ideas. The shear magnitude of applying specialized treatments over areas as large as those affected by the spruce budworm is daunting, especially when there is no guarantee of success. In the few cases where such methods have been tried, the results have not lived up to expectations (eg. Croome 1970).

Interest in the spruce budworm has waxed and waned along with outbreaks in the past (Sanders 1991). Speculation in 1993 that the outbreak in the Black Sturgeon Lake area was on the verge of collapse has been confirmed. The outbreak remained strong in 1993, but declined significantly

throughout the Northwestern Region of Ontario in 1994 (Constable *et al.* 1994). The budworm may all but disappear for the next 30 years, but one thing is certain ... it will return. Rather than becoming complacent during its absence, forest managers should be exploring ways to increase the spruce component of the boreal mixedwood forest and make it less susceptible to the spruce budworm.

LITERATURE CITED

Albert, P.J. 1991. A review of some host-plant chemicals affecting the feeding and oviposition behaviours of the eastern spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae). Memoirs of the Entomological Society of Canada, 159: 13-18.

Alexander, M. E. 1980. Forest fire history research in Ontario: A problem analysis. pp. 96-109 *in* Stokes, M.A. and J.H. Dieterich (tech. coord.) Proceedings of the Fire History Workshop. Oct. 20-24, 1980, Tuscon, Arizona. USDA Forest Service General Technical Report RM-81, Rocky Mtn. Forest and Range Experiment Station, Fort Collins, Colorado. 142 pp.

Alexander, M.E. and D.L. Euler. 1981. Ecological role of fire in the uncut boreal mixedwood forest. pp. 42-64 *in* Whitney, R.D. and K.M. McClain (ed.) Boreal Mixedwood Symposium. COJFRC Symposium Proceedings O-P-9, Sault Ste. Marie, Ontario, Sept. 16-18, 1980. 278 pp.

Allen, D.C., L. Dorais, and E.G. Kettela. 1984. Survey and detection. pp. 21-36 *in* Managing the Spruce Budworm in Eastern North America. USDA Forest Service, Agriculture Handbook 620. 101 pp.

Anderson, R.S., R.B. Davis, N.G. Miller, and R. Stuckenrath. 1986. History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. Canadian Journal of Botany, 64: 1977-1986.

Atwood, C.E. 1944. The feeding habits of young spruce budworm larvae. The Canadian Entomologist, 76: 64-66.

Baldwin, K.A. 1991. An introduction to the boreal forest in Ontario. Proceedings of the Entomological Society of Ontario, 122: 73-86.

Baskerville, G.L. 1975. Spruce budworm: super silviculturist. The Forestry Chronicle, 51: 138-140.

Baskerville, G.L. and D.A. MacLean. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Canadian Forest Service, Maritimes Forest Research Centre, Information Report M-X-102. 23 pp.

Batzer, H.O. 1969. Forest character and vulnerability of balsam fir to spruce budworm in Minnesota. Forest Science, 15: 17-25.

Batzer, H.O. and M.P. Popp. 1985. Forest succession following a spruce budworm outbreak in Minnesota. The Forestry Chrohnicle, 61: 75-80.

Bean, J.L. and H.O. Batzer. 1957. Mean head width for spruce budworm larval instars in Minnesota and associated data. Journal of Economic Entomology, 50: 499.

Beckwith, R.C. and D.G. Burnell. 1982. Spring larval dispersal of the western spruce budworm (Lepidoptera: Tortricidae) in north-central Washington. Environmental Entomology, 11: 828-832.

Belyea, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. II. An assessment of the role of associated insect species in the death of severely weakened trees. Journal of Forestry, 50: 729-738.

Bergeron, Y. and M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. Vegetario, 79: 51-63.

Bess, H.A. 1946. Staminate flowers and spruce budworm abundance. Dominion Department of Agriculture, Science Service - Division of Entomology, Forest Insect Investigations Bi-monthly Progress Report. 2(2): 3-4.

Binotto, A.P. and R.R. Locke. 1981. The impact of budworm damaged fir on pulp quality. Pulp & Paper Canada, 82: 32-36.

Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Canadian Journal of Zoology, 30: 1-29.

Blais, J.R. 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. The Canadian Entomologist, 85: 446-448.

Blais, J.R. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology, 35: 62-71.

Blais, J.R. 1957. Some relationships of the spruce budworm, *Choristoneura fumiferana* (Clem.) to black spruce, *Picea mariana* (Moench) Voss. The Forestry Chronicle, 33: 364-372.

Blais, J.R. 1958a. Effects of defoliation by spruce budworm (*Choristoneura fumiferana* Clem.) on radial growth at breast height of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.). The Forestry Chronicle, 34: 39-47.

Blais, J.R. 1958b. The vulnerability of balsam fir to spruce budworm attack in northwestern Ontario, with special reference to the physiological age of the tree. The Forestry Chronicle, 34: 405-422.

Blais, J.R. 1959. Spruce budworm outbreaks and the climax of the boreal forest in eastern North America. pp. 69-75 *in* 41st Report of the Quebec Society for the Protection of Plants.

Blais, J.R. 1962. Collection and analysis of radial-growth data from trees for evidence of past spruce budworm outbreaks. The Forestry Chronicle, 38: 474-484.

Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Quebec. Forest Science, 11: 130-138.

Blais, J.R. 1974. The policy of keeping trees alive via spray operations may hasten the recurrence of spruce budworm outbreaks. The Forestry Chronicle, 50: 19-21.

Blais, J.R. 1979. Rate of defoliation of balsam fir in relation to spruce budworm attack and timing of spray application. Canadian Journal of Forest Research, 9: 354-361.

Blais, J.R. 1981a. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Canadian Journal of Forest Research, 11: 620-629.

Blais, J.R. 1981b. Recurrence of spruce budworm outbreaks for two hundred years in western Quebec. The Forestry Chronicle, 57: 273-275.

Blais, J.R. 1981c. Population trends of the spruce budworm and characteristics of outbreaks. pp. 22-24 *in* Hudak, J. and A.G. Raske (ed.). Review of the Spruce Budworm Outbreak in Newfoundland - Its Control and Forest Management Implications. Canadian Forest Service, Newfoundland Forest Research Centre, St. John's, Newfoundland. Information Report N-X-205. 280 pp.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research, 13: 539-547.

Blais, J.R. 1985. Epidemiology of the spruce budworm in western Ontario: a discussion. The Forestry Chronicle, 61: 494-498.

Blum, B.M. 1990. Red spruce. pp. 250-259 *in* Burns, R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume 1, Conifers. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 675 pp.

Blum, B.M. and D.A. MacLean. 1984. Silviculture, forest management, and the spruce budworm. pp. 83-101 *in* Managing the Spruce Budworm in Eastern North America. USDA Forest Service, Agriculture Handbook 620. 101 pp.

Brown, K.M. 1993. Design and Analysis of Experiments. Lakehead University, Thunder Bay, Ontario. 221 pp.

Burns, R.M. and B.H. Honkala. 1990a. Silvics of North America, Volume 1, Conifers. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 675 pp.

Burns, R.M. and B.H. Honkala. 1990b. Silvics of North America, Volume 2, Hardwoods. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 877 pp.

Carleton, T.J. and P.F. Maycock. 1978. Dynamics of the boreal forest south of James Bay. Canadian Journal of Botany, 56: 1157-1173.

Cogbill, C.V. 1985. Dynamics of the boreal forest of the Laurentian Highlands, Canada. Canadian Journal of Forest Research, 15: 252-261.

Constable, D.C., W.D. Biggs, A.J. Keizer, and P.M. Bolan. 1994. Results of Forest Insect and Disease Surveys in the Northwest Region of Ontario, 1994. Natural Resources Canada, Information Report O-X-445. 23 pp.

Craighead, F.C. 1924. Part II. General bionomics and possibilities of prevention and control. pp. 28-88 *in* Swaine, J.M., F.C. Craighead, and I.W. Bailey. Studies on the spruce budworm *Cacoecia fumiferana* Clem. Dominion of Canada, Department of Agriculture, Bulletin 37, New Series (technical). 91 pp.

Crawford, H.S. and D.T. Jennings. 1985. Effects of bird predation of spruce budworm: a pilot study. pp. 98-99 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Croome, G.C.R. 1970. A trial of selection management in a mature fir-spruce-birch forest. The Forestry Chronicle, 46: 317-321.

Davis, W. 1991. The role of advance growth in regeneration of red spruce and balsam fir in east central Maine. pp. 157-168 *in* Simpson, C.M. (ed). Proceedings of the Conference on Natural Regeneration Management. Forestry Canada - Maritimes Region. 261 pp.

Day, R.J. and E.M. Harvey. 1981. Forest dynamics in the boreal mixedwood. pp. 29-41 *in* Whitney, R.D. and K.M. McClain (ed.) Boreal Mixedwood Symposium. COJFRC Symposium Proceedings 0-P-9, Sault Ste. Marie, Ontario, Sept. 16-18, 1980. 278 pp.

