PHENOTYPIC VARIATION IN CONE AND NEEDLE CHARACTERS OF *Pinus banksiana* LAMB. (JACK PINE) IN NORTHWESTERN ONTARIO

by

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ABSTRACT

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Keywords: cone morphology; jack pine; needle morphology; northwestern Ontario; *Pinus banksiana* Lamb.; phenotypic variation.

To assess the patterns of phenotypic variation in cone and needle characters of jack pine relative to spatial, climatic and ecological data, collections were made from ten trees in each of 64 sites in northwestern Ontario. Nineteen cone and forty needle characters were measured on five cones and five needles per tree. Climatic data from 27 Canadian and 10 American weather stations in and surrounding the study area were interpolated, using a geographic information system, to produce weather data for each collection site. Vegetation and soil data for each collection site were determined using the system developed by the Ontario Ministry of Natural Resources in the Northwestern and North Central regions for the Forest Ecosystem Classification program.

Discriminant analysis indicated that the populations in the study areas formed a single group but were spatially organized into two groups, west and east, including the Armstrong area, of Lake Nipigon. A trend surface of the discriminant scores revealed a steep cline at a longitude of 88°15', Nipigon area. Simple regression of discriminant scores against the spatial, climatic and ecological data indicated that the patterns of variation expressed by cone and needle characters may be a result of adaptation to local environments. The first axis scores of the cone data were most closely associated with longitude (r^2=0.23**); elevation (r^2=0.21**); maximum June temperature (r^2=0.10**); and extreme minimum temperature (r^2=0.11**). Similarly, the first axis scores of the needle data were most closely associated with longitude (r^2=0.10**); elevation (r^2=0.13**); maximum June temperature (r^2=0.07**); and extreme minimum temperature (r^2=0.05**).

Multiple regression coefficients from regressions of spatial and climatic data against discriminant scores for both cone and needle data were compared with the variance component among groups from the nested analysis of variance to assess the amount of the total variation attributable to the local environment. The comparison revealed that most of the variation among sites could be explained by spatial and climatic data. In addition, a steep cline could be discerned at a longitude of 88°15' on the the trend surface of maximum June temperature.

The correlations of the patterns of variation with the spatial and climatic data suggest that climate may be the causal agent for the patterns of variation in cone and needle characters in Northwestern Ontario. However, the patterns of cone and needle characters are similar suggesting that the modern patterns of variation may be a result of two migration routes or two refugia.

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MLM

INTRODUCTION

Pinus banksiana Lamb. (jack pine) is the most widely distributed pine in Canada. The range extends from the Maritime provinces to the Mackenzie River Valley in the Northwest Territories and south into the United States, east of the great plains (Critchfield and Little 1966 as modified by Rudloph and Yeatman 1982). Jack pine is predominant in the eastern and central portions of the boreal forest region and is also a component of the transition zone between the Great Lakes-St. Lawrence forest and the boreal forest regions (Rowe 1972).

Jack pine, second only to *Picea mariana* (Mill.) B.S.P. (black spruce) in importance to the forest industry in Ontario, constitutes 28 percent of the total volume and 30 percent of the total stumpage of timber extracted from Crown lands in Ontario (OMNR 1984). In the last 30 years interest in jack pine as a commercial species has increased due to the excellent and early return on the management investment (OMNR 1986). Currently, the province of Ontario commits 80 percent of its regeneration effort to jack pine and black spruce. The level of harvesting and silvicultural effort coupled with the amount of natural variation present in jack pine has led the Ontario Ministry of Natural Resources (OMNR) to group jack pine with black spruce to receive 70 percent of the total tree improvement effort in the province of Ontario (OMNR 1987a).

Assessment of seedling growth (Yeatman 1966); height, diameter, crown width and bark thickness (Hyun 1979); and bud burst (Steiner 1979) in range-wide provenance tests indicates that variation in jack pine is primarily clinal. The patterns of variation correspond to latitude (Yeatman 1966; Hyun 1979; Steiner 1979) and to a lesser degree longitude (Hyun 1979). More specifically patterns of variation in jack pine correspond to growing degree days for seedling growth (Yeatman 1966); and temperature isotherms for bud burst (Steiner 1979). Local provenance tests in the Lake States show that rate of growth (Canavera 1975) and biomass production (Zavitkovski *et al.* 1981; Strong and Grigal 1987) are correlated with latitude. Similarly, variation in tree size in an Ontario provenance test corresponds to latitude (Magnussen *et al.* 1985). In addition, Skeates (1979) and Yeatman (1966) both note a break in the otherwise continual pattern of variation in growth in the area north of Lake Superior.

Patterns of phenotypic variation of cone and needle traits are clinal and follow temperature and latitudinal gradients (Schoenike 1962; Beshir 1975; Schoenike 1976). In addition, there is an intersection of clines that produces a particularly complex pattern of variation in the Lake Superior area (Schoenike 1976).

The climate of northwestern Ontario is classified as modified continental (Chapman and Thomas 1968). The modification is due to the presence of the Great Lakes to the south and, to a lesser degree, Hudson Bay to the north. There are two major climatic gradients, one of increasing temperatures to the south and a second of increasing precipitation from west to east. Northwestern Ontario can be divided into three climatic regions: (1) the Rainy River-Thunder Bay, west of Lake Superior; (2) the Superior, a narrow band north of Lake Superior extending to Sault Ste. Marie; and (3) the Height of Land, north of the first two climatic regions extending to the edge of the Hudson Bay Lowlands. The first two climatic regions have a longer, drier growing season than the third. The Height of Land climatic region is characterized by local climatic variation as a result of the rugged topography of the area and the increased distance from the moderating effect of Lake Superior (Chapman and Thomas 1968).

There are two major physiographic landscapes in northwestern Ontario (Chapman and Thomas 1968). The first is the rugged knobs and ridges of the Precambrian rocks covered with a thin discontinuous layer of soil. Included are several areas in which lacustrine sediments fill bedrock hollows. These areas constitute the farming areas of Kenora-Rainy River and Thunder Bay that are associated with the Rainy River-Thunder Bay climatic region. The second physiographic area, the Hudson Bay Lowlands, is made up of the flat, boggy plains underlain by younger sedimentary rock bordering Hudson Bay and James Bay (Chapman and Thomas 1968).

The forests of northwestern Ontario are classified, based on vegetation and physiography, in the Boreal Forest Region except for area between Lake Superior and Lake of the Woods which is classified in the Quetico Forest Section of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). The Quetico Forest Section is associated with the Rainy River-Thunder Bay climatic region and the areas of lacustrine deposits in bedrock hollows (Chapman and Thomas 1968). The Boreal Forest Region in northwestern Ontario is comprised of four Forest Sections: (1) the Central Plateau, northeast of Lake Superior to the lowlands around James Bay; (2) the Superior, immediately north of Lake Superior corresponding to the Superior climatic region; (3) the Nipigon, the basin surrounding Lake Nipigon; and (4) the Upper English River, west of Lake Superior, This last Section is the transition between the Quetico Forest Section to the south and the boreal forest of the Central Plateau to the east and north (Rowe 1972).

In 1983, the OMNR and the Canadian Forestry Service initiated a Forest Ecosystem Classification (FEC) Project funded in part by the Canada Ontario Forest Development Agreement (COFRDA) (Sims *et al.* 1987). The goal of the project is to provide foresters and resource managers with a field based classification system for silvicultural planning in the North Central Region, an administrative region of the OMNR in northwestern Ontario. Since 1983, 1300 mature forest stands have been located and described in terms of vegetation, soil and site. Based on the information collected a system of field classification has been developed. The FEC system identified 38 vegetation types (eight of which are jack pine dominant or co-dominant) and 34 associated soil types. Eventually each vegetation type will have associated management options from which the forest manager can develop a harvesting and reforestation strategy.

Selection is probably the primary cause of variation in jack pine (Schoenike 1962). The climatic, ecological and physiographic diversity of the North Central Region would lead to complex patterns of variation in jack pine if selection for locally adapted genotypes were strong. The variation patterns are further attributed to post-glacial migration from one or more refugia (Critchfield 1985). Although a single refugium for jack pine in the Appalachian Highlands is generally supported (Wright 1964; Yeatman 1967; Wright 1968; Schoenike 1976; Critchfield 1984; Critchfield 1985), other evidence indicates that there may have been refugia in the western cordillera (Löve 1959; Ritchie 1969; Ritchie 1976; Ritchie and Yarranton 1978) and/or the central United States (Rudolph and Yeatman 1982; Critchfield 1984; Critchfield 1985). In addition, Skeates (1979) speculated that two separate migration routes contributed to, if not caused, the current patterns of variation in the Lake Superior area.

Hills (1952) established a system of site classification that was used in northwestern Ontario for decision making in forest management. Northwestern Ontario was classified into three major (4W, 3W and 2W) and two minor (2E and 3E) site regions (Hills 1960). In the North Central Region the initial tree improvement program established two breeding zones, based on Hills (1960) site regions. One of the breeding zones was particularly large, and local adaptation within the breeding zone could dilute the genetic gain. Consequently, five smaller breeding zones were established using management unit boundaries and patterns of climatic variation rather than anticipated variation in growth corresponding to environmental parameters. As information on population variation becomes available the breeding zones will be realigned if warranted (OMNR 1987b).

The objectives of this study were twofold. The first was to discern the patterns of phenotypic variation in cone and needle traits of jack pine in the North Central Region of Ontario. The second was to assess the level of correlation of the variation present with climatic, spatial and ecological (FEC) data. The results of this study should indicate if the patterns of morphological variation in natural stands are random or adaptive. Further, if the variation is adaptive, this study will indicate the most probable cause(s).

LITERATURE REVIEW

NOMENCLATURE AND TAXONOMIC RELATIONSHIPS

Jack pine is classified in the genus *Pinus*, subgenus *Pinus*, section *Pinus*, and subsection *Contortae* (Little and Critchfield 1969). There are three additional species in the subsection *Contortae*: *Pinus contorta* Dougl. ex Loud (lodgepole pine); *Pinus virginiana* Mill. (Virginia pine); and *Pinus clausa* Vasey ex Sarg. (sand pine). Jack pine and lodgepole pine are a "species pair" exhibiting evidence of successful mating in areas of sympatry (Rudolph and Yeatman 1982). Crosses between Virginia pine and sand pine have been successful and putative hybrids have been reported between jack pine and Virginia pine. Sand pine crosses with other pines that are not classified within its subsection and, therefore, may be more closely related to pine species outside the subsection *Contortae*. (Rudolph and Yeatman 1982).

Schantz-Hansen and Jensen (1952) concluded from a provenance test that geographic races of jack pine exist and research by Wright (1971) indicates that distinct jack pine races exist both in the Upper and Lower Peninsulas of Michigan (Wright 1971). However, other studies (Schoenike 1962; Schoenike 1976) conclude that there are no geographic races of jack pine. A variant (*Pinus banksiana* forma *procumbens*) with a low, bushy structure from the Atlantic coast (Mt. of the Islets, St. Urbain, Quebec; Cape Canso, Nova Scotia; Acadia National Park, Bar Harbor, Maine) has been reported (Rousseau 1938; Schantz-Hansen and Jensen 1952; Schoenike 1962; Schoenike 1976). In addition, a horticultural variety 'Annae' (*Pinus banksiana* var *annae* Schwerin) with yellow, variegated foliage was reported in Germany in 1908 (Schoenike 1962; Krüssmann 1985). Other variants, from natural populations and populations with a history of ionizing radiation, have been reported and include: dwarfs, varigated needle colour and abnormal branch characteristics (Rudolph and Yeatman 1982).

The ranges of jack pine and lodgepole pine overlap in central and northern Alberta (Peace River, Lesser Slave Lake and Pigeon Lake) and the southwest corner of the Northwest Territories (south Nahanni River) (Moss 1949; Scotter 1974) (Figure 1). In these areas, morphological, chemical and allozyme evidence has identified putative hybrids of jack pine and lodgepole pine (Mirov 1956, Critchfield 1957; Zavarin *et al.* 1969; Pollack and Dancik 1985). The hybrid swarms occupy those areas that are intermediate in climate, between the cool montane niche occupied by lodgepole pine and the warmer, dry continental environment to which jack pine is adapted (Yeatman and Teich 1969). The zone of recognizable hybrid populations is narrower than that of another species pair, *Abies balsamea* (L.) Mill (balsam fir) and *Abies lasiocarpa* (Hook.) Nutt. (alpine fir) (Critchfield 1984). This may be due to barriers to crossing between the two pines, such as timing of reproductive phenology or a high incidence of aborted pollen in hybrid individuals (Critchfield 1980).

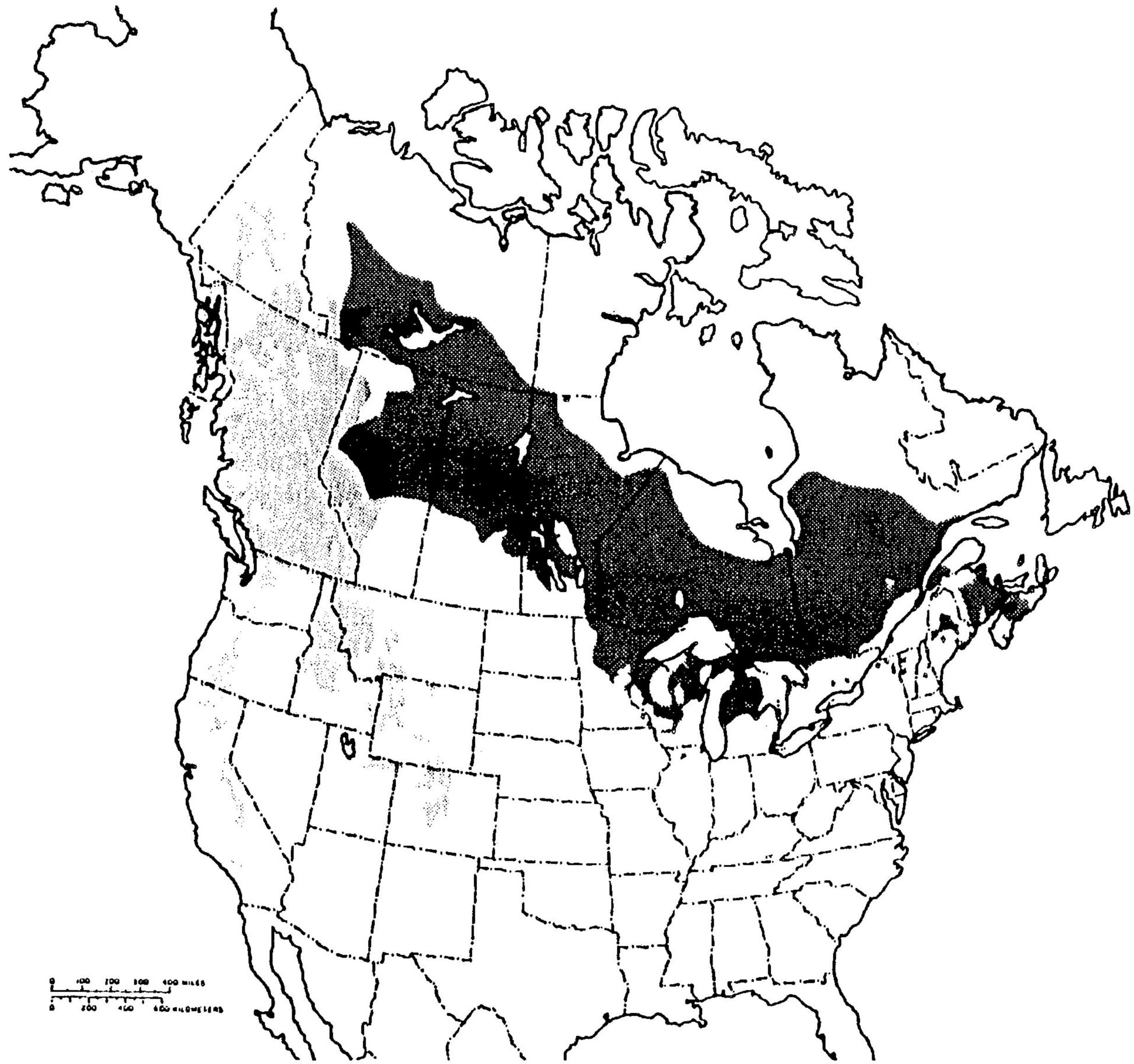


Figure 1. Distribution of *Pinus banksiana* and *Pinus contorta* (Little 1971)

In addition to the area of overlap, other studies (Lotan and Joyce 1970; Pauly and von Rudloff 1971; Forrest 1980) have shown evidence of the presence of jack pine type terpenes (α-pinene and β-pinene) in some individuals in lodgepole pine stands located some distance from the zone of sympatry but evidence that introgression (i.e. backcrosses with parental taxa) has taken place is limited (Wheeler and Guries 1987). Von Rudloff (1975) reported the presence of jack pine individuals which resembled lodgepole pine in monoterpene composition in Ontario and Saskatchewan but rejected the introgression hypothesis due to the large geographic distance to the nearest lodgepole pine population. However, Forrest (1987) speculated that the monoterpene patterns in lodgepole pine indicate a relatively long-term permeation of lodgepole pine populations by jack pine genes through hybridization and may possibly be a relict of the common ancestry of the two species. Critchfield (1985) noted that monoterpene α-phellandrene is a reliable indicator of lodgepole pine but that resins of jack pine have no such diagnostic content. A-pinene is present in both lodgepole pine and jack pine, and so even large increases in α-pinene are subject to interpretations other than introgression (Critchfield 1985).

Schoenike (1962, 1976) demonstrated that the western portion of the range of jack pine exhibits greater within stand variation for some morphological characters (i.e. cone angle). Cone angle was also emphasized as an indicator of jack pine influence in lodgepole pine populations by Critchfield (1957). However, the climate in western Canada differs from central and eastern Canada, and most of the variation in the study traits could conceivably be accounted for by the environment. Based on evaluation of morphological characters, introgression has played a minor role in the variation of jack pine but is evolutionarily significant in the zone of sympatry (Schoenike 1962).

In a range-wide study of phenotypic variation in jack pine, Beshir (1975) found that, within most locations studied, the species had homogeneous populations. However, populations in the prairies appear heterogeneous (Beshir 1975). Variation within individual populations may be a response to many factors one of which, but not the most probable, is introgression.

In a study incorporating morphological and allozyme data for lodgepole and jack pine and their hybrids, backcrossed individuals could not be identified (Wheeler and Guries 1987). However, based on the hybrid index generated by the allozyme data and the effect of glaciation upon the ecology of western Canada, Wheeler and Guries (1987) speculated that multiple, localized introgressive hybridization events have taken place in the lodgepole-jack pine complex in Alberta and the Yukon. Within the unglaciated portion of the Yukon Territory, lodgepole pine exhibits unusual gene frequencies at a number of loci that differentiate between lodgepole and jack pine (Wheeler and Guries 1982, 1987). In addition, lodgepole from this area and the Liard River, Northwest Territories, have a leaf oil pattern that is similar to lodgepole-jack pine hybrids and western jack pine. The lodgepole pine in this area may resemble the phylogenetic ancestor from which the modern species of lodgepole and jack pine evolved (von Rudloff and Nyland 1979). An alternative hypothesis is that the Yukon populations were affected by ancient hybridization between the taxa and have survived the most recent glaciation in a refugia in the Yukon (Wheeler and Guries 1982, 1987). There is limited support for either of these hypotheses. It is more probable that the sporadic and uncorrelated individuals that exhibit jack pine influence and are distributed from the Yukon to western Montana, are the result of previous contact during interglacials (Critchfield 1984).

RANGE AND ECOLOGY

Jack pine is the most widely distributed pine in Canada with a range extending from the east on Cape Breton Island, Nova Scotia, across Quebec, Ontario and the Prairie provinces to northern British Columbia and the Mackenzie River Valley in the Northwest Territories. The southern edge of the range extends into the states of Minnesota, Wisconsin, Michigan and Maine (Figure 1) (Critchfield and Little 1966 as modified by Rudloph and Yeatman 1982).

Local populations of jack pine can be found in northern Illinois, northwestern Indiana, northern New York, Vermont, New Hampshire and the central and southern Mackenzie Basin (Mirov 1967). The origin of some of the local populations in the northeastern United States is doubtful. Progeny from plantations established in the northeastern United States as early as 1847 and 1888 have formed local populations that may be misinterpreted as outliers from the natural range when in fact they are introduced (Baldwin 1979).

The geographic center of the range is in northern Ontario and southern Manitoba, north of Lake Superior and south of Hudson Bay. This general area between Lake Winnipeg and Lake Superior is also the area of best growth, form and abundance (Halliday and Brown 1943; Dallimore and Jackson 1966; Schoenike 1976). In addition, populations from the area north of Lake Superior and east of Lake Nipigon represent the norm for cone and needle characters. The greater the distance from this centre, the greater the deviation from average for needle and cone characters (Schoenike 1962).

The range of jack pine is characterized by warm to cool summers with mean temperatures of 13 degrees Celcius (°C) to 22°C, and cold winters with mean temperatures of -29°C to 4°C, low rainfall 57 centimetres (cm) to 89 cm and 80 to 120 frost free days (Fowells 1965; Cayford *et al.* 1967; Mirov 1967). Jack pine is generally found on level to rolling terrain of glacial outwash, fluvial or lacustrian origin and less commonly on eskers, sand dunes, rock outcrops and bald rock ridges (Fowells 1965). The soils are generally podzolic, ranging from fine sands to clays with best growth occurring on well drained loamy sand. Jack pine can occasionally be found on heavy soils or peat (Rudolf and Schoenike 1963; Cayford *et al.* 1967; Fowells 1965).

Jack pine, a pioneer species, usually has serotinous cones that open, allowing for seed dispersal, after a fire has moved through an area and exposed a seedbed of mineral soil. The fire-controlled ecology has created extensive, even aged stands of pure jack pine that characterize the species in the boreal forest. Cone serotiny in jack pine is a highly heritable trait that is apparently controlled by a one gene-two allele system at maturity (Teich 1970; Sittman and Tyson 1971). Cone serotiny in closely related lodgepole pine is not expressed until the trees are 30 to 50 years old (Perry and Lotan 1979). Observations indicate that cone serotiny in jack pine may not exist in the juvenile portion of its life-history (Schantz-Hansen and Jensen 1952).

Jack pine is generally succeeded by spruce (*Picea mariana* (Mill) B.S.P. or *Picea glauca* (Moench) Voss) or a spruce/balsam fir mix in Canada. In the northern Lake States jack pine stands are replaced by either red (*Pinus resinosa* Ait) or white pine (*Pinus strobus* L.) followed by northern oaks (*Quercus rubra* L. or *Quercus palustris* Muenchh.) or by an aspen (*Populus tremuloides* Michx. or *Populus grandidentata* Michx.)/birch (*Betula papyrifera* Marsh.) mix followed by a spruce/balsam fir mix which in turn is replaced by northern oaks Jack pine is a climax species only on the poorest, driest sites (Chrosciewicz 1963; Rudolf and Schoenike 1963; Fowells 1965; Cayford *et al.* 1967; Rowe 1972; Hosie 1979).

Jack pine also occurs in mixedwood stands and is most often associated with trembling aspen, white birch and black spruce and less often with white spruce in the Boreal Forest Region of northern Ontario. In the Great Lakes-St. Lawrence Forest Region, jack pine is commonly associated with aspen (trembling and largetooth) and white birch, and, less commonly, with red pine, black and white spruce, and red and northern pin oak. West of Lake Nipigon scattered red and white pine may be found in jack pine stands. (Chrosciewicz 1963; Rudolf and Schoenike 1963; Fowells 1965; Cayford *et al.* 1967; Rowe 1972; Hosie 1979).

In the North Central Region of Ontario, the FEC system recognizes 10 vegetation types that have a considerable jack pine component (Sims *et al.* 1987). Four are classified as mixedwood: hardwood (trembling aspen or white birch) with jack pine as the primary conifer and *Acer spicatum* Lamb. (mountain maple) and *Corylus cornuta* Marsh. (beaked hazel) in the shrub layer (V8); trembling aspen with jack pine as the primary conifer and *A. crispa* (Ait.) Pursh) (green alder) in the shrub layer (V9); jack pine dominant with trembling aspen, birch, and occasionally black spruce and balsam fir in the canopy with a shrub rich layer of beaked hazel and *Diervilla lonicera* Mill. (bush honeysuckle) (V17); jack pine dominant with black spruce common in the canopy, a minor hardwood component (trembling aspen or white birch) and generally shrub and herb poor (V18). There are six conifer types: pure, even-aged jack pine with abundant shrub cover of beaked hazel, green alder and, occasionally, mountain maple (V27); pure, even-aged jack pine with an understory of *Vaccinium angustifolium* Ait. (low sweet blueberry) and *Vaccinium myrtilloides* Michx. (velvet-leaf blueberry) (V28); jack pine with black spruce present in the canopy and an understory characterized by *Aralia nudicaulis* L. (wild sarsaparilla), bush honeysuckle or *Aster macrophyllus* L. (large-leaved aster) (V29); jack pine with black spruce in the canopy and an understory dominated by blueberry and *Ledum groenlandicum* Oeder (labrador tea) (V30); sparse black spruce and/or jack pine stands with exposed bedrock (V31); black spruce with jack pine in the canopy with the understory typically dominated by black spruce and balsam fir (V32). All the jack pine vegetation types are located in dry, nutritionally poor to dry-fresh, moderately rich sandy sites within the North Central Region (Sims *et al.* 1987).

BIOGEOGRAPHY

The pines are generally thought to have originated at the beginning of the Mesozoic era (ca. 225 million years before present (mybp)) (Mirov 1967). The earliest known pine fossils are from the Jurassic period (136 to 190 mybp). By the lower Cretaceous period (136 mybp) the pines had separated into two groups: haploxylon (soft pines) and diploxylon (hard pines) (Mirov and Stanley 1959). Although there is limited (lodgepole pine) or non-existent (jack pine) representation in the Tertiary period (ca. 5 to 10 mybp) fossil record, jack pine is thought to have originated in this period, following the cooling of the climate and crustal uplift in western North America (Yeatman 1967; Critchfield 1984). Kuc and Hills (1971) noted that fossil cones from late Miocene/early Pliocene epoch (ca. 2 to 25 mybp) conifer forests, found in the Beaufort Formation of northwest Banks Island, were assignable to the genus *Pinus* and exhibited a similarity to modern jack pine cones.

Alternatively, jack pine may have diverged during the Pleistocene epoch (ca. 2 million to 10,000 years before present (ybp)) from an ancestral taxon resembling lodgepole pine (Critchfield 1984). Analysis of allozyme data by Dancik and Yeh (1983) and Wheeler *et al.* (1983) indicated that there was relatively little genetic differentiation between lodgepole pine and jack pine. Based on this information, Dancik and Yeh (1983) concluded that the two species arose from a common progenitor as recently as the Pleistocene epoch.

The present patterns of variation in boreal tree species are principally determined by the extent of the Wisconsin glaciation (Halliday and Brown 1943). Approximately 95 percent of Canada was covered with late-Pleistocene ice, which removed the previous vegetative cover. The variation in current species is primarily a result of the interaction of the environment and the gene pool. Post-glacial migration and population dynamics also contribute to current patterns of variation (Ritchie 1987).

At the maximum extent of the late-Wisconsin glaciation (18000 ybp) the entire present-day jack pine range was covered with ice except for: the Cypress Hills, Saskatchewan; the adjacent areas of southern Saskatchewan and Alberta; large areas of the northern Yukon Territory and the adjacent Northwest Territories; lowland Alaska; south-central United States (Ritchie 1987); and, possibly, the 'driftless area' southwest of the Great Lakes in Wisconsin (Flint 1957). Most plant taxa, including jack pine, that are represented in the pollen and macrofossil history of continental Canada and the adjacent United States persisted in refugia in the mid-continental United States. Boreal species were present from Kansas to the Carolinas and intermittently as far south as Texas and Missouri, and spread north with the retreating ice, following the same general paths but with differing chronologies (Schoenike 1976; Ritchie 1987). The historical spread of jack pine is difficult to reconstruct because of the large volume of pollen that is widely dispersed and the number of species involved, lodgepole pine in the west and red and white pine in the east (Ritchie 1976).

Between 12,000 and 13,000 ybp, southern Newfoundland, southern Ontario and Alberta, and the northwestern portions of the Yukon and Northwest Territories became ice-free. These areas were occupied by a park-tundra ecosystem with stands of spruce, ash and elm. Between 11,100 and 10,200 ybp, a climatic deterioration resulted in an arctic-type environment during which the ash and elm disappeared (Ritchie 1987). At this time high values of pine pollen were restricted to the Appalachian Mountain area (Webb 1981). By 10,000 ybp, the ice-margin coincided with the southern limit of the Canadian Shield and several large proglacial lakes had formed along the edge of the continental ice-sheet in central Manitoba and Saskatchewan, Quebec, and Ontario. At this time a warming trend allowed the rapid migration of spruce, larch, birch followed by pine (red and/or jack) into the Quetico-Superior and adjacent areas. Red and/or jack pine became the dominant species in this area between 9,500 and 8,800 ybp with the transition from spruce to pine forest taking between 100 to 600 years to occur. The continental glacial ice retreated to Hudson Bay by 8,000 ybp but small ice-caps persisted in the western Cordillera and the Appalachian Highlands, and the Tyrrell Sea occupied a large area of northern Manitoba and Ontario. The warm dry period of the hypsithermal, between 8,000 and 4,000 ybp, created an influx of prairie taxa, especially at the southern edge of the boreal forest in the Lake States area, where pine pollen percentages dropped abruptly. It is not clear whether jack pine moved back into this area from stands that persisted through the hypsithermal period or from more northerly seed sources (Potzger 1953; Björck 1985; Critchfield 1985; Ritchie 1987).

There are several general areas of possible jack pine refugia; the Appalachian Highlands in northeastern Pennsylvania, the unglaciated areas of the western Cordillera and the Yukon Valley, the central United States and the exposed continental shelf (Yeatman 1967; Halliday and Brown 1943). Current literature supports the existence of a single large refugium in the Appalachian Highlands (Wright 1964; Yeatman 1967; Wright 1968; Schoenike 1976; Critchfield 1984; Critchfield 1985). There is limited evidence for refugia in the western cordillera (Löve 1959; Ritchie 1969; Ritchie 1976; Ritchie and Yarranton 1978) or in the central United States (Critchfield 1984). Halliday and Brown (1943) recognized the possibility of refugia on the exposed continental shelf, however, there is no evidence to corroborate this theory.

Although jack pine exhibits clinal variation across the range, a range-wide study of cone and needle morphology suggested that discontinuities in the Lake States/Lake Superior area may represent the presence of unique races (Schoenike 1976). Research to date indicates that: distinct jack pine races exist in both the Upper and Lower Peninsulas of Michigan (Wright 1971); there is a steep cline across northern Minnesota that separates genetically-different populations (Schoenike 1962; Zavarin *et al.* 1969; Schoenike 1976; Hyun 1979); and possible break in the continuous pattern of variation at, or in the vicinity of, Lake Nipigon in northwestern

Ontario (Yeatman 1966; Schoenike 1962, Schoenike1976; Skeates 1979).

Pollen evidence is inconclusive (Wright 1968), although more recent investigations indicate that jack pine pollen was present in northwestern Manitoba 7,500 ybp (Ritchie and Yarranton 1978), in the Lake Winnipeg area (central Manitoba) at 6,000 ybp (Ritchie and Hadden 1975) and in Riding Mountain (southeastern Manitoba) at 2,500 ybp (Ritchie 1969). Based on this information, Ritchie and Yarranton (1978) concluded that jack pine spread into the region west and north of Lake Winnipeg from western centers, following Löve (1959) but noted in an earlier paper that there was no other evidence to confirm or refute this idea (Ritchie 1976). Yeatman (1967) noted that dwarf mistletoe (*Arceuthobium americanum* Nutt. ex. Englem.) apparently transfers from lodgepole pine to jack pine and has only spread as far east as Lake Winnipeg, indicating that contact between the two pines was relatively recent. Zavarin *et al.* (1969) countered this theory by stating that interglacial or pre-Pleistocene contacts could have been responsible for the presence of dwarf mistletoe 500 miles east of the range of lodgepole pine. Jack pine is a relatively recent species in the MacKenzie Basin in the northwestern extreme of the range and there is evidence of only lodgepole pine south of the ice in the Rocky Mountains and eastern foothills in the northwestern United States (Rudolph and Yeatman 1982).

An alternative interpretation of the break in the pattern of variation in the Lake Superior area is the presence of a single or multiple refugia in the central United States (Critchfield 1984).