De Gryse, J.J. 1944. Enemies of the forest - man or insect? pp. 52-63 *in* Proceedings of the Royal Canadian Institute, Series IIIA, Volume IX.

Dix, R.L. and J.M.A. Swan. 1971. The role of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Jouurnal of Botany, 49: 657-676.

Dobesberger, E.J., K.P. Lim, and A.G. Raske. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flight from New Brunswick to Newfoundland. The Canadian Entomologist, 115: 1641-1645.

Durzan, D.J. and S.M. Lopushanski. 1968. Free and bound amino acids of spruce budworm larvae feeding on balsam fir and red and white spruce. Journal of Insect Physiology, 14: 1485-1497.

Eidt, D.C. and M.D. Cameron. 1972. Measuring growth and development in post-diapause spruce budworms (Lepidoptera: Tortricidae). The Canadian Entomologist, 104:1901-1910.

Elliott, K.R. 1960. A history of recent infestations of the spruce budworm in northwestern Ontario, and an estimate of resultant timber losses. The Forestry Chronicle, 36: 61-82.

Environment Canada. 1993. Annual Meteorological Summary, Thunder Bay "A" Ontario. Atmospheric Environment Service, Environment Canada.

Fettes, J.J. 1950. Investigations of Sampling Techniques for Population Studies of the Spruce Budworm on Balsam Fir in Ontario. Ph.D. Thesis, University of Toronto. (Cited *in* Elliott 1960).

Fellin, D.G. 1985. Dispersal of western spruce budworm larvae and adults as related to silvicultural treatments. pp. 116-117 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Fowle, C.D. 1983. The impact of spruce budworm on the forest community. pp. 7-16 *in* Sanders, C.J. and Carrow, R. (cochairmen). The Spruce Budworm Problem in Ontario -- Real or Imaginary? COJFRC Symposium Proceedings O-P-11. 116 pp.

Frank, R.M. 1990. Balsam fir. pp. 26-35 *in* Burns, R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume 1, Conifers. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 675 pp.

Fye, R.E. and J.B. Thomas. 1963. Regeneration of balsam fir and spruce about fifteen years following release by spruce budworm attack. The Forestry Chronicle, 39: 385-397.

Ghent, A.W. 1958a. Studies of regeneration in forest stands devastated by the spruce budworm, II. Age, height growth, and related studies of balsam fir seedlings. Forest Science, 4: 135-146.

Ghent, A.W. 1958b. Mortality of overstory trembling aspen in relation to outbreaks of the forest tent caterpillar and the spruce budworm. Ecology, 39: 222-232.

Ghent, A.W. 1963. Studies of regeneration in forest stands devastated by the spruce budworm, III. Problems of sampling precision and seedling distribution. Forest Science, 9: 295-310.

Ghent, A.W., D.A. Fraser, and J.B. Thomas. 1957. Studies of regeneration in forest stands devastated by the spruce budworm, I. Evidence of trends in forest succession during the first decade following budworm devastation. Forest Science, 3: 184-208.

Gordon, A.G. 1985. Budworm! What about the forest? USDA Forest Sevice, Report GTR-NE-99. 29 pp.

Graham, S.A. 1941. Climax forest of the upper peninsula of Michigan. Ecology, 22: 355-362.

Greenbank, D.O. 1963. Climate and the spruce budworm. pp. 174-180 in Morris, R.F. (ed.) The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada 31. 332 pp.

Greenbank, D.O. 1973. The dispersal process of spruce budworm moths. Canadian Forest Service, Maritimes Forest Research Centre, Fredricton, New Brunswick. Information Report M-X-39. 25 pp.

Greenbank, D.O., G.W. Schaefer, and R.C. Rainey. 1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: New understanding from canopy observations, radar, and aircraft. Entomological Society of Canada, Memoir 110. 49 pp.

Grigal, D.F. and L.F. Ohmann. 1973. Upland plant communities of the Boundary Waters Canoe Area. Naturalist, 24: 16-20.

Halliday, W.E.D. and A.W.A. Brown. 1943. The distribution of some important forest trees in Canada. Ecology, 24: 353-373.

Harvey, G.T. 1985. The taxonomy of the coniferophagous Choristoneura (Lepidoptera: Tortricidae): A review. pp. 16-48 in Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Hatcher, R.J. 1964. Spruce budworm damage to balsam fir in immature stands, Quebec. The Forestry Chronicle, 40: 372-383.

Hearnden, K.W., S.V. Millson, and W.C. Wilson. 1992. A Report on the Status of Forest Regeneration, by the Ontario Independent Forest Audit Committee. Queen's Printer for Ontario. 117 pp.

Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. pp. 374-405 *in* West, D.C., H.H. Shugart, and D.B. Botkin (ed.) Forest Succession: Concepts and Application. Springer-Verlag, New York, New York. 517 pp.

Henson, W.R. 1951. Mass flights of the spruce budworm. The Canadian Entomologist, 83: 240.

Hudes, E.S. and C. A. Shoemaker. 1984. Statistical comparison of spruce budworm (Lepidoptera: Tortricidae) development on balsam fir and on red and black spruce. Environmental Entomology, 13: 1602-1603.

Irland, L.C. and K. Runyon. 1984. Economics of spruce budworm management strategy. pp. 65-81 *in* Managing the Spruce Budworm in Eastern North America. USDA Forest Service, Agriculture Handbook 620. 101 pp.

Jaynes, H.A. and C.F. Speers. 1949. Biological and ecological studies of the spruce budworm. Journal of Economic Entomology, 42: 221-225.

Jennings, D.T., M.W. Houseweart, and J.B. Dimond. 1983. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce-fir forests of Maine. Environmental Entomology, 12: 1787-1792.

Kayll, A.J. 1968. The role of fire in the boreal forest of Canada. Canadian Forest Service, Petawawa Forest Experiment Station, Chalk River, Ontario. Information Report PS-X-7. 15 pp.

Kelly, B. and J. Régnière. 1985. Predation on pupae of the spruce budworm (Lepidoptera: Tortricidae) on the forest floor. The Canadian Entomologist, 117: 33-38.

Ketcheson, D.E. 1981. Some thoughts on the economics of boreal mixedwood management. pp. 17-20 *in* Whitney, R.D. and K.M. McClain (ed.) Boreal Mixedwood Symposium. COJFRC Symposium Proceedings 0-P-9, Sault Ste. Marie, Ontario, Sept. 16-18, 1980. 278 pp.

Kimmins, J.P. 1971. Variations in the foliar amino acid composition of flowering and non-flowering balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) in relation to outbreaks of the spruce budworm (*Choristoneura fumiferana* (Clem.)). Canadian Journal of Biology, 49: 1005-1011.

Kimmins, J.P. 1987. Forest Ecology. Macmillan Publ. Co., New York, New York. 531 pp.

Klein, R. 1985. Future plans of the Ministry of Natural Resources regarding spruce budworm. 13 pp. *in* The Spruce Budworm and Our Future Forest, Proceedings of the 17th Annual Lakehead University Forestry Association Symposium. Lakehead University, Thunder Bay, Ontario.

Koller, C.N. and D.E. Leonard. 1981. Comparison of energy budgets for spruce budworm *Choristoneura fumiferana* (Clemens) on balsam fir and white spruce. Oecologia, 49: 14-20.

Lawrence, R.K. and M.W. Houseweart. 1981. Impact of the spruce budworm in the Maine spruce-fir region. Cooperative Forestry Research Unit, School of Forest Resources, University of Maine, Orono, Maine. Research Bulletin 3, Misc. Report 250. 106 pp.

Loucks, O.L. 1970. Evolution of Diversity, Efficiency, and Community Stability. American Zoologist, 10: 17-25.

Lysyk, T.J. 1989. Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir. Journal of Economic Entomology, 82: 1161-1168.

Lysyk, T.J. 1990. Relationships between spruce budworm (Lepidoptera: Tortricidae) egg mass density and resultant defoliation of balsam fir and white spruce. The Canadian Entomologist, 122: 253-262.

MacDonell, N.R. 1994. The Effect of Balsam Fir (*Abies balsamea* (L.) Mill.) and White Spruce (*Picea glauca* (Moench) Voss) on the Growth and Development of Spruce Budworm (*Choristoneura fumiferana* Clemens). B.Sc. thesis. Lakehead University, Thunder Bay, Ontario. 36 pp.

MacKay, D. 1978. The Lumberjacks. McGraw-Hill Ryerson Limited, Toronto, Ontario. 319 pp.

MacKay, D. 1985. Heritage Lost: The Crisis in Canada's Forests. Macmillan of Canada, Toronto, Ontario. 272 pp.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. The Forestry Chronicle, 56: 213-221.

MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. The Forestry Chronicle, 60: 273-279.

MacLean, D.A. 1985. Effects of spruce budworm outbreaks on forest growth and yield. pp. 148-175 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

MacLean, D.A. 1988. Effects of spruce budworm outbreaks on vegetation, structure, and succession of balsam fir forests on Cape Breton Island, Canada. pp. 253-261 *in* Werger, M.J.A., P.J.M. van der Aart, H.J. During, and J.T.A. Verhoeven (ed.). 1988. Plant Form and Vegetation Structure: Adaptation, Plasticity and Relation to Herbivory. SBP Academic Publishing, The Hague, The Netherlands.

Marshall, K.B. 1975. The spruce budworm and the dollar in New Brunswick. The Forestry Chronicle, 51: 143-146.

Mattson, W.J. 1985. Role of host plants in the population dynamics of the spruce budworm. pp. 124-125 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Mattson, W.J., R.A. Haack, R.K. Lawrence, and S.S. Slocum. 1991a. Considering the nutritional ecology of the spruce budworm in its management. Forest Ecology and Management, 39: 183-210.

Mattson, W.J., D.A. Herms, J.A. Witter, and D.C. Allen. 1991b. Woody plant grazing systems: North American outbreak folivores and their host plants. pp. 53-84 *in* Baranchikov, Y.N., W.J. Mattson, F.P. Hain, and T.L. Payne (ed.) Forest Insect Guilds: Patterns of Interaction with Host Trees. Proceedings of a Conference held at Abakan, Siberia, USSR, August 13-17, 1989. USDA Forest Service, Northeastern Experimental Station, General Technical Report NE-153. 400 pp.

Mattson, W.J., G.A. Simmons, and J.A. Witter. 1988. The spruce budworm in eastern North America. pp. 309-330 *in* Berryman, A.A. 1988. Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Press, New York, New York. 603 pp.

Maycock, P.F. and J.T. Curtis. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. Ecological Monographs, 30: 1-35.

McClain, K.M. 1981. Definition and distribution of the boreal mixedwood forest in Ontario. pp. 5-9 *in* Whitney, R.D. and K.M. McClain (ed.) Boreal Mixedwood Symposium. COJFRC Symposium Proceedings O-P-9, Sault Ste. Marie, Ontario, Sept. 16-18, 1980. 278 pp.

McClave, J.T. and F.H. Dietrich, II. 1988. Statistics, 4th ed. Dellen Publ. Co., Riverside, New Jersey. 1014 pp.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. The Canadian Entomologist, 10: 439-453.

McIntosh, R.P. 1981. Succession and Ecological Theory. pp. 10-23 *in* West, D.C., H.H. Shugart, and D.B. Botkin (ed.) Forest Succession: Concepts and Application. Springer-Verlag, New York, New York. 517 pp.

Miller, A. and P. Rusnock. 1993. The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. Forest Ecology and Management, 61: 171-189.

Miller, C.A. 1975. Spruce budworm: how it lives and what it does. The Forestry Chronicle, 51: 136-138.

Morris, R.F. (ed.) 1963. The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada 31. 332 pp.

Morris, R.F. and D.G. Mott. 1963. Dispersal and the spruce budworm. pp. 180-189 *in* Morris, R.F. (ed.) The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada 31. 332 pp.

Mott, D.G. 1963. The forest and the spruce budworm. pp.189-202 *in* Morris, R.F. (ed.) The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada 31. 332 pp.

Moulton, T.A. 1982. Assessment of Natural Regeneration in Spruce Budworm Damaged Stands of Bowater Newfoundland Limited. B.Sc. thesis. Lakehead University, Thunder Bay, Ontario. 61 pp.

Nienstaedt, H. and J.C. Zasada. 1990. White spruce. pp. 204-226 *in* Burns, R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume 1, Conifers. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 675 pp.

Norusis, M.J. 1992. SPSS / PC+: Base System User's Guide. SPSS Inc., Chicago, Illinois. 910 pp.

Perala, D.A. 1990. Quaking aspen. pp. 555-569 *in* Burns, R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume 2, Hardwoods. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 877 pp.

Piene, H. and D.A. MacLean. 1984. An evaluation of growth response of young, spaced balsam fir to 3 years of spruce budworm spraying with *Bacillus thuringiensis*. Canadian Journal of Forest Research, 14: 404-411.

Powell, G.R. 1973. The spruce budworm and megasporangiate strobili of balsam fir. Canadian Journal of Forest Research, 3: 424-429.

Prévost, Y.H. and J.E. Laing. 1986. Phenology of spruce budworm, *Choristoneura fumiferana* (Clem.), in relation to the development of cones and foliage of black spruce, *Picea mariana* (Mill.) B.S.P. pp. 225-239 *in* Roques, A. (ed.) Proc. 2nd Conference of the Cone and Seed Insects Working Party. Briancon, France, Sept. 3-5, 1986. 312 pp.

Raske, A.G. 1981. Damage caused by the spruce budworm: Damage to trees. pp. 28-30 *in* Hudak, J. and A.G. Raske (ed.). Review of the Spruce Budworm Outbreak in Newfoundland - Its Control and Forest Management Implications. Canadian Forest Service, Newfoundland Forest Research Centre, St. John's, Newfoundland. Information Report N-X-205. 280 pp.

Régnière, J. 1982. A process-oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). The Canadian Entomologist, 114: 811-825.

Régnière, J. and R.M. Fletcher. 1983. Direct measurement of spruce budworm (Lepidoptera: Tortricidae) larval dispersal in forest stands. Environmental Entomology, 12: 1532-1538.

Régnière, J., T.J. Lysyk, and M. Auger. 1989. Population density estimation of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) on balsam fir and white spruce from 45-cm mid-crown branch tips. The Canadian Entomologist, 121: 267-281.

Régnière, J. and C.J. Sanders. 1983. Optimal sample size for the estimation of spruce budworm (Lepidoptera: Tortricidae) populations on balsam fir and white spruce. The Canadian Entomologist, 115:1621-1626.

Régnière, J. and M. You. 1991. A simulation model of spruce budworm (Lepidoptera: Tortricidae) feeding on balsam fir and white spruce. Ecological Modelling, 54: 277-297.

Renwick, J.A.A. and C.D. Radke. 1982. Ovipositional choice and larval survival of the spruce budworm, Choristoneura fumiferana (Lepidoptera: Tortricidae). Environmental Entomology, 11: 503-505.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Canadian Journal of Botany, 39: 1007-1017.

Rowe, J.S. 1972. Forest Regions of Canada. Publ. No. 1300, Canadian Forest Service, Department of the Environment, Ottawa, Ontario. 172 pp.

Royama, T. 1984. Population dynamics of the spruce budworm Choristoneura fumiferana. Ecological Monographs, 54: 429-462.

Ruel, J-C. and M. Huot. 1993. Impact de la tordeuse des bourgeons de l'épinette [Choristoneura fumiferana (Clem.)] sur la régénération des sapinières après la coupe à blanc. The Forestry Chronicle, 69: 163-172.

Safford, L.O., J.C. Bjorkbom, and J.C. Zasada. 1990. Paper birch. pp. 158-171 in Burns, R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume 2, Hardwoods. Agricultural Handbook 654, USDA Forest Service, Washington, DC. 877 pp.

Sanders, C.J. 1969. Extrusion of the female sex pheromone gland in the eastern spruce budworm Choristoneura fumiferana (Lepidoptera: Tortricidae). The Canadian Entomologist, 101: 760-762.

Sanders, C.J. (compiler). 1980. A summary of current techniques used for sampling spruce budworm populations and estimating defoliation in eastern Canada. Canadian Forest Service, Sault Ste. Marie, Ontario. Report 0-X-306. 33 pp. + Appendices.

Sanders, C.J. 1991. Biology of North American spruce budworms. pp.579-620 in van der Geest, L.P.S. and H.H. Evenhuis (ed.) Tortricid Pests, Their Biology, Natural Enemies and Control. Elsevier Science Publ., Amsterdam, The Netherlands.

Sanders, C.J., and G.S. Lucuik. 1972. Factors affecting calling by female eastern spruce budworm, Choristoneura fumiferana (Lepidoptera: Tortricidae). The Canadian Entomologist, 104: 1751-1762.

Sanders, C.J., and G.S. Lucuik. 1975. Effects of photoperiod and size on flight activity and oviposition in the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). The Canadian Entomologist, 107: 1289-1299.

Schooley, H.O. 1978. Effects of spruce budworm on cone production by balsam fir. The Forestry Chronicle, 54: 298-301.

Schooley, H.O. 1980. Damage to black spruce cone crops by the spruce budworm. Newfoundland Forest Research Centre, St. John's, Newfoundland. Information Report N-X-187. 15 pp.