Pollen evidence indicates that there may or may not have been jack pine present in the late-glacial forest in the Great Lakes region (Critchfield 1985). Migration into the northern Lakes States was extremely rapid (Wright 1968) and jack pine appeared at locations in southern Ontario and in Minnesota within 1,000 years of each other, with little east-west progression in date of arrival (Critchfield 1984). In addition, migration north of the Great Lakes between 9,500 and 9,000 ybp, long after pine reached northern Minnesota and western Ontario, was not possible (Critchfield 1985) due to glacial ice that did not retreat from the Marathon area, on the shore of Lake Superior in northwestern Ontario, until 9,000 ybp (Saarnisto 1974). Migration south of the Great Lakes is not supported as most of the spruce forests were replaced by hardwood forests not pine forests (Kapp and Gooding 1964; Ogden 1966). In addition, pine pollen appears earlier in western Ohio than in the northern or northeastern portions of the State (Shane 1980) indicating that the pine in western Ohio did not arrive there via a migration route south of the Great Lakes. A central migration route from southern Ontario across lower Michigan and Lake Michigan to Wisconsin or alternatively north of Lake Erie was proposed by Davis (1981) and Wright (1971) respectively. However, the arrival of pine is the reverse of what would be predicted with either of these routes, arriving in southern Michigan and Indiana before Ontario (McAndrews 1970; Kerfoot 1974; Williams 1974; Karrow *et al.* 1975; Manny *et al.* 1978; Anderson 1982).

Jack pine may have been present in small numbers in the late-glacial forests of the Lake States and survived south of the ice in at least two refugia in the central United States, migrating into Michigan, Wisconsin and Minnesota as the ice retreated (Rudolph and Yeatman 1982; Critchfield 1984; Critchfield 1985). The proposed areas of refugia are the central Ohio River Valley (southwestern Ohio/central Kansas) and the 'driftless area' in southwestern Wisconsin (Critchfield 1985). The presence of isolated jack pine outside the range associated with the Mississippi River and its tributaries has led to the speculation that these are relics from refugia (Rudolph and Yeatman 1982). However, the outliers may actually be of a more recent origin, rather than glacial relics (Wright 1964).

From the Appalachian Highlands refugium, jack pine apparently migrated along a single route westerly following the moraines, outwashes and eskers left by the retreating ice and the shorelines and beaches created by the fluctuating glacial lakes (Yeatman 1967; Wright 1968). If the presence of refugia in the central United States is accepted, jack pine would have migrated north from these refugia in the 'driftless area' and other areas in the central United States and colonized lower Michigan and the Wisconsin/Minnesota area.

VARIATION

Genetic variation is caused by changes in gene and genotype frequencies as a result of the evolutionary forces of mutation, migration, selection, recombination and drift (Hartl 1981). Mutation is the ultimate source of variation and genetic recombination, the immediate source of variation (Stebbins 1950), is influenced by migration, the flow of genetic information into a population. Selection, the force by which variation is manipulated in a population, and drift, the random fixation of genetic information in a population (Hartl 1981) act upon the variation present producing either random or non-random patterns. The evolutionary forces are not autonomous; and so, seemingly random patterns of variation may be due to the complexity of the interaction. In addition to the complexity, the environment has two effects on variation. The first is the direct effect on the expression or plasticity of the phenotype. The second is the indirect effect of evolution of the genotype through adaptation (Callaham 1964; Gould and Johnston 1972).

Studies of geographic variation are complex due to the difficulty of evaluating genetic variation via the phenotype (Gould and Johnston 1972). A technique used to assess the two components of phenotypic variation, genetic and environmental, is the common garden test (Clausen, Keck and Hiesey 1940; Clausen, Keck and Hiesey 1948). However, one of the most desired aims of the study of variation is evaluation in natural habitats under natural conditions (Gould and Johnston 1972). A study of natural populations can define the level of variation in a population and estimate the amount of variation associated with the genotype by correlating characters with the environment (Schoenike 1962) in a biologically sound manner.

Virtually all characters will exhibit variation among populations; however, phenological traits are under strong genetic control and often show the strongest expression of variation across an environmental gradient. Physiological traits, such as disease resistance, historically show less correlation with the environment followed by morphological traits, biochemical and allozyme data.

Phenological

Range-wide studies of growth and development in juvenile and mature jack pine correlate variation to the geographic location of the seed source and the associated climate (Giertych and Farrar 1962; Yeatman 1966; Canavera 1975; Hyun 1979; Steiner 1979; Zavitkovski *et al.* 1981; Magnussen *et al.* 1985; Kremer and Larson 1983; Strong and Grigal 1987). A series of studies of geographic variation in seedling size and growth by Yeatman (1966) based on 19 to 50 provenances of seed collected from natural stands across the range showed strong provenance differences. Variation in seedling size was equally affected by growing degree days at the point of origin and seed weight (76 percent of the total variation), confirming an earlier study by Holst and Yeatman (1959). The relationship between growing degree days and seedling growth was significantly different east and west of 91°W longitude (the western tip of Lake Superior) and may reflect distinct relationships between longitude and growing degree days in the eastern and western section of the continent. A similar relationship was noticed by Skeates (1979) who was able to group seed sources from Ontario into 3 subpopulations (north-western, north-central and north-eastern) based on 10 year height growth. The division separating the north-western and north-central subpopulations extends from 93°W latitude in the north and crosses Lake Superior at 88°W in the south.

Evaluation of 90 provenances of 10 year-old jack pine in a range-wide test plantation in the University of Minnesota Experimental Forest, showed a large amount of variation between provenances based on 5 growth and 5 morphological traits (Hyun 1979). Seed source location had the greatest effect on height, diameter, crown width and bark thickness. All four traits were moderately negatively correlated with latitude. In addition, diameter and crown width was negatively correlated with longitude resulting in the smallest trees originating from the northwest portion of the range (Hyun 1979). Using D^2 values derived from the Mahalanobis distance function, Hyun (1979) derived 5 clusters. The two most distinct clusters cover (a) the Lake States area and (b) western Canada (and a small section of northern Quebec). The rest overlap, especially in the southern Ontario and Quebec area. An earlier evaluation of 23 seed sources in a range-wide test plantation by Schantz-Hansen and Jensen (1952) revealed similar findings to Hyun (1979). There were large differences in growth and form between provenances with the fastest growth occurring in trees that originated from southern seed sources leading the authors to conclude that there are races in jack pine (Schantz-Hansen and Jensen 1952). Variation in seedling growth from the Lake States showed no correlation with length of growing season or place of origin (Canavera 1975; Kremer and Larson 1983). However, there was a significant correlation of rate of growth with latitude

(Canavera 1975); and, by the second season of growth, there were recognizable differences between provenances in height increment (Kremer and Larson 1983). Evaluation of total biomass in 25 and 30 year old Lake States provenance tests showed significant differences among provenances that were negatively correlated with latitude (Zavitkovski *et al.* 1981; Strong and Grigal 1987). Similar results were found for 12 Ontario provenances, with latitude explaining 50 to 70 percent of the total variation in average tree size (Magnussen *et al.* 1985).

Bud-burst timing of jack pine evaluated in a range-wide provenance test represented by 92 populations, revealed that populations from the north burst bud earlier than their southern counterparts (Steiner 1979). The trends in jack pine closely paralleled temperature isotherms which are strongly influenced by Pacific air masses moving eastward. Populations from southern Michigan were significantly later in burst bud than populations from Wisconsin on the same latitude. The variation reflected the climate of the region where winter temperatures are lower in Wisconsin than all but the northern tip of southern Michigan.

Photoperiod was the major factor influencing seedling development of 19 to 50 provenances in a series of range-wide studies, whereas, temperature played a minor role in growth rate and contributed little to discrimination among provenances (Yeatman 1966). A study of nine provenances (Saskatchewan to New York) by Giertych and Farrar (1962) showed that northern provenances were more responsive to photoperiod in terms of seedling growth. The differential correlation of response to photoperiod supports the hypothesis put forth by Vaartaja (1959) that the more severe the climate, the more necessary adaptation is to photoperiod in order for the plant to survive drought and cold (Giertych and Farrar 1962).

Variation in rates of photosynthesis in 10 jack pine provenances (Maine to the Northwest Territory) did not vary (variation was minor or inconsistent) among provenances until September, after which there was provenance variation in the rate of decline in photosynthesis. Continental provenances had the highest rate of photosynthesis in October and November, and also exhibited the greatest total height. Maritime provenances also had a high photosynthetic rate but had lower growth possibly due to other growth-limiting factors for these provenances when grown in a continental climate (Petawawa Forest Experiment Station, Chalk River, Ontario) (Logan 1971).

Significant differences among seven Ontario provenances in above-ground dry matter coupled with a lack of variation in relative growth rate and net assimilation rate led Magnussen *et al.* (1986) to believe that provenance variation was attributable to allocation of shoot and root resources, not to differences in rate of photosynthesis, and that provenances will continue to maintain their relative performance in growth and yield to maturity.

Disease and Insect Resistance

Resistance of 29 provenances of jack pine from the natural range in the northern Lake States to *Hypodermella ampla* (J. Davis)

Dearn. (a fungus that causes jack pine needle cast) was studied in two test plantations eight years after outplanting. There were strong differences among provenances in susceptibility to the fungus and these differences were consistent between years and test locations, indicating that resistance was genetically controlled. The highest resistance was found in those provenances from the lower peninsula of Michigan and the lowest from northeastern Minnesota. However, no explanation for these results was offered (King and Nienstaedt 1965).

The mortality of jack pine in a local provenance trial of western Quebec sources due to *Ascocalyx abietina* (Lager.) Morelet (Scleroderris canker) showed differences among provenances. Those from the south were more susceptible to the canker. Again, no explanation for the differential infection was offered (Yeatman 1976).

Resistance to *Cronartiun comptoniae* Arth. (sweet fern rust), a rust on several two- and three-needled pine taxa in Canada and the United States (Sinclair et al. 1987), also shows strong differences among jack pine provenances in range-wide provenance test plantations (Hunt and Van Sickle 1984). Variation in infection is apparently related to the ranges of *Comptonia peregrina* (L.) Coult. (sweet fern) and *Myrica gale* L. (sweet gale), the telial hosts. Sweet gale is distributed throughout the range of jack pine, whereas sweet fern is generally found in the southeastern portion of the range, south of latitude 49°N. Isolated populations of sweet fern have been found in Thunder Bay district, adjacent to the Minnesota border (Soper and Heimburger 1982). Northern provenances, beyond the natural range of sweet fern, were much more susceptible to infection (Tauer 1978; Hunt and Van Sickle 1984). The high susceptibility of some of the southern provenances may reflect lowered local selection pressure for rust resistant genotypes due to absence of sweet fern or adverse environmental conditions for infection (Hunt and Van Sickle 1984).

Pissodes strobi (Peck) (white pine weevil) is most commonly found on white pine but will attack all pine and spruces (Rose and Linquist 1984). Incidence of infection by white pine weevil was assessed in a plantation of thirty seed sources from Minnesota, Michigan and Wisconsin at Chippewa National Forest, Minnesota. There were highly significant differences between seed sources and no seed source had significantly less damage than the local source. The reason for this phenomenon was unknown but was speculated to be due to coexistence of the trees and the weevil population. Establishment of the local seed source in another location may result in higher levels of infestation (Batzer 1961).

Morphological and Anatomical

Using cone and needle morphological traits, jack pine can be differentiated into a number of regional populations, although the pattern of variation is generally clinal and follows the main climatic gradient (Schoenike, 1962; Beshir 1975; Schoenike 1976). Schoenike (1962) conducted a range-wide study of variation in jack pine based on thirteen cone, eleven needle and seven mensuration characters. There were 90 populations sampled, located from the

Northwest Territories to New Brunswick and south into the Lake States and the eastern seaboard. All 31 traits showed highly significant differences among populations. Based on climatic data, Schoenike (1962) derived four regional populations: south-central, eastern, north-central and western. Thirty of the phenotypic traits exhibited a significant relationship with the regions. However, two-thirds of the traits did not have discontinuous variation (ecotypic) but rather represented intermediate or end-points along a continuous gradient. In this light, there is no validity for recognizing subpopulations in jack pine.

Further univariate analysis of the data confirmed that, for most traits, the pattern of variation in jack pine is continuous with a combination of clinal trends and complex regional patterns. The the regional patterns appear to be a result of the intersection of climatic gradients and the corresponding differential selection pressures. Complex patterns of variation could also result from different selection pressure in different portions of the range (i.e. precipitation in one location and temperature in another). It is also possible that variation is due to non-climatic environmental variables such as soil characters. The major cline in the pattern of jack pine variation has end-points in the western and southern Lake States portions of the range and is primarily temperature and latitudinal based. A minor cline extends from eastern to western Canada with the steepest portion located in the Lake Superior area (Schoenike 1976).

Multivariate analysis of the data (D^2 values generated from the Mahalanobis distance function) described a steep cline south from central Canada into the southern Lake States (Schoenike 1976). In contrast, the cline from the eastern to western edges of the range is less steep except at the end-points (Alberta and New Brunswick) where they rise sharply. Cluster analysis of the data based on D^2 values resulted in eight clusters: maritime; eastern interior; south-central; mid-central; north-central; western interior; northwest; and western border. However, each cluster was most similar to its neighbours, indicating the clinal nature of variation across the species range. Of interest is the area north of Lake Superior which appears to be located at the intersection of two clines (Schoenike 1976).

Beshir (1975) conducted a smaller (22 populations) range-wide study of morphological variation in jack pine cone and needle characters. The pattern of variation was clinal along a southeast to northwest gradient that followed the main climatic gradient. Jack pine appeared to form a single homogeneous group with the exception of the Prairie and peripheral populations. The Prairie populations were heterogeneous in contrast to the rest of the stands sampled. Beshir (1975) speculated that introgression with lodgepole pine may have been the cause.

Schoenike *et al.* (1959) examined cone traits of 23 seed sources located in the Cloquet provenance test at the University of Minnesota Experimental Forest. Although there was no statistical testing, the data indicated trends in variation of cone morphology among geographically distinct populations. In general, the frequency of closed cones increased with increasing latitude, paralleling the findings of Roe (1963). Curved cones with a small cone angle (the angle between the axis from cone tip to point of attachment and the branch) were generally associated with western sources. Eastern and Lake States sources had the straightest cones with the largest cone angle.

Jeffers (1972) evaluated cone morphology in 11 provenances (east coast to Alberta) and found similar trends. In addition, Jeffers (1972) recognized that cones from Wisconsin and Michigan had the straightest cones with the largest cone angle; cones from central Canada showed intermediate values for these traits; and cones from the west were the most curved with the most acute cone angle.

The pattern of variation in bark thickness in a range-wide provenance test of jack pine appears similar to the distribution of stands with primarily open or closed cones. In the southern and western Lake States most of the jack pine are thick-barked and show a propensity to the open cone condition. In contrast, individuals from the northern portion of the range have the thinnest bark and primarily closed cones (Schoenike *et al.* 1959; Schoenike and Brown 1963). Areas that show a predominance of the open cone condition generally have fewer and less intense fires than those areas with closed cones. In the southern and western Lake States jack pine is generally mixed with deciduous trees and, in contrast with the destructive crown fires associated with the pure coniferous forests of the boreal forest region, the fires in this region are usually light surface fires (Schoenike 1962). In areas with low intensity ground fires, thick bark would protect the individual while the open cones would provide a continual seed source. In areas where forest trees cannot survive the intense crown fires, thick bark would offer little protection and would drain valuable resources. The closed cones would only open under conditions of the extreme heat of an intense crown fire providing seed only when there was an exposed mineral soil seedbed.

Variation in other morphological and anatomical characteristics such as wood formation (Kennedy 1971), nuclear volume (Mergen and Thielges 1967), mineral content (Mergen and Worrall 1965) and free sugars, amino acids and soluble proteins (Durzan and Chalupa 1968) all show some relationship with the environment of the seed source.

The cessation of cambial activity appears to be under strong genetic control, while its initiation is less so (Kennedy 1971). As a result, xylem attributes showed a significant relationship with growing degrees days at the point of origin. As the number of growing degree days increased so did early- and late-wood ring width. In contrast, specific gravity decreased with increasing number of growing degree days (Kennedy 1971).

An evaluation of intraspecific variation in nuclear volume of seedlings grown from seed collected throughout the range showed an increase in nuclear volume with increasing latitude (Mergen and Thielges 1967). Correlations of increasing nuclear volume to increasing cold hardiness in other genera led Mergen and Thielges (1967) to speculate that the same relationship may exist in jack pine. Therefore, variation in nuclear volume is not random and may have adaptive significance.

Internal differences in the nitrogen, potassium phosphorus and ash content of jack pine seedlings grown under controlled environmental conditions from seed collected throughout the range were associated with seed source (Mergen and Worrall 1965). However, the variation could not be attributed to north-south or east-west trends because the western sources were also the most northerly sources.

Seed from 16 locations across the natural range of jack pine was assayed for free sugars, free and protein amino acids and soluble protein (Durzan and Chalupa 1968). Levels of these chemical components correlated well with the environment of seed source, in particular, length of growing season, difference in minutes of photoperiod between the longest and shortest day, precipitation and temperature

Biochemical

The genus *Pinus* is characterized by the presence of resin systems in the needles, cones and stem tissues (cortex, secondary phloem and secondary xylem). Many of the taxa within the genus can be identified by the monoterpene complexes in the turpentine (a fraction of wood resin) (Zavarin *et al.* 1969). The terpenes present in the leaves of many North American conifers are apparently under strict genetic control and are well suited to studies of geographic variation (von Rudloff 1975). The major components of the terpenes of jack pine are α-pinene and β-pinene (Zavarin *et al.* 1969).

Jack pine from the eastern portion of the range (southeastern Ontario to the maritimes) can be subdivided into two major and eight minor leaf terpene types. There was no obvious relationship between the terpene leaf types and their geographic location (Lapp and von Rudloff 1982), except that the minor clusters and outliers tended to occur at the southern and eastern edges of the study area. The variation in jack pine leaf terpenes does not appear to have a geographic origin. In addition, a few samples from western Canada were analyzed and appeared to fit into the cluster system established by the eastern Canada samples, indicating that the conclusions for eastern Canada would also hold true for the entire range (Lapp and von Rudloff 1982).

Allozyme

Variation in jack pine based on allozyme data is generally less than other conifer species (Cheliak *et al.* 1985). Mean heterozygosity (43.5 percent) and number of polymorphic loci (13.0 percent) (weighted by the number of loci) were calculated by Ross and Hawkins (1986) from a number of jack pine allozyme studies (Hamrick *et al.* 1981; Dancik and Yeh 1983; Cheliak et al 1985; Ross and Hawkins 1986). These values are much less than the summary values of 67.7 percent and 20.7 percent respectively for 20 conifer species reported by Hamrick *et al.* (1981). A significant proportion of the differences in genetic variation among plant species can be accounted for by life history and ecology. In general, species that occupy later successional stages, mesic habitats, have open cones and are located in the southern and western portions of North America exhibit more variation than those with alternate combinations (Hamrick *et al.* 1981). However, most of the species included in the Hamrick *et al.* study are of western origin and the boreal species that are included have limited sample locations.

The genetic structure of jack pine populations has been observed to be similar among widely and closely spaced populations (Dancik and Yeh 1983; Ross and Hawkins 1986). Dancik and Yeh (1983) speculated that long distance pollen flow produced the homogeneity among jack pine populations located between 100 km (kilometres) and 600 km apart However, in a study of populations located 10 km to 20 km apart Ross and Hawkins (1986) observed approximately the same level of homogeneity as Dancik and Yeh (1983) not greater, as expected. The effects of long distance transport of pollen are apparently negated by adaptation to different environments. This process maintains population integrity.

MATERIALS AND METHODS

COLLECTION SITES

The general location of the study area was selected using two criteria. The first was the break in the pattern of clinal variation of jack pine in the Lake Superior area (Yeatman 1966; Schoenike 1962; Schoenike 1976). The second was the boundaries of the FEC program, from which ecological data could be gleaned, in the OMNR's administrative area of the North Central Region. The FEC program is confined to that area of the North Central Region north of Lake Superior to the limit of commercial forestry at the Hudson Bay Lowlands, approximately 125 km north of Lake Nipigon (Sims 1986).

Between late May and early August, 1987, jack pine cone and needle material was collected from 64 sites (populations) in the study area located to the immediate east and west of Lake Nipigon in the North Central Region of Ontario (Figures 2 and 3). The locations of the sites and brief site descriptions are in Appendices 1 and 2.

The criteria for site selection were: jack pine dominance or co-dominance; accessibility by road; and, if possible, previous survey by the FEC program. Ten trees were selected at each site

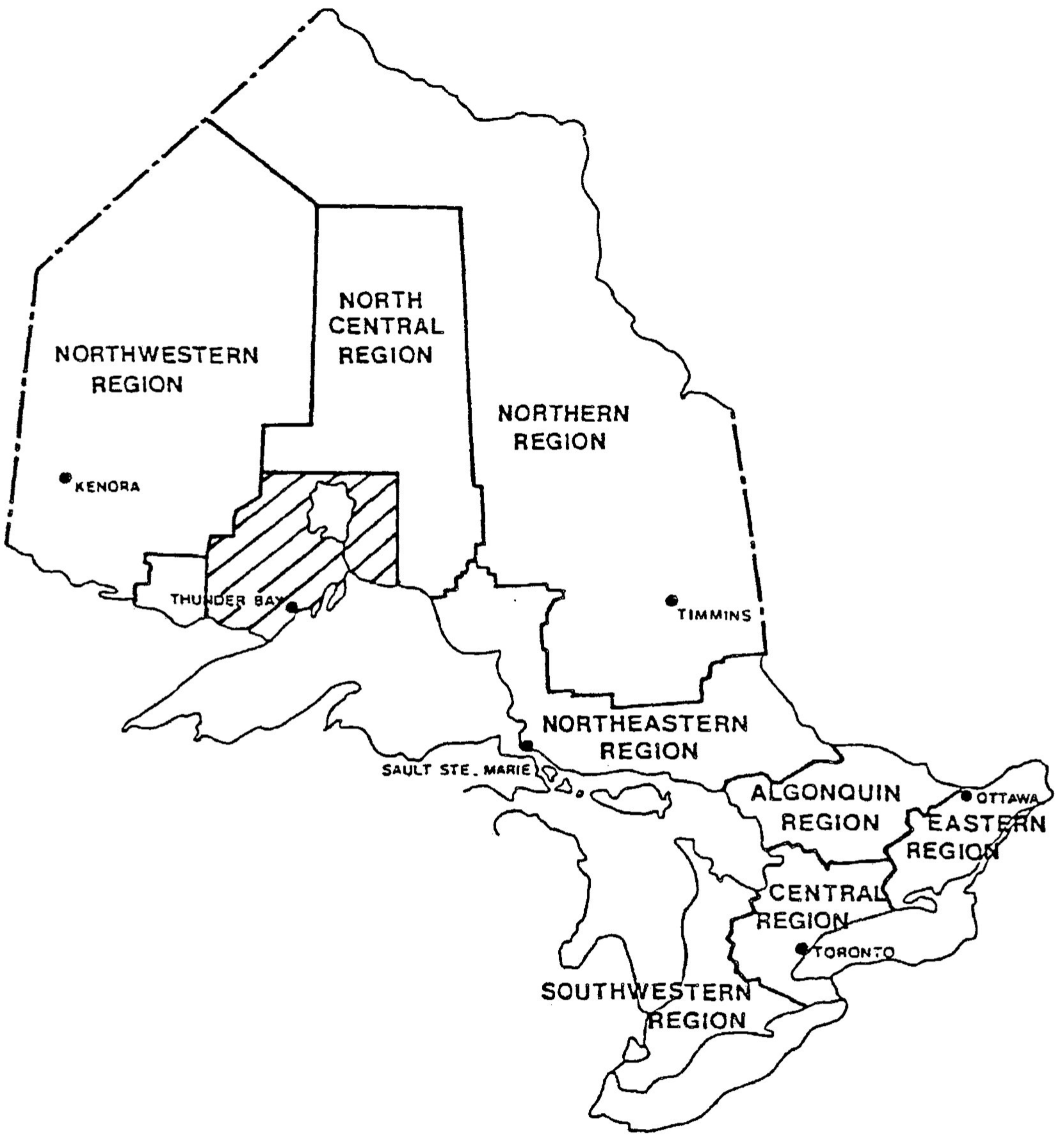


Figure 2. Location of the study area (shaded) with reference to the administrative regions of the Ontario Ministry of Natural Resources (OMNR 1987a).

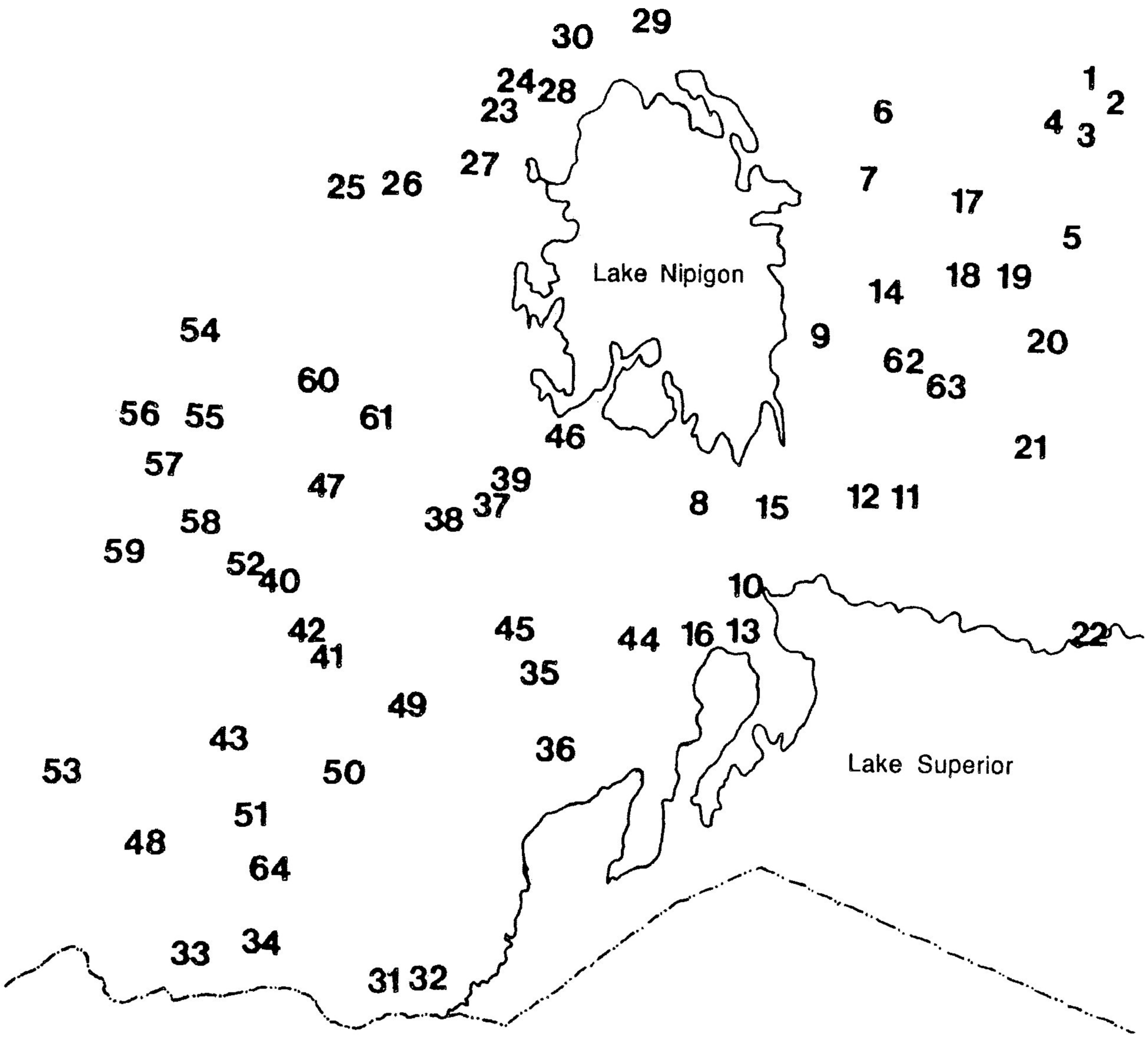


Figure 3. Locations of *Pinus banksiana* collection sites.

using the following criteria: cone bearing, with a minimum of 10 cones; disease and insect damage free and easily cut down to facilitate sample collection. The individuals were located at least 20 metres (m) apart to minimize familial relationships. Standard mensuration data, height (m); diameter at breast height, centimetres (cm); and age (years) at 0.5 m above the ground, were collected for each tree sampled (Table 1). If the site had already been surveyed by the FEC program, vegetation and soil information was made available by W. Towill, Mixedwood Specialist at the Technology Development Unit, O.M.N.R., Thunder Bay, Ontario. Otherwise, vegetation and soil type were surveyed using the methodology developed by the FEC program (Sims et al. 1987).

A minimum of ten current year (if possible) cones were collected from the mid-portion of the crown of each tree and stored in paper bags labelled by collection site and tree number. Ten needles per tree from the previous seasons' growth were plucked from cone bearing branches located in the mid-section of the crown, fixed in formalin-acetic-alcohol (FAA) (Berlyn and Miksche 1976) and stored in vials labelled by site and tree number. Prior to fixation the needles were first cut in half, the tip removed by a diagonal slice, and the lower half of the needle discarded to ensure that all ensuing needle cross-sections came from the same location on each needle. In addition, standard herbarium collections were made for each tree in the study, and these are located at the School of Forestry, Lakehead University, Thunder Bay, Ontario.

Table 1. Mean and range of height, diameter and age for each *Pinus banksiana* collection site.

Site	Height (m)		Diameter (cm)[a]		Age (yrs)[b]	
	Mean	Range	Mean	Range	Mean	Range
1	15.2	12.3 - 18.0	14.5	10.5 - 20.2	42	38 - 49
2	13.6	12.8 - 14.3	11.7	9.8 - 13.2	45	43 - 48
3	13.4	11.9 - 14.8	11.7	9.8 - 12.3	57	49 - 67
4	16.2	13.8 - 18.6	14.4	10.4 - 18.0	37	27 - 44
5	12.9	9.7 - 16.2	11.6	10.8 - 13.2	30	27 - 31
6	14.5	12.1 - 17.8	15.2	13.2 - 19.4	51	45 - 57
7	17.0	14.5 - 19.6	18.6	15.3 - 22.0	62	54 - 67
8	17.3	13.0 - 19.4	22.1	17.7 - 26.3	48	40 - 66
9	15.7	12.1 - 20.4	16.3	14.4 - 21.4	42	36 - 47
10	16.7	13.1 - 18.7	22.0	17.2 - 32.4	47	34 - 56
11	9.8	8.3 - 17.8	14.2	10.3 - 17.0	22	22 - 25
12	11.3	8.5 - 13.9	13.6	10.0 - 19.7	37	35 - 40
13	16.3	11.6 - 19.3	17.8	12.8 - 20.1	44	35 - 50
14	16.9	13.8 - 21.6	17.2	13.6 - 20.1	56	45 - 65
15	20.1	17.4 - 21.8	16.4	14.6 - 18.7	60	55 - 63
16	17.0	16.3 - 18.6	16.5	12.5 - 21.3	38	36 - 40
17	18.4	15.6 - 20.3	15.6	11.7 - 21.3	61	40 - 68
18	19.6	17.5 - 22.2	16.5	13.5 - 18.8	53	42 - 60
19	15.1	12.6 - 17.3	11.9	10.2 - 15.5	53	51 - 57
20	17.6	16.2 - 19.8	13.6	10.9 - 17.4	61	50 - 67
21	15.2	13.4 - 16.8	13.3	10.4 - 15.8	63	58 - 68
22	17.5	16.5 - 18.2	16.1	13.5 - 17.7	74	62 - 83
23	17.6	16.4 - 18.8	19.2	16.9 - 25.2	52	38 - 63
24	16.4	13.6 - 19.9	17.5	13.3 - 23.8	52	42 - 64
25	11.9	9.9 - 14.1	13.2	10.8 - 17.0	41	34 - 47
26	14.4	12.9 - 16.1	13.6	10.6 - 17.5	43	37 - 52
27	18.7	16.1 - 20.0	20.4	17.3 - 23.0	82	77 - 91
28	16.7	13.6 - 20.2	21.6	12.7 - 17.0	48	38 - 60
29	14.8	13.0 - 17.3	14.5	13.9 - 19.9	66	63 - 71
30	17.2	13.7 - 19.1	17.5	11.2 - 29.5	62	53 - 69
31	10.7	8.5 - 13.5	15.8	14.0 - 25.7	24	18 - 41
32	12.8	8.0 - 18.2	19.2	17.3 - 23.5	49	25 - 59

[a] diameter measured at 1.3 m

[b] age measured at 0.5 m above the ground

Table 1. (Continued).