Shepherd, R.F. 1958. Factors controlling the internal temperatures of spruce budworm larvae, *Choristoneura fumiferana* (Clem.). Canadian Journal of Zoology, 36: 779-786.

Solomon, D.S. and T.B. Brann. 1992. Ten-year impact of spruce budworm on spruce-fir forests of Maine. USDA Forest Service, General Technical Report NE-165. 44 pp.

Sprugel, D.G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. Journal of Ecology, 64: 889-911.

SPSS. 1994. The Basics: SPSS for Windows. SPSS Inc., Chicago, Illinois. 12 Chapters + Appendix.

Stocks, B.J. 1985. Forest-fire behavior in spruce budworm-killed balsam fir. pp. 188-199 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Stocks, B.J. 1987. Fire potential in the spruce budworm-damaged forests of Ontario. The Forestry Chronicle, 63: 8-14.

Swaine, J.M. 1933. The relation of insect activities to forest development as exemplified in the forests of eastern North America. Scientific Agriculture, 14: 8-31.

Swaine, J.M. and F.C. Craighead. 1924. Part I. A general account of the outbreaks, injury and associated insects. pp. 3-27 *in* Swaine, J.M., F.C. Craighead, and I.M. Bailey. Studies on the Spruce Budworm *Cacoecia fumiferana* Clem. Dominion of Canada, Department of Agriculture, Bulletin 37, New Series (tech.). 91 pp.

Swaine, J.M., F.C. Craighead, and I.M. Bailey. 1924. Studies on the Spruce
    Budworm *Cacoecia fumiferana* Clem. Dominion of Canada, Department
    of Agriculture, Bulletin 37, New Series (tech.). 91 pp.

Swift, J. 1983. Cut and Run: The Assault on Canada's Forests. Between the
    Lines Publ., Toronto, Ontario. 283 pp.

Talerico, R.L. 1983. Summary of life history and hosts of the spruce budworm.
    pp.1-4 in Talerico, R.L. and M. Montgomery (tech. coord.) Proceedings,
    Forest Defoliator - Host Interactions: A Comparison Between Gypsy Moth
    and Spruce Budworms. New Haven, Connecticut, April 5-7, 1983.
    General Technical Report NE-85, USDA Forest Service. 141 pp.

Torgersen, T.R. 1985. Role of birds and ants in western spruce budworm
    dynamics. pp. 97-98 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J.
    Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc.
    CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept.
    16-20, 1984. 527 pp.

Towill, W.D. and D.A. Archibald. 1991. A competition index methodology for
    Northwestern Ontario: Ministry of Natural Resources, Northwestern
    Ontario Forest Technology Development Unit, Technical Note TN-10.
    12 pp.

Tripp, H.A. 1950. Injury to white spruce cones by spruce budworm. Forest
    Insect Investigations Bi-Monthly Progress Report, Dominion Department
    of Agriculture, 6(5): 1-2.

Tripp, H.A. and A.F. Hedlin. 1956. An ecological study and damage appraisal
    of white spruce cone insects. The Forestry Chronicle, 32: 400-410.

Turner, K.B. 1952. The relation of mortality of balsam fir, caused by the spruce
    budworm, to forest competition in the Algoma forest of Ontario. Pub.
    875, Canada Department of Agriculture, Ottawa. 107 pp.

Vescio, S. A. 1995. Varying Food Quality and Its Influence on Spruce
    Budworm Growth, Development, and Fecundity. M.Sc.F. thesis.
    Lakehead University, Thunder Bay, Ontario. 175 pp.

Viereck, L.A. and W.F. Johnston. 1990. Black spruce. pp. 227-237 *in* Burns,
    R.M. and B.H. Honkala (tech. coord.). Silvics of North America, Volume
    1, Conifers. Agricultural Handbook 654, USDA Forest Service,
    Washington, DC. 675 pp.

Vincent, A.B. 1956. Balsam fir and white spruce regeneration on the Green River watershed. Department of Northern Affairs and Natural Resources, Forest Research Division, Technical Note No. 40. 24 pp.

Wein R.W. and M.A. El-Bayoumi. 1983. Limitations to predictability of plant succession in northern ecosystems. pp. 214-225 *in* *in* Wein, R.W., R.R. Riewe, and I.R. Methven (ed.) Resources and Dynamics of the Boreal Zone. (Proceedings of a Conference held at Thunder Bay, Ontario, August 1982). 544 pp.

Wein, R.W. and J.M. Moore. 1979. Fire history and recent fire rotation periods in the Nova Scotia Acadian Forest. Canadian Journal of Forest Research, 9: 166-178.

Weingartner, D.H. and J.T. Basham. 1979. Forest management and research needs in the boreal mixedwood forest of Ontario. The Spruce-Fir-Aspen Forestry Research Committee. 90 pp.

Wellington, W.G. 1948. The light reactions of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). The Canadian Entomologist, 80: 56-82.

Wellington, W.G. and W.R. Henson. 1947. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). The Canadian Entomologist, 79: 168-170.

Welsh, D.A. 1985. Preliminary studies of the relation between spruce budworm and birds in the boreal forest of Ontario. pp. 100-101 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Westveld, M. 1946. Forest management as a means of controlling the spruce budworm. Journal of Forestry, 44: 949-953.

Westveld, M. 1953. Ecology and silviculture of the spruce-fir forests of eastern North America. Journal of Forestry, 51: 422-431.

Westveld, M. 1954. A budworm vigor-resistance classification for spruce and balsam fir. Journal of Forestry, 52: 11-24.

White, P.S., M.D. MacKenzie, and R.T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. Canadian Journal of Forest Research, 15: 233-240.

Wile, B.C. 1979. Natural regeneration under mature and overmature stands of balsam fir on the Cape Breton Highlands. Maritimes Forest Research Centre, Fredericton, New Brunswick. Information Report M-X-104. 5 pp.

Wilson, L.F. 1963. Host preference for oviposition by the spruce budworm in the Lake States. Journal of Economic Entomology, 56: 285-288.

Witter, J., D. Ostaff, and B. Montgomery. 1984. Damage assessment. pp. 37-61 *in* Managing the Spruce Budworm in Eastern North America. USDA Forest Service, Agriculture Handbook 620. 101 pp.

Yang, R.C. and R.D. Fry. 1981. Natural succession following harvesting in the boreal mixedwood forest. pp. 65-77 *in* Whitney, R.D. and K.M. McClain (ed.) Boreal Mixedwood Symposium. COJFRC Symposium Proceedings 0-P-9, Sault Ste. Marie, Ontario, Sept. 16-18, 1980. 278 pp.

Youngs, L. 1985. Ant predators of the western spruce budworm: species composition and patterns of occurrence in eastern Oregon and western Montana. p. 96 *in* Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy (ed.). Recent Advances in Spruce Budworms Research. Proc. CANUSA Spruce Budworms Research Symposium, Bangor, Maine, Sept. 16-20, 1984. 527 pp.

Zoladeski, C.A. and P.F. Maycock. 1990. Dynamics of the boreal forest in northwestern Ontario. American Midland Naturalist, 124: 289-300.

APPENDICES

APPENDIX I

RECENT NEWSPAPER ARTICLES THAT EXEMPLIFY THE SPRUCE BUDWORM PROBLEM AND CURRENT CONTROVERSY

Budworm plague mounts in North warns industry

☐ Infested area may have grown by 500,000 km

By RON McGREGOR
The Chronicle-Journal

Timber areas in the far Northwest and Northeast of here have borne the brunt of a major increase in spruce budworm infestation, according to a federal report.

The area infested by the spruce budworm, which can kill spruce and balsam trees through repeated attacks, has grown by as much as 500,000 square kilometres, according to the latest survey bulletin issued by Forestry Canada. The cool, wet summer did not limit their numbers.

Most of that was concentrated in Sioux Lookout, Red Lake and Hearst districts.

Dryden and Atikokan districts experienced some decline in budworm numbers, but that's because "the budworm has basically eaten itself out of house and home," in those areas already, said Ministry of Natural Resources forestry technician Eldon Kangas.

The forest industy has slammed the provincial government for discontinuing its usual program of spring spraying this year because of budget cuts.

The area of infestation has already covers an area from from the Manitoba border east to Wawa and Hearst.

The death of spruce caused by budworm infestation is a serious threat to timber stands cut by pulp and paper companies and the industry faces problems if spraying isn't resumed, say industry spokesman.

The area of severe tree defoliation tracked by the industry has expanded this year, said Bill Klages, forestry services superintendent with Canadian Pacific Forest Products Ltd. in Thunder Bay.

The infestation is also moving east. Foresters for Kimberly-Clark Canada Ltd. near Terrace Bay are seeing serious budworm defoliation, Klages said.

(Kimberly-Clark doesn't allow its employees to answer press inquiries without prior approval from management. A company spokesman said it would likely take weeks to arrange an interview with Kimberly-Clark chief district forester James Harrison.)

It's not just the forest industry that's affected, Klages said.

The Sibley Peninsula, home to Sleeping Giant Provincial Park and heavily used by hikers and campers, has been "devastated" by budworm.

He also dismissed suggestions that cold wet weather this year has reduced budworm larvae survival rates.

"I thought this year wouldn't be as severe as it's been in the past, but it was," Klages said. "It just occurred later because of the weather."

The one piece of good news in the bug wars is that jackpine budworm populations in Northwestern Ontario crashed this year, said the MNR's Kangas.

But it's difficult to isolate the cause exactly, he said.

Jackpine budworm numbers fluctuate greatly in a cycle that's not completely understood.

"'It's a more dynamic insect," he said. "It will build quickly in good years and when you get ready to spray, they fall out of the trees."

Thunder Bay Chronicle Journal, October 26, 1992

Spruce hurt by spraying contends one scientist

SAULT STE. MARIE (CP) — Government efforts to kill the spruce budworm through blanket spraying may be doing spruce trees more long-term harm than good, says a scientist who has done years of research.

Alan Gordon, with the Ontario Forest Research Institute, says samples taken from more than 400 plots of balsam fir and spruce trees across Ontario indicate the budworm is a spruce tree's best friend.

"I didn't set out to destroy conventional wisdom on the budworm," said Gordon, who has spent decades studying forest ecosystems. But that may be the ultimate result.

For years, scientists have believed spruce budworm infestations kill spruce forests. Governments across the country spent millions of dollars using sprays to eliminate the pest.

Gordon's research indicates, however, that the budworm actually helps maintain the growth of spruce because the insect helps destroy balsam fir trees that would normally crowd out the more valuable spruce.

"Where spruce and fir grow together it is necessary to have budworm in it to regenerate the spruce component in the stand," Gordon said.

Gordon's studies show that less than 10 per cent of mature spruce and more than 90 per cent of balsam fir trees are killed by the budworms, which like to eat foliage of the two tree species. Repeated attacks can kill the trees and browned, damaged trees are vulnerable to fires.

Before the budworm appears, a forest may contain 12 fir trees for every spruce, a valuable tree used for construction and to make newsprint, high-grade paper and musical instruments.

But after the infestation, there are an even number or more spruce trees left, Gordon found. And when the stand of trees regrows, there are as many or more spruce than balsam fir.

Blanket spraying kills the budworm, enabling the less valuable balsam fir trees to survive, Gordon concludes.

But government officials responsible for forest protection in New Brunswick and Quebec — two provinces hit hard by spruce budworm — argue that spraying is the only alternative during epidemics.

Nelson Carter and Louis Dorais, directors of forest pest management in the two provinces, respectively, say they are examining other methods of saving forests. But the trees and economies of the provinces can't be risked by using unproven remedies, the said.

"The issue facing provincial managers is, 'Can I afford to let these trees die?'" said Carter.

☐ Anti-spray activists to buy N.S.'s claim

HALIFAX (CP) — Anti-spray activists in Cape Breton don't buy the province's claim that an Ontario study that suggests the spruce budworm is beneficial doesn't apply to Nova Scotia.

"It's amazing the bunk these guys are willing to come up with to protect their agenda," said Charles Restino, spokesman for the Cape Breton Coalition for Alternatives to Pesticides.

A study by the Ontario Forest Research Institute recently concluded that the budworm helps spruce tree growth by destroying trees that normally crowd them out.

That may be so in Ontario, but the study "breaks down in Nova Scotia," Tom Smith, an insect expert for the Department of Natural Resources, said earlier this week.

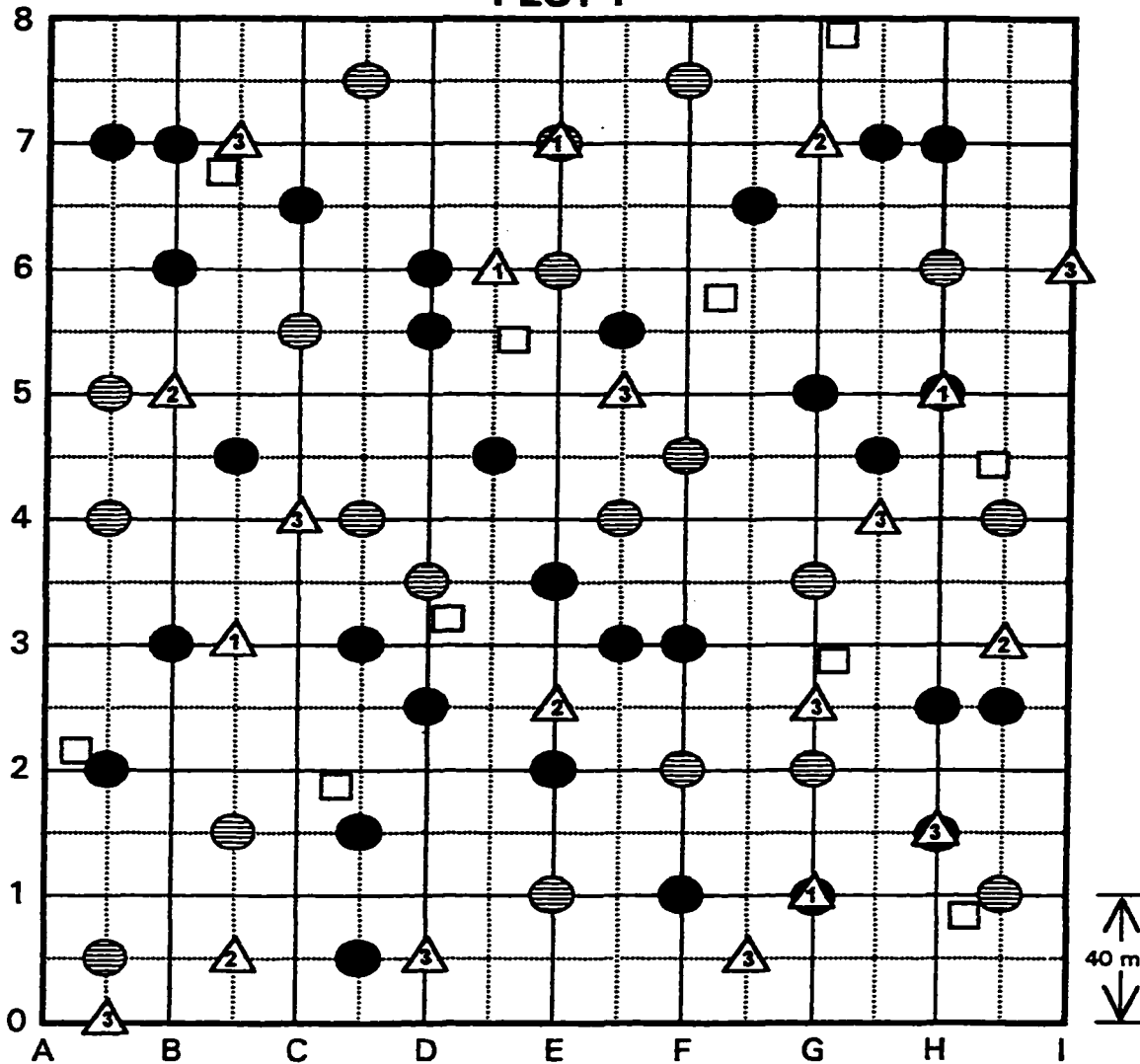**Thunder Bay Chronicle Journal**
October 27, 1992