Site	Height (m)		Diameter (cm)[a]		Age (yrs)[b]	
	Mean	Range	Mean	Range	Mean	Range
33	16.2	13.2 - 18.8	21.2	17.3 - 23.5	55	40 - 65
34	16.0	13.8 - 19.9	22.3	16.0 - 33.5	48	41 - 63
35	18.6	14.8 - 21.7	22.5	17.4 - 26.5	81	67 - 97
36	15.5	12.2 - 18.8	19.2	14.1 - 25.0	45	35 - 56
37	18.1	16.0 - 19.5	21.3	16.4 - 27.9	52	49 - 56
38	18.4	10.7 - 22.6	24.5	18.0 - 30.8	74	20 - 85
39	16.0	13.3 - 17.7	17.9	15.1 - 25.5	53	50 - 56
40	14.6	11.6 - 16.6	14.8	12.0 - 16.9	55	50 - 62
41	15.2	11.9 - 19.7	19.5	14.3 - 24.8	47	40 - 53
42	19.2	13.9 - 22.1	20.5	13.4 - 29.1	61	55 - 74
43	11.2	7.9 - 13.8	18.2	12.7 - 23.4	27	25 - 32
44	16.1	11.6 - 17.3	21.0	17.5 - 24.2	49	41 - 56
45	9.5	7.3 - 11.6	18.1	12.7 - 23.5	22	20 - 26
46	17.6	16.0 - 19.5	22.7	18.3 - 29.0	61	58 - 63
47	11.3	9.0 - 14.1	19.7	16.2 - 28.0	23	20 - 31
48	18.5	12.5 - 21.9	26.9	18.1 - 34.6	65	60 - 70
49	13.9	11.8 - 16.4	18.4	21.4 - 25.8	63	57 - 69
50	13.6	12.2 - 15.5	19.3	14.3 - 28.2	38	26 - 44
51	16.7	13.3 - 19.2	21.6	17.1 - 27.9	55	50 - 61
52	16.5	11.5 - 19.2	21.1	17.8 - 23.0	71	63 - 78
53	15.6	12.1 - 17.8	19.1	14.0 - 25.0	48	41 - 54
54	15.3	13.2 - 17.9	16.6	13.3 - 20.0	67	61 - 73
55	18.3	15.5 - 20.5	21.0	16.5 - 26.3	58	54 - 62
56	17.5	15.9 - 19.7	19.8	16.2 - 24.0	67	63 - 71
57	15.9	12.8 - 22.0	18.2	12.3 - 25.5	65	59 - 72
58	17.0	15.4 - 19.2	21.6	18.6 - 27.2	47	45 - 50
59	13.3	10.3 - 17.4	20.2	14.3 - 26.8	35	22 - 44
60	19.2	17.6 - 20.9	19.5	15.5 - 23.4	105	96 - 115
61	14.2	11.8 - 16.6	14.4	10.8 - 18.8	79	72 - 85
62	21.2	19.3 - 23.4	26.1	21.1 - 30.9	107	90 - 118
63	21.5	19.2 - 25.5	25.5	17.5 - 35.9	81	67 - 94
64	14.9	12.2 - 17.4	17.1	14.9 - 22.4	54	50 - 58

[a] diameter measured at 1.3 m

[b] age measured at 0.5 m above the ground

LABORATORY PROCEDURES

CONES

Five cones were selected without bias from the sample from each tree. Cone length (millimeters (mm)), cone width (mm), cone depth (mm), apophysis length (mm), apophysis width (mm), distance from the umbo to the cone scale tip (mm) were measured using metric calipers on unopened cones (Figure 4). In addition, cone volume (milligrams (mg)), measured by water displacement, and cone weight (mg) were also assessed on closed cones.

A single cone scale was selected for all measurements. It was located on the top of the cone corresponding to the mid-ordinate point. If there were two scales at this point the one closer to the woody base of the cone was selected. Cone width and cone depth (perpendicular to the curve) were measured at the point halfway between the mid-ordinate point and the cone base.

An estimate of cone curvature (percent) using closed cones was made following Schoenike (1962, 1976). The cones were oriented with the woody base to the right and the curve of the cone (assuming that the curve made up a portion of the circumference of a circle) was drawn on the cone surface. The point at the top of the arc was designated the mid-ordinate and from this point to the intersection of a line between the tip and base of the cone (cone length) was the mid-ordinate distance (Figure 4). A simple trigonometric ratio calculation was made to estimate percent curvature (Appendix 3).

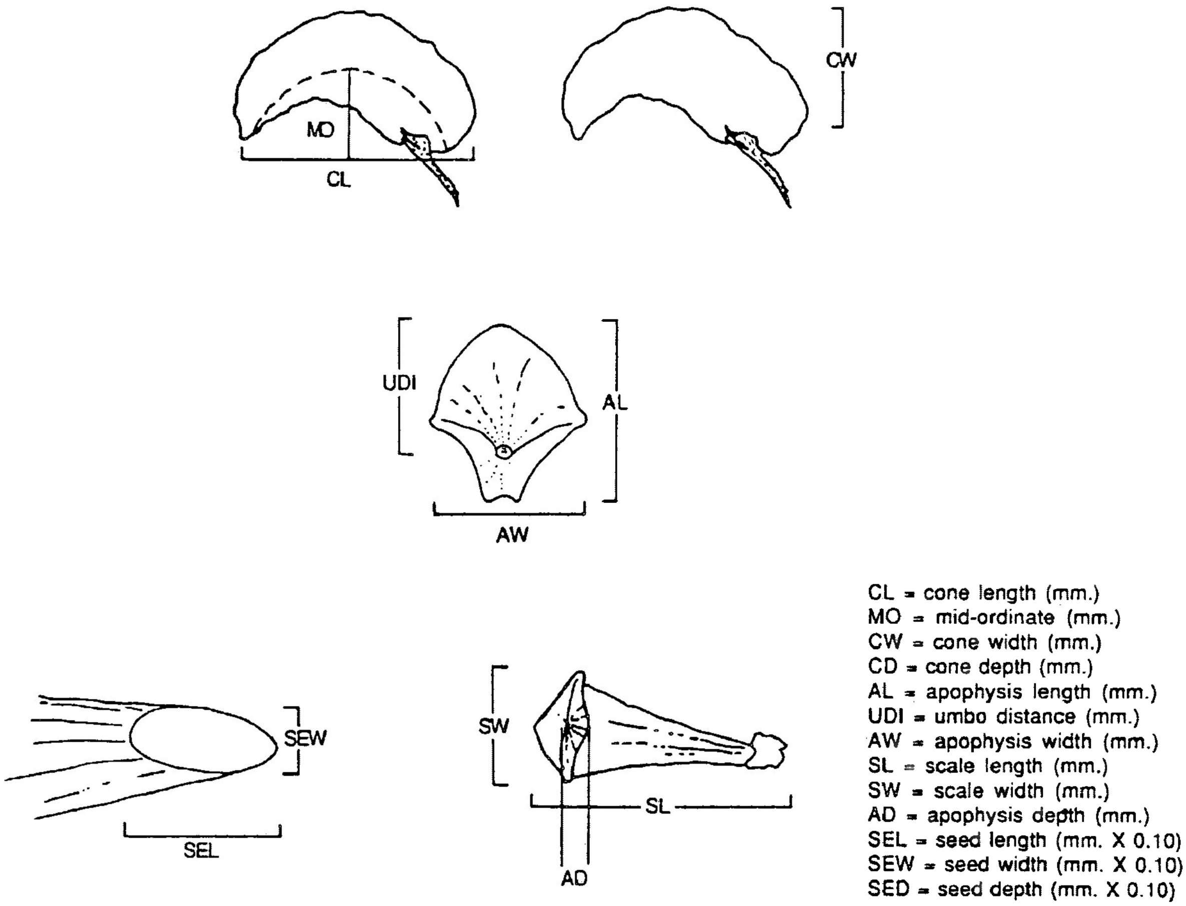


Figure 4. *Pinus banksiana* cone characters.

The cones were then placed in an oven at 65°C for $2^1/_2$ hours to facilitate opening. The seeds were extracted from the opened cones using tweezers, and counted. One seed was selected without bias and the width, depth and length measured using a calibrated eyepiece on a dissecting microscope (Figure 4). An additional nine seeds were selected, again without bias, and all ten seeds weighed. If there were less than ten seeds the seed weight of all the seeds was measured, divided by the number of seeds and then multiplied by ten.

The same cone scale selected for the closed cone measurements was detached from the cone axis, and scale length, scale width (measured at the point on the scale where the top of the seed wing is located), and apophysis depth were measured using metric calipers (Figure 4). Number of scales on the cone was also recorded. All the data were entered on tally sheets and then on the MicroVAX II™ computer facility at Lakehead University, Thunder Bay, Ontario.

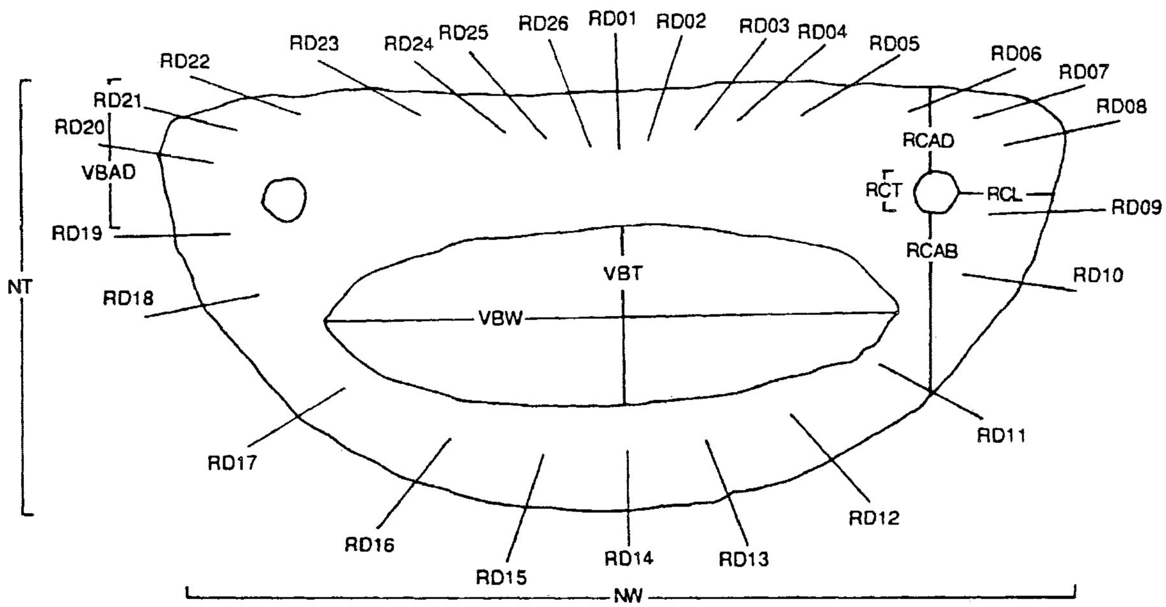
NEEDLES

Needle traits, except needle length, were determined from permanently mounted cross sections. First, the ten needles were processed through a tertiary butyl alcohol series (Johansen 1940) and the tissues permeated with paraffin, after the removal of FAA by two, 24 hour soakings in 70% ethanol. Then five of the ten needles were selected without bias, embedded in paraffin blocks, sectioned (7 µm) and then permanently mounted on gelatin-coated slides (Berlyn and Miksche 1976). Before sectioning, the paraffin blocks were trimmed to expose the needle cross section and soaked in water, at room temperature, for 2 hours. This process softened the needle tissue and minimized tearing in the resulting sections (A. Macdonald 1987 pers. comm.). The slides were stained with safranin O (Johansen 1940) and Fast Green FCF (Gray 1964). The needle cross-sections were measured using an Apple IIe™ computer attached to a Houston Hipad Digitizer™, with a light microscope and drawing arm.

A BASIC program, developed by W.H. Parker, created two files of needle cross-sectional measurements. The first defined the size of the needle, vascular bundle, including transfusion tissue and endodermis, and resin canal(s) via 13 conventional measurements and the second defined the shape of the needle via 26 radial distance measures from a fixed reference point (Figure 5). In addition, needle length for each individual was estimated by measuring five needles, selected without bias, from the herbarium samples. The data were stored on floppy diskettes and transferred to the MicroVAX II™ using VersaTerm-PRO™ and Kermit™ via a Macintosh™ computer.

SPATIAL, ECOLOGICAL AND CLIMATIC DATA BASE

Each site was assigned an FEC vegetation and soil code derived from the data collected when the site was sampled or from the FEC data base made available by W. Towill (Table 2). The FEC vegetation and soil types are classified by dichotomous keys (Sims



NL = needle length (mm.)
NW = needle width (mm.X 0.10)
NT = needle thickness (mm.X 0.10)
VBT = vascular bundle thickness (mm.X 0.10)
VBAD = vascular bundle adaxial distance (mm.X 0.10)
RCT = resin canal depth (right and left) (mm.X 0.10)
RCAD = resin canal adaxial distance (right and left) (mm.X 0.10)
RCL = resin canal distance to needle surface (right and left) (mm.X 0.10)
RCAB = left resin canal abaxial distance (right and left) (mm.X 0.10)
VBW = vascular bundle width (mm.X 0.10)
RD01 to RD26 = radial distances (mm.X 0.10)

Figure 5. *Pinus banksiana* needle characters.

Table 2. Latitude, longitude, elevation, FEC vegetation type and FEC soil type for each *Pinus banksiana* collection site (see Appendices 1 and 2 for location descriptions).

SITE NO.	LAT[a].	LONG.	ELEV.(m).	FEC VEGETATION TYPE		FEC SOIL TYPE	
1	50°12'	86°52'	1050	V30	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
2	50°07'	86°47'	1080	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
3	50°03'	86°54'	1150	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
4	50°05'	87°01'	1100	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry coarse sandy
5	49°48'	87°00'	1150	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry coarse sandy
6	50°09'	87°39'	1050	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
7	49°59'	87°44'	1050	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
8	49°11'	88°25'	950	V28	Pj - Blueberry - Feathermoss	S2	Fresh fine sandy
9	49°37'	87°57'	1050	V27	Pj - Shrub Rich	S3	Fresh coarse loamy
10	49°01'	88°20'	950	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry coarse sandy
11	49°12'	87°43'	1500	V31	Sb/Pj - Blueberry - Lichen	SS1	Discontinuous organic mat on rock
12	49°13'	87°52'	1400	V31	Sb/Pj - Blueberry - Lichen	SS1	Discontinuous organic mat on rock
13	48°54'	88°21'	650	V27	Pj - Shrub Rich	S1	Dry coarse sandy
14	49°43'	87°44'	1150	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
15	49°12'	88°13'	800	V28	Pj - Blueberry - Feathermoss	S1	Dry very coarse sandy
16	48°54'	88°31'	900	V27	Pj - Shrub Rich	S1	Dry coarse sandy
17	49°54'	87°24'	1100	V29	Pj (Sb) - Feathermoss	S3	Fresh coarse loamy
18	49°43'	87°27'	1100	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry coarse sandy
19	49°43'	87°16'	1100	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry coarse sandy
20	49°33'	87°10'	1250	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
21	49°17'	87°13'	1300	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
22	48°47'	87°06'	900	V28	Pj - Blueberry - Feathermoss	S2	Fresh fine sandy
23	50°16'	89°03'	1200	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
24	50°18'	89°01'	1150	V29	Pj (Sb) - Feathermoss	S4	Fresh silt loamy fine loamy
25	50°04'	89°42'	1450	V31	Sb/Pj - Blueberry - Lichen	SS1	Discontinuous organic mat on rock
26	50°02'	89°29'	1350	V29	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
27	50°07'	89°13'	1100	V29	Pj (Sb) - Feathermoss	SS3	Very to mod. shallow soil on rock
28	50°17'	88°53'	1050	V31	Sb/Pj - Blueberry - Lichen	S2	Fresh fine sandy
29	50°26'	88°32'	1050	V29	Pj (Sb) - Feathermoss	S2	Fresh fine sandy
30	50°27'	88°42'	1050	V29	Pj (Sb) - Feathermoss	S4	Fresh silt-loamy fine loam
31	48°05'	89°47'	1100	V28	Pj - Blueberry - Feathermoss	S5	Fresh clayey
32	48°10'	89°37'	1250	V31	Sb/Pj - Blueberry - Lichen	SS2	Extremely shallow soil on bedrock

[a] LAT = latitude; LONG = longitude; ELEV = elevation (m).

Table 2. (Continued).

SITE NO.	LAT.	LONG.	ELEV.(m).	FEC VEGETATION TYPE		FEC SOIL TYPE	
33	48°14'	90°30'	1700	V28	Pj - Blueberry - Feathermoss	SS3	Very to mod. shallow soil on rock
34	48°14'	90°11'	1600	V27	Pj - Shrub Rich	SS6	Moderately deep coarse loamy
35	48°50'	89°06'	1550	V30	Pj (Sb) - Feathermoss	SS6	Moderately deep coarse loamy
36	48°39'	89°04'	1500	V18	Pj (Sb) - Hardwood - Feathermoss	S3	Fresh coarse loamy
37	49°17'	89°14'	1350	V27	Pj - Shrub Rich	SS5	Moderately deep sandy
38	49°15'	89°25'	1450	V30	Pj (Sb) - Feathermoss	SS2	Extremely shallow soil on bedrock
39	49°20'	89°09'	1150	V30	Pj (Sb) - Feathermoss	S4	Fresh fine loamy
40	49°07'	90°03'	1550	V30	Pj (Sb) - Feathermoss	S2	Fresh fine sandy
41	48°55'	89°53'	1600	V30	Pj (Sb) - Feathermoss	S4	Fresh silt-loamy fine loam
42	48°59'	89°57'	1450	V17	Pj - Hardwood - Shrub Rich	S3	Fresh coarse loamy
43	48°44'	90°15'	1600	V18	Pj (Sb) - Hardwood - Feathermoss	S1	Dry very coarse sand
44	48°54'	88°44'	1100	V17	Pj - Hardwood - Shrub Rich	SS6	Moderately deep coarse loamy
45	48°57'	89°11'	1500	V31	Sb/Pj - Blueberry - Lichen	SS1	Discontinuous organic mat on rock
46	49°26'	88°56'	750	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
47	49°21'	89°50'	1500	V24	Sw - Other Conifer	S3	Fresh coarse loamy
48	48°30'	90°36'	1600	V29	Pj (Sb) - Wild Sarsaparilla	SS6	Moderately deep coarse loamy
49	48°47'	89°36'	1500	V31	Sb/Pj - Blueberry - Lichen	SS6	Moderately deep coarse loamy
50	48°38'	89°51'	1450	V30	Pj (Sb) - Feathermoss	S1	Dry very coarse sand
51	48°35'	90°09'	1500	V29	Pj (Sb) - Wild Sarsaparilla	SS6	Moderately deep coarse loamy
52	49°18'	90°11'	1600	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
53	48°41'	90°54'	1600	V29	Pj (Sb) - Wild Sarsaparilla	SS6	Moderately deep coarse loamy
54	49°46'	90°17'	1450	V18	Pj (Sb) - Hardwood - Feathermoss	SS7	Moderately deep silty - fine loamy
55	49°33'	90°17'	1550	V29	Pj (Sb) - Wild Sarsaparilla	S3	Fresh coarse loamy
56	49°34'	90°32'	1600	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
57	49°26'	90°26'	1550	V30	Pj (Sb) - Feathermoss	S1	Dry coarse sandy
58	49°17'	90°20'	1550	V27	Pj - Shrub Rich	SS6	Moderately deep coarse loamy
59	49°13'	90°37'	1550	V28	Pj - Blueberry - Feathermoss	S1	Dry coarse sandy
60	49°37'	89°51'	1450	V28	Pj - Blueberry - Feathermoss	S2	Fresh fine sandy
61	49°31'	89°38'	1500	V28	Pj - Blueberry - Feathermoss	S2	Fresh fine sandy
62	49°32'	87°40'	1350	V30	Pj (Sb) - Feathermoss	S1	Dry very coarse sand
63	49°28'	87°32'	1450	V30	Pj (Sb) - Feathermoss	S1	Dry very coarse sand
64	48°25'	90°08'	1450	V31	Sb/Pj - Blueberry - Lichen	SS1	Discontinuous organic mat on rock

[a] LAT = latitude; LONG = longitude; ELEV = elevation (m).

et al. 1987). Corresponding to each couplet of the dichotomous key, where the choice would lead to one or more of the vegetation or soil types present in the study, an effort was made to quantify the character state of the diagnostic variable. In this manner eight vegetation variables and five soil variables were defined: percent cover conifer; percent cover hardwood; percent cover jack pine; percent cover black spruce; percent cover white spruce; percent cover lichen; percent cover feathermoss; soil depth; sand texture, average grain size; percent sand, grain size between 0.05 to 2.00 mm; percent silt, grain size between 0.002 and 0.05 mm; and percent clay, grain size less than 0.002 mm. Sand texture was estimated by using the average sand grain size for the sand texture designated in the field. Percent sand, silt and clay was designated by using the average values from a soil textural triangle (USDA 1951) for each soil type designated in the field. The information was entered on the MicroVAX II™ (Table 3).

Climatic data from 27 Canadian (Environment Canada 1982a; Environment Canada 1982b) and 10 American (Gale Research Company 1985a; Gale Research Company 1985b) weather stations within and immediately adjacent to the study area were obtained (Appendices 4 and 5). The climatic information consisted of mean value per month for each of 12 variables resulting from data collected between 1950 and 1980 (Canada) and 1951 and 1980 (United States): maximum June temperature; minimum January temperature; mean daily temperature; extreme minimum temperature; extreme maximum temperature; total precipitation; precipitation from snow; heating degree days; growing degree days;

Table 3. Ecological records for each *Pinus banksiana* collection site.

SITE NO.	SODP[a]	SATX	PERS	PERC	PERSI	PERCO	PERHW	PERPJ	PERSB	PERSW	PERLI	PERBD	PERF
1	100	750	91	4	5	40	0	40	0	0	1	0	68
2	100	750	91	4	5	60	0	60	0	0	1	0	83
3	100	1500	91	4	5	60	0	60	0	0	1	0	86
4	100	375	91	4	5	60	10	60	0	0	N/A	N/A	N/A
5	100	375	91	4	5	56	0	56	0	0	N/A	N/A	N/A
6	100	375	91	4	5	40	0	40	0	0	1	0	90
7	100	375	91	4	5	60	0	60	0	0	0	0	75
8	100	175	91	4	5	30	0	30	0	0	0	0	78
9	100	75	60	5	35	60	0	60	0	0	0	0	38
10	100	750	91	4	5	50	0	50	0	0	0	0	56
11	15	N/A	91	4	5	15	0	15	0	0	30	50	0
12	N/A	N/A	N/A	N/A	N/A	40	0	40	0	0	40	50	10
13	100	375	91	4	5	70	0	70	0	0	0	0	20
14	100	750	91	4	5	70	0	70	0	0	0	0	86
15	100	1500	91	4	5	55	0	40	0	15	0	0	60
16	100	375	91	4	5	80	0	80	0	0	5	0	1
17	100	N/A	82	6	12	70	0	70	0	0	0	0	88
18	100	1500	91	4	5	40	0	40	0	0	0	0	1
19	100	750	91	4	5	5	2	5	0	0	1	0	80
20	100	750	91	4	5	50	0	50	0	0	0	0	91
21	100	1500	91	4	5	65	0	50	15	0	1	0	86
22	100	175	91	4	5	32	0	32	0	0	0	0	93
23	100	750	91	4	5	19	0	19	0	0	1	0	87
24	100	375	91	4	5	60	0	60	0	0	0	0	80
25	20	N/A	N/A	N/A	N/A	40	0	40	0	0	60	10	25
26	100	375	91	4	5	70	0	70	0	0	1	0	85
27	20	N/A	N/A	N/A	N/A	N/A	0	N/A	0	0	0	0	85
28	100	75	91	4	5	70	0	70	0	0	85	0	1
29	100	175	91	4	5	45	0	45	0	0	5	0	85
30	100	N/A	33	34	33	60	0	60	0	0	10	0	85
31	100	N/A	18	65	17	30	0	30	0	0	1	0	90
32	3	N/A	N/A	N/A	N/A	4	0	4	0	0	83	10	0

[a] SODP = soil depth (cm); SATX = sand texture (mm); PERS = percent sand; PERC = percent clay; PERSI = percent silt; PERCO = percent conifer; PERHW = percent hardwood; PERPJ = percent jack pine; PERSB = percent black spruce; PERSW = percent white spruce; PERLI = percent lichen; PERBD = percent bedrock; PERF = percent feather moss.

Table 3. (Continued).

SITE NO.	SODP	SATX	PERS	PERC	PERSI	PERCO	PERHW	PERPJ	PERSB	PERSW	PERLI	PERBD	PERF
33	9	N/A	N/A	N/A	N/A	27	0	27	0	0	3	0	68
34	77	175	60	5	35	70	0	70	0	0	1	0	3
35	40	175	60	5	35	25	0	15	10	0	1	0	96
36	100	750	82	6	12	35	0	35	0	0	0	0	80
37	90	175	91	4	5	75	0	60	0	15	0	0	35
38	3	N/A	N/A	N/A	N/A	30	0	30	0	0	1	0	70
39	100	N/A	10	34	56	35	0	35	0	0	0	0	70
40	100	75	91	4	5	40	0	40	0	0	1	0	85
41	100	N/A	33	34	33	70	0	55	15	0	1	0	65
42	100	750	82	6	12	40	0	40	0	0	0	0	5
43	100	1500	91	4	5	45	0	45	0	0	1	0	55
44	70	N/A	82	6	12	70	0	70	0	0	1	0	15
45	10	N/A	N/A	N/A	N/A	25	0	25	0	0	0	20	0
46	100	750	91	4	5	30	0	30	0	0	0	0	75
47	100	N/A	82	6	12	50	0	15	0	35	0	0	55
48	35	N/A	N/A	N/A	N/A	40	0	40	0	0	1	40	10
49	45	N/A	67	15	18	40	0	40	0	0	65	10	20
50	75	1500	91	4	5	60	0	60	0	0	1	0	55
51	65	N/A	82	6	12	65	0	65	0	0	0	0	40
52	100	375	91	4	5	75	0	75	0	0	1	0	85
53	65	N/A	42	17	41	65	0	40	25	0	0	0	37
54	30	N/A	N/A	N/A	N/A	70	0	40	30	0	1	0	60
55	100	75	60	5	35	75	0	75	0	0	0	0	5
56	100	1500	91	4	5	75	0	75	0	0	1	0	80
57	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
58	25	N/A	N/A	N/A	N/A	75	0	75	0	0	0	0	52
59	100	375	91	4	5	80	0	80	0	0	1	0	72
60	100	175	91	4	5	N/A	0	N/A	N/A	N/A	0	N/A	N/A
61	100	175	91	4	5	60	0	60	0	0	0	0	84
62	10	1500	91	4	5	60	0	60	0	0	0	0	78
63	10	1500	91	4	5	70	0	70	0	0	0	0	80
64	20	N/A	N/A	N/A	N/A	70	0	70	0	0	1	0	25

[a] SODP = soil depth (cm); SATX = sand texture (mm); PERS = percent sand; PERC = percent clay; PERSI = percent silt; PERCO = percent conifer; PERHW = percent hardwood; PERPJ = percent jack pine; PERSB = percent black spruce; PERSW = percent white spruce; PERLI = percent lichen; PERBD = percent bedrock; PERF = percent feather moss.

frost free days; date of last spring frost; and date of first fall frost. Degree days are a cumulative measure of the departure from a given base temperature and are calculated by subtracting the average temperature from a base temperature every day over a given period. The resulting values, positive and negative, are systematically accumulated. The base temperature for heating degree days is 18°C and for growing degree days is 5°C (Environment Canada 1982a).

The climatic data were entered on ARC/INFO (Environmental Systems Research Institute 1987), a geographic information system (GIS) used to manipulate geographic data. Using the TIN ("triangulated irregular network") subpackage of ARC/INFO a three dimensional trend surface was generated for each of the climatic variables. In this manner, a climatic record was interpolated for each of the 64 sites in the study (Parker, pers. comm. 1988) which was then entered on the MicroVAX II™. Each climatic record consisted of a unique value for the 12 climatic variables based on the variation patterns of temperature, precipitation and frost across northwestern Ontario (Table 4).

Spatial information (latitude, longitude and elevation) was obtained for each population from 1:50,000 scale topographic maps (The National Topographic System, Series A751 (5th. ed.)) made available by the Geography Department Map Library at Lakehead University, Thunder Bay, Ontario (Table 2).

Table 4. Interpolated climatic records for each *Pinus banksiana* collection site.

SITE	JUMAX[a]	JAMIN	MNDLY	EXMAX	EXMIN	PCIPSN	PCIPTL	DDH	DDG	FFDYS	FFS	FFA
1	22.9	-26.0	-0.6	35.1	-46.9	290.0	807.8	6819.1	1167.6	74.9	166.0	240.9
2	22.9	-26.0	-0.6	34.9	-46.8	291.4	809.3	6820.0	1166.4	74.4	166.2	240.6
3	23.0	-26.2	-0.6	34.8	-47.0	292.8	806.7	6815.1	1172.9	73.7	166.4	240.1
4	23.0	-26.3	-0.6	34.9	-47.2	294.7	804.1	6816.3	1173.5	74.3	166.2	240.5
5	23.5	-27.3	-0.2	34.0	-48.1	281.9	801.3	6679.7	1279.3	64.0	168.5	232.5
6	23.2	-27.0	-0.7	35.8	-48.8	291.8	780.9	6851.0	1168.1	67.2	169.6	236.8
7	23.4	-27.3	0.2	34.0	-48.3	335.7	784.0	6530.3	1273.5	80.0	163.0	243.0
8	23.9	-22.8	1.6	39.5	-46.8	245.9	792.2	6050.9	1379.3	98.8	155.1	253.7
9	23.4	-26.6	0.2	34.0	-48.3	335.7	784.0	6530.3	1273.5	80.0	163.0	243.0
10	23.2	-22.1	1.6	37.5	-44.4	208.6	768.2	6021.3	1317.4	98.9	155.3	254.4
11	22.4	-23.8	0.9	33.0	-43.4	365.7	798.8	6272.2	1234.0	94.2	155.9	251.0
12	22.8	-23.7	1.2	34.1	-44.4	268.1	797.2	6173.3	1281.1	95.2	155.9	251.8
13	22.7	-22.6	1.4	35.6	-43.0	180.2	716.3	6096.1	1258.5	88.6	159.9	248.7
14	23.4	-27.0	0.0	33.9	-48.7	338.9	785.3	6601.1	1263.9	77.1	164.5	241.6
15	23.6	-22.4	1.7	38.7	-46.6	243.7	801.7	6002.2	1359.4	103.1	153.8	257.0
16	23.0	-23.0	1.3	36.1	-43.4	108.7	703.5	6117.7	1277.5	85.7	161.2	246.8
17	23.2	-27.0	-0.4	34.2	-48.4	322.6	792.4	6732.3	1221.2	74.1	166.2	240.2
18	23.4	-27.1	0.0	33.8	-48.4	320.6	789.4	6617.6	1270.0	73.7	165.5	239.1
19	23.4	-27.2	-0.1	33.9	-49.0	303.1	792.6	6801.0	1281.7	69.7	166.6	236.3
20	23.5	-27.9	-0.5	35.7	-46.5	260.5	706.1	6801.0	1247.3	63.6	169.9	233.5
21	22.5	-26.0	-0.2	34.9	-46.5	236.9	716.0	6669.5	1184.1	75.8	164.2	240.4
22	19.0	-19.6	1.3	32.6	-42.1	214.4	861.7	6108.3	1090.3	112.4	144.7	256.9
23	23.6	-28.2	-1.1	38.4	-49.9	258.8	737.5	6985.6	1136.1	50.3	177.7	228.0
24	23.6	-28.2	-1.1	38.4	-50.5	259.7	737.1	6990.8	1130.8	49.9	178.1	228.0
25	23.6	-27.7	-0.9	37.8	-45.3	257.1	753.3	6909.9	1181.9	61.2	172.1	233.3
26	23.6	-27.9	-0.9	38.0	-46.7	256.9	746.8	6928.9	1165.5	56.1	174.6	230.7
27	23.6	-28.0	-1.0	38.1	-48.5	259.0	741.4	6946.4	1149.4	52.1	176.6	228.7
28	23.6	-28.2	-1.1	38.3	-50.6	262.3	738.6	6990.3	1130.2	50.0	178.0	228.0
29	23.5	-28.2	-1.1	38.2	-51.7	266.5	742.4	6990.8	1119.9	50.8	178.0	228.8
30	23.6	-28.2	-1.1	36.6	-51.7	262.2	737.2	6990.8	1119.3	49.2	178.8	227.9
31	23.5	-20.0	2.7	36.5	-39.9	217.3	692.5	5653.8	1449.0	125.6	141.4	268.9
32	23.4	-19.7	2.8	36.5	-39.2	209.4	696.8	5612.9	1448.8	121.8	142.6	264.3

[a] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperature EXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost.

Table 4. (Continued).

SITE	JUMAX[a]	JAMIN	MNDLY	EXMAX	EXMIN	PCIPSN	PCIPTL	DDH	DDG	FFDYS	FFS	FFA
33	23.6	-22.8	1.7	36.1	-43.8	304.2	705.4	6012.4	1373.6	142.7	135.0	277.7
34	24.0	-23.6	1.3	36.4	-45.4	348.6	709.3	6120.4	1330.1	152.0	130.7	282.7
35	24.0	-24.1	1.1	37.1	-42.8	217.1	725.1	6216.8	1363.4	88.4	157.9	246.2
36	24.1	-22.9	1.7	37.1	-42.5	198.4	707.7	6002.0	1373.5	90.0	157.3	247.4
37	23.8	-25.3	0.4	37.9	-44.3	249.5	736.0	6467.7	1318.6	69.3	162.9	232.2
38	23.8	-25.4	0.3	37.7	-42.9	246.5	737.2	6490.1	1313.5	66.3	164.3	230.7
39	23.8	-25.3	0.4	38.0	-44.6	252.7	736.3	6469.5	1317.1	69.6	162.7	232.3
40	23.6	-25.4	0.4	36.1	-44.3	237.4	784.4	6471.4	1314.8	71.1	167.6	238.7
41	23.9	-25.6	0.1	36.3	-46.0	217.3	761.2	6568.6	1224.2	31.0	185.0	216.0
42	23.8	-25.6	0.2	36.2	-45.5	223.3	769.8	6546.2	1249.4	40.1	181.2	221.3
43	23.8	-24.8	0.9	36.1	-47.6	266.6	755.2	6293.4	1331.6	97.8	157.8	255.6
44	23.4	-23.5	1.2	36.7	-43.4	191.7	704.0	6456.6	1310.0	85.7	160.7	246.2
45	24.1	-24.9	0.7	37.1	-42.7	232.0	735.7	6350.2	1363.1	85.8	158.3	244.2
46	23.7	-25.6	0.3	37.4	-45.4	270.8	739.4	6499.0	1304.6	70.9	162.4	233.3
47	23.6	-26.0	-0.1	36.7	-40.0	255.0	760.3	6617.1	1286.0	68.9	164.3	233.2
48	23.9	-24.4	1.1	36.5	-45.7	292.9	733.2	6191.6	1344.3	114.7	149.1	263.8
49	24.3	-25.0	0.6	37.3	-45.3	222.9	742.0	6399.7	1291.9	51.6	174.2	225.8
50	23.2	-24.8	0.5	37.1	-46.9	229.5	741.8	6404.0	1246.6	43.4	179.2	222.6
51	23.0	-24.4	1.0	36.5	-47.2	297.1	740.6	6236.8	1326.5	114.8	148.9	263.8
52	23.5	-25.6	0.3	35.8	-43.4	238.4	790.7	6486.3	1319.4	74.1	166.7	240.8
53	23.9	-25.0	1.0	36.5	-46.1	258.8	742.5	6225.2	1361.1	94.4	159.6	254.0
54	23.4	-26.6	-0.4	35.9	-37.0	226.7	795.2	6745.2	1262.1	84.3	160.8	245.2
55	23.4	-26.4	-0.3	35.2	-34.9	268.5	804.9	6711.8	1264.8	84.0	161.0	245.0
56	23.4	-26.3	-0.2	35.2	-34.4	266.9	805.7	6674.8	1286.5	89.5	158.5	248.0
57	23.4	-26.2	-0.2	34.8	-33.5	268.5	811.2	6669.4	1280.3	87.4	159.5	247.0
58	23.4	-26.2	-0.2	34.6	-33.1	269.3	813.5	6653.5	1277.0	84.6	160.6	245.2
59	23.4	-26.0	-0.0	34.3	-32.3	266.8	817.2	6607.5	1296.7	89.1	159.2	248.2
60	23.5	-26.7	-0.5	36.1	-38.9	265.0	780.4	6756.6	1238.1	71.8	165.6	237.4
61	23.7	-26.3	-0.2	37.4	-42.3	256.0	741.7	6661.4	1274.4	64.5	165.3	229.8
62	23.3	-26.5	-0.1	34.0	-48.0	314.3	770.9	6555.8	1261.8	79.2	163.2	242.5
63	23.1	-26.6	-0.0	34.4	-47.8	290.3	749.0	6610.2	1242.8	76.9	164.1	241.1
64	24.0	-24.1	1.1	36.6	-46.5	320.7	727.9	6192.6	1325.3	129.6	161.4	271.0

[a] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperature EXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost.

DATA ANALYSIS

Cone and needle data were analyzed separately using parallel procedures. Earlier analyses of morphological variation of other North American conifers, black spruce (Parker et al 1983), *Abies procera* Rehd. (noble fir) (Maze and Parker 1983), *Abies lasiocarpa* (Hook.) Nutt. (alpine fir) (Parker et al 1981; Parker and Maze 1984) and *Abies balsamea* (L.) Mill. (Parker et al.1981), indicate that vegetative and reproductive structures exhibited different patterns of variation. Reproductive structures are produced later in the life-cycle than vegetative structures, differentiate from different meristems, grow and mature under different annual environmental conditions and are not necessary for yearly survival. Thus, they may respond to different selection pressures than vegetative structures (Maze and Parker 1983).

Univariate Analysis

Using the Statistical Package for the Social Sciences (SPSSx™) (SPSS Inc. 1988) software on the MicroVAX II™, mean values for all characters were generated for each individual tree from the measurements of five cones and five needles associated with each tree. The mean data sets were checked for general trends and anomalies by generating means and standard deviations, and frequency histograms for each variable by site.

The trees ranged in age from approximately 20 to 120 years. To ensure that the cone and needle characters did not vary due to tree age, individual tree means for all cone and needle variables were regressed against tree age. The coefficients of determination (r^2) for the regression of age against cone characters and needle characters were significant in a few cases but, it was concluded that these relationships would not affect subsequent analyses.

Variance Components

Components of variation, for each character, corresponding to sites, trees within sites and cones or needles within trees within sites were determined from the raw data sets by a two-level nested analysis of variance (ANOVA) using an algorithm developed by W.H. Parker, adapted from Sokal and Rohlf (1981) on a Macintosh™ computer

Multivariate Analysis

Principal Component Analysis

Principal component analysis (PCA) was used to determine the number of dimensions that accounted for the variation within the data and to create a new data set of uncorrelated variables to use in regression analysis (Stevens 1986). PCA is a mathematical technique for which there are no assumptions made about the probability distribution of the original variables. In addition, there is no requirement for specification of the underlying statistical model used to explain the error structure (Chatfield and Collins

1980). The components were extracted from the correlation matrix which was generated from individual tree means for cone and needle data. The correlation matrix provides standardized variables for analysis independent of scales of measurement (Pimental 1979). PCA is a mathematical maximization procedure that produces components that account for the maximum amount of variation left after each successive component is generated (Stevens 1986). Components with an eigenvalue greater than one were interpreted as accounting for a biologically significant level of variation (Kaiser 1960).

PCA was run separately on the 26 needle radial distances to reduce the number of variables in that portion of the data set by generating new summary variables. The radial distances were highly correlated thus each single radial distance could not explain variation in needle shape Groups of radial distances could show the variation in shape over all surfaces and so PCA was used to produce uncorrelated variables that effectively summarize the variation in needle shape.

The component scores of the first three principal components were retained for regression analysis against environmental variables. Geographic variation is probably a multidimensional system due to the adaptation of many characters to a complex pattern of environmental variables (Sokal and Rinkle 1963). In this light, correlations of variation patterns with the environment will be more meaningful using multidimensional variables to represent the patterns of variation.

PCA evaluates the relationship between variables based on individuals rather than individuals within groups. Nonetheless, ordination of the individual PCA component scores from the first two or three eigenvectors may show some population trends. Generally, ordination is most useful if the bulk of the variation is concentrated in the first two or three eigenvectors. A program developed by W.H. Parker for the Macintosh™ computer was used to produce ordinations of the first versus the second principal component and the first versus the third principal component. The plotting program locates the population centroid and designates standard deviations for all individuals within the population.

Discriminant Analysis

Discriminant function analysis (DA) was used to produce a set of linear combinations of the original variables which maximized the among to within group variability (Green 1978; Stevens 1986). DA then allocated individuals to one of the 64 groups (sites) on the basis of the variation of the individual in p-dimensional space: where p is the number of variables used to describe each individual (Chatfield and Collins 1980). Unlike PCA, DA requires that each individual must belong to a sample from a recognized population (Pimental 1979). In addition, in order to minimize the probability of misclassification the data must meet the assumptions of a multivariate normal distribution (Norusis 1985). However, Klecka (1975) notes that DA on SPSSx™ is a robust procedure and that these assumptions need not be strongly adhered to in order to produce meaningful results.

DA was run on the individual tree mean data sets for cones and needles. All the cone variables were analyzed together. The needle data set was comprised of 14 morphometric variables and three needle shape summary variables derived using PCA. The component scores associated with the first three axes of the DA were retained for each tree for regression analysis.

Ordinations of the first versus the second discriminant function and the first versus the third discriminant function were made. Ordination of the populations based on DA were made to examine how the populations clustered.

Regression Analysis

The use of the linear regression model assumes that the errors are independent and follow a normal distribution with constant variance (Stevens 1986). Scatterplots of residuals versus predicted values were generated for the climatic and FEC data sets to assess the level of normality. Any systematic pattern or clustering of the residuals indicates a violation of the linear model (Stevens 1986). Scatterplots of residual versus predicted values of the climatic and spatial data did not show a systematic pattern or clustering. Climatic and spatial data were therefore assumed not to violate the regression model. The FEC data were primarily percent data, therefore, scatterplots of residual versus predicted values should have approximated a diamond pattern (Stevens 1986).

However, the scatterplots all had some form of clustering that did not follow a detectable pattern. The clustering is probably a function of the variables chosen to summarize the FEC data and the corresponding values. The data were not transformed as trial transformations did not remedy the problem. The regressions of FEC data should, therefore, be viewed with caution.

Simple Regression Analysis

Simple regressions of PCA and DA component scores on climate and FEC data sets were used to evaluate the relationship of the multidimensional pattern of variation with individual predictors. Six separate simple regressions were run with the first three PCA and the first three DA component (function) scores for both cone and needle data sets as the dependent variables and the climatic and FEC data as the independent variables.

Multiple Regression Analysis

Six separate multiple regressions were run with the first three PCA and the first three DA component (function) scores for the cone and needle data sets as the dependent variables and the spatial and selected climatic data variables as the independent variables. Climatic data variables with correlations greater than 0.75 to each other, from the correlation matrix (Table 5), resulted in one variable being eliminated from the model. The variables were selected based on correlations with all other variables and

Table 5. Correlation matrix of climatic data.

	LAT	LONG	ELEV	JUMAX	JAMIN	MNDLY	EXMAX	EXMIN	PCIPSN	PCIPTL	DDH	DDG	FFDYS	FSP
LAT														
LONG	-0.461													
ELEV	-0.363	0.654												
JUMAX	-0.109	0.493	0.370											
JAMIN	-0.815	0.128	-0.060	-0.264										
MNDLY	-0.893	0.212	0.041	-0.009	0.938									
EXMAX	0.000	0.397	-0.060	0.552	-0.011	0.025								
EXMIN	-0.356	0.522	0.406	-0.089	0.324	0.256	-0.202							
PCIPSN	-0.328	-0.201	0.084	0.090	-0.469	-0.368	-0.374	-0.286						
PCIPTL	0.394	-0.275	-0.067	-0.473	-0.189	-0.325	-0.546	0.213	0.319					
DDH	0.895	-0.214	-0.042	0.025	-0.943	-1.000	-0.017	-0.265	0.372	0.316				
DDG	-0.775	0.437	0.315	0.434	0.603	0.797	0.104	0.394	-0.171	-0.324	-0.789			
FFDYS	-0.668	0.198	0.139	-0.143	0.703	0.733	-0.180	0.327	0.141	-0.115	-0.735	0.599		
FSP	0.692	-0.191	-0.141	0.159	-0.729	-0.752	0.181	-0.377	-0.110	0.123	0.755	-0.632	-0.986	
FAA	-0.686	0.246	0.206	-0.095	0.673	0.705	-0.183	0.271	0.102	-0.106	-0.707	0.540	0.898	-0.860

[a] LAT = latitude; Long = longitude; ELEV = elevation; JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperature; EXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost.

the type of data it represented. High correlations among predictors can limit the size of the correlation coefficient (r) and create difficulty in determining the importance of the predictor because of confounding relationships with other predictors (Stevens 1986). Due to the low r^2 values generated by the simple regressions of FEC data on the PCA and DA summary variables the FEC data were not included in the multiple regressions.

The approach to variable selection for the model was the backwards elimination. It was chosen in lieu of the stepwise procedure because the stepwise method assumes an order of importance as the variables enter the model and early termination of the regression may result in some potentially important variables being eliminated (Hocking 1983).

Components of variation were calculated for each of the PCA and DA axes from one-way ANOVA's (Sokal and Rohlf 1981). The percent variation between groups was compared to the r^2 values obtained from multivariate regression analysis in order to determine the fraction of among-group variation associated with the environment (climate, vegetation and soils). The r^2 value represents the relationship between the environment and the PCA/DA component scores regardless of group, whereas, the component of variation value represents the level of variation between groups. From this it is possible to determine what percent of the variation manifested between populations is associated with the environment and possibly represents adaptive variation.

Trend Surface Mapping

Mean DA component scores were computed for each site for the first axes of both cone and needle data. Using the ARC/INFO software package on a GIS, a database with site locations (coverage) was created. The mean DA scores were added to the coverage as a third dimension (z axis) using the TIN (triangulated irregular network) subpackage of ARC/INFO. The TIN software generates a continuous trend surface by interpolating the DA scores. The trend surface is represented by contour intervals (interval = one standard deviation) that correspond to the variation in DA component scores by site (Parker, per. comm. 1988). A comparison of the DA trend surfaces with each other and trend surfaces of climatic data will give additional insight into the patterns of variation.

RESULTS

UNIVARIATE ANALYSIS

The means and standard deviations for selected cone and needle characters for each collection site are presented in Table 6. A complete listing of the means and standard deviations for both cone and needle data is presented in Appendices 6 and 7. It was difficult to discern any trends in the data from the means and standard deviations, due to the complexity of the patterns of variation. Scattergrams of residual versus predicted values for the cone and needle characters resulted in a "shotgun" pattern indicating a normal distribution (Stevens 1986). In addition, frequency distributions followed a "bell-shaped" curve, indicative of normality.

Analysis of Variance

Nested analysis of variance of the cone and needle characters demonstrated that there were significant differences among groups (sites) and within groups (between trees within sites) (Tables 7 and 8). The percent of the total variance associated with the sites ranged from 1.62 percent (apophysis depth) to 18.85

Table 6. Means and standard deviations (in parentheses) for selected cone and needle characters of *Pinus banksiana.*

SITE NO	CD	SL	SEL	SEW	SED	NW	NT	VBW
1	16.6	18.0	3.7	1.9	1.2	32.1	76.3	102.2
	(1.6)	(2.5)	(0.2)	(0.2)	(0.1)	(3.4)	(4.0)	(8.6)
2	17.7	18.7	3.9	2.0	1.3	30.4	76	103
	(2.1)	(2.6)	(0.3)	(0.2)	(0.1)	(2.0)	(1.5)	(10.0)
3	18.9	19.2	3.6	1.8	1.2	30.5	77.9	105.3
	(2.0)	(2.5)	(0.2)	(0.2)	(0.1)	(3.0)	(6.0)	(7.8)
4	18.3	20.1	4.1	2.1	1.2	35.2	78.1	101.8
	(1.4)	(2.2)	(0.5)	(0.2)	(0.1)	(3.3)	(4.4)	(7.5)
5	18.0	17.4	3.8	2.0	1.2	33	76.5	100.2
	(2.1)	(2.0)	(0.4)	(0.2)	(0.2)	(4.3)	(7.1)	(10.4)
6	17.2	18.4	4.2	2.2	1.4	35.8	79.9	98.6
	(1.7)	(2.0)	(0.3)	(0.1)	(0.2)	(5.9)	(5.3)	(6.6)
7	18.4	20.1	3.9	1.9	1.1	36.2	78.3	10.4
	(1.5)	(2.2)	(0.5)	(0.2)	(0.1)	(3.1)	(4.2)	(5.5)
8	18.3	17.2	3.6	1.8	1.2	34.7	79.7	104.9
	(2.6)	(1.3)	(0.4)	(0.3)	(0.1)	(2.5)	(4.1)	(10.3)
9	18.9	18.4	4.0	2.0	1.2	34	75.8	94.5
	(1.7)	(2.9)	(0.6)	(0.2)	(0.1)	(6.2)	(6.1)	(11.8)
10	18.6	19.2	4.1	2.1	1.3	38.9	85.4	98.3
	(2.0)	(1.1)	(0.3)	(0.2)	(0.1)	(7.2)	(4.7)	(9.2)
11	20.4	15.6	4.0	2.0	1.2	35.2	83.8	95.3
	(2.7)	(1.1)	(0.3)	(0.3)	(0.2)	(3.4)	(6.0)	(5.8)
12	19.4	17.5	4.1	2.1	1.2	31.7	81.6	100.1
	(1.5)	(1.2)	(0.3)	(0.2)	(0.1)	(3.7)	(4.8)	(10.5)
13	18.4	18.5	4.2	2.3	1.3	34.8	78.6	101.5
	(1.7)	(1.7)	(0.2)	(0.1)	(0.1)	(3.4)	(4.1)	(8.4)
14	18.5	19.1	4.1	2.2	1.3	33.9	77.1	97.5
	(1.8)	(2.3)	(0.3)	(0.2)	(0.1)	(5.3)	(5.2)	(10.9)
15	18.0	18.1	3.8	1.9	1.2	32.3	76.6	97.4
	(1.4)	(2.4)	(0.5)	(0.2)	(0.1)	(4.1)	(3.3)	(10.6)
16	18.5	18.7	4.2	2.2	1.5	34.2	78.8	94.4
	(1.7)	(2.2)	(0.2)	(0.2)	(0.2)	(2.4)	(2.9)	(8.4)

[a] CD = cone depth; SL = scale length; SEL = seed length; SEW = seed weight; NW = needle width; NT = needle thickness; VBW = vascular bundle width (all cone measurements in mm; all needle measurements in mm X 0.10).

Table 6. (Continued).

SITE NO	CD	SL	SEL	SEW	SED	NW	NT	VBW
17	17.6	18.2	4.0	2.1	1.2	166.7	81.1	102.2
	(1.5)	(2.5)	(0.2)	(0.3)	(0.1)	(11.8)	(4.5)	(8.6)
18	19.0	18.8	4.0	2.1	1.2	164.8	79.4	103
	(1.0)	(2.0)	(0.1)	(0.2)	(0.1)	(15.4)	(6.2)	(10.0)
19	18.5	17.9	4.1	2.2	1.3	166.6	78.1	105.3
	(1.0)	(1.1)	(0.4)	(0.2)	(0.1)	(11.5)	(4.7)	(7.8)
20	19.0	18.5	4.0	2.1	1.2	162	77.4	101.8
	(2.1)	(2.1)	(0.3)	(0.2)	(0.1)	(10.2)	(4.7)	(7.5)
21	19.8	19.4	4.0	2.1	1.2	159.2	76.3	100.2
	(1.6)	(3.3)	(0.3)	(0.2)	(0.1)	(13.2)	(4.5)	(10.4)
22	17.5	16.7	3.8	2.0	1.2	161.5	79.9	98.6
	(1.3)	(2.0)	(0.3)	(0.2)	(0.1)	(9.5)	(4.6)	(6.6)
23	19.1	17.6	3.9	2.0	1.2	160.7	77.2	10.4
	(1.7)	(0.8)	(0.4)	(0.3)	(0.1)	(8.3)	(6.0)	(5.5)
24	19.1	17.3	4.1	2.1	1.2	167.5	80.5	104.9
	(2.3)	(2.5)	(0.4)	(0.2)	(0.1)	(14.2)	(7.2)	(10.3)
25	18.4	18.5	3.9	2.0	1.2	154.2	75.1	94.5
	(1.8)	(2.5)	(0.3)	(0.2)	(0.1)	(13.8)	(5.1)	(11.8)
26	18.2	19.0	4.1	1.9	1.2	157	78.3	98.3
	(1.5)	(1.7)	(0.2)	(0.2)	(0.1)	(10.5)	(5.6)	(9.2)
27	17.3	17.0	4.1	2.1	1.3	155.6	76.1	95.3
	(1.7)	(1.3)	(0.2)	(0.1)	(0.1)	(8.4)	(4.3)	(5.8)
28	17.0	16.3	3.9	2.0	1.2	161	78.5	100.1
	(2.3)	(2.3)	(0.3)	(0.2)	(0.1)	(12.5)	(5.6)	(10.5)
29	20.1	18.3	4.0	2.1	1.2	157.9	78.9	101.5
	(1.1)	(1.9)	(0.5)	(0.1)	(0.2)	(11.1)	(6.2)	(8.4)
30	19.2	18.8	4.1	2.1	1.2	157.8	77.1	97.5
	(0.8)	(1.7)	(0.1)	(0.1)	(0.1)	(12.2)	(4.3)	(10.9)
31	19.4	17.4	4.2	2.2	1.2	155.2	74.4	97.4
	(1.6)	(1.5)	(0.4)	(0.2)	(0.1)	(17.7)	(8.7)	(10.6)
32	19.0	18.5	4.1	2.1	1.2	153.3	75.5	94.4
	(0.9)	(1.4)	(0.3)	(0.1)	(0.1)	(8.8)	(4.1)	(8.4)

[a] CD = cone depth; SL = scale length; SEL = seed length; SEW = seed weight; NW = needle width; NT = needle thickness; VBW = vascular bundle width (all cone measurements in mm; all needle measurements in mm X 0.10).

Table 6. (Continued).

SITE NO	CD	SL	SEL	SEW	SED	NW	NT	VBW
33	17.7	17.3	4.0	2.1	1.2	154.2	72.9	96.2
	(2.0)	(2.3)	(0.2)	(0.1)	(0.1)	(13.6)	(4.6)	(11.2)
34	17.7	17.6	4.2	2.1	1.2	168.9	81.5	105.5
	(1.1)	(2.4)	(0.3)	(0.1)	(0.1)	(12.4)	(5.8)	(10.5)
35	18.0	16.4	3.9	0.2	1.2	155	75.8	95.4
	(1.9)	(1.3)	(0.4)	(0.2)	(0.1)	(9.7)	(4.1)	(7.3)
36	18.4	17.4	3.9	1.9	1.2	162.4	77.8	101.2
	(1.7)	(1.7)	(0.5)	(0.2)	(0.0)	(12.5)	(5.2)	(10.8)
37	18.1	16.9	3.8	1.9	1.2	157.5	76.1	97.3
	(2.0)	(1.7)	(0.3)	(0.2)	(0.1)	(13.6)	(4.0)	(11.7)
38	18.2	16.9	3.6	1.8	1.1	161.6	77.4	99.6
	(1.4)	(1.1)	(0.4)	(0.2)	(0.1)	(11.1)	(4.8)	(9.6)
39	17.5	16.4	3.7	1.7	1.1	150.7	71.4	93.6
	(1.6)	(1.0)	(0.4)	(0.2)	(0.0)	(7.5)	(2.6)	(6.2)
40	15.9	16.9	3.8	1.8	1.2	155.9	73.8	97
	(1.1)	(1.6)	(0.2)	(0.2)	(0.1)	(13.9)	(6.4)	(10.2)
41	18.0	18.6	3.9	2.0	1.2	157.7	76.2	97.8
	(1.7)	(2.6)	(0.4)	(0.1)	(0.1)	(9.7)	(2.8)	(7.8)
42	16.8	17.6	3.6	1.8	1.1	158	73.7	98.9
	(1.4)	(2.0)	(0.2)	(0.2)	(0.1)	(12.8)	(4.8)	(10.5)
43	16.7	16.5	3.6	1.9	1.1	167.6	80.1	106.3
	(1.3)	(2.1)	(0.3)	(0.1)	(0.1)	(10.9)	(5.1)	(6.2)
44	17.4	16.7	3.4	1.7	1.1	166.5	78.6	105.5
	(2.0)	(1.4)	(0.2)	(0.2)	(0.1)	(7.1)	(3.2)	(8.2)
45	17.2	17.3	3.4	1.8	1.1	165.6	79.4	105.9
	(1.4)	(1.3)	(0.3)	(0.2)	(0.1)	(14.1)	(6.1)	(10.1)
46	17.4	18.2	3.6	1.8	1.2	159.3	76.3	100.5
	(1.4)	(1.5)	(0.3)	(0.2)	(0.1)	(11.9)	(3.2)	(9.5)
47	18.9	18.2	3.8	1.9	1.2	166.9	79	105.4
	(1.1)	(1.4)	(0.3)	(0.2)	(0.1)	(11.0)	(5.2)	(5.4)
48	16.6	16.7	3.6	1.9	1.2	152.6	74.8	94.8
	(1.5)	(1.8)	(0.3)	(0.1)	(0.1)	(12.3)	(3.8)	(9.6)

[a] CD = cone depth; SL = scale length; SEL = seed length; SEW = seed weight; NW = needle width; NT = needle thickness; VBW = vascular bundle width (all cone measurements in mm; all needle measurements in mm X 0.10).

Table 6. (Continued).

SITE NO	CD	SL	SEL	SEW	SED	NW	NT	VBW
49	17.2	17.0	3.6	1.8	1.1	157.8	75.6	99.4
	(1.4)	(1.8)	(0.4)	(0.3)	(0.1)	(10.7)	(3.4)	(7.2)
50	18.1	16.6	3.5	1.8	1.1	153.2	74.8	98.2
	(1.3)	(1.8)	(0.1)	(0.3)	(0.1)	(14.6)	(3.9)	(11.7)
51	16.3	17.5	3.6	1.8	1.1	150.7	72.4	92.7
	(1.9)	(1.8)	(0.2)	(0.1)	(0.1)	(12.8)	(4.8)	(8.6)
52	17.4	16.6	3.5	1.9	1.2	161.5	77.5	101.9
	(2.3)	(1.4)	(0.4)	(0.1)	(0.1)	(11.8)	(4.5)	(7.0)
53	15.7	15.1	3.3	1.8	1.1	150	74.9	91.8
	(1.6)	(1.6)	(0.2)	(0.2)	(0.0)	(15.7)	(7.9)	(11.1)
54	17.7	16.5	3.7	1.9	1.3	156.4	76.2	95.2
	(1.8)	(2.2)	(0.1)	(0.1)	(0.1)	(10.2)	(4.5)	(7.6)
55	17.9	15.6	3.7	2.0	1.2	163.5	79.6	102.5
	(1.5)	(1.1)	(0.2)	(0.3)	(0.1)	(11.4)	(2.8)	(10.0)
56	17.5	15.4	3.8	2.1	1.2	155.4	75.1	97
	(1.9)	(1.3)	(0.3)	(0.1)	(0.1)	(12.5)	(4.9)	(10.1)
57	17.4	15.7	3.6	1.9	1.1	165.6	78.6	103.8
	(1.4)	(2.2)	(0.3)	(0.2)	(0.1)	(10.6)	(5.3)	(7.5)
58	17.4	15.5	3.7	2.1	1.1	159.7	75.4	98.2
	(1.1)	(1.5)	(0.3)	(0.2)	(0.1)	(17.0)	(6.0)	(12.6)
59	19.4	16.3	3.6	2.0	1.1	155	75.3	96.2
	(2.3)	(2.5)	(0.3)	(0.2)	(0.1)	(10.2)	(6.7)	(8.2)
60	17.2	15.1	3.8	2.0	1.0	154.5	75.6	97.1
	(1.6)	(2.1)	(0.4)	(0.2)	(0.1)	(10.7)	(3.6)	(7.2)
61	19.1	14.7	3.5	1.9	1.1	148.6	72.6	91.2
	(2.0)	(1.7)	(0.3)	(0.2)	(0.1)	(14.7)	(6.9)	(10.8)
62	19.0	18.8	3.7	1.8	1.1	159	73.9	101.9
	(1.7)	(2.0)	(0.4)	(0.3)	(0.1)	(7.1)	(4.6)	(4.7)
63	18.8	17.9	3.7	1.9	1.2	153.3	73.4	96.9
	(2.4)	(2.0)	(0.2)	(0.1)	(0.1)	(14.5)	(5.8)	(11.8)
64	17.7	18.0	3.6	1.9	1.1	150.3	71.8	94.6
	(1.8)	(2.5)	(0.3)	(0.1)	(0.1)	(9.2)	(3.3)	(6.9)

[a] CD = cone depth; SL = scale length; SEL = seed length; SEW = seed weight; NW = needle width; NT = needle thickness; VBW = vascular bundle width (all cone measurements in mm; all needle measurements in mm X 0.10).

percent (seed length) for the cone characters (Figure 4) and from 2.71 percent (left resin canal depth) to 15.42 percent (needle width) for the needle characters (Figure 5). The percent variance associated between trees within sites ranged from 20.75 percent (seed depth) to 62.44 percent (cone curvature) for the cone characters (Figure 4) and from 20.27 percent (right resin canal distance to the needle edge) to 72.56 percent (needle length) for the needle characters (Figure 5). Variance associated within trees within sites (error term) ranged from 30.89 percent (cone curvature) to 72.31 percent (seed number) for the cone characters (Figure 4) and from 17.10 percent (needle width) to 76.30 percent (right resin canal distance to the needle edge) for the needle characters (Figure 5) (Tables 7 and 8).

The best cone traits for distinguishing among sites were: cone depth; scale length; seed length; seed width; and seed depth (Figure 4). The needle characters that best distinguished among sites were: needle width, needle thickness; and vascular bundle thickness (Figure 5). In addition, the radial distances that defined the curve of the needle cross-section, RD05 to RD12 and RD17 to RD19 (Figure 5), also had a high percentage (between 12 and 15 percent) of the total variance associated with the sites (Table 8). The radial distances from the right side of the needle cross-section had higher percentages of variation associated with among site differences than the distances from the left side of the needle. The difference, in the partitioning of the total variance, between the two sides of the needle is not large but indicates an asymmetry in needle shape.

Table 7. Percent of the total variance associated with site, individuals within site, and within individuals within site for cone characters of *Pinus banksiana*.

VARIABLE[a]	SITE	W/IN SITE	W/IN TREES
CL	6.84	60.94	32.22
MO	3.61	50.23	46.09
CW	6.30	50.47	46.70
CD	11.91	43.29	44.80
AL	5.16	46.82	48.01
UDI	4.30	47.04	48.66
AW	5.44	40.03	54.53
CV	5.81	50.56	43.63
CWT	4.33	51.21	44.46
SN	5.73	28.32	65.95
SL	15.95	45.49	38.55
SW	5.76	37.57	56.67
AD	1.62	50.17	48.21
SEN	2.72	24.97	72.31
SEL	18.75	37.70	43.55
SEW	14.57	24.93	60.50
SED	13.50	20.75	65.75
SEWT	6.41	45.23	48.36
CUV	6.67	62.44	30.89

[a] CL = cone length; MO = mid-ordinate length; CW = cone width; CD = cone depth; AL = apophysis length; UDI = umbo distance; AW = apophysis width; CV = cone volume (mg); apophysis depth; SEN = seed number; SEL = seed length; SEW = seed width; SED = seed depth; SEWT = seed weight; and CUV = cone curvature (all measurements in mm except where noted).

Table 8. Percent of the total variance associated with site, individuals within site, and within individuals within sites for needle characters of *Pinus banksiana*.

VARIABLE[a]	SITE	W/IN SITE	W/IN TREES
NLEN	5.92	72.56	21.51
NW	15.42	67.48	17.10
NT	12.22	57.14	30.64
VBT	7.51	59.01	33.47
VBAD	6.70	33.36	59.95
RCLT	2.71	41.39	55.88
RCLAD	9.24	27.78	62.99
RCLL	3.43	20.27	76.30
RCLAB	6.91	25.16	67.93
RCRT	9.23	24.86	65.92
RCRAD	9.72	20.66	69.62
RCRL	4.68	26.96	68.36
RCRAB	9.22	24.86	65.92
VBW	13.40	67.31	19.29
RD01	8.42	45.75	45.83
RD02	10.17	44.65	45.48
RD03	10.74	41.98	47.28
RD04	11.38	38.23	50.39
RD05	12.68	13.40	12.97
RD06	13.40	28.99	57.62
RD07	12.97	36.89	50.14
RD08	14.39	57.24	28.37
RD09	15.06	59.79	25.15
RD10	15.14	58.05	28.82
RD11	14.59	56.02	29.39
RD12	12.35	55.07	32.58
RD13	11.14	58.85	30.01
RD14	10.61	61.85	27.54
RD15	10.23	60.31	29.46
RD16	10.53	57.35	32.12
RD17	12.59	59.72	27.69
RD18	12.72	61.62	25.66
RD19	12.68	63.25	24.07
RD20	11.92	59.46	28.63
RD21	10.35	38.69	50.96
RD22	11.30	28.33	60.36
RD23	9.86	33.84	56.30
RD24	8.44	39.01	52.54
RD25	7.63	43.28	49.09
RD26	7.56	46.08	46.35

[a] NLEN = needle length (mm); NW = needle width; NT = needle thickness; VBT = vascular bundle thickness; VBAD = vascular bundle adaxial distance; RCLT (RCRT) = resin canal depth (left & right); RCLAD (RCRAD) = resin canal adaxial distance (left & right); RCLL (RCRL) = resin canal distance to needle surface (left & right); RCLAB (RCRAB) = resin canal abaxial distance; VBW = vascular bundle width; and RD01 - RD26 = radial distances (all measurements in mm X 0.10 except where noted).