Thunder Bay Chronicle Journal
October 26, 1992

194

APPENDIX II

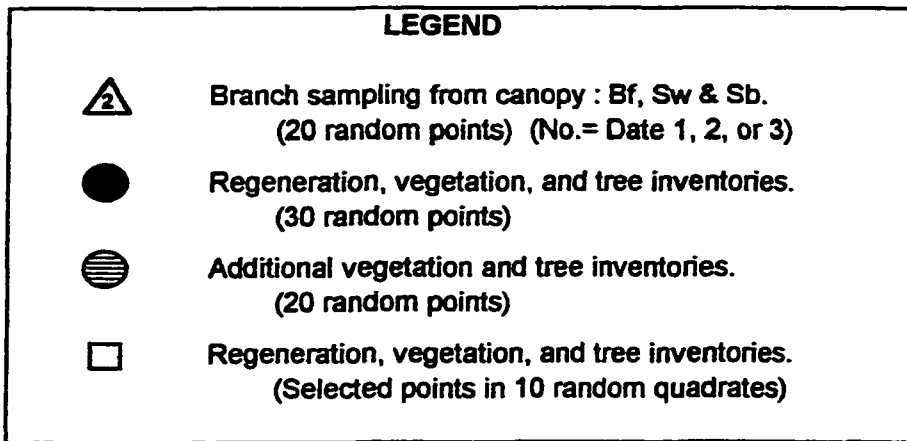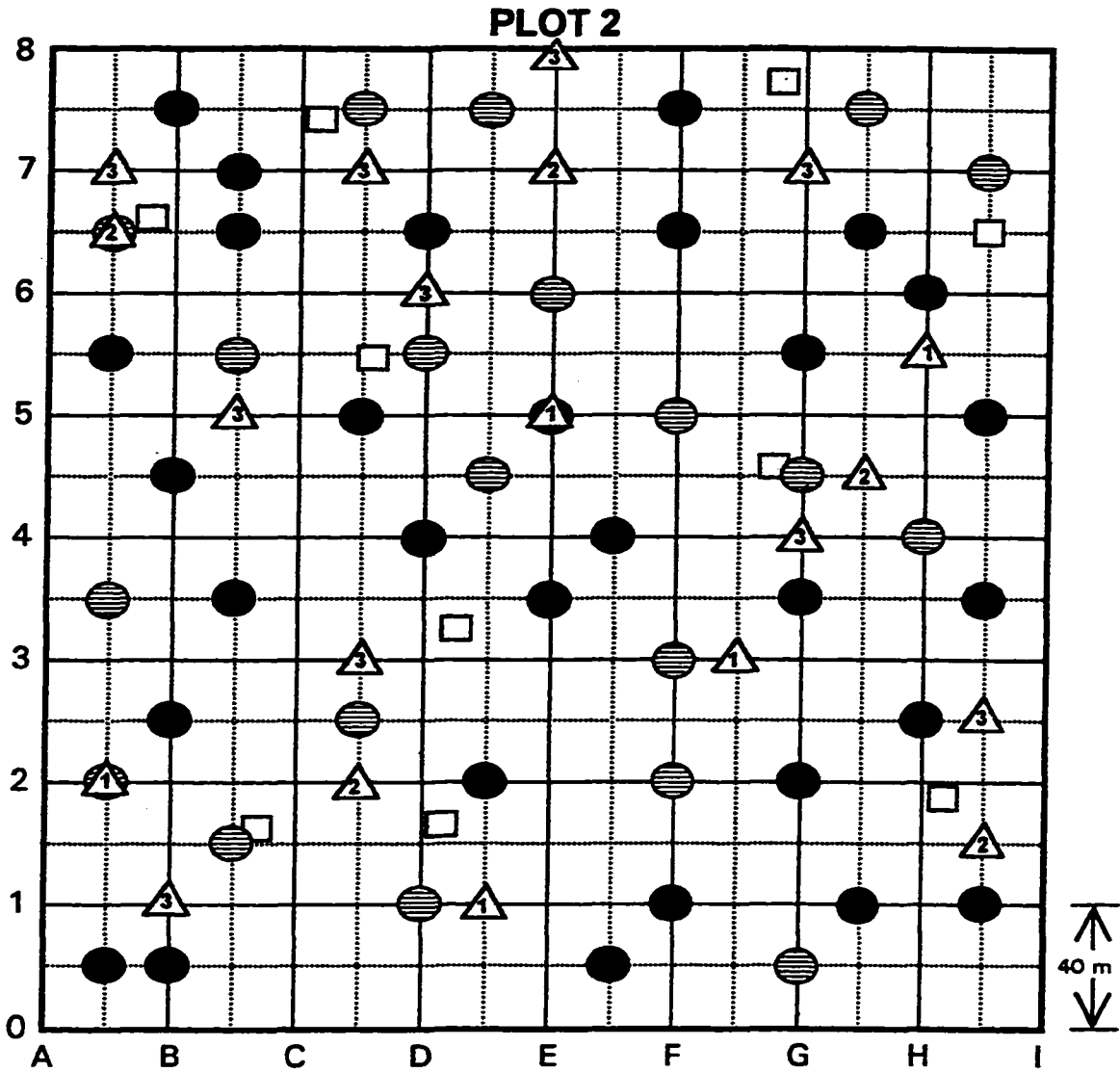# LOCATIONS OF SUB-PLOTS USED FOR SAMPLING WITHIN 10-HA STUDY PLOTS

PLOT 1

LEGEND

Branch sampling from canopy : Bf, Sw & Sb.
(20 random points) (No.= Date 1, 2, or 3)

Regeneration, vegetation, and tree inventories.
(30 random points)

Additional vegetation and tree inventories.
(20 random points)

Regeneration, vegetation, and tree inventories.
(Selected points in 10 random quadrates)

PLOT 2

PLOT 3
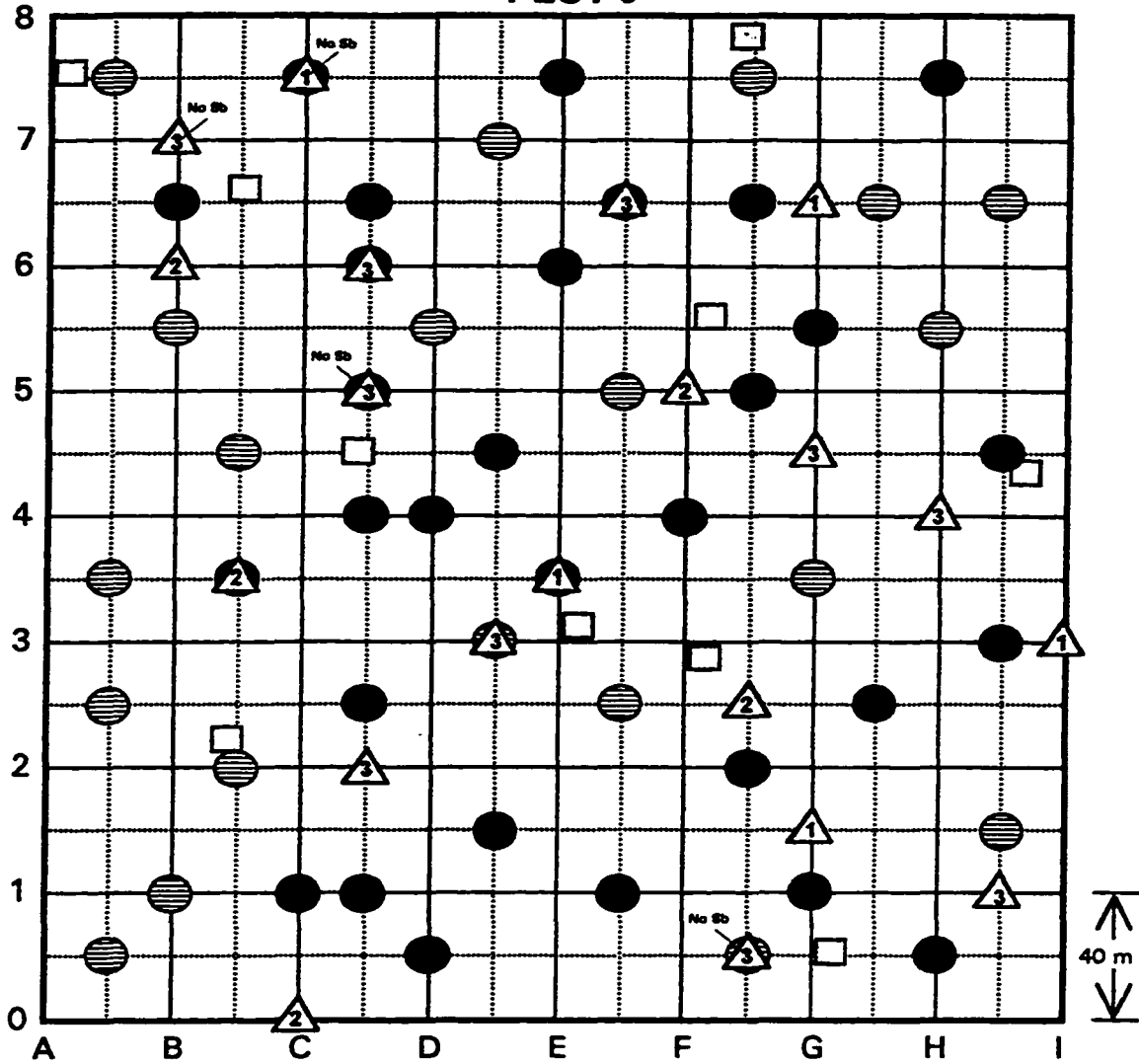
LEGEND

△ Branch sampling from canopy : Bf, Sw & Sb.
(20 random points) (No.= Date 1, 2, or 3)

● Regeneration, vegetation, and tree inventories.
(30 random points)

⊜ Additional vegetation and tree inventories.
(20 random points)

☐ Regeneration, vegetation, and tree inventories.
(Selected points in 10 random quadrates)