MULTIVARIATE ANALYSIS

Principal component Analysis

Principal component analysis generated uncorrelated summary variables from the correlation matrices of cone and needle data (Appendix 8). Cone width, cone depth, cone volume, cone weight (Figure 4) were all correlated to each other with r greater than 0.75. In addition, apophysis length, apophysis depth and umbo distance (Figure 5) were also correlated to each other at r greater than 0.75. The conventional needle characters of needle width, needle thickness, vascular bundle thickness, distance from the vascular bundle to the adaxial surface, and vascular bundle width were correlated at r greater than 0.75 with the radial distances that define needle shape, RD07-RD11 and RD17-RD21, RD10-RD18, RD12-RD16, RD02, and RD07-RD11 and RD17-RD21 respectively (Figure 5). The greatest correlation between radial distances was generally between neighbouring distance measurements. The radial distances that defined the curves on the right and left surfaces were highly correlated with each other. However, the correlations showed that the curves were not mirror images of each other, indicating asymmetry of the needle shape.

Principal component analysis of the cone characters generated four significant (eigenvalue greater than 1) principal components that accounted for 35.4 percent, 19.5 percent, 13.7 percent and 5.4 percent of the variation respectively (Table 9). The first principal

Table 9. Results of principal component analysis for 19 cone characters of *Pinus banksiana*.

	COMPONENTS			
	1	2	3	4
EIGENVALUE	6.72	3.7	2.6	1.02
% OF VARIANCE	35.4	19.5	13.7	5.4
	COMPONENT LOADINGS			
VARIABLE				
CL	0.47	-0.79	0.10	-0.04
MO	0.65	0.32	-0.43	0.31
CW	0.70	-0.45	-0.04	-0.11
CD	0.73	-0.58	0.04	-0.04
AL	0.72	0.50	-0.19	-0.09
UDI	0.72	0.46	-0.24	-0.08
AW	0.66	0.37	-0.14	-0.30
CV	0.86	-0.45	-0.11	0.06
CWT	0.83	-0.47	-0.14	0.07
SN	0.16	-0.66	-0.43	0.27
SL	0.73	0.04	-0.01	0.14
SW	0.67	0.12	0.09	-0.37
AD	0.65	0.46	-0.20	-0.19
SEN	0.06	-0.06	0.39	-0.55
SEL	0.42	0.12	0.64	0.24
SEW	0.36	0.20	0.72	0.14
SED	0.32	0.31	0.70	0.15
SEWT	0.55	0.11	0.55	0.25
CUV	0.20	0.77	0.39	0.26

[a] CL = cone length; MO = mid-ordinate length; CW = cone width; CD = cone depth; AL = apophysis length; UDI = umbo distance; AW = apophysis width; CV = cone volume (mg); apophysis depth; SEN = seed number; SEL = seed length; SEW = seed width; SED = seed depth; SEWT = seed weight; and CUV = cone curvature (all measurements in mm except where noted).

component was general; all the eigenvectors were positive, indicating that it is associated with size, although size is not always independent of shape (Pimental 1979). Cone volume and cone weight (Figure 4) had the largest loadings. The subsequent principal components were all bipolar; eigenvectors were positive and negative, indicating that they define shape. The largest loadings on the eigenvectors were associated with the following variables: cone length (negative) and cone curvature (positive) on the second principal component; seed length (positive), seed width (positive), and seed depth (positive) on the third principal component; and seed number (negative) (Figure 5) on the fourth principal component (Table 9). The variables that exhibit the greatest contribution to the first principal component are not the ones that best distinguish between collection sites, as demonstrated by the partitioning of the variance (Table 7), indicating that the first principal component is not associated with the geographic location of the collection sites.

Principal component analysis of needle characters generated six significant (eigenvalues greater than one) principal components that accounted for 58.0 percent, 15.3 percent, 6.0 percent, 3.9 percent, 2.6 percent and 2.5 percent respectively of the total variation (Table 10). The first principal component was general with positive eigenvectors. The eigenvectors associated with needle width, needle thickness, vascular bundle thickness, and the radial distances describing the curve between the abaxial and adaxial surface (RD07 to RD11 and RD17 to RD21) (Figure 5) had the

Table 10. Results of principal component analysis for 40 needle characters of *Pinus banksiana*.

	COMPONENTS					
	1	2	3	4	5	6
EIGENVALUES	23.20	6.12	2.39	1.54	1.03	1.00
% OF VARIENCE	58.0	15.3	6.0	3.9	2.6	2.5
	COMPONENT LOADINGS					
VARIABLE[a]						
NLEN	0.35	0.17	-0.12	-0.18	0.14	-0.10
NW	0.94	0.09	-0.24	-0.16	-0.01	-0.01
NT	0.92	0.18	0.17	0.18	0.10	-0.07
VBT	0.50	0.76	0.13	0.17	0.05	-0.01
VBAD	0.77	-0.41	0.01	0.03	0.09	-0.03
RCLT	0.46	0.11	-0.40	0.60	0.02	0.14
RCLAD	0.58	0.18	0.35	-0.19	0.24	-0.37
RCLL	0.63	0.11	0.44	-0.08	-0.24	0.14
RCLAB	0.62	0.07	0.45	0.05	-0.09	0.43
RCRT	0.39	0.12	-0.44	0.60	0.10	0.15
RCRAD	0.60	0.22	0.33	-0.12	0.08	-0.41
RCRL	0.61	0.07	0.47	-0.19	-0.11	0.21
RCRAB	0.64	0.00	0.46	0.04	-0.39	0.22
VBW	0.87	0.01	-0.34	-0.24	-0.05	0.04
RD01	0.77	-0.46	0.19	0.20	0.12	-0.13
RD02	0.76	-0.46	0.18	0.10	0.31	0.05
RD03	0.75	-0.47	0.17	0.01	0.37	0.13
RD04	0.76	-0.49	0.14	-0.01	0.33	0.14
RD05	0.78	-0.52	0.08	-0.04	0.20	0.12
RD06	0.77	-0.51	-0.01	-0.10	0.02	0.12
RD07	0.87	-0.32	-0.12	-0.16	-0.04	0.11
RD08	0.92	0.04	-0.25	-0.21	0.00	0.07
RD09	0.91	0.17	-0.25	-0.19	-0.01	0.02
RD10	0.91	0.25	-0.23	-0.15	-0.04	-0.01
RD11	0.87	0.41	-0.11	-0.04	-0.10	-0.06
RD12	0.78	0.56	0.03	0.09	-0.11	-0.09
RD13	0.72	0.63	0.15	0.17	-0.06	-0.07
RD14	0.70	0.64	0.19	0.18	0.04	-0.02
RD15	0.72	0.63	0.16	0.13	0.12	0.05
RD16	0.78	0.57	0.06	0.05	0.14	0.08
RD17	0.87	0.42	-0.10	-0.06	0.09	0.05
RD18	0.91	0.25	-0.25	-0.14	0.01	0.00
RD19	0.91	0.17	-0.29	-0.16	-0.03	-0.02
RD20	0.91	0.04	-0.31	-0.17	-0.09	-0.02
RD21	0.86	-0.30	-0.21	-0.10	-0.13	0.05
RD22	0.78	-0.51	-0.09	0.01	-0.13	0.04
RD23	0.78	-0.53	0.00	0.12	-0.20	-0.11
RD24	0.76	-0.50	0.02	0.19	-0.23	-0.21
RD25	0.74	-0.47	0.03	0.23	-0.23	-0.27
RD26	0.75	-0.45	0.12	0.24	-0.13	-0.26

[a] NL = needle length (mm); NW = needle width; NT = needle thickness; VBT = vascular bundle thickness; VBAD = vascular bundle adaxial distance; RCLT = left resin canal depth; RCLAD = left resin canal adaxial distance; RCLL = left resin canal distance to needle edge; RCLAB = left resin canal abaxial distance; RCRT = right resin canal depth; RCRAD = right resin canal adaxial distance; RCRL = right resin canal distance to needle edge; RCRAB = right resin canal abaxial distance; VBW = vascular bundle width (all measured in mm X 0.10 except where noted).

largest loadings on the first axis. The rest of the principal components were bipolar with the largest eigenvectors associated with: vascular bundle thickness (positive) on the second principal component; vascular bundle width (positive) on the third principal component; the radial distances that define the curve on the adaxial surface (RD2 to RD4 and RD23 to RD25) (mixed positive and negative) on the fifth principal component; the radial distances that define the adaxial surface (negative) on the sixth principal component (Figure 5). The characters that define the location and size of the resin canals had high loadings on the fourth, fifth and sixth principal components (Figure 5) (Table 10). Interestingly, the variables that had the greatest loading on the first principal component were also the variables that best distinguished between sites as demonstrated by the variance components (Table 8), indicating that the pattern of variation expressed by first principal component of the needle characters is associated with the location of the collection sites.

Principal component analysis also was used to generate a set of component scores from the needle radial distances to be used for discriminant analysis. The first three principal components accounted for 66.2 percent, 20.1 percent and 5.0 percent of the variation respectively (Table 11). The first principal component was general with positive eigenvectors. The eigenvectors associated with the largest loadings represented the curves between the adaxial and abaxial surfaces on the widest part of the needle (RD07 to RD10 and RD18 to RD21) (Figure 5). The second and

Table 11. Results of principal component analysis for 26 needle radial distances of *Pinus banksiana*.

	COMPONENTS		
	1	2	3
EIGENVALUE	17.22	5.22	1.30
% VARIATION	66.1	20.1	5.0
	COMPONENT LOADINGS		
VARIABLE[a]			
RD01	0.80	-0.43	0.35
RD02	0.78	-0.42	0.29
RD03	0.77	-0.44	0.22
RD04	0.79	-0.45	0.16
RD05	0.80	-0.48	0.04
RD06	0.80	-0.46	-0.14
RD07	0.89	-0.25	-0.25
RD08	0.93	0.13	-0.28
RD09	0.91	0.26	-0.25
RD10	0.90	0.33	-0.20
RD11	0.84	0.48	-0.04
RD12	0.74	0.61	0.15
RD13	0.66	0.65	0.24
RD14	0.64	0.65	0.29
RD15	0.66	0.65	0.34
RD16	0.73	0.62	0.18
RD17	0.84	0.49	-0.01
RD18	0.90	0.34	-0.19
RD19	0.91	0.26	-0.25
RD20	0.92	0.13	-0.31
RD21	0.88	-0.23	-0.28
RD22	0.81	-0.45	-0.15
RD23	0.81	-0.49	0.01
RD24	0.79	-0.46	0.11
RD25	0.77	-0.43	0.17
RD26	0.77	-0.42	0.27

[a] RD01 - RD26 = radial distances (mm X 0.10).

third principal components were bipolar, with the largest eigenvector loadings representing: the lower portion of the curve on the abaxial surface on the second principal component (RD12 to RD16); and the upper portion of the abaxial curve (RD01, RD02, RD07 to RD09, RD13 to RD15, RD19 to RD21, and RD26) on the third principal component (Figure 5) (Table 11). The variables associated with the largest loadings on the first principal component were also those that had the highest component of among-site variation in the nested ANOVA.

Discriminant Analysis

The first three discriminant functions based on the cone data were retained for subsequent analyses and accounted for 33.08 percent, 12.53 percent and 11.65 percent of the variation respectively (Table 12). The contributions associated with the cone characters were strongly unbalanced with most characters contributing a relatively small amount and cone volume, cone weight and the characters associated with cone curvature (cone length and mid-ordinate distance) contributing relatively large amounts. The largest standardized discriminant function coefficients were associated with: cone volume (positive) and cone weight (negative) on the first discriminant function; cone weight (positive) and cone volume (negative) on the second discriminant function; and cone curvature (positive) and cone weight (negative) on the third discriminant function. Discriminant analysis classified 38.44 percent of the trees into the correct group (site).

Table 12. Results of discriminant functions analysis for 19 cone characters of *Pinus banksiana*.

	DISCRIMINANT FUNCTIONS		
	1	2	3
EIGENVALUE	2.08	0.79	0.73
% VARIANCE	33.08	12.53	11.65
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS			
VARIABLES[a]			
CL	0.36	0.73	1.30
MO	-0.53	-0.28	-1.14
CW	0.21	-0.35	-0.46
CD	0.28	0.14	1.50
AL	-0.10	0.45	-0.23
UDI	-0.08	0.21	-0.04
AW	-0.15	-0.61	0.42
CV	1.45	-2.40	0.97
CWT	-2.16	2.64	-1.69
SN	0.70	0.11	-0.18
SL	0.63	-0.72	-0.73
SW	0.18	-0.06	0.01
AD	-0.11	0.00	0.08
SEN	-0.38	0.17	0.06
SEL	0.55	0.28	0.23
SEW	0.35	0.48	0.13
SED	0.64	0.40	-0.29
SEWT	-0.65	-0.45	-0.23
CUV	0.38	0.98	1.82

[a] CL = cone length; MO = mid-ordinate length; CW = cone width; CD = cone depth; AL = apophysis length; UDI = umbo distance; AW = apophysis width; CV = cone volume (mg); apophysis depth; SEN = seed number; SEL = seed length; SEW = seed width; SED = seed depth; SEWT = seed weight; and CUV = cone curvature (all measurements in mm except where noted).

Three populations: two (Nakina); eight (Cameron Falls); and nine (Beardmore) (Figure 3) had no individuals correctly classified. These populations appear to be less coherent, exhibiting more variation within the site than the other populations. The discriminant analysis correctly classified 41.08 percent of the thirty-six western populations; but only 34.81 percent of the twenty-eight eastern populations, including eight populations from Armstrong, were correctly classified.

The data set used for discriminant analysis of the needle characters consisted of 14 parametric measures and the three new summary variables generated from principal component analysis of the 26 radial distances. This discriminant analysis produced five significant functions. The first three were used for subsequent analyses and accounted for 20.90 percent, 16.27 percent and 9.29 percent of the variation respectively (Table 13). In contrast to the cone discriminant analysis, the first discriminant function derived from the needle data was fairly small with small balanced contributions associated with most variables. The largest standardized discriminant function coefficients were associated with: needle width (negative) and radial distance summary variable 1 (positive) on the first discriminant function; right resin canal depth (positive) and radial distance summary variable 1 (positive) on the second discriminant function; and radial distance summary variable 1 (positive) on the third discriminant function. Discriminant analysis correctly classified 26.14 percent of the trees into the correct group (site). Only one site, twenty-eight (Armstrong), had none of its individuals correctly classified. Of the

Table 13. Results of discriminant functions analysis for 14 morphometric characters and 3 summary variables of needle shape of *Pinus banksiana.*

	DISCRIMINANT FUNCTIONS		
	1	2	3
EIGENVALUE	0.77	0.51	0.34
% VARIANCE	21.07	14.03	9.19
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS			
VARIABLES[a]			
NLEN	-0.04	-0.15	-0.21
NW	-0.71	-3.71	-0.21
NT	-0.19	-2.63	-0.56
VBT	-0.07	0.19	-0.67
VBAD	0.00	1.00	-0.42
RCLT	0.06	-0.53	0.08
RCLAD	0.40	-0.45	0.03
RCLL	-0.10	0.55	0.45
RCLAB	0.49	-0.87	-0.87
RCRT	-0.03	8.05	0.21
RCRAD	0.57	-0.19	-0.33
RCRL	0.22	0.12	-0.17
RCRAB	0.19	0.00	0.20
VBW	-0.04	0.09	-0.44
RSC1	0.60	5.69	2.31
RSC2	-0.11	2.17	0.22
RSC3	-0.49	0.48	0.62

[a] NLEN = needle length (mm); NW = needle width; NT = needle thickness; VBT = vascular bundle thickness; VBAD = vascular bundle adaxial distance; RCLT (RCRT) = resin canal depth (left & right); RCLAD (RCRAD) = resin canal adaxial distance (left & right); RCLL (RCRL) = resin canal distance to needle surface (left & right); RCLAB (RCRAB) = resin canal abaxial distance; VBW = vascular bundle width; and RSC1 - RSC3 = radial distance summary variables from PCA (all measurements in mm X 0.10 except where noted).

twenty-eight eastern populations, including eight from Armstrong, 31.09 percent were correctly classified, whereas, 25.65 percent of the thirty-six western populations were correctly classified. The first radial distance summary variable contributes strongly to all three discriminant functions. The radial distances that define the curve between the adaxial and abaxial surfaces have the largest loadings on the first radial distance summary variable thus indicating that needle shape is important for discriminating among groups. In addition to defining needle shape the radial distances are an indication of the size of the needle. Therefore, needle size is also an important factor in discrimination among groups. The variables that best distinguish among groups, needle width and the radial distances that define the curve between the adaxial and abaxial surfaces, are also the variables that contribute the most to the first principal component.

Ordination Of Populations

Ordination of the first versus the second, and first versus third principal component and discriminant scores were used to examine the relationships of the populations to each other. For both cone and needle data the populations formed a single cluster with overlapping standard deviations (Figures 6 and 7; Appendix 9). Although the populations formed a single group, examination of the centroids revealed that the location of the populations along the axes corresponded to longitude.

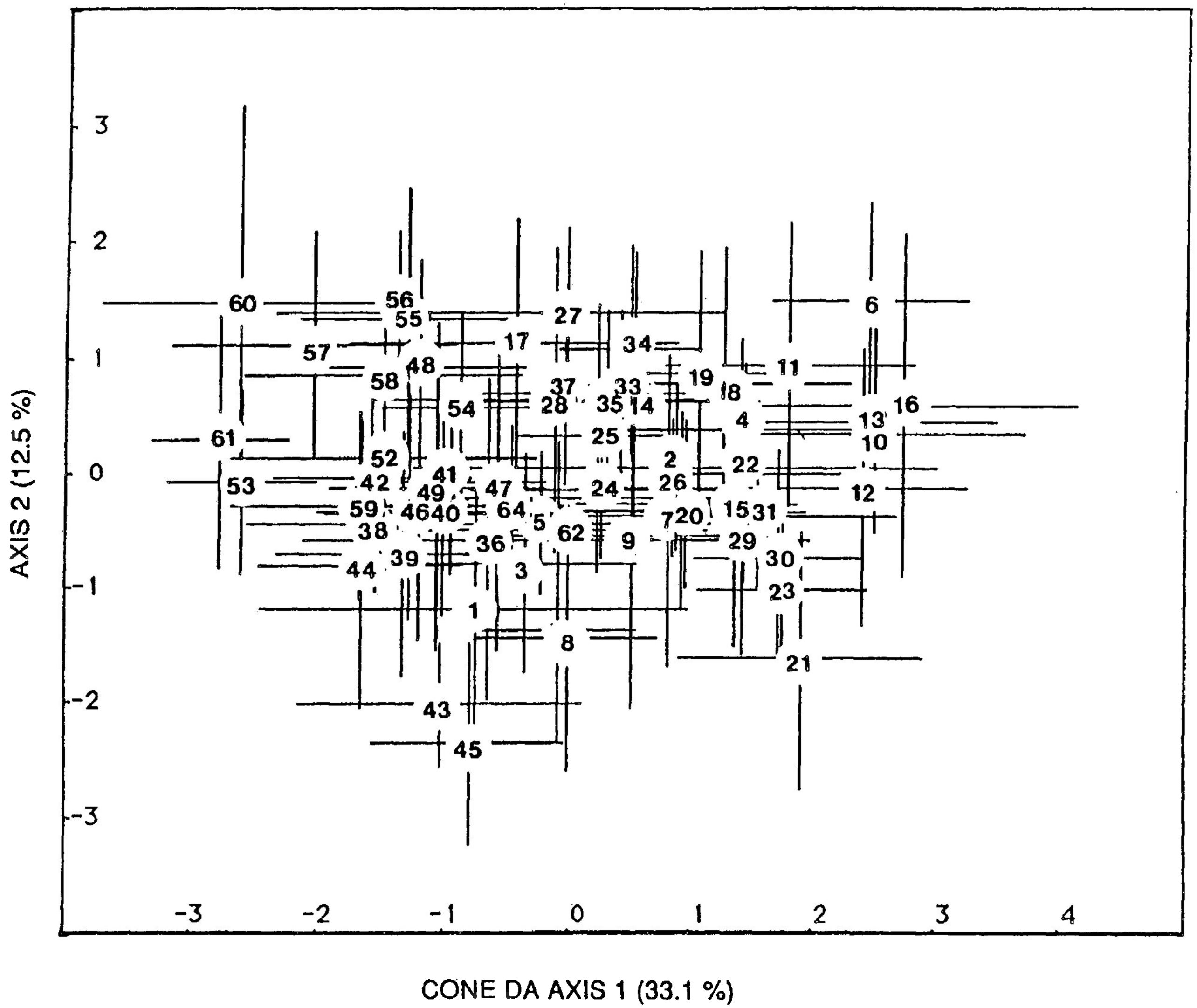


Figure 6. Ordination of discriminant cone axes one and two.

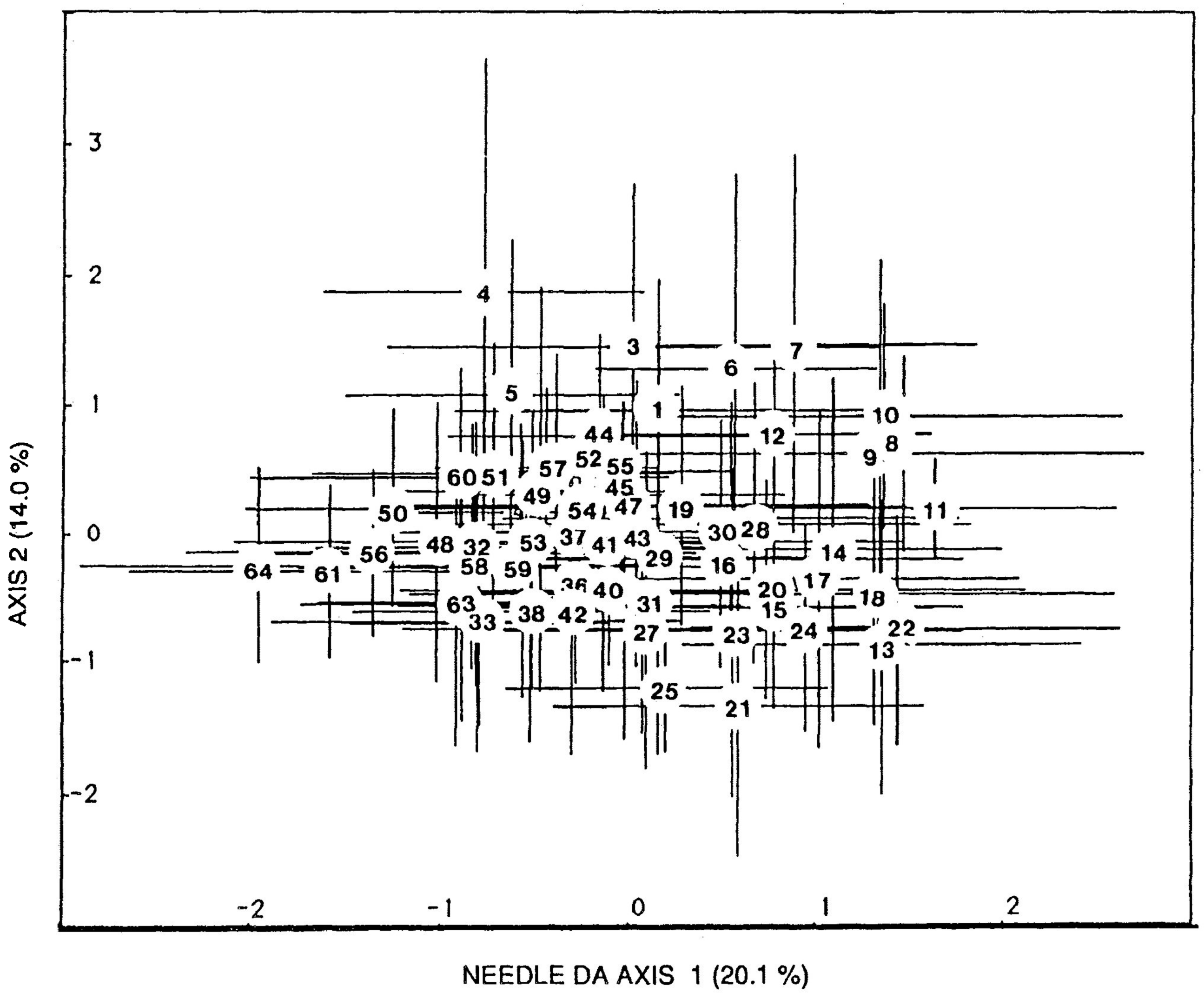


Figure 7. Ordination of discriminant needle axes one and two.

The populations appear to form two groups east and west of longitude 88°15', the Lake Nipigon area. The separation of the populations into the two groups was most easily distinguished on the ordination of the discriminant scores.

Regression Analysis

Simple Regression Analysis

Simple regressions of cone principal component and discriminant analysis scores (dependent variables) with spatial and climatic data (independent variables) produced r^2 values ranging from $0.00^{n.s.}$ to 0.06^{**} for principal component scores and from $0.00^{n.s.}$ to 0.23^{**} for discriminant analysis scores (Table 14). The largest r^2 values were associated with the first discriminant function and: longitude (0.23^{**}), elevation (0.21^{**}), maximum June temperature (0.10^{**}), and extreme minimum temperature (0.11^{**}).

The regression coefficients for cone principal component and discriminant analysis scores with FEC data were less, ranging from $0.00^{n.s.}$ to 0.02^{*} for the principal component scores and from $0.00^{n.s.}$ to 0.08^{**} discriminant analysis scores (Table 14). The largest values were for: the second discriminant function and soil texture (0.06^{**}), the third discriminant function and percent bedrock (0.04^{**}), and the first discriminant function and percent conifer (0.03^{**}).

The needle principal component and discriminant analysis scores showed slightly less correlation with the climatic and

Table 14. Coefficient of determination (r^2) for simple regression of cone DA summary variables of *Pinus banksiana* against spatial, climatic and ecological data.

	DEPENDENT VARIABLES[a]		
INDEPENDENT VARIABLES[b]	DFA1	DFA2	DFA3
LAT	0.01*	0.01	0.00
LONG	0.23**	0.01*	0.01**
ELEV	0.21**	0.00	0.03**
JUMAX	0.10**	0.00	0.00
JAMIN	0.02**	0.01*	0.00
MNDLY	0.01*	0.01*	0.00
EXMAX	0.02*	0.02**	0.00
EXMIN	0.11**	0.04**	0.04**
PCIPSN	0.00	0.02**	0.01
PCIPTL	0.01	0.02**	0.00
DDH	0.01*	0.01*	0.00
DDG	0.05**	0.00	0.00
FFDYS	0.01	0.00	0.00
FSP	0.00	0.00	0.00
FFA	0.00	0.00	0.00
SODP	0.02*	0.00	0.01*
SATX	0.00	0.06**	0.01
PERS	0.01	0.00	0.01
PERC	0.00**	0.00	0.01
PERSI	0.00	0.01	0.01*
PERCO	0.03**	0.02**	0.01
PERHW	0.01**	0.00	0.01
PERPJ	0.01**	0.02**	0.01*
PERSB	0.02**	0.00	0.01
PERSW	0.00	0.00	0.01
PERLI	0.01*	0.00	0.02**
PERBD	0.01**	0.00	0.04**
PERF	0.00	0.01*	0.00

* significant at $\alpha = 0.05$.

** significant at $\alpha = 0.01$.

[a] DFA1 to DFA3 = discriminant functions from DA of 19 cone characters.

[b] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperatureEXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost; SODP = soil depth (cm); SATX = sand texture (mm); PERS = percent sand; PERC = percent clay; PERSI = percent silt; PERCO = percent conifer; PERHW = percent hardwood; PERPJ = percent jack pine; PERSB = percent black spruce; PERSW = percent white spruce; PERLI = percent lichen; PERBD = percent bedrock; and PERF = percent feather moss

Table 15. Coefficient of determination (r^2) for simple regression of needle DA summary variables of *Pinus banksiana* against spatial, climatic and ecological data

	DEPENDENT VARIABLES[a]		
INDEPENDENT VARIABLES[b]	DFA1	DFA2	DFA3
LAT	0.03**	0.01**	0.01*
LONG	0.10**	0.02**	0.00
ELEV	0.13**	0.01	0.00
JUMAX	0.07**	0.00	0.00
JAMIN	0.00	0.00	0.02*
MNDLY	0.00	0.00	0.01*
EXMAX	0.01*	0.02**	0.00
EXMIN	0.05**	0.00	0.00
PCIPSN	0.00	0.02**	0.01*
PCIPTL	0.02**	0.05**	0.01*
DDH	0.00	0.00	0.01*
DDG	0.04**	0.00	0.01
FFDYS	0.00	0.00	0.01*
FSP	0.00	0.00	0.01**
FFA	0.00	0.00	0.01
SODP	0.04**	0.01*	0.04**
SATX	0.01*	0.01*	0.00
PERS	0.00	0.00	0.00
PERC	0.04**	0.01*	0.02**
PERSI	0.00	0.01*	0.00
PERCO	0.01*	0.00	0.01*
PERHW	0.01	0.05**	0.01*
PERPJ	0.00	0.00	0.01
PERSB	0.00	0.00	0.00
PERSW	0.00	0.00	0.01
PERLI	0.00	0.00	0.00
PERBD	0.00	0.01	0.00
PERF	0.00	0.00	0.02**

* significant at $\alpha = 0.05$.

** significant at $\alpha = 0.01$.

[a] DFA1 to DFA3 = discriminant functions from DA of 19 cone characters.

[b] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperatureEXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost; SODP = soil depth (cm); SATX = sand texture (mm); PERS = percent sand; PERC = percent clay; PERSI = percent silt; PERCO = percent conifer; PERHW = percent hardwood; PERPJ = percent jack pine; PERSB = percent black spruce; PERSW = percent white spruce; PERLI = percent lichen; PERBD = percent bedrock; and PERF = percent feather moss

spatial, and FEC data than the cone scores. The values for the simple regressions with climatic and spatial data ranged from $0.00^{n.s.}$ to 0.05^{**} for the principal component scores and from $0.00^{n.s.}$ to 0.10^{**} for the discriminant analysis scores (Table 15). The largest values were for the first discriminant function and elevation (0.13^{**}), longitude (0.11^{**}) and maximum June temperature (0.07^{**}).

The range of values for the simple regressions with the FEC data was less, for all but the second discriminant function, than the climatic data: $0.00^{n.s.}$ to 0.02^{**} for the principal component scores and $0.00^{n.s.}$ to 0.05^{**} for the discriminant analysis scores for FEC data as compared to $0.00^{n.s.}$ to 0.05^{**} for the principal component scores and $0.00^{n.s.}$ to 0.10^{**} for the discriminant analysis scores for climatic and spatial data. The largest value was associated with the second discriminant function and percent hardwood (0.05^{**}).

The regressions of the cone discriminant scores with environmental data shows a much stronger relationship than with the cone principal component scores. The strong relationship between environmental variables and discriminant scores indicates that much of the variation expressed among sites corresponds to spatial and /or climatic differences among sites.

Multiple Regression Analysis

The multiple regressions of cone and needle principal component and discriminant analysis summary variables (dependent variables) against spatial and climatic variables (independent variables) resulted in higher r^2 values than the simple regressions (Tables 16 and 17). The variables included in the regression model were not necessarily those that had the strongest relationships in the simple regressions. The multiple regression process creates a model that, using a combination of variables rather than a single variable, will result in the strongest relationship of dependent with independent variables. The complexity of the model may be a function of the complexity of the variation in climate and in cone and needle morphology.

The r^2 from the multiple regression analysis gives an indication of the relationship of the dependent variables to the independent variables. As individual tree summary variables were regressed against the climatic information for each site, the r^2 actually reflects the relationship of the variation in cone and needle morphology between sites to spatial and climatic data. The r^2 value can be compared to the percent variation expressed among sites, produced from a oneway ANOVA of each set of summary variables. Such a comparison will give an indication of how much of the variation among sites is attributable to spatial and climatic variation among sites.

The multiple regressions of cone and needle principal component scores with spatial and climatic data were weaker than those with the discriminant scores. The pattern of variation expressed by the first principal component does not appear to be

Table 16. Results of multiple regression of selected climatic variables and DA scores, and oneway ANOVA of the among groups variation of the DA scores for the cone data of *Pinus banksiana*.

DEPENDENT VARIABLE[a]	INDEPENDENT VARIABLES IN IN THE REGRESSION MODEL[b]	r^2	% VARIATION AMONG GROUPS
DFA1	FFDYS; PCIPTL; ELEV; PCIPSN; EXMAX; EXMIN; LAT	0.60**	64.27
DFA2	ELEV; PCIPSN; EXMAX; EXMIN; LONG; LAT	0.33**	38.24
DFA3	PCIPTL; ELEV; EXMIN; JUMAX; LAT	0.28**	36.27

* significant at $\alpha = 0.05$

** significant at $\alpha = 0.01$.

[a] DFA1 to DFA3 = discriminant functions from DA of 14 morphometric needle characters and 3 needle shape summary variables.

[b] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperatureEXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost.

Table 17. Results of multiple regression of selected climatic variables and DA scores, and oneway ANOVA of the among groups variation of the DA scores for the needle data of *Pinus banksiana*.

DEPENDENT VARIABLE	INDEPENDENT VARIABLES IN IN THE REGRESSION MODEL	r^2	% VARIATION AMONG GROUPS
DFA1	FFDYS; ELEV; PCIPSN; EXMAX; EXMIN; LAT	0.42**	36.74
DFA2	FFDYS; PCIPTL; JUMAX; LONG	0.33**	24.59
DFA3	FFDYS; EXMAX; EXMIN; LONG	0.17**	16.56

* significant at α = 0.05

** significant at α = 0.01.

[a] DFA1 to DFA3 = discriminant functions from DA of 14 morphometric needle characters and 3 needle shape summary variables.

[b] JUMAX = maximum June temperature; JAMIN = minimum January temperature; MNDLY = mean daily temperature; EXMAX = extreme maximum temperatureEXMIN = extreme minimum temperature; PCIPSN = precipitation from snow (cm); PCIPTL = total precipitation (cm.); DDH = heating degree days; DDG = growing degree days; FFDYS = frost free days; FFS = date of last spring frost; FFA = date of first fall frost.

strongly related to collection site, from the nested ANOVAs, and therefore probably not to the environment, and so low r^2 values are expected (Tables 16 and 17). The first principal component generated from the needle data does appear to be a result of collection site location based on nested ANOVAs but not strongly related to the variation in climate as demonstrated by the low r^2 values of the multiple regression.

The multiple regression of discriminant analysis summary variables against spatial and climatic data resulted in higher r^2 values ranging from 0.28** to 0.66** for the cone data and 0.17** to 0.42** in the needle data. A comparison of the r^2 values with the percent variation indicated by the oneway ANOVA revealed that most, if not all, of the variation between groups corresponds to collection site environment.

The relationship between the patterns of variation expressed by the first discriminant scores and the spatial and climatic variables was stronger for cone data. Although the variation in needle morphology is connected to collection site, it is not as highly correlated to spatial and climatic data as variation between groups based on cone morphology.

Trend Surface Mapping

The trend surface of both cone and needle discriminant scores revealed a steep cline between the eastern and western populations in the study area (Figures 8 and 9) with the trend from lower values in the west to higher values in the east. Both cone and needle trend

Figure 8. Trend surface of the first cone discriminant axis scores.

Figure 9. Trend surface of the first needle discriminant axis scores.

surfaces exhibit valleys to the east and west of Lake Nipigon. In addition, both cone and needle trend surfaces show a peak in the Armstrong area. The overall similarities are coupled with slight differences in the specific location of the peaks and valleys. A comparison of the trend surface of extreme maximum temperature (Figure 10) with the trend surface of discriminant function scores, for both cone and needle data, clearly shows the strength of the relationship between spatial and climatic data and the variation expressed by the discriminant scores reflected by simple and multiple regression analyses.

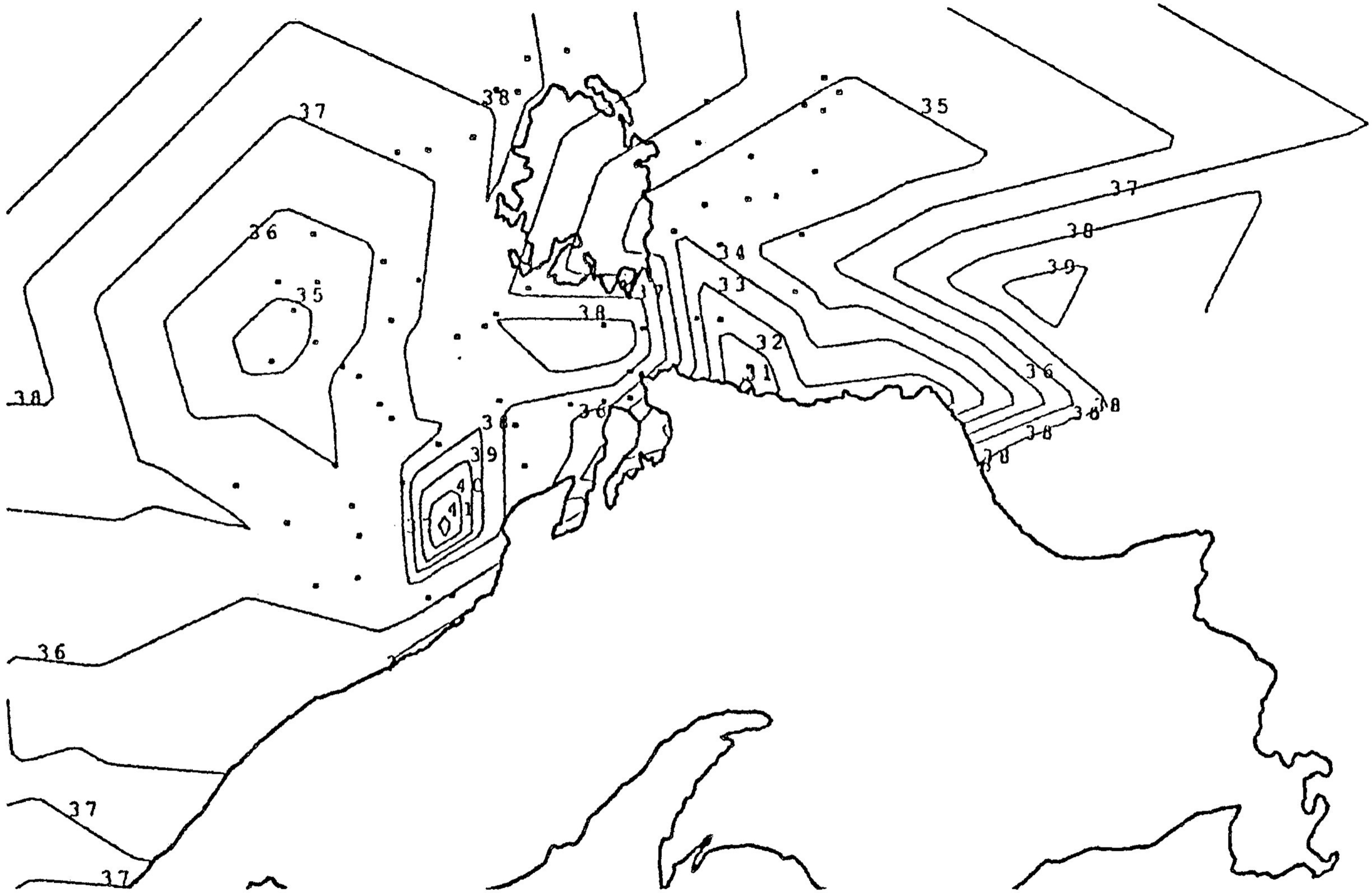


Figure 10. Trend surface of extreme maximum temperature (°C).

DISCUSSION

The patterns of variation in jack pine in the Lake Superior area have been attributed to adaptation to the present environment (Schoenike 1962; Schoenike 1976; Beshir 1975; Yeatman 1966), adaptation to the environment along two migration routes (Skeates 1979) or having originated from more than one glacial refugium (Schoenike 1962; Schoenike 1976; Beshir 1975; Yeatman 1966). The results of this northwestern Ontario study indicate that variation in jack pine is probably a reflection of the climate in the area. However, the data also support the hypothesis that the variation in jack pine may be a result of historical events.

Range-wide studies of variation in needle and cone characters indicate that jack pine forms a single group across the entire range (Schoenike 1962; Schoenike 1976; Beshir 1975). Schoenike (1976) subdivided the range of jack pine into eight clusters using cluster analysis. The cluster that includes the present study area, north central cluster, exhibited the least differentiation. Ordination of principal component and discriminant function scores of jack pine in northwestern Ontario indicates that the populations are similar enough to form a single group.

Similar to the present study in northwestern Ontario, most of the variation in cone and needle characters was attributed to among-groups differences by earlier research (Schoenike 1962;

Schoenike 1976; Beshir 1975). Variation among groups was greater for the range-wide studies compared to the present study. Presumably, this is due to the difference in size of the study areas and the climatic and ecological differences that the areas cover. In addition, some of the among group differences may be attributable to the inclusion of lodgepole pine X jack pine from the western extremity of the jack pine range (Schoenike 1962; Schoenike 1976; Beshir 1975).

Although the populations form a single group, closer examination of the ordinations, particularly those from the discriminant function scores, revealed that the populations tended to cluster by longitude. The populations were clustered into two groups, east and west of Lake Nipigon at longitude 88°15'W. A trend surface of the discriminant function scores demonstrated that the clustering of the populations is indicative of a steep cline (Figures 8 and 9). This cline was also noted by Schoenike (1976) in a range-wide study of variation in cone and needle morphology. Skeates' (1979) evaluation of a provenance test in Ontario separated the north-western population from the north-central by a line extending from longitude 93°W (Armstrong area) in the north to longitude 88°W (Nipigon area) in the south. The location of this division corresponds to the location of the cline and the clustering of the populations east and west of Lake Nipigon. Yeatman (1966), in a study of seedling growth, also noted differences between populations in the eastern and western portions of northwestern Ontario. However, the longitude designating the split between east and west was more westerly, longitude 91°W, than Schoenike's (1976), Skeates' (1979) or than noted in the present study.

Most of the variation in jack pine in northwestern Ontario can be accounted for by variation in spatial and climatic data, based on regression analyses. Both Schoenike (1976) and Beshir (1975) note that variation in individual traits across the entire range correspond to broad climatic changes. Yeatman (1966) proposed that the different relationships between seedling growth and growing degree days that was significantly different east and west of longitude 91°W, may reflect climatic differences in the eastern and western sections of the continent. A trend surface of maximum June temperature approximated the trend surface generated from both cone and needle discriminant scores with a steep cline at approximately longitude 88°15'W, indicating that the climate does indeed vary east and west of Lake Nipigon. From the results of this study in northwestern Ontario, it appears that variation in jack pine may be a response to climatic differences on a finer scale than those demonstrated in the range-wide studies.

The strong correlation of the patterns of variation with climatic data demonstrated by regression analyses and the trend surfaces suggests a causal relationship. However, there is evidence from the northwestern Ontario study that lends support to the hypothesis that the patterns of variation are a result of migration via two routes from one or more refugia. The trend surfaces based on cone and needle data were similar indicating that the patterns of variation are similar for reproductive and vegetative characters. As a species becomes reproductively isolated into two or more groups, each group will exhibit greater correlation among functionally unrelated characters than will a single undiverged group (Maze 1983). The overall similarity between the patterns of variation of cone and needle characters reported here supports the existence of the two groups of jack pine as a result of a single group split by two migration routes or having originated from two refugia. A closer look at the two groups, east and west of Lake Nipigon, further substantiates the existence of two migration waves or two refugia as the patterns of cone and needle variation are similar within each group. The data do not indicate if jack pine followed two migration routes from a single refugium or is a result of migration from two refugia. However, there is some evidence indicating that other species, white pine and alder, moved into northwestern Ontario via two migration routes, above and below Lake Superior (Bjorck 1985).

The discriminant analysis correctly classified more populations in the west than in the east based on cone data but *visa versa* based on needle data. However, the number of populations correctly classified was greater for cone data that needle data. If differences among populations are a result of adaptation to climate *via* selection, it would appear that selection pressures are greater in the west for cone characters and in the east for needle characters. In addition, selection pressure is greater for reproductive than vegetative parts. However, correct classification of cones is almost all based on cone volume and cone weight, whereas, all needle characters contribute equally.

The currently most accepted hypothesis, supported by modern patterns of variation, and macro- and micro-fossils, is that the jack pine occupying most of the present range originated from a single refugium located in the Appalachian Highlands. On the other hand, the patterns of variation in the Lake States area indicates the presence of two or more refugia located in the midwestern United States (Critchfield 1985). Jack pine apparently migrated from the refugia following the moraines, outwashes and eskers left by the retreating ice (Yeatman 1967; Wright 1968). However, the historical spread of jack pine is difficult to assess due to the large volumes of widely dispersed pollen and the number of species involved, lodgepole pine in the west, and red and white pine in the east (Ritchie 1976).

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APPENDICES

APPENDIX I

JACK PINE COLLECTION SITE LOCATIONS

SITE 1 From the junction of Hwy584 and Hwy 643, travel 2 km. east down Hwy 643, plot on right.	**SITE 9** From the junction Hwy 11/17, go 80.6 km. north on Hwy 11, plot on left.
SITE 2 From the junction of Crib rd. and Hwy 584, travel 24.75 km. north on Hwy 584, plot on right.	**SITE 10** From the OPP Stat. on Hwy 11/17, take road directly west from OPP Station, travel 1.4 km, plot at T-Intersection
SITE 3 From the junction of Crib Rd. and Hwy 584, travel 17.2 km. east on Crib Rd., plot on left	**SITE 11** Junct Hwy 17/ Domtar Haul Rd to Unit 81, N. on Haul Rd. 45.1 km., right, travel 5.6 km. to plot (both sides of road).
SITE 4 From junction of Crib Rd. and Hwy 584, travel 20.4 km. on Crib Rd. to Fleming Rd., 8.2 km. down Fleming Rd. plot on right.	**SITE 12** Junction Hwy 17/ Domtar Haul Rd. to Unit 81, N. on Haul Rd. 45.1 , turn left 4.55 km. to plot on right.
SITE 5 From junction Greta Lk. Rd. and Hwy 584, travel 3.8 km. east on Greta Lk. Rd., plot on left by gravel pit.	**SITE 13** Junct of Hwy11/17 and Red Rock Rd., W.~ 7 km. to Everard Rd. down Everard Rd. 2.2 km., plot left
SITE 6 From junct. Kinghorn Rd. and Hwy 11, travel 59.65 km. N. on Kinghorn Rd. to Onaman River Camp Rd., turn right and travel 24.1 km., plot on right.	**SITE 14** Junction Hwy 11 and Hwy 801, travel 9.4 km. N. on Hwy 801, plot on left by dump.
SITE 7 Junction Kinghorn Rd. and Hwy 11, travel north on Kinghorn Rd. 55.3 km., plot on left behind older stand.	**SITE 15** Junction Hwy 11 and Hwy 801, travel 1.6 km. N. on Hwy 801, plot on left.
SITE 8 Junction Hwy 585 and Hwy 11/17, travel N on Hwy 585 past Camaron Falls (~15 km.), turn left 6.7 km., plot on right.	**SITE 16** Junct. Hwy 11/17 and Hurkett Rd., travel 5.75 km. N to Stewart Lk. Rd., turn right, go 9.65 km., turn left, go 6.35 km. plot at junction of Driftwood Rd. on right.

SITE 17 From the junct Hwy 11/Kinghorn Rd., travel 14.65 km. on Kinghorn Rd., right, travel 15 km. plot on right	**SITE 25** From junct. Hwy 527/Obonga Lk Rd travel 33.4 km. down Obonga Lk Rd left, travel 14.5 km plot on left
SITE 18 From junct. Hwy 11/ Kinghorn Rd., travel 3.05 km. on Kinghorn Rd., plot on left - (just over tracks)	**SITE 26** From junct Hwy 527/Obonga Lk Rd travel 29.6 km down Obonga Lk Rd plot on left
SITE 19 From junct. Hwy11/Geraldton Rd. travel 28.3 km west on Hwy 11 turn rt, travel 0.65 km. plot on rt (next to gravel pit)	**SITE 27** Junct McKenzie Lk Rd./Hwy 527 travel south on Hwy 527 22.55 km turn right travel 2.8 km, turn right 3.65 km plot on left
SITE 20 From junct. Hwy 11/Geraldton Rd. 4.8 km. west on Hwy 11, left 18.1 km on Goldfield Rd right 3.4 km., plot on left	**SITE 28** From post office in Armstrong, north past Airport onto Pikatigushi Rd 16.6 km to White Sand River plot on left just past river
SITE 21 N/A	**SITE 29** From post office in Armstrong, north past Airport onto Pikatigushi Rd 38.2 km, take East Branch 11.2 km turn rt 1.35 km plot on right
SITE 22 From junct. Hwy17/Airport Rd at Terrace Bay, travel to airport 0.25 km. - plot on left	**SITE 30** From post office in Armstrong, north past Airport onto Pikatigushi Rd 38.2 km, take West branch 11.6 km plot just across creek (end of rd)
SITE 23 Junct. McKenzie Lk Rd/ Hwy 527 N on Hwy 527 0.32 km - plot on left	**SITE 31** From junct Hwy 61/Hwy 593 travel 9 km down Hwy 593 to Devon Rd/ Pigeon River Rd turn rt travel 17.3 km on Devon Rd plot on rt
SITE 24 From church in Armstrong, travel towards the airport 2.4 km. plot on the left	**SITE 32** From junct Hwy 597/Hwy 608 travel s on Hwy 597 to Moores Ck Bridge 1.7 km further plot on right

SITE 33 From Madeleine Lk JR Camp E on Northern Lts Lk Rd 10.16 km plot on left	**SITE 41** Junct Hwy 17/Dog R Rd, 4.2 km down Dog R. Rd to fork, straight (rt) 0.7 km, right 3.35 km, left 2.45 km. plot on left
SITE 34 From Madeleine Lk JR Camp e on Northern Lights Lk Rd 9.12 km plot on left	**SITE 42** Junct Dog R. Rd/Hwy 17 15 km on Dog R. Rd (to 15 km marker) plot on right
SITE 35 From junct Hwy 527/Dorion Cutoff 5 km south on Hwy 527 plot on left	**SITE 43** Junct Hwy 11/Hwy 586 west on Hwy 11 10.3 km, right 4.6 km, left 5.3 km., left 2.35 km, left 1.4 km, left 2.05 km, plot on right
SITE 36 From junct Hwy 527/Dorion Cutoff 25 km south on Hwy 527 plot on left	**SITE 44** Junct Hwy 527/Dorion C.off 14.2 km e. down Dorion C., go down small rd on left (1 ch.), across intermit stream plot on ridge
SITE 37 Junct Hwy 527/Camp 45 Rd 15.2 km down Camp 45 Rd, left 5.02 km, left 0.9 km (thru C.O.) plot on right	**SITE 45** Junct Hwy 527/Dorion C., 11.6 km N on Hwy 527 to Mott Lk Rd, 5.6 km on Mott Lk Rd, plot 0.1 km down side rd (right) on left
SITE 38 From Rinker Lk JR Camp, north on Hwy 527 7.2 km plot on left	**SITE 46** Junct Hwy 527/Pace Lk Rd. N on 527 33.55 km to Sturgeon R. Rd, right 65.05 km to Hurkett C., left 49.7 km, right 1.9 km plot on left by gravel pit
SITE 39 Camp 45 Rd. to Black Sturgeon Rd to Little Posh Rd (~96 km) south river rd	**SITE 47** Dog R. Rd to CP Camp 234 (~24 km), past camp 18.1 km, right 6.6 km, left 10.3 km, left 3.8 km, right 9.1 km plot on right
SITE 40 Junct Dog River Rd/Hwy 17 to CP Camp 234, turn left just before camp, 7.5 km, turn right 5.15 km plot on left	**SITE 48** Junct Hwy 11/Hwy 801 (S) left on Hwy 801 6.05 km, left 15.5 km. plot on left

SITE 49 Junct Hwy 17/Rd to Michener Twp, 22.5 km on main rd to plot on right	**SITE 57** Junct Wawang Lk Rd/Graham Rd S 2.25 km , plot on right across creek/swamp
SITE 50 Junct Hwy 11/Hwy 17 5.15 km down Hwy 17 to Hydro Rd (64-1+9.27) right 0.15 km, 1 ch. into gravel pit plot on right	**SITE 58** Junct Snipe lk Rd/Graham Rd, E on Snipe Lk Rd 18.3 km, plot on right, edge of creek/swamp
SITE 51 Junct Hwy 11/Shebandowan Rd 9.6 km down Shebandowan Rd, left 3.6 km to plot	**SITE 59** Junct Hwy 17/Graham Rd, N on Graham Rd 23.05 km, plot on right
SITE 52 Junct Hwy 17/Dog R. Rd, 24 km to CP Camp 234, left 18.2 km, left 10.05 km, plot on left	**SITE 60** Junct Madden Lk Rd (811)/Hwy 527 W on Madden Lk Rd 17.56 km, plot on right
SITE 53 N/A	**SITE 61** Junct Hwy 811/Hwy 527 W on Hwy 811 15.15 km, stand on left
SITE 54 Junct Graham Rd/Brightsand Rd S on Graham Rd 0.2 km, plot on right	**SITE 62** Junct Hwy 11/RD 76 (2.81 km S. of Beardmore, 13.6 km, left, 6.2 km, keep left, 13.65 km, left, 0.8 km, stand at C.O. boundary on left and rt.
SITE 55 Junct Hwy 17/Graham Rd N on Graham Rd 71.8 km, right 2.25 km, right 5.70 km, across C.O by lake	**SITE 63** Junct Hwy 11/RD 76 (2.81 km S. of Beardmore, 13.6 km, left, 6.2 km, S to Gorge Ck Rd (14.5 km), left 28.1 km, plot on rt behind gravel pit
SITE 56 Junct Wawang Lk Rd/Graham Rd N 18.95 km to Moberly Lk Rd, left 13.50 km, stand on right	**SITE 64** 20.95 km down Boreal Rd., stand on right

APPENDIX II

JACK PINE COLLECTION SITE DESCRIPTIONS

COLLECTION SITE	SITE DESCRIPTION
1	Lower slope; black spruce co-dominant (40%); feather moss (65%); fairly closed canopy; deep coarse sand.
2	Level site; black spruce understory; young stand (may have been thinned); feather moss (80%); coarse sand.
3	Level site; black spruce sub-dominant (7%); feather moss (85%); young stand; very coarse sand.
4	Jack pine with some aspen (10%); approximately 70% cover; birch and spruce in the understory; deep medium sandy soil; stand on the upper slope.
5	Gently rolling; fairly dense stand of younger (30 years) trees; understory of aspen black spruce and birch; deep medium/coarse sandy soil; 70% cover.
6	Upper slope; black spruce understory; feather moss (80%); coarse/very coarse sand.
7	Gently rolling; black spruce understory with old growth black spruce/jack pine nearby; deep silty very fine sand/medium sand; feather moss (80%).
8	Crest of small hill; sub-dominant white spruce (20%); birch/balsam fir understory; feather moss (78%); deep very fine/fine sand.
9	Level site; co-dominant aspen (not in plot); feather moss (35%); litter/debris (60%); silty very fine sand.

10	Level site; aspen/spruce/balsam fir understory with some aspen co-dominant (20%); leaf litter (40%); feather moss (50%); deep medium/coarse sand.
11	Upper slope; jack pine (15%) and spruce (5%) growing in pockets of soil; exposed bedrock (50%); shallow medium sand; lichens (30%).
12	Bedrock knob; some spruce (5%); exposed bedrock (50%); lichens (30%); shallow medium sand.
13	Aspen with pockets of pure jack pine; gently rolling/level; leaf litter (80%); deep medium sand.
14	Level site; black spruce understory; feather moss (80%); litter/debris (10%); deep coarse sand.
15	Level site; white spruce/balsam fir understory; open areas with mountain maple and green alder; litter/debris (35%); feather moss (60%); very coarse sand.
16	Level site; fairly open; birch understory and aspen in stand (not in plot); litter/debris (95%); rich site; medium sand.
17	Crest of hill; black and white spruce understory; litter/debris (10%); feather moss (85%); loamy sand.
18	Level site sloping gently to lake; aspen co-dominant (not in plot); birch/aspen understory; litter/debris (99%); deep very coarse sand.
19	Hilly terrain; co-dominant aspen (2%); black spruce understory; feather moss (80%); litter/debris (15%); deep coarse sand.

20	Upper slope; black spruce understory; feather moss (90%); litter/debris (5%); deep coarse sand.
21	Level site; black spruce co-dominant (15%); litter/debris (10%); feather moss (< 10%); very coarse sand.
22	Level site; no understory; feather moss (90%); fine sand.
23	Upper slope; black spruce co-dominant (4%); feather moss (90%); litter/debris (10%); coarse sand.
24	Level site; black spruce co-dominant (10%); feather moss (82%); litter/debris (18%); medium sand.
25	Shallow to bedrock with bedrock outcrops (10%); jack pine and spruce in pockets of soil; lichens (60%); shallow loam.
26	Fairly level sloping down to lake; black spruce understory; feather moss (85%); deep medium sand.
27	Level site; black spruce sub-dominant; feather moss (83%); shallow to bedrock (20 cm); silty loam.
28	Gently rolling; aspen in the openings (5%); litter/debris (10%); deep very fine sand.
29	Level site; sub-dominant black spruce; feather moss (85%); deep fine sand.
30	Level site; sub-dominant black spruce; feather moss (85%); lichen (1%); deep clay loam.

31	Level site; sub-dominant black spruce; feather moss (90%); lichen (1%); deep clay.
32	Crest of slope; shallow pockets of silt loam (3 cm); lichen (84%).
33	Upper slope; shallow pockets of loamy fine sand (9 cm); feather moss (77%); lichen (3%); litter/debris (20%).
34	Upper slope; white birch and aspen understory; feather moss (10%); litter/debris (86%); very fine sand; bedrock (70 cm).
35	Level site; black spruce understory; feather moss (99%); silty fine sand; bedrock (40 cm).
36	Upper slope; sub-dominant aspen (5%); feather moss (80%); litter/debris (15%); loamy coarse sand.
37	Level site; co-dominant white spruce (15%); balsam fir understory; litter/debris (60%); feather moss (35%); fine sand.
38	Mid-slope; black spruce understory (25%); bedrock (3 cm); sandy loam; feather moss (70 %); litter/debris (30%).
39	Level site; black spruce understory (40%); feather moss (78%); litter/debris (20%); deep silty clay loam.
40	Gently rolling; black spruce understory; litter/debris (10%); deep very fine sand.
41	Level site; co-dominant black spruce (15%); balsam fir understory; litter/debris (30%); feather moss (70%); deep clay loam.
42	Level site; sub-dominant balsam fir/white birch; herb rich; feather moss (5%); litter/debris (95%); deep loamy coarse sand.

43	Gently rolling; old growth jack pine (5%); co-dominant aspen (10%); feather moss (60%); litter/debris (40%); deep very coarse sand.
44	Shallow to bedrock; young jack pine; black spruce, balsam fir; white birch understory; litter/debris (80%); feather moss (20%); loamy sand (70 cm).
45	Bedrock knob; barren and scattered jack pine; exposed bedrock (20%); debris/litter (80%); silty very fine sand (10 cm).
46	Level site; black spruce/balsam fir understory; feather moss (80%); litter/debris (20%); deep coarse sand.
47	Gently rolling; mature white spruce (scattered); young jack pine; feather moss (60%); litter/debris (40%); deep loamy sand.
48	Rock outcrop; black spruce/white birch understory; feather moss (10%); exposed bedrock (40%); litter/debris (40%); silty sand (35 cm).
49	Bedrock outcrop; very open stand; some black spruce (5%); feather moss (20%); lichens (65%); exposed bedrock (10%); sandy loam (45 cm).
50	Gently rolling; black spruce understory; feather moss (60%); litter/debris (40%); deep very coarse sand.
51	Mid-slope; white birch,balsam fir, black spruce understory; feather moss (40%); litter/debris (60%); deep loamy sand.
52	Level site; feather moss (90%); deep medium sand.

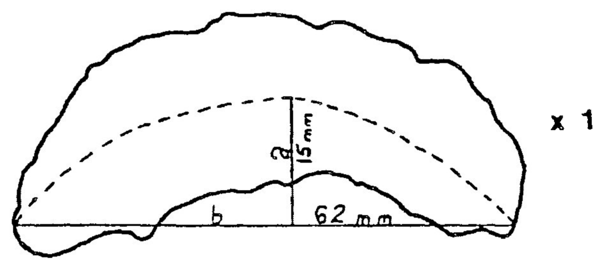
53	Gently rolling; co-dominant black spruce (25%); feather moss (37%); litter/debris (35%); loam (65 cm).
54	Level site; co-dominant black spruce (30%); feather moss (80%); litter/debris (20%); boulder pavement; sandy clay loam (30 cm).
55	Mid-slope; sub-dominant black spruce (7%); litter/debris (95%); deep silty very fine sand.
56	Level site; litter/debris (15%); feather moss (85%); deep very coarse sand.
57	N/A
58	Mid-slope; litter/debris (95%); white spruce/white birch understory; boulder pavement; loamy very coarse sand (25 cm).
59	Level site; litter/debris (25%); feather moss (74%); deep medium sand.
60	Upper slope; no understory; feather moss (87%); litter/debris (10%); deep fine sand.
61	Gently rolling; sub-dominant black spruce; feather moss (88%); litter/debris (15%); deep fine sand.
62	Crest of depression; sub-dominant black spruce; feather moss (82%); litter/debris (15%); deep very coarse sand.
63	On an esker; sub-dominant black spruce; litter/debris (10%); feather moss (75%); very coarse sand.
64	Bedrock knob; sub-dominant black spruce; feather moss (25%); lichen (1%); litter/debris (60%); loamy fine sand (20 cm).

APPENDIX III

METHOD OF CALCULATION OF CONE CURVATURE

Method of determining cone curvature

a. Projected outline of a typical jack pine cone



The ratio of "b," the long chord, to "a," the mid-ordinate, is a constant for a circle of any radius. This ratio describes a portion of the arc of a circle which can be expressed in degrees of arc or percentage curvature (degrees of arc/3.6). In the illustration above, $b/a = 4.01$. This describes an arc of about 106° or 29 percent curvature. The method assumes that the outline of a cone describes a portion of a circle. This is only approximately correct, but satisfactory for a rough approximation.