PLOT 4

APPENDIX III

DIAMETER CLASS DISTRIBUTIONS
BY TREE SPECIES AND PLOT

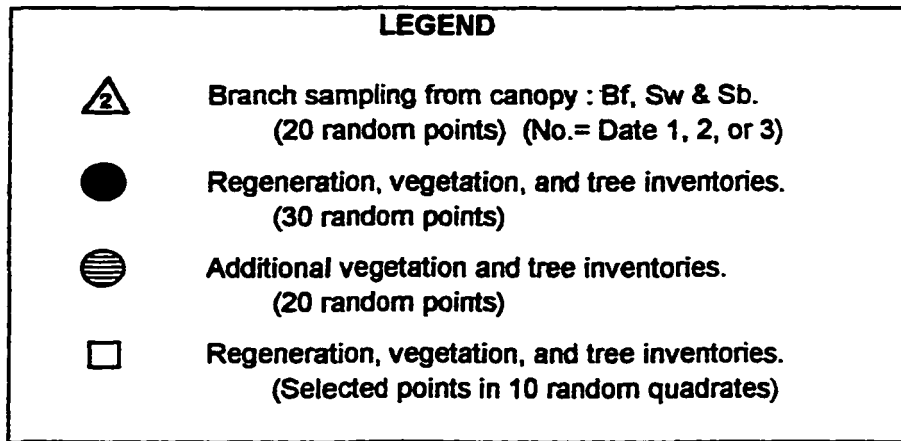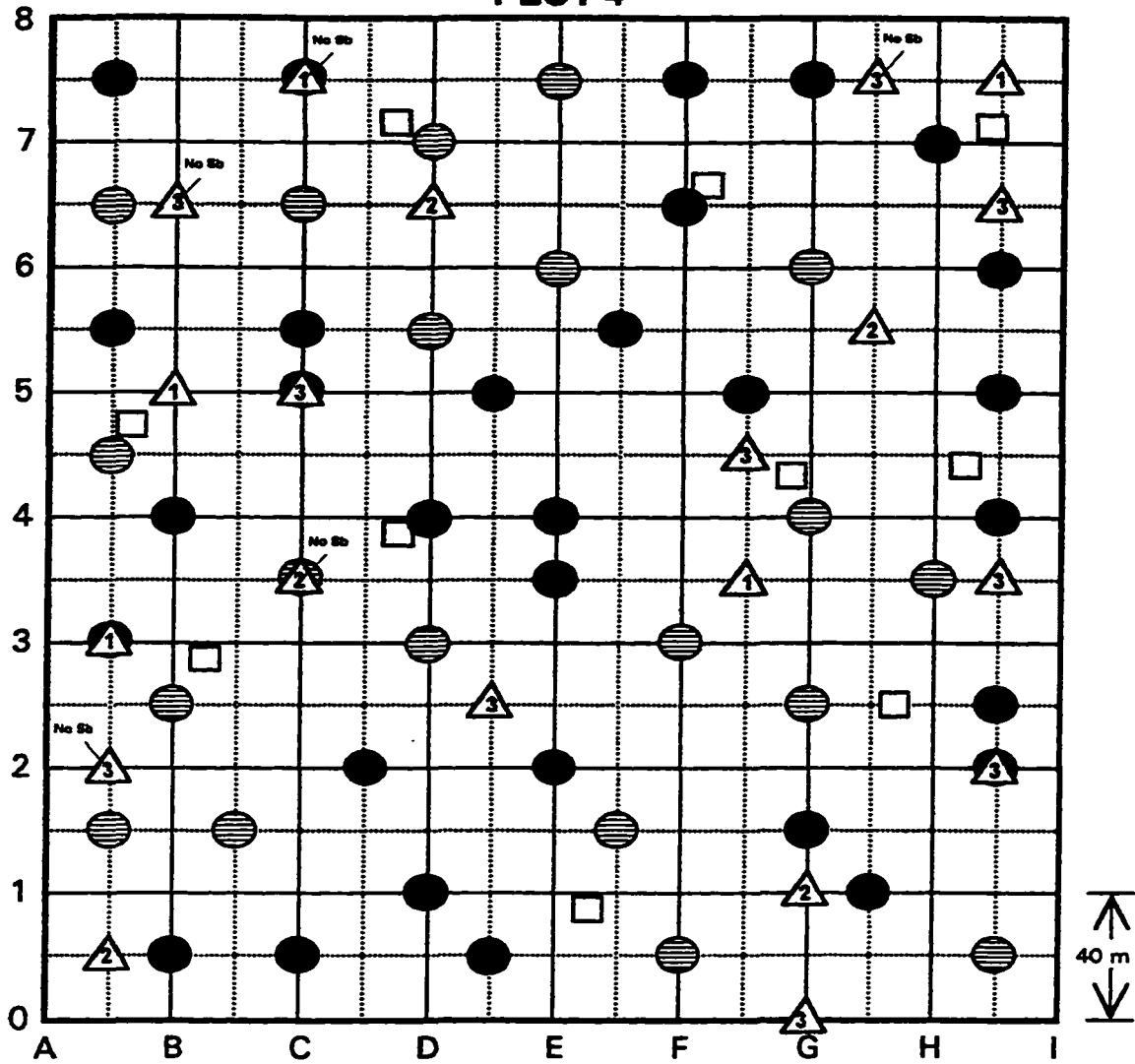**Live stems per hectare.**

DBH Class	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	All
Balsam fir																		
Plot 1	170	126	134	106	66	24	20	14	2	0	0	0	0	0	0	0	0	662
Plot 2	68	70	36	80	68	36	12	14	2	0	0	2	0	0	0	0	0	388
Plot 3	52	42	32	62	70	62	38	26	18	10	8	0	0	0	0	0	0	420
Plot 4	32	10	14	40	38	26	24	28	18	16	0	0	2	0	0	0	0	248
All plots	80.5	62.0	54.0	72.0	60.5	37.0	23.5	20.5	10.0	6.5	2.0	0.5	0.5	0.0	0.0	0.0	0.0	429.5
White spruce																		
Plot 1	4	8	0	2	6	10	8	10	6	4	2	4	2	0	0	0	0	66
Plot 2	14	12	8	10	14	18	10	14	8	18	12	4	0	4	0	0	0	146
Plot 3	2	2	4	6	6	18	18	12	10	10	16	10	6	2	2	2	2	128
Plot 4	8	2	6	8	4	18	24	10	14	18	24	8	6	6	4	0	2	162
All plots	7.0	6.0	4.5	6.5	7.5	16.0	15.0	11.5	9.5	12.5	13.5	6.5	3.5	3.0	1.5	0.5	1.0	125.0
Black spruce																		
Plot 1	12	16	40	30	28	32	22	16	10	4	2	4	2	0	0	0	0	218
Plot 2	2	2	0	2	4	4	8	0	0	4	4	0	0	0	0	0	0	30
Plot 3	6	4	2	4	2	8	4	16	0	4	2	0	0	0	0	0	0	52
Plot 4	0	0	4	0	0	0	8	0	0	2	0	2	0	0	0	0	0	16
All plots	5.0	5.5	11.5	9.0	8.5	11.0	10.5	8.0	2.5	3.5	2.0	1.5	0.5	0.0	0.0	0.0	0.0	79.0
Jack pine																		
Plot 1	0	0	0	0	0	2	4	2	2	4	0	0	0	0	0	0	0	14
Plot 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plot 3	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2
Plot 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
All plots	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.5	0.5	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
White birch																		
Plot 1	58	78	66	70	44	26	12	12	2	4	0	0	0	0	0	0	0	372
Plot 2	38	86	62	24	28	6	6	0	0	0	2	0	0	0	0	0	0	252
Plot 3	14	18	4	4	0	0	0	0	0	4	0	0	0	0	0	0	2	48
Plot 4	4	6	6	6	4	2	6	4	0	0	0	4	0	0	0	0	2	44
All plots	28.5	47.0	34.5	26.0	19.0	8.5	6.0	4.0	0.5	2.0	0.5	1.0	0.0	0.0	0.0	0.0	1.0	179.0
Trembling aspen																		
Plot 1	2	10	16	40	28	22	16	28	28	24	16	2	8	0	0	0	0	240
Plot 2	0	16	18	22	24	36	34	28	16	20	16	4	6	6	0	0	0	246
Plot 3	4	20	32	24	28	16	28	26	26	14	8	2	2	4	2	0	0	236
Plot 4	6	8	12	20	16	18	22	14	22	16	12	6	4	2	0	2	0	182
All plots	3.0	13.5	19.5	26.5	24.0	23.0	25.0	24.0	23.0	18.5	13.0	3.5	5.0	3.0	0.5	0.5	0.0	226.0

Dead stems per hectare.