APPENDIX IV

LOCATION OF WEATHER STATIONS

WEATHER STATION	LOCATION	LATITUDE	LONGITUDE	ELEVATION (m.)
101	ABITIBI 228	48 56'	89 15'	472
102	ABITIBI 230	49 02'	89 22'	457
103	ARMSTRONG	50 17'	88 54'	320
104	ATIKOKAN	48 45'	91 37'	393
105	BEARDMORE	49 37'	87 57'	305
106	CAMERON FALLS	49 09'	88 21'	229
107	DORION	48 49'	88 31'	193
108	GERALDTON	49 42'	86 57'	331
109	GRAHAM	49 15'	90 40'	350
110	KAKABEKA FALLS	48 24'	89 37'	278
111	LONGLAC	49 46'	86 32'	343
112	NAKINA	50 11'	86 42'	325
113	NOLALU	48 09'	89 53'	381
114	RAITH	48 44'	89 52'	433
115	SCHREIBER	48 49'	87 16'	302
116	THUNDER BAY	48 22'	89 19'	199
117	MANITOUWADGE	49 09'	85 48'	332
118	MARATHON	48 43'	86 24'	189
119	MATTICE	49 36'	83 10'	233
120	MINE CENTRE	48 46'	92 38'	366
121	PAYS PLAT	48 52'	87 36'	285
122	PICKLE LAKE	51 28'	90 12'	369
123	RED LAKE	51 04'	93 48'	375
124	UPSALA	49 03'	90 28'	484
125	WHITE RIVER	48 36'	85 17'	379
126	CENTRAL PATRICIA	51 30'	90 09'	373
127	DRYDEN	49 46'	92 51'	372
128	BABBITT	47 41'	91 55'	485
129	BAUDETTE	48 43'	94 37'	323
130	BEMIDJI	47 30'	94 56'	418
131	CLOQUET	46 42'	92 31'	380
132	GRAND MARAIS	47 47'	90 20'	206
133	GRAND RAPIDS	47 14'	93 30'	393
134	TWO HARBOURS	47 01'	91 40'	188
135	VIRGINIA	47 30'	92 33'	431
136	DULUTH	46 50'	92 11'	428
137	INTERNATIONAL FALLS	48 34'	93 23'	354

APPENDIX V

CLIMATIC DATA FROM WEATHER STATIONS FROM THE PERIOD 1950 -1980

LOCATION	STAT. NO.	JUMAX	JAMIN	MNDLY	EXMAX	EXMIN	PCIPSN	PCIPTL	DDH	DDG	FFDYS	FSP	FFA
ABITIBI 228	101	24.2	-25.0	0.7	37.2	-42.8	232.4	734.8	6357.1	1364.3	84	159	243
ABITIBI 230	102	23.8	-25.6	0.2	37.8	-43.9	251.5	734.4	6531.0	1306.0	66	164	230
ARMSTRONG	103	23.6	-28.2	-1.1	38.3	-50.6	262.0	738.4	6990.8	1130.4	50	178	228
ATIKOKAN	104	24.5	-25.6	1.1	37.3	-45.6	237.4	724.0	6208.6	1411.9	81	165	246
BEARDMORE	105	23.4	-26.6	0.2	34.0	-48.3	335.7	784.0	6530.3	1273.5	80	163	243
CAMERON FALLS	106	23.6	-22.3	1.7	38.9	-46.1	233.6	793.3	6005.0	1361.4	102	154	256
DORION	107	22.8	-22.8	1.4	35.5	-42.8	168.6	685.0	6094.7	1261.8	84	162	246
GERALDTON	108	22.9	-27.0	-0.4	36.1	-47.8	239.6	697.0	6752.7	1219.1	68	168	236
GRAHAM	109	23.4	-26.1	-0.1	34.4	-32.2	268.1	816.6	6626.4	1291.7	89	159	248
KAKABEKA	110	25.4	-22.2	2.5	41.7	-48.3	191.6	710.0	5714.8	1500.5	94	153	247
LONGLAC	111	23.6	-27.3	-0.1	34.4	-47.8	268.7	813.3	6645.6	1310.1	59	170	229
NAKINA	112	22.9	-25.9	-0.6	35.0	-46.7	291.1	810.9	6815.5	1166.0	75	166	241
NOLALU	113	24.2	-23.4	1.4	36.7	-45.6	369.8	0.0	6096.3	1320.4	163	125	288
RAITH	114	24.1	-25.2	0.3	36.7	-46.7	221.0	749.8	6489.9	1225.2	31	185	216
SCHREIBER	115	19.6	-20.2	1.2	32.8	-42.8	212.5	860.2	6129.2	1090.3	109	146	255
THUNDER BAY	116	24.3	-21.3	2.3	37.2	-41.1	213.0	711.8	5767.9	1425.4	105	150	255
MANITOUWADGE	117	24.0	-23.5	1.1	39.4	-42.2	309.5	861.7	6215.5	1410.3	94	157	251
MARATHON	118	18.3	-19.1	1.9	32.2	-36.1	242.2	838.4	5899.8	1117.5	118	147	265
MATTICE	119	23.6	-25.7	0.2	37.2	-48.9	339.9	845.6	6566.6	1301.2	47	178	225
MINE CENTRE	120	25.5	-23.7	2.3	41.7	-47.2	179.9	706.2	5825.4	1628.4	101	151	252
PAYS PLAT	121	21.2	-21.1	0.0	30.6	-38.3	217.0	836.5	N/A	N/A	109	148	259
PICKLE LAKE	122	22.9	-26.9	-0.9	40.0	-51.1	265.7	760.9	6911.8	1276.4	92	158	250
RED LAKE	123	23.7	-26.5	0.7	37.2	-45.6	180.5	588.5	6350.2	1519.9	120	143	263
UPSALA	124	23.5	-25.4	0.6	35.6	-45.6	234.8	798.2	6395.0	1345.8	81	166	247
WHITE RIVER	125	23.1	-25.8	0.3	38.3	-51.7	291.6	823.3	6479.2	1206.7	57	170	227
CENTRAL PATRICIA	126	23.6	-27.9	-1.4	36.7	-53.9	321.9	697.5	7116.0	1197.0	43	177	220
DRYDEN	127	24.5	-24.4	1.6	39.4	-46.7	170.8	711.2	6086.6	1578.2	120	142	262

LOCATION	STAT. NO.	JUMAX	JAMIN	MNDLY	EXMAX	EXMIN	PCIPSN	PCIPTL	DDH	DDG	FFDYS	FSP	FFA
BABBITT	128	25.2	-20.0	3.7	35.6	-40.6	135.6	573.8	5459.0	1904.0	124	140	264
BAUDETTE	129	26.4	-23.8	3.2	37.2	-43.3	104.4	577.1	5644.0	1956.0	120	142	262
BEMIDJI	130	26.3	-23.1	3.2	38.3	-44.4	102.1	760.9	5669.0	1932.0	121	141	262
CLOQUET	131	26.6	-19.7	4.0	36.1	-40.6	76.1	670.6	5321.0	1893.0	104	153	257
GRAND MARAIS	132	21.4	-16.6	3.7	35.0	-36.1	143.0	669.5	5352.0	1511.0	138	135	273
GRAND RAPIDS	133	26.6	-20.8	4.2	37.8	-41.7	145.5	723.9	5295.0	1989.0	113	146	259
TWO HARBOURS	134	24.1	-16.5	4.4	37.2	-37.2	130.8	688.1	5128.0	1719.0	135	138	273
VIRGINIA	135	26.3	-21.2	3.7	36.1	-43.3	157.2	753.9	5468.0	1911.0	105	150	255
DULUTH	136	24.7	-19.4	3.4	36.1	-39.4	N/A	618.5	5501.0	N/A	N/A	N/A	N/A
INTERNATIONAL FALLS	137	25.8	-23.9	2.4	36.7	-43.3	N/A	N/A	5891.0	N/A	N/A	N/A	N/A

APPENDIX VI

MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) FROM CONE DATA

SITE NO.	CL	MO	CW	CD	AL	UDI	AW	CV	CWT	SN	SL	SW	AD	SEN	SEL	SEW	SED	SEWT	CUV
1	35.1	14.6	19.5	16.6	8.6	5.5	8.2	6.2	5.6	74.1	18.0	7.0	3.5	15.7	3.7	1.9	1.2	3.2	43.9
	(4.1)	(3.0)	(2.3)	(1.6)	(1.0)	(0.7)	(1.2)	(2.1)	(2.0)	(10.1)	(2.5)	(0.9)	(1.0)	(6.7)	(0.2)	(0.2)	(0.1)	(0.5)	(5.5)
2	35.0	15.8	19.6	17.7	8.6	5.8	8.7	6.8	6.2	81.4	18.7	7.2	3.8	18.6	3.9	2.0	1.3	2.8	46.6
	(4.4)	(2.5)	(2.7)	(2.1)	(1.1)	(0.8)	(1.2)	(2.2)	(1.7)	(7.5)	(2.6)	(0.6)	(0.8)	(6.6)	(0.3)	(0.2)	(0.1)	(0.5)	(5.9)
3	40.8	16.2	22.0	18.9	8.9	5.8	8.4	8.5	7.8	84.4	19.2	7.4	3.8	20.7	3.6	1.8	1.2	3.0	42.7
	(5.6)	(2.5)	(1.9)	(2.0)	(0.6)	(0.6)	(0.8)	(1.9)	(1.8)	(10.9)	(2.5)	(0.7)	(0.6)	(8.8)	(0.2)	(0.2)	(0.1)	(0.4)	(7.5)
4	40.2	16.5	20.3	18.3	9.0	5.8	8.3	8.3	7.5	88.2	20.1	7.2	3.8	23.6	4.1	2.1	1.2	2.8	43.8
	(7.4)	(2.3)	(1.5)	(1.4)	(1.2)	(0.9)	(1.3)	(1.9)	(1.7)	(8.9)	(2.2)	(0.8)	(1.1)	(6.2)	(0.5)	(0.2)	(0.1)	(0.8)	(7.7)
5	36.0	16.1	20.2	18.0	9.0	5.6	9.2	7.4	6.8	85.4	17.4	7.3	3.7	12.2	3.8	2.0	1.2	2.9	45.9
	(3.7)	(2.0)	(2.2)	(2.1)	(1.3)	(0.8)	(1.0)	(1.9)	(1.7)	(10.6)	(2.0)	(0.8)	(0.8)	(7.6)	(0.4)	(0.2)	(0.2)	(0.7)	(4.6)
6	38.8	14.5	20.1	17.2	8.3	5.4	8.0	7.0	6.6	83.9	18.4	6.7	3.2	19.5	4.2	2.2	1.4	2.9	40.9
	(6.1)	(1.9)	(1.8)	(1.7)	(1.4)	(0.9)	(1.0)	(2.1)	(4.8)	(8.6)	(2.0)	(0.6)	(0.8)	(9.1)	(0.3)	(0.1)	(0.2)	(0.5)	(5.8)
7	39.6	16.4	21.8	18.4	9.0	5.6	8.2	8.5	8.0	95.0	20.1	6.9	3.6	14.4	3.9	1.9	1.1	2.9	43.8
	(4.7)	(2.4)	(1.8)	(1.5)	(1.3)	(1.1)	(0.9)	(1.6)	(1.6)	(8.7)	(2.2)	(0.6)	(1.0)	(5.3)	(0.5)	(0.2)	(0.1)	(0.5)	(6.5)
8	38.3	14.6	21.0	18.3	7.9	5.2	8.5	7.3	6.5	88.2	17.2	6.7	3.3	16.5	3.6	1.8	1.2	2.7	40.8
	(5.3)	(3.2)	(2.3)	(2.6)	(0.7)	(0.7)	(0.7)	(2.7)	(2.2)	(14.9)	(1.3)	(0.3)	(0.7)	(8.4)	(0.4)	(0.3)	(0.1)	(0.5)	(3.5)
9	39.2	14.9	21.6	18.9	8.7	5.4	9.1	8.2	7.6	84.7	18.4	7.4	3.4	20.6	4.0	2.0	1.2	3.1	41.3
	(6.2)	(2.5)	(2.2)	(1.7)	(1.4)	(1.0)	(1.2)	(1.9)	(1.7)	(14.1)	(2.9)	(0.8)	(1.0)	(11.3)	(0.6)	(0.2)	(0.1)	(0.5)	(6.8)
10	39.7	15.2	21.8	18.6	8.3	5.5	8.0	8.1	7.4	88.5	19.2	6.7	3.4	15.3	4.1	2.1	1.3	3.0	41.6
	(5.0)	(1.4)	(2.3)	(2.0)	(1.2)	(0.8)	(0.8)	(2.1)	(1.9)	(10.3)	(1.1)	(0.5)	(0.8)	(5.7)	(0.3)	(0.2)	(0.1)	(0.4)	(5.5)
11	43.1	14.5	21.8	20.4	7.7	5.0	8.5	8.7	8.1	96.2	15.6	7.2	3.1	13.6	4.0	2.0	1.2	2.6	37.8
	(6.1)	(2.1)	2..6	(2.7)	(0.9)	(0.9)	(0.6)	(2.5)	(2.2)	(14.8)	(1.1)	(0.7)	(0.7)	(8.8)	(0.3)	(0.3)	(0.2)	(0.7)	(5.1)
12	40.2	14.4	21.0	19.4	7.9	4.9	8.8	8.1	7.2	91.4	17.5	7.4	3.2	18.5	4.1	2.1	1.2	2.4	39.8
	(7.2)	(2.1)	(2.0)	(1.5)	(0.8)	(0.7)	(0.7)	(1.8)	(1.5)	(10.6)	(1.2)	(0.4)	(0.6)	(11.0)	(0.3)	(0.2)	(0.1)	(0.3)	(6.8)
13	38.5	14.4	20.8	18.4	8.2	5.3	8.3	7.2	6.7	82.8	18.5	6.8	3.4	13.0	4.2	2.3	1.3	3.1	41.0
	(4.6)	(1.8)	(2.7)	(1.7)	(1.2)	(0.7)	(1.0)	(2.0)	(1.8)	(9.4)	(1.7)	(0.5)	(0.6)	(2.9)	(0.2)	(0.1)	(0.1)	(0.6)	(5.0)
14	37.7	16.1	20.9	18.5	9.3	6.0	8.9	8.1	7.5	75.9	19.1	7.5	4.1	22.7	4.1	2.2	1.3	3.2	44.7
	(4.9)	(3.3)	(2.5)	(1.8)	(1.5)	(1.0)	(0.9)	(2.8)	(2.7)	(10.4)	(2.3)	(0.8)	(0.9)	(5.6)	(0.3)	(0.2)	(0.1)	(0.5)	(5.0)
15	38.4	14.2	20.4	18.0	7.4	4.7	7.5	7.2	6.6	90.6	18.1	6.7	2.9	22.7	3.8	1.9	1.2	2.5	40.2
	(4.9)	(2.0)	(1.7)	(1.4)	(1.0)	(0.7)	(0.6)	(1.5)	(1.3)	(11.0)	(2.4)	(0.5)	(0.8)	(9.8)	(0.5)	(0.2)	(0.1)	(0.4)	(6.1)
16	38.8	14.9	21.2	18.5	8.0	5.1	8.3	7.5	6.8	80.2	18.7	7.0	3.4	18.1	4.2	2.2	1.5	3.4	41.6
	(3.6)	(2.6)	(2.7)	(1.7)	(1.3)	(0.8)	(0.9)	(1.8)	(1.4)	(9.8)	(2.2)	(0.8)	(0.8)	(8.5)	(0.2)	(0.2)	(0.2)	(0.4)	(6.6)

SITE NO.	CL	MO	CW	CD	AL	UDI	AW	CV	CWT	SN	SL	SW	AD	SEN	SEL	SEW	SED	SEWT	CUV
17	38.2	17.7	20.5	17.6	9.3	6.0	8.9	7.8	7.4	84.6	18.2	7.2	3.7	21.1	4.0	2.1	1.2	3.0	47.4
	(4.0)	(2.1)	(1.9)	(1.5)	(0.7)	(0.6)	(1.1)	(1.5)	(1.3)	(7.6)	(2.5)	(0.8)	(0.8)	(6.8)	(0.2)	(0.3)	(0.1)	(0.8)	(5.5)
18	43.0	16.0	20.9	19.0	8.5	6.4	8.2	8.9	8.3	91.5	18.8	7.1	3.4	18.3	4.0	2.1	1.2	2.8	40.8
	(6.5)	(2.7)	(1.3)	(1.0)	(1.1)	(0.9)	(1.0)	(1.9)	(1.7)	(8.7)	(2.0)	(0.5)	(1.0)	(4.7)	(0.1)	(0.2)	(0.1)	(0.4)	(7.3)
19	36.1	15.7	20.9	18.5	6.7	5.5	8.6	7.5	6.9	82.4	17.9	7.5	3.5	22.1	4.1	2.2	1.3	3.2	45.3
	(2.6)	(2.1)	(9.0)	(1.0)	(1.4)	(1.0)	(1.3)	(0.5)	(0.5)	(12.0)	(1.1)	(0.6)	(0.8)	(8.4)	(0.4)	(0.2)	(0.1)	(0.6)	(6.0)
20	42.3	14.2	20.7	19.0	8.0	4.9	8.1	8.1	7.7	88.7	18.5	7.2	3.0	16.4	4.0	2.1	1.2	3.0	37.8
	(4.9)	(1.4)	(2.5)	(2.1)	(1.2)	(0.8)	(1.1)	(1.7)	(1.7)	(10.3)	(2.1)	(0.7)	(0.8)	(7.3)	(0.3)	(0.2)	(0.1)	(0.5)	(5.1)
21	41.2	14.4	22.9	19.8	8.3	5.3	8.7	9.0	8.0	87.6	19.4	7.5	3.7	14.9	4.0	2.1	1.2	3.0	39.1
	(9.5)	(2.5)	(1.7)	(1.6)	(1.3)	(0.7)	(1.2)	(3.3)	(3.1)	(10.2)	(3.3)	(0.6)	(0.6)	(6.5)	(0.3)	(0.2)	(0.1)	(0.7)	(5.7)
22	37.3	14.4	19.6	17.5	6.9	4.3	7.3	6.4	5.9	90.1	16.7	6.6	2.8	16.8	3.8	2.0	1.2	3.5	41.4
	(2.7)	(2.5)	(1.7)	(1.3)	(1.2)	(0.9)	(0.9)	(1.2)	(1.2)	(7.4)	(2.0)	(0.6)	(1.0)	(5.7)	(0.3)	(0.2)	(0.1)	(0.4)	(6.1)
23	38.1	14.6	21.5	19.1	7.9	5.0	8.6	7.6	6.8	90.2	17.6	7.3	3.1	11.5	3.9	2.0	1.2	2.6	41.5
	(4.2)	(2.0)	(1.9)	(1.7)	(0.9)	(0.6)	(1.3)	(1.2)	(1.2)	(13.4)	(0.8)	(0.8)	(0.7)	(5.7)	(0.4)	(0.3)	(0.1)	(0.5)	(6.2)
24	37.1	15.0	21.4	19.1	8.3	5.1	8.8	7.5	6.9	77.2	17.3	7.2	3.7	23.1	4.1	2.1	1.2	2.8	43.2
	(6.5)	(2.0)	(2.4)	(2.3)	(1.1)	(0.6)	(0.7)	(2.4)	(2.0)	(7.6)	(2.5)	(0.5)	(0.6)	(6.5)	(0.4)	(0.2)	(0.1)	(0.6)	(5.3)
25	38.8	15.1	20.4	18.4	8.4	5.4	8.4	7.4	7.2	83.9	18.5	6.9	3.7	21.7	3.9	2.0	1.2	2.8	42.0
	(5.8)	(2.7)	(1.7)	(1.8)	(1.2)	(0.8)	(0.6)	(2.0)	(1.8)	(9.2)	(2.5)	(0.6)	(0.8)	(7.0)	(0.3)	(0.2)	(0.1)	(0.6)	(6.4)
26	36.2	16.1	20.7	18.2	8.6	5.3	8.4	7.5	7.0	87.0	19.0	7.1	3.8	18.4	4.1	1.9	1.2	2.7	45.9
	(2.7)	(2.2)	(2.8)	(1.5)	(0.8)	(0.8)	(0.8)	(1.6)	(1.4)	(7.5)	(1.7)	(0.7)	(0.7)	(5.2)	(0.2)	(0.2)	(0.1)	(0.4)	(4.5)
27	38.1	15.9	19.9	17.3	8.5	5.6	8.3	7.7	7.3	84.2	17.0	6.7	3.5	20.3	4.1	2.1	1.3	3.0	43.7
	(3.8)	(4.4)	(2.1)	(1.7)	(1.6)	(1.3)	(1.3)	(1.9)	(1.6)	(6.6)	(1.3)	(0.6)	(1.1)	(5.9)	(0.2)	(0.1)	(0.1)	(0.7)	(9.8)
28	36.0	15.9	19.1	17.0	8.3	5.4	8.6	6.5	6.0	83.9	16.3	6.9	3.4	19.5	3.9	2.0	1.2	2.5	46.3
	(6.4)	(1.9)	(3.3)	(2.3)	(0.6)	(0.9)	(1.0)	(2.2)	(1.9)	(9.2)	(2.3)	(0.9)	(0.7)	(6.2)	(0.3)	(0.2)	(0.1)	(0.4)	(5.7)
29	41.6	15.3	22.5	20.1	8.1	5.0	8.7	8.8	7.9	91.0	18.3	7.0	3.4	22.6	4.0	2.1	1.2	2.9	39.8
	(3.9)	(3.0)	(1.8)	(1.1)	(1.3)	(1.0)	(1.5)	(1.8)	(1.3)	(10.4)	(1.9)	(0.8)	(0.9)	(10.0)	(0.5)	(0.1)	(0.2)	(0.7)	(6.6)
30	39.0	14.0	22.0	19.2	7.9	4.9	8.4	7.8	7.2	85.3	18.8	7.2	3.3	18.5	4.1	2.1	1.2	2.9	39.7
	(3.6)	(1.1)	(1.1)	(0.8)	(1.0)	(0.7)	(1.0)	(0.9)	(1.0)	(10.3)	(1.7)	(0.4)	(0.7)	(9.0)	(0.1)	(0.1)	(0.1)	(0.3)	(3.1)
31	40.5	13.9	21.0	19.4	7.8	5.0	8.5	7.9	7.1	88.4	17.4	7.0	3.0	16.6	4.2	2.2	1.2	3.2	38.2
	(4.5)	(1.5)	(1.1)	(1.6)	(0.8)	(0.6)	(0.9)	(1.4)	(1.3)	(11.4)	(1.5)	(0.6)	(0.5)	(8.7)	(0.4)	(0.2)	(0.1)	(0.9)	(4.9)
32	37.7	15.0	21.5	19.0	8.3	5.2	9.0	8.2	7.6	85.9	18.5	7.5	3.4	22.9	4.1	2.1	1.2	2.8	42.7
	(3.5)	(1.4)	(1.8)	(0.9)	(0.8)	(0.6)	(0.6)	(1.6)	(1.3)	(5.9)	(1.4)	(0.6)	(0.6)	(8.0)	(0.3)	(0.1)	(0.1)	(0.4)	(3.3)

SITE NO.	CL	MO	CW	CD	AL	UDI	AW	CV	CWT	SN	SL	SW	AD	SEN	SEL	SEW	SED	SEWT	CUV
33	37.3	14.7	20.0	17.7	7.5	4.7	7.4	6.9	6.5	81.7	17.3	6.4	2.9	21.7	4.0	2.1	1.2	2.9	42.5
	(5.7)	(2.8)	(2.8)	(2.0)	(1.1)	(0.9)	(0.8)	(2.0)	(1.8)	(8.2)	(2.3)	(0.5)	(1.0)	(10.5)	(0.2)	(0.1)	(0.1)	(0.8)	(7.5)
34	37.6	16.3	19.8	17.7	8.5	5.5	8.2	7.2	6.7	8.0	17.6	6.7	3.4	19.5	4.2	2.1	1.2	2.9	45.2
	(4.5)	(3.2)	(1.7)	(1.1)	(1.4)	(1.1)	(0.7)	(1.4)	(1.3)	(11.3)	(2.4)	(0.4)	(0.8)	(10.4)	(0.3)	(0.1)	(0.1)	(0.4)	(7.5)
35	37.6	14.7	20.5	18.0	7.7	5.1	7.7	6.8	6.5	88.7	16.4	6.6	3.3	20.4	3.9	0.2	1.2	2.6	42.4
	(5.6)	(2.1)	(2.1)	(1.9)	(1.1)	(0.8)	(0.8)	(1.5)	(1.3)	(8.6)	(1.3)	(0.6)	(0.8)	(11.6)	(0.4)	(0.2)	(0.1)	(0.6)	(7.7)
36	37.9	16.3	21.8	18.4	8.6	5.2	9.0	8.0	7.4	82.2	17.4	7.0	3.5	18.2	3.9	1.9	1.2	2.8	45.2
	(7.4)	(2.6)	(2.5)	(1.7)	(0.6)	(0.6)	(0.7)	(2.6)	(2.2)	(10.5)	(1.7)	(0.7)	(0.6)	(3.8)	(0.5)	(0.2)	(0.0)	(0.2)	(5.8)
37	36.2	16.1	20.1	18.1	8.4	5.4	8.3	7.2	6.9	88.1	16.9	6.8	3.4	17.1	3.8	1.9	1.2	2.5	46.0
	(5.1)	(3.2)	(2.6)	(2.0)	(0.8)	(0.7)	(1.1)	(2.2)	(1.9)	(8.9)	(1.7)	(0.7)	(0.7)	(7.0)	(0.3)	(0.2)	(0.1)	(0.5)	(6.7)
38	37.7	15.7	19.6	18.2	8.0	5.1	8.3	6.9	6.7	83.6	16.9	6.8	3.3	17.2	3.6	1.8	1.1	2.6	43.8
	(3.7)	(2.8)	(1.9)	(1.4)	(0.6)	(0.6)	(0.8)	(1.6)	(1.4)	(12.7)	(1.1)	(0.9)	(0.5)	(5.9)	(0.4)	(0.2)	(0.1)	(0.8)	(6.6)
39	35.6	14.8	19.6	17.5	7.9	4.8	8.3	6.2	6.0	80.7	16.4	6.8	3.2	16.4	3.7	1.7	1.1	2.5	44.0
	(5.6)	(2.1)	(1.6)	(1.6)	(0.9)	(0.7)	(1.1)	(1.5)	(1.4)	(9.3)	(1.0)	(0.7)	(0.8)	(8.3)	(0.4)	(0.2)	(0.0)	(0.5)	(5.8)
40	35.0	14.3	19.2	15.9	8.5	5.2	8.8	6.1	6.0	81.2	16.9	6.7	3.4	15.6	3.8	1.8	1.2	2.8	43.3
	(3.7)	(1.9)	(1.8)	(1.1)	(0.8)	(0.6)	(0.9)	(1.3)	(2.5)	(10.2)	(1.6)	(0.7)	(0.4)	(5.7)	(0.2)	(0.2)	(0.1)	(0.4)	(4.3)
41	38.4	16.8	20.7	18.0	8.8	5.8	8.0	8.1	7.6	82.4	18.6	7.1	3.8	21.4	3.9	2.0	1.2	2.9	45.4
	(5.2)	(3.5)	(2.3)	(1.7)	(1.3)	(0.8)	(1.3)	(2.6)	(1.7)	(7.4)	(2.6)	(0.6)	(0.9)	(8.2)	(0.4)	(0.1)	(0.1)	(0.4)	(6.9)
42	36.5	15.5	20.2	16.8	8.8	5.6	8.5	7.0	7.0	85.9	17.6	6.6	3.7	15.8	3.6	1.8	1.1	2.6	44.5
	(4.1)	(2.6)	(2.3)	(1.4)	(1.1)	(0.9)	(1.0)	(1.8)	(1.5)	(8.7)	(2.0)	(0.9)	(0.9)	(4.5)	(0.2)	(0.2)	(0.1)	(0.6)	(6.0)
43	36.4	13.4	19.7	16.7	7.8	5.0	9.3	6.4	5.9	81.1	16.5	6.9	3.2	13.8	3.6	1.9	1.1	2.9	40.7
	(5.9)	(1.6)	(1.5)	(1.3)	(1.0)	(0.8)	(0.9)	(1.5)	(1.9)	(10.3)	(2.1)	(0.6)	(0.6)	(5.4)	(0.3)	(0.1)	(0.1)	(0.3)	(5.9)
44	38.5	14.2	20.9	17.4	8.4	5.4	8.4	7.5	7.2	88.5	16.7	6.9	3.5	16.0	3.4	1.7	1.1	2.6	40.2
	(4.3)	(2.5)	(2.6)	(2.0)	(1.0)	(0.7)	(0.8)	(2.1)	(1.3)	(9.3)	(1.4)	(0.6)	(1.0)	(3.0)	(0.2)	(0.2)	(0.1)	(0.5)	(4.3)
45	36.8	14.5	20.1	17.2	8.2	5.5	9.7	7.3	6.6	85.0	17.3	7.4	3.2	14.1	3.4	1.8	1.1	2.4	42.2
	(3.1)	(1.6)	(2.0)	(1.4)	(0.4)	(0.6)	(0.8)	(1.5)	(2.0)	(12.6)	(1.3)	(0.6)	(0.3)	(6.6)	(0.3)	(0.2)	(0.1)	(0.5)	(3.2)
46	37.7	17.8	21.1	17.4	8.7	5.5	8.8	8.1	7.7	88.4	18.2	6.9	3.4	18.8	3.6	1.8	1.2	2.8	47.7
	(2.7)	(2.9)	(1.9)	(1.4)	(1.0)	(0.9)	(0.7)	(2.2)	(1.2)	(7.1)	(1.5)	(0.6)	(0.7)	(7.6)	(0.3)	(0.2)	(0.1)	(0.4)	(3.0)
47	40.0	16.8	21.2	18.9	8.9	5.6	9.1	8.3	7.8	87.3	18.2	7.1	3.8	19.6	3.8	1.9	1.2	2.9	44.3
	(5.2)	(2.8)	(1.0)	(1.1)	(1.2)	(1.0)	(1.0)	(1.2)	(1.1)	(7.7)	(1.4)	(0.5)	(0.8)	(6.3)	(0.3)	(0.2)	(0.1)	(0.6)	(7.3)
48	34.2	16.4	19.2	16.6	7.9	5.1	8.1	5.9	6.1	81.3	16.7	6.5	3.2	15.6	3.6	1.9	1.2	2.4	48.2
	(3.0)	(2.8)	(2.2)	(1.5)	(1.0)	(0.8)	(0.8)	(1.7)	(1.8)	(12.8)	(1.8)	(0.5)	(0.6)	(6.7)	(0.3)	(0.1)	(0.1)	(0.3)	(4.7)

SITE NO.	CL	MO	CW	CD	AL	UDI	AW	CV	CWT	SN	SL	SW	AD	SEN	SEL	SEW	SED	SEWT	CUV
49	35.6	16.6	19.6	17.2	8.0	5.1	8.4	6.6	6.4	84.8	17.0	6.8	3.4	17.2	3.6	1.8	1.1	2.5	47.2
	(4.3)	(2.5)	(2.2)	(1.4)	(1.0)	(0.8)	(0.7)	(1.6)	(1.5)	(12.2)	(1.8)	(0.4)	(0.6)	(6.8)	(0.4)	(0.3)	(0.1)	(0.7)	(4.6)
50	37.4	13.6	19.9	18.1	7.3	4.5	8.3	6.3	5.9	87.4	16.6	6.6	2.9	16.8	3.5	1.8	1.1	2.3	39.7
	(3.2)	(2.2)	(1.5)	(1.3)	(1.0)	(0.8)	(1.3)	(1.5)	(1.3)	(9.4)	(1.8)	(0.6)	(0.7)	(7.4)	(0.1)	(0.3)	(0.1)	(0.3)	(4.0)
51	34.6	15.5	19.1	16.3	8.3	5.3	8.3	6.3	6.1	83.0	17.5	6.3	3.4	16.9	3.6	1.8	1.1	2.5	46.0
	(1.5)	(2.1)	(2.1)	(1.9)	(1.0)	(0.7)	(0.9)	(1.2)	(1.1)	(7.1)	(1.8)	(0.5)	(0.7)	(5.3)	(0.2)	(0.1)	(0.1)	(0.3)	(4.7)
52	37.4	14.9	19.9	17.4	7.8	5.0	7.9	6.7	6.7	84.0	16.6	6.6	3.1	16.5	3.5	1.9	1.2	2.8	42.9
	(6.2)	(2.7)	(2.3)	(2.3)	(1.2)	(0.9)	(1.2)	(2.0)	(1.9)	(7.3)	(1.4)	(0.7)	(0.8)	(5.2)	(0.4)	(0.1)	(0.1)	(0.5)	(8.5)
53	32.0	14.5	18.0	15.7	7.8	5.1	8.3	4.9	4.8	74.3	15.1	6.4	3.3	19.4	3.3	1.8	1.1	2.2	46.4
	(3.2)	(2.2)	(2.2)	(1.6)	(0.6)	(0.7)	(1.1)	(1.2)	(1.1)	(7.4)	(1.6)	(0.7)	(0.9)	(4.4)	(0.2)	(0.2)	(0.0)	(0.4)	(3.4)
54	35.0	15.9	19.3	17.7	8.3	5.3	8.4	6.5	6.1	76.1	16.5	6.8	3.7	19.9	3.7	1.9	1.3	2.8	46.9
	(5.2)	(2.4)	(2.1)	(1.8)	(0.9)	(0.8)	(0.9)	(2.0)	(1.7)	(9.9)	(2.2)	(0.6)	(0.7)	(4.8)	(0.1)	(0.1)	(0.1)	(0.6)	(4.8)
55	36.7	16.6	19.6	17.9	8.1	5.2	8.5	7.1	7.2	85.7	15.6	6.8	3.5	21.0	3.7	2.0	1.2	2.6	46.5
	(3.3)	(2.1)	(1.8)	(1.5)	(0.9)	(0.6)	(0.9)	(0.6)	(0.7)	(5.9)	(1.1)	(0.5)	(0.6)	(7.1)	(0.2)	(0.3)	(0.1)	(0.4)	(6.0)
56	35.8	14.7	19.2	17.5	8.2	5.1	8.2	6.9	6.5	78.8	15.4	7.2	3.4	22.9	3.8	2.1	1.2	2.9	43.7
	(6.1)	(2.7)	(2.0)	(1.9)	(1.1)	(0.8)	(1.3)	(2.0)	(1.9)	(8.7)	(1.3)	(0.9)	(0.9)	(8.2)	(0.3)	(0.1)	(0.1)	(0.3)	(7.4)
57	37.3	16.2	20.1	17.4	8.3	5.4	8.2	7.1	6.9	83.6	15.7	6.7	3.8	23.1	3.6	1.9	1.1	2.4	45.4
	(6.0)	(3.1)	(2.4)	(1.4)	(1.2)	(0.7)	(1.2)	(1.8)	(1.6)	(9.3)	(2.2)	(0.6)	(0.9)	(7.9)	(0.3)	(0.2)	(0.1)	(0.5)	(7.9)
58	35.8	14.5	20.0	17.4	8.0	5.1	8.2	6.7	6.6	82.5	15.5	7.0	3.1	19.2	3.7	2.1	1.1	2.9	43.3
	(4.5)	(1.6)	(1.4)	(1.1)	(1.3)	(0.6)	(0.9)	(1.1)	(1.1)	(10.8)	(1.5)	(0.5)	(0.7)	(9.0)	(0.3)	(0.2)	(0.1)	(0.7)	(5.7)
59	41.0	14.9	21.1	19.4	8.0	5.3	8.5	8.3	7.6	79.9	16.3	6.9	3.8	20.5	3.6	2.0	1.1	3.1	40.4
	(7.4)	(1.3)	(1.3)	(2.3)	(1.0)	(0.7)	(0.8)	(2.5)	(2.2)	(10.4)	(2.5)	(0.7)	(0.7)	(9.0)	(0.3)	(0.2)	(0.1)	(0.8)	(6.9)
60	36.1	16.8	19.2	17.2	8.4	5.4	8.3	6.9	6.7	76.7	15.1	7.0	3.6	23.0	3.8	2.0	1.0	3.1	47.5
	(2.8)	(2.2)	(2.7)	(1.6)	(0.8)	(0.7)	(0.6)	(1.2)	(1.2)	(6.3)	(2.1)	(0.5)	(0.7)	(5.8)	(0.4)	(0.2)	(0.1)	(0.6)	(5.1)
61	37.8	15.5	21.0	19.1	7.5	4.9	8.2	7.2	7.1	85.2	14.7	6.7	3.4	22.9	3.5	1.9	1.1	2.9	43.5
	(3.6)	(2.0)	(2.1)	(2.0)	(0.9)	(0.7)	(0.9)	(1.5)	(1.6)	(10.8)	(1.7)	(0.7)	(0.7)	(9.0)	(0.3)	(0.2)	(0.1)	(0.5)	(6.1)
62	42.5	16.4	21.6	19.0	8.2	5.1	8.2	8.9	8.4	94.5	18.8	6.8	3.1	15.9	3.7	1.8	1.1	3.0	41.8
	(7.2)	(3.0)	(2.2)	(1.7)	(0.9)	(0.7)	(0.6)	(2.6)	(2.5)	(11.8)	(2.0)	(0.5)	(0.5)	(4.7)	(0.4)	(0.3)	(0.1)	(0.7)	(6.4)
63	40.0	15.7	20.9	18.8	8.2	5.3	7.9	7.8	7.1	87.3	17.9	6.7	3.3	17.1	3.7	1.9	1.2	2.6	42.3
	(4.7)	(2.4)	(2.6)	(2.4)	(0.8)	(0.7)	(0.7)	(2.4)	(2.2)	(8.0)	(2.0)	(0.5)	(0.7)	(8.9)	(0.2)	(0.1)	(0.1)	(0.5)	(5.1)
64	35.5	16.3	20.1	17.7	8.2	5.1	7.7	6.9	6.4	82.7	18.0	6.6	3.6	18.6	3.6	1.9	1.1	2.5	47.1
	(6.1)	(3.7)	(1.6)	(1.8)	(0.9)	(0.8)	(0.8)	(2.5)	(2.0)	(5.8)	(2.5)	(0.8)	(0.8)	(7.5)	(0.3)	(0.1)	(0.1)	(0.5)	(7.5)