DBH Class	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	All
Balsam fir																		
Plot 1	526	576	402	290	120	52	14	4	0	0	0	0	0	0	0	0	0	1984
Plot 2	446	384	340	264	148	94	44	10	2	0	0	0	0	0	0	0	0	1732
Plot 3	152	192	158	164	104	72	44	18	8	2	2	0	0	0	0	0	0	916
Plot 4	186	128	112	148	100	90	80	38	14	2	6	0	0	0	0	0	0	904
All plots	327.5	320.0	253.0	216.5	118.0	77.0	45.5	17.5	6.0	1.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	1384.0
White spruce																		
Plot 1	4	0	4	6	2	2	2	0	0	0	0	0	0	0	0	0	0	20
Plot 2	8	18	10	10	8	0	4	2	0	0	2	0	0	0	0	0	0	62
Plot 3	12	12	6	2	0	0	4	0	4	0	0	0	0	0	0	0	0	40
Plot 4	2	4	6	4	10	0	6	2	0	4	0	2	0	0	0	0	0	40
All plots	6.5	8.5	6.5	5.5	5.0	0.5	4.0	1.0	1.0	1.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	40.5
Black spruce																		
Plot 1	4	4	8	6	2	0	0	0	2	0	0	0	0	0	0	0	0	26
Plot 2	2	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	6
Plot 3	6	4	2	4	0	0	4	0	0	0	0	0	0	0	0	0	0	20
Plot 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
All plots	3.0	2.5	2.5	2.5	0.5	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0
Jack pine																		
Plot 1	0	0	0	0	0	0	0	0	4	0	2	2	0	0	0	0	0	8
Plot 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plot 3	0	0	0	0	2	0	4	0	0	0	0	0	0	0	0	0	0	6
Plot 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
All plots	0.0	0.0	0.0	0.0	0.5	0.0	1.0	0.0	1.0	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	3.5
White birch																		
Plot 1	12	6	10	4	0	2	2	0	0	0	0	2	2	0	0	0	0	40
Plot 2	10	6	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	18
Plot 3	2	0	2	0	0	0	2	0	2	0	0	0	0	0	0	0	0	8
Plot 4	0	0	0	0	0	0	0	0	0	2	0	0	2	2	0	0	0	6
All plots	6.0	3.0	3.0	1.0	0.0	0.5	1.5	0.0	0.5	0.5	0.0	0.5	1.0	0.5	0.0	0.0	0.0	18.0
Trembling aspen																		
Plot 1	6	8	6	2	0	0	2	0	0	0	0	0	0	0	0	0	0	24
Plot 2	4	14	4	4	2	2	0	0	0	0	0	0	0	0	0	0	0	30
Plot 3	4	4	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	14
Plot 4	4	2	10	2	2	0	0	0	2	0	0	0	0	0	0	0	0	22
All plots	4.5	7.0	6.0	2.5	1.0	0.5	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.5

APPENDIX IV

SCIENTIFIC NAMES OF NON-HOST UNDERSTORY SPECIES TALLIED IN VEGETATION SUB-PLOTS
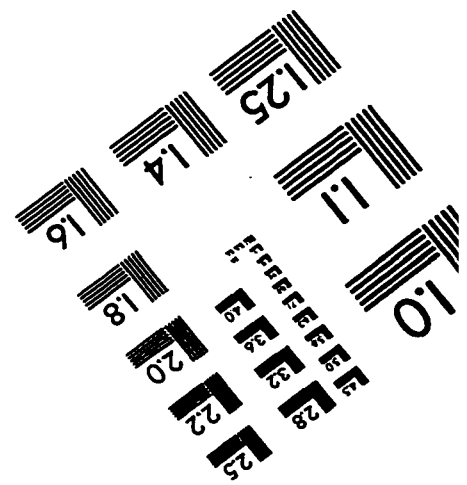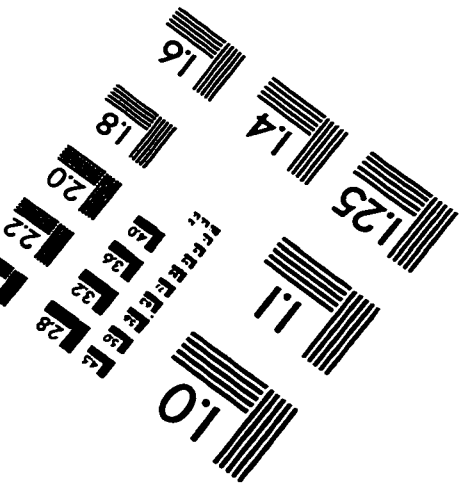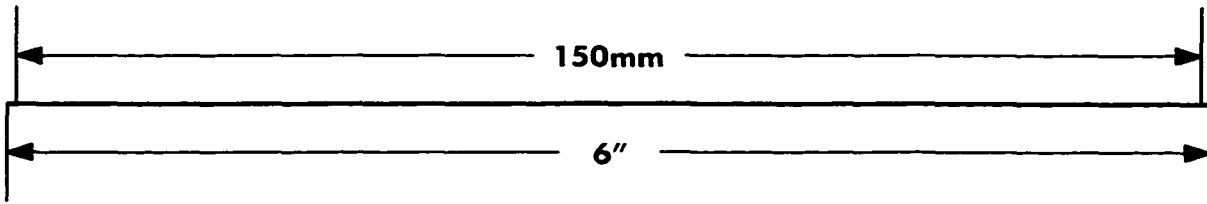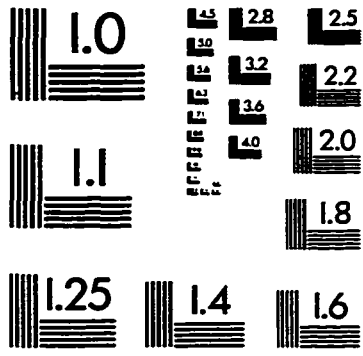
Species List for Understory Vegetation

High Shrub

Common Name	Scientific Name	Auth.
Mountain Maple	*Acer spicatum*	Lam.
Beaked Hazel	*Corylus cornuta*	Marsh.
White Birch	*Betula papyrifera*	Marsh.
Trembling Aspen	*Populus tremuloides*	Michx.
Speckled Alder	*Alnus rugosa*	(Du Roi) Spreng.
Willow	*Salix spp.*	L.
Saskatoon	*Amelanchier spp.*	Medik.
Mountain Ash		
American Mountain Ash	*Sorbus americana*	Marsh.
Showy Mountain Ash	*Sorbus decora*	(Sarg.) Schneid.

Low Shrub, Herbaceous, and Others

Honeysuckle		
Bush Honeysuckle	*Diervilla Lonicera*	Mill.
Canada Fly Honeysuckle	*Lonicera canadensis*	Bartr.
Squashberry	*Viburnum edule*	Raf.
Red Baneberry	*Actaea rubra*	(Ait.) Willd.
Sarsaparilla	*Aralia nudicaulis*	L.
Twisted Stalk	*Streptopus roseus*	Michx.
Prickly Wild Rose	*Rosa acicularis*	Lindl.
Red Raspberry	*Rubus idaeus*	L.
Ribes: Currants & Gooseberries	*Ribes spp.*	L.
Lady Fern	*Athyrium filix-femina*	(L.) Roth
Bracken Fern	*Pteridium aquilinum*	(L.) Kuhn
Labrador Tea	*Ledum groenlandicum*	Oeder
Blueberry	*Vaccinium spp.*	L.
Blue Bead Lily	*Clintonia borealis*	(Ait.) Raf.
Large-Leaved Aster	*Aster macrophyllus*	L.
Clematis (Purple)	*Clematis occidentalis*	(Hornem.) DC.
Bunchberry	*Cornus canadensis*	L.
Twinflower	*Linnaea borealis*	L.
Dwarf Raspberry	*Rubus pubescens*	Raf.
Running Clubmoss	*Lycopodium clavatum*	L.
Misc. Lily		
Wild Lily-of-the-Valley	*Maianthemum canadense*	Desf.
Ground Pine	*Lycopodium obscurum*	L.
Ground Cedar	*Lycopodium complanatum*	L.
Starflower	*Trientalis borealis*	Raf.
Strawberry (Common)	*Fragaria virginiana*	Duchesne
Fragrant Bedstraw	*Galium triflorum*	Michx.
Round-Leaved Orchid	*Plantanthera orbiculata*	(Pursh) Lindl.
Dwarf Rattlesnake Plantain	*Goodyera repens*	(L.) R. Brown
Sweet Coltsfoot	*Petasites palmatus*	(Ait.) Gray.
Violets and Mitreworts		
Kidney-Leaved Violet	*Viola renifolia*	Gray
Naked Mitrewort	*Mitella nuda*	L.
Pyrola	*Pyrola spp.*	
Goldthread	*Coptis trifolia*	(L.) Salisb.
Creeping Snowberry	*Gaultheria hispidula*	(L.) Muhl.
Wood Anemone	*Anemone quinquefolia*	L.

IMAGE EVALUATION
TEST TARGET (QA-3)

150mm

6"