APPENDIX VII

MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) FROM NEEDLE DATA

SITE NO	NLEN	NW	NT	VBT	VBAD	RCLT	RCLAD	RCLL	RCLAB	RCRT	RCRAD	RCRL	RCRAB	VBL
33	34.8	154.2	72.9	29.3	28.2	7.5	13.8	15.5	30.5	7.6	13.4	15.1	29.7	96.2
	(4.9)	(13.6)	(4.6)	(2.0)	(4.4)	(0.9)	(1.0)	(1.8)	(2.6)	(1.2)	(1.1)	(1.4)	(2.8)	(11.2)
34	35	168.9	81.5	32.6	30.7	8	15.1	17.8	33.4	7.8	15.5	17.4	32.9	105.5
	(3.7)	(12.4)	(5.8)	(2.3)	(4.6)	(0.8)	(1.2)	(1.6)	(2.9)	(0.8)	(1.0)	(1.9)	(3.2)	(10.5)
35	34	155	75.8	32.3	26	8	13.6	15.7	31.5	8.1	13.9	15.5	31.2	95.4
	(4.7)	(9.7)	(4.1)	(2.9)	(3.0)	(0.8)	(1.2)	(1.9)	(3.8)	(1.0)	(1.2)	(1.7)	(2.9)	(7.3)
36	33.6	162.4	77.8	33	27.3	7.5	14.3	16.6	32.9	7.9	14.4	16.6	31.4	101.2
	(4.6)	(12.5)	(5.2)	(2.3)	(4.0)	(1.0)	(0.8)	(1.6)	(2.7)	(0.9)	(1.1)	(1.4)	(3.1)	(10.8)
37	32.3	157.5	76.1	31.6	26.7	7.5	14.2	16.6	32	7.6	14.1	16.3	31.5	97.3
	(7.2)	(13.6)	(4.0)	(2.3)	(1.8)	(1.1)	(1.2)	(1.6)	(2.0)	(1.3)	(0.9)	(2.0)	(2.2)	(11.7)
38	32.7	161.6	77.4	31.5	29.2	8	14.8	16.8	30.2	7.6	14	17.7	31.5	99.6
	(4.5)	(11.1)	(4.8)	(2.3)	(4.3)	(1.4)	(1.4)	(0.9)	(2.1)	(1.6)	(0.9)	(1.6)	(2.6)	(9.6)
39	31.3	150.7	71.4	30	24.9	7.1	14.1	15.4	39.4	7.3	13.6	15.6	29	93.6
	(4.2)	(7.5)	(2.6)	(1.4)	(2.3)	(1.3)	(0.8)	(1.2)	(2.1)	(1.2)	(0.8)	(1.0)	(2.5)	(6.2)
40	31.6	155.9	73.8	31.1	26.7	7.3	14.3	16.7	32.1	7.1	14	17	31.1	97
	(3.0)	(13.9)	(6.4)	(3.3)	(4.4)	(0.9)	(1.0)	(1.4)	(2.5)	(0.8)	(1.2)	(1.5)	(2.1)	(10.2)
41	34.5	157.7	76.2	31.6	26.4	7.6	14	16.7	33	7.4	14	17	32.6	97.8
	(4.6)	(9.7)	(2.8)	(2.3)	(2.3)	(1.0)	(0.7)	(1.0)	(2.4)	(0.8)	(1.0)	(0.8)	(1.9)	(7.8)
42	36	158	73.7	30.5	28.3	6.8	14.5	15.9	31	6.9	14	16.3	29.8	98.9
	(4.0)	(12.8)	(4.8)	(2.9)	(4.6)	(1.6)	(1.1)	(1.9)	(2.9)	(1.4)	(1.1)	(1.5)	(2.6)	(10.5)
43	35.8	167.6	80.1	32.9	28.9	8.1	14.7	16.8	32.6	7.9	15	16.6	32.4	106.3
	(2.4)	(10.9)	(5.1)	(3.7)	(2.7)	(1.0)	(1.5)	(1.4)	(2.3)	(1.2)	(1.3)	(1.2)	(2.7)	(6.2)
44	31.7	166.5	78.6	32.6	28.5	8.1	14	17	32.9	7.9	14	17.3	34.2	105.5
	(4.1)	(7.1)	(3.2)	(2.1)	(2.8)	(0.8)	(1.0)	(1.7)	(2.2)	(1.1)	(1.0)	(0.9)	(2.4)	(8.2)
45	31.6	165.6	79.4	32.3	28.7	7.7	14.9	16.6	31.9	8	14.7	16.4	32.1	105.9
	(4.2)	(14.1)	(6.1)	(2.8)	(3.0)	(1.4)	(1.6)	(1.8)	(2.5)	(1.1)	(1.5)	(2.0)	(2.5)	(10.1)
46	33.6	159.3	76.3	34.1	25.3	7.6	14	16.1	31.6	7.3	14.4	16.3	31.3	100.5
	(2.8)	(11.9)	(3.2)	(2.6)	(1.9)	(1.2)	(0.9)	(1.1)	(1.2)	(1.3)	(0.9)	(1.2)	(1.9)	(9.5)
47	39.8	166.9	79	35.1	27.5	7.7	14.9	17	33.4	7.3	14.9	16.8	31.6	105.4
	(6.3)	(11.0)	(5.2)	(2.4)	(3.2)	(1.2)	(1.3)	(1.5)	(2.3)	(0.8)	(0.9)	(1.7)	(2.0)	(5.4)
48	35.5	152.6	74.8	33.1	25.5	7.7	14.1	15.3	30.8	7.8	14	14.5	29.5	94.8
	(4.3)	(12.3)	(3.8)	(2.7)	(3.5)	(1.3)	(1.0)	(1.2)	(2.7)	(1.5)	(1.3)	(1.1)	(3.0)	(9.6)

SITE NO	NLEN	NW	NT	VBT	VBAD	RCLT	RCLAD	RCLL	RCLAB	RCRT	RCRAD	RCRL	RCRAB	VBL
49	32.0	157.8	75.6	32.8	27.2	7.4	13.9	16.1	31.9	7.5	14.2	16.1	31.8	99.4
	(3.7)	(10.7)	(3.4)	(3.2)	(3.7)	(1.2)	(0.8)	(1.4)	(1.9)	(1.3)	(1.1)	(1.1)	(2.3)	(7.2)
50	32.2	153.2	74.8	33.5	25.6	6.4	13.3	15.6	31.9	6.3	13.4	15.4	30.4	98.2
	(5.4)	(14.6)	(3.9)	(3.3)	(2.5)	(1.1)	(0.9)	(1.4)	(2.4)	(0.6)	(1.0)	(1.1)	(1.3)	(11.7)
51	30	150.7	72.4	32	24.3	5.5	14	16	31.3	6.3	13.6	16.2	30.3	92.7
	(3.8)	(12.8)	(4.8)	(2.7)	(3.2)	(2.4)	(1.0)	(1.6)	(2.1)	(1.2)	(1.4)	(1.5)	(2.2)	(8.6)
52	33.5	161.5	77.5	33.1	28.2	7.3	14.1	16.8	34	7.1	14.2	16.1	31.8	101.9
	(4.5)	(11.8)	(4.5)	(2.1)	(3.3)	(1.3)	(0.7)	(0.8)	(2.5)	(1.2)	(0.9)	(1.4)	(1.8)	(7.0)
53	32.1	150	74.9	31.4	26.2	7.1	13.9	15.5	32.5	7.4	13.9	15.6	31.3	91.8
	(3.4)	(15.7)	(7.9)	(3.1)	(3.8)	(1.0)	(1.5)	(2.0)	(3.8)	(1.0)	(1.0)	(2.0)	(3.6)	(11.1)
54	34.7	156.4	76.2	32.8	26.3	7.7	14.7	16.6	31.5	7.4	14.4	16.2	31.9	95.2
	(4.1)	(10.2)	(4.5)	(2.8)	(2.7)	(1.0)	(1.0)	(1.3)	(2.8)	(1.0)	(1.4)	(1.3)	(2.5)	(7.6)
55	35	163.5	79.6	35.1	27.2	8	14.6	16.8	33.3	7.5	14.6	16.9	32.6	102.5
	(2.2)	(11.4)	(2.8)	(2.4)	(3.1)	(1.0)	(0.7)	(1.1)	(3.7)	(0.9)	(1.1)	(1.2)	(2.6)	(10.0)
56	32.7	155.4	75.1	33.2	25.2	7.8	13.6	15.1	31.4	7.5	13.3	15.1	29.2	97
	(3.9)	(12.5)	(4.9)	(3.3)	(1.5)	(0.8)	(1.6)	(0.7)	(2.2)	(0.8)	(1.3)	(1.0)	(2.0)	(10.1)
57	34	165.6	78.6	33.8	28.4	8	14.3	16.6	32.9	7.8	14.3	16.4	31	103.8
	(5.3)	(10.6)	(5.3)	(3.8)	(2.8)	(1.2)	(1.5)	(1.1)	(1.6)	(1.3)	(0.9)	(1.4)	(2.2)	(7.5)
58	33.9	159.7	75.4	32.6	26.2	7.5	14.3	16.3	30.6	7.5	13.9	16	29.7	98.2
	(5.1)	(17.0)	(6.0)	(2.6)	(3.2)	(0.9)	(1.6)	(1.6)	(1.6)	(1.1)	(1.5)	(1.7)	(1.8)	(12.6)
59	34.9	155	75.3	33.8	25.1	7.7	14.3	15.3	31.7	7.5	14.4	15.3	29.7	96.2
	(4.8)	(10.2)	(6.7)	(4.1)	(2.8)	(0.7)	(1.6)	(1.5)	(3.6)	(0.9)	(1.5)	(1.6)	(3.4)	(8.2)
60	32.2	154.5	75.6	33.3	26.3	8.1	13.7	16	31.1	8	14.1	15.4	31.4	97.1
	(7.0)	(10.7)	(3.6)	(2.8)	(1.8)	(1.8)	(1.6)	(1.8)	(2.7)	(0.9)	(1.2)	(2.1)	(3.3)	(7.2)
61	32	148.6	72.6	31.2	25.4	7.8	13.4	14.5	29.3	7.9	13	14.6	29.4	91.2
	(1.8)	(14.7)	(6.9)	(3.0)	(3.5)	(1.5)	(1.2)	(1.8)	(3.7)	(1.2)	(1.2)	(1.4)	(2.9)	(10.8)
62	36.9	159	73.9	31.1	27.5	7.7	13.7	15	30.1	7.9	13.6	15	29.6	101.9
	(6.1)	(7.1)	(4.6)	(2.1)	(2.1)	(1.2)	(1.6)	(1.0)	(1.6)	(0.9)	(1.4)	(1.4)	(2.1)	(4.7)
63	36	153.3	73.4	33	25.4	7.2	13.2	16.3	32.5	7.7	13.8	15.4	29.2	96.9
	(6.8)	(14.5)	(5.8)	(2.6)	(3.6)	(1.7)	(0.9)	(2.1)	(2.8)	(1.3)	(0.8)	(1.4)	(2.9)	(11.8)
64	31.2	150.3	71.8	30.8	25.2	8.1	12.6	14.1	30	8.1	12.3	14.7	28.5	94.6
	(4.9)	(9.2)	(3.3)	(2.0)	(3.1)	(1.3)	(0.5)	(1.5)	(1.8)	(1.8)	(0.9)	(1.3)	(2.8)	(6.9)

APPENDIX VIII

CORREALTION MATRICES FROM CONE AND NEEDLE DATA

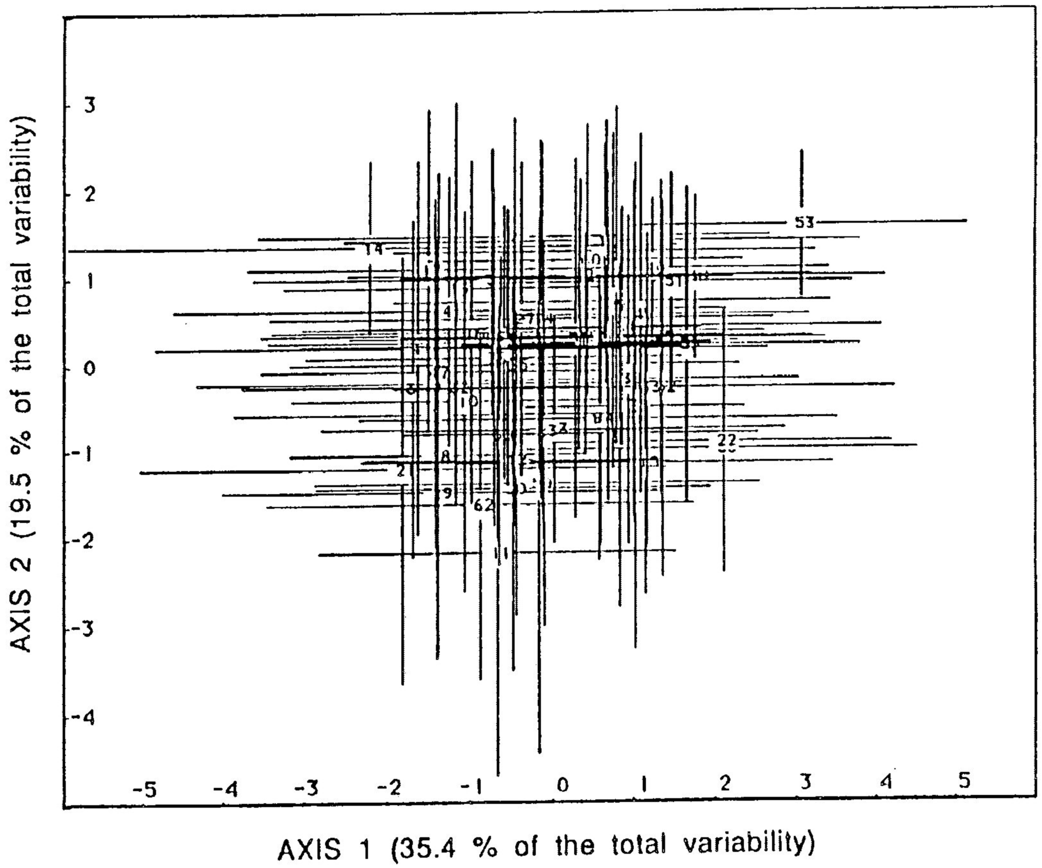
	CL	MO	CW	CD	AL	UDI	AW	CV	CWT	SN	SL	SW	AD	SEN	SEL	SEW	SED	SEWT
CL																		
MO	0.03																	
CW	0.56	0.26																
CD	0.71	0.25	0.80															
AL	0.00	0.62	0.26	0.17														
UDI	0.00	0.63	0.31	0.19	0.85													
AW	0.00	0.44	0.29	0.26	0.70	0.63												
CV	0.76	0.51	0.79	0.84	0.40	0.42	0.39											
CWT	0.76	0.52	0.76	0.82	0.38	0.40	0.36	0.98										
SN	0.49	0.14	0.34	0.44	-0.15	-0.09	-0.12	0.46	0.49									
SL	0.34	0.47	0.40	0.41	0.61	0.54	0.39	0.58	0.55	0.11								
SW	0.18	0.31	0.45	0.43	0.47	0.45	0.66	0.48	0.44	-0.03	0.36							
AD	-0.05	0.54	0.31	0.22	0.73	0.78	0.57	0.34	0.32	-0.16	0.43	0.42						
SEN	0.16	-0.08	0.04	0.08	-0.01	-0.04	-0.07	0.03	0.04	-0.18	0.05	0.09	0.01					
SEL	0.16	0.10	0.18	0.23	0.25	0.18	0.16	0.24	0.20	-0.20	0.37	0.26	0.16	0.17				
SEW	0.05	0.04	0.13	0.19	0.19	0.17	0.18	0.15	0.11	-0.28	0.21	0.35	0.14	0.17	0.58			
SED	0.00	0.05	0.08	0.07	0.23	0.20	0.17	0.07	0.03	-0.36	0.25	0.22	0.20	0.20	0.52	0.61		
SEWT	0.23	0.21	0.29	0.33	0.32	0.28	0.29	0.38	0.36	-0.19	0.34	0.35	0.25	0.06	0.52	0.56	0.57	
CUV	-0.62	75.00	-0.17	-0.28	0.50	0.49	0.34	-0.10	-0.10	-0.23	0.15	0.13	0.46	-0.16	-0.02	0.01	0.05	0.03

	NLEN	NW	NT	VBT	VBAD	RCLT	RCLAD	RCLL	RCLAB	RCRT	RCRAD	RCRL	RCRAB	VBL	RD01	RD02	RD03	RD04	RD05	RD06
NLEN																				
NW	0.35																			
NT	0.30	0.80																		
VBT	0.26	0.46	0.67																	
VBAD	0.20	0.69	0.69	0.75																
RCLT	0.17	0.44	0.44	0.31	0.30															
RCLAD	0.26	0.50	0.60	0.40	0.38	0.09														
RCLL	0.19	0.54	0.60	0.38	0.43	0.17	0.50													
RCLAB	0.17	0.45	0.61	0.42	0.45	0.12	0.31	0.65												
RCRT	0.14	0.39	0.36	0.28	0.25	0.76	0.09	0.12	0.13											
RCRAD	0.23	0.53	0.62	0.46	0.35	0.15	0.71	0.53	0.37	0.09										
RCRL	0.19	0.52	0.56	0.32	0.42	0.15	0.55	0.72	0.54	0.06	0.51									
RCRAB	0.17	0.45	0.62	0.36	0.46	0.19	0.36	0.60	0.64	0.03	0.38	0.68								
VBL	0.37	0.94	0.71	0.38	0.68	0.36	0.36	0.42	0.41	0.31	0.41	0.4	0.42							
RD01	0.16	0.62	0.73	0.10	0.79	0.30	0.41	0.46	0.48	0.24	0.37	0.45	0.51	0.56						
RD02	0.15	0.62	0.70	0.08	0.80	0.30	0.41	0.44	0.50	0.22	0.36	0.46	0.44	0.57	0.92					
RD03	0.16	0.62	0.67	0.07	0.80	0.24	0.41	0.42	0.51	0.19	0.38	0.47	0.47	0.58	0.87	0.96				
RD04	0.18	0.64	0.66	0.05	0.80	0.25	0.40	0.42	0.51	0.22	0.38	0.48	0.51	0.61	0.86	0.93	0.98			
RD05	0.20	0.66	0.63	0.02	0.80	0.27	0.39	0.42	0.49	0.24	0.38	0.46	0.53	0.65	0.83	0.87	0.92	0.96		
RD06	0.21	0.68	0.58	0.00	0.76	0.30	0.37	0.43	0.46	0.3	0.43	0.45	0.54	0.68	0.75	0.77	0.8	0.86	0.94	
RD07	0.27	0.83	0.67	0.16	0.75	0.35	0.42	0.49	0.49	0.37	0.5	0.5	0.47	0.81	0.72	0.73	0.75	0.8	0.86	0.92
RD08	0.34	0.97	0.77	0.42	0.69	0.41	0.47	0.51	0.48	0.38	0.52	0.52	0.45	0.92	0.6	0.63	0.64	0.66	0.69	0.71
RD09	0.35	0.97	0.79	0.51	0.63	0.42	0.48	0.51	0.46	0.39	0.54	0.51	0.48	0.93	0.54	0.56	0.57	0.58	0.6	0.62
RD10	0.36	0.96	0.81	0.57	0.60	0.43	0.49	0.52	0.47	0.39	0.58	0.5	0.55	0.91	0.52	0.52	0.52	0.53	0.55	0.58
RD11	0.35	0.89	0.85	0.70	0.52	0.44	0.52	0.55	0.49	0.37	0.6	0.49	0.56	0.83	0.47	0.43	0.41	0.42	0.44	0.46
RD12	0.32	0.76	0.85	0.83	0.39	0.42	0.52	0.55	0.51	0.34	0.59	0.48	0.55	0.66	0.38	0.32	0.29	0.29	0.29	0.3
RD13	0.30	0.66	0.84	0.90	0.30	0.40	0.53	0.54	0.53	0.33	0.58	0.47	0.53	0.54	0.33	0.28	0.25	0.24	0.23	0.22
RD14	0.29	0.63	0.84	0.92	0.28	0.40	0.53	0.52	0.56	0.35	0.57	0.47	0.5	0.5	0.33	0.3	0.28	0.26	0.23	0.21
RD15	0.30	0.66	0.84	0.90	0.31	0.40	0.54	0.52	0.59	0.37	0.56	0.5	0.48	0.54	0.33	0.34	0.33	0.31	0.27	0.23
RD16	0.34	0.76	0.84	0.84	0.39	0.41	0.55	0.52	0.59	0.39	0.55	0.51	0.48	0.66	0.37	0.4	0.39	0.37	0.34	0.3
RD17	0.37	0.89	0.85	0.71	0.52	0.44	0.55	0.53	0.55	0.4	0.51	0.52	0.45	0.82	0.47	0.48	0.48	0.48	0.46	0.45
RD18	0.37	0.96	0.81	0.57	0.60	0.45	0.50	0.51	0.45	0.39	0.49	0.48	0.44	0.91	0.53	0.53	0.53	0.54	0.56	0.57
RD19	0.36	0.97	0.78	0.51	0.62	0.44	0.47	0.50	0.41	0.38	0.47	0.46	0.45	0.93	0.54	0.54	0.54	0.56	0.59	0.61
RD20	0.34	0.96	0.75	0.41	0.66	0.44	0.44	0.50	0.41	0.35	0.39	0.45	0.5	0.92	0.59	0.58	0.58	0.6	0.64	0.68
RD21	0.28	0.84	0.66	0.16	0.74	0.40	0.38	0.47	0.45	0.31	0.34	0.45	0.5	0.82	0.7	0.69	0.69	0.73	0.78	0.84
RD22	0.21	0.70	0.59	0.00	0.77	0.36	0.35	0.41	0.47	0.27	0.36	0.39	0.53	0.7	0.76	0.73	0.74	0.78	0.85	0.9
RD23	0.16	0.66	0.63	0.01	0.79	0.34	0.34	0.44	0.46	0.27	0.38	0.39	0.53	0.65	0.84	0.77	0.74	0.77	0.82	0.85
RD24	0.15	0.64	0.65	0.04	0.78	0.34	0.32	0.43	0.41	0.27	0.37	0.36	0.52	0.59	0.87	0.75	0.71	0.72	0.77	0.78
RD25	0.15	0.62	0.65	0.05	0.76	0.33	0.32	0.43	0.38	0.25	0.4	0.34	0.52	0.56	0.87	0.73	0.67	0.69	0.73	0.72
RD26	0.16	0.60	0.68	0.08	0.77	0.31	0.35	0.45	0.41	0.25	0.4	0.38	0.52	0.58	0.91	0.77	0.72	0.73	0.74	0.71

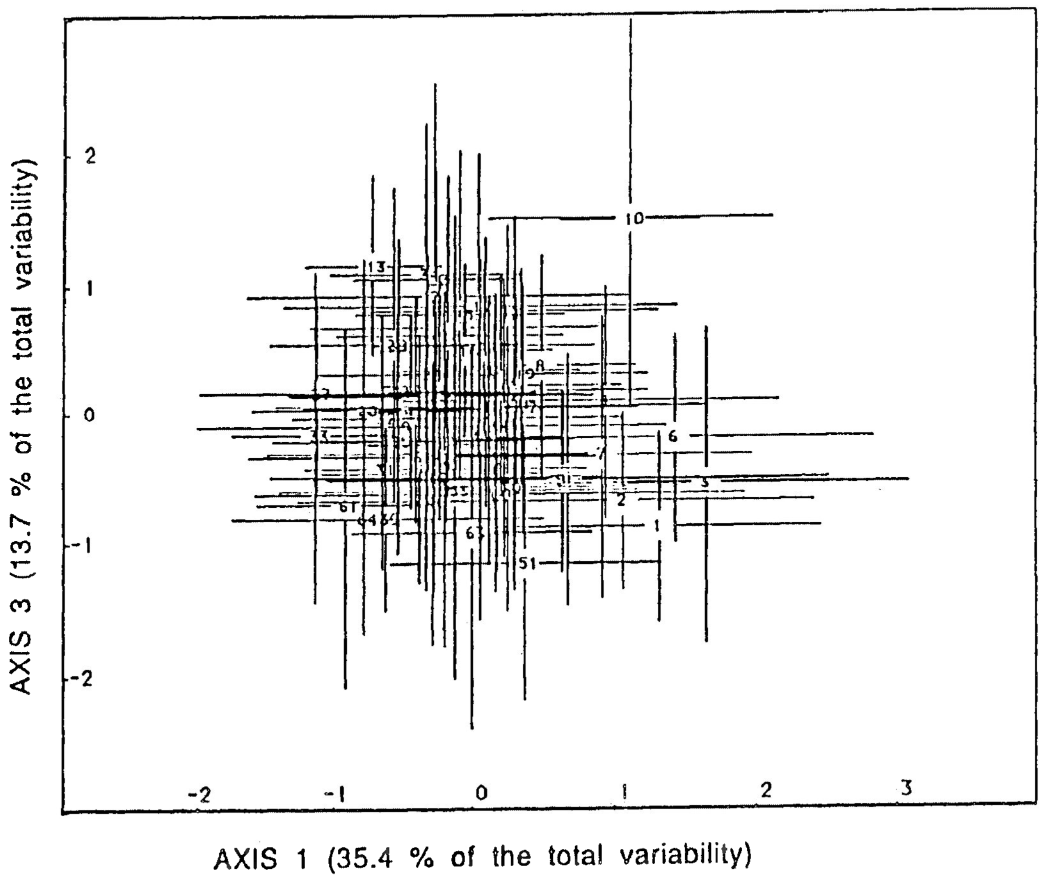
	RD07	RD08	RD09	RD10	RD11	RD12	RD13	RD14	RD15	RD16	RD17	RD18	RD19	RD20	RD21	RD22	RD23	RD24	RD25
NLEN																			
NW																			
NT																			
VBT																			
VBAD																			
RCLT																			
RCLAD																			
RCLL																			
RCLAB																			
RCRT																			
RCRAD																			
RCRL																			
RCRAB																			
VBL																			
RD01																			
RD02																			
RD03																			
RD04																			
RD05																			
RD06																			
RD07																			
RD08	0.88																		
RD09	0.8	0.98																	
RD10	0.75	0.95	0.99																
RD11	0.64	0.86	0.92	0.96															
RD12	0.48	0.71	0.79	0.85	0.95														
RD13	0.38	0.61	0.69	0.75	0.88	0.97													
RD14	0.35	0.58	0.66	0.71	0.83	0.93	0.98												
RD15	0.38	0.62	0.69	0.73	0.83	0.91	0.95	0.98											
RD16	0.46	0.71	0.78	0.81	0.87	0.9	0.91	0.93	0.97										
RD17	0.62	0.85	0.9	0.92	0.93	0.89	0.84	0.84	0.89	0.95									
RD18	0.73	0.93	0.96	0.96	0.92	0.82	0.73	0.72	0.75	0.84	0.95								
RD19	0.77	0.94	0.96	0.96	0.89	0.77	0.68	0.65	0.69	0.78	0.91	0.99							
RD20	0.83	0.96	0.94	0.92	0.84	0.7	0.6	0.57	0.59	0.69	0.84	0.95	0.97						
RD21	0.93	0.86	0.78	0.75	0.63	0.48	0.37	0.35	0.37	0.46	0.63	0.75	0.8	0.88					
RD22	0.87	0.71	0.63	0.59	0.47	0.32	0.24	0.22	0.23	0.3	0.45	0.58	0.63	0.72	0.91				
RD23	0.81	0.66	0.59	0.56	0.47	0.34	0.26	0.23	0.22	0.27	0.42	0.55	0.6	0.68	0.85	0.94			
RD24	0.75	0.62	0.57	0.55	0.48	0.38	0.3	0.25	0.23	0.28	0.42	0.54	0.58	0.66	0.79	0.87	0.96		
RD25	0.71	0.59	0.55	0.53	0.48	0.4	0.31	0.26	0.24	0.28	0.41	0.52	0.57	0.64	0.75	0.81	0.92	0.97	
RD26	0.69	0.58	0.53	0.52	0.48	0.4	0.34	0.3	0.28	0.32	0.43	0.52	0.55	0.61	0.71	0.76	0.88	0.93	0.95

APPENDIX IX

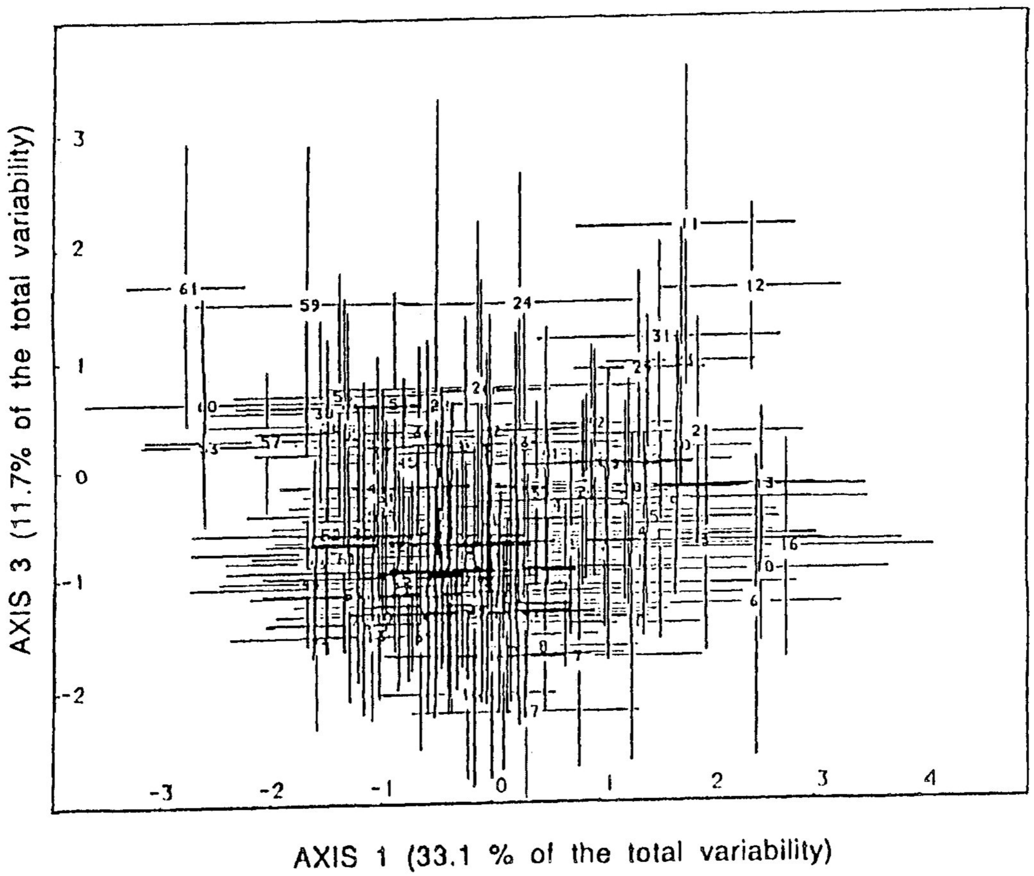
ORDINATIONS OF PRINCIPAL COMPONENT AND DISCRIMINANT FUNCTION SCORES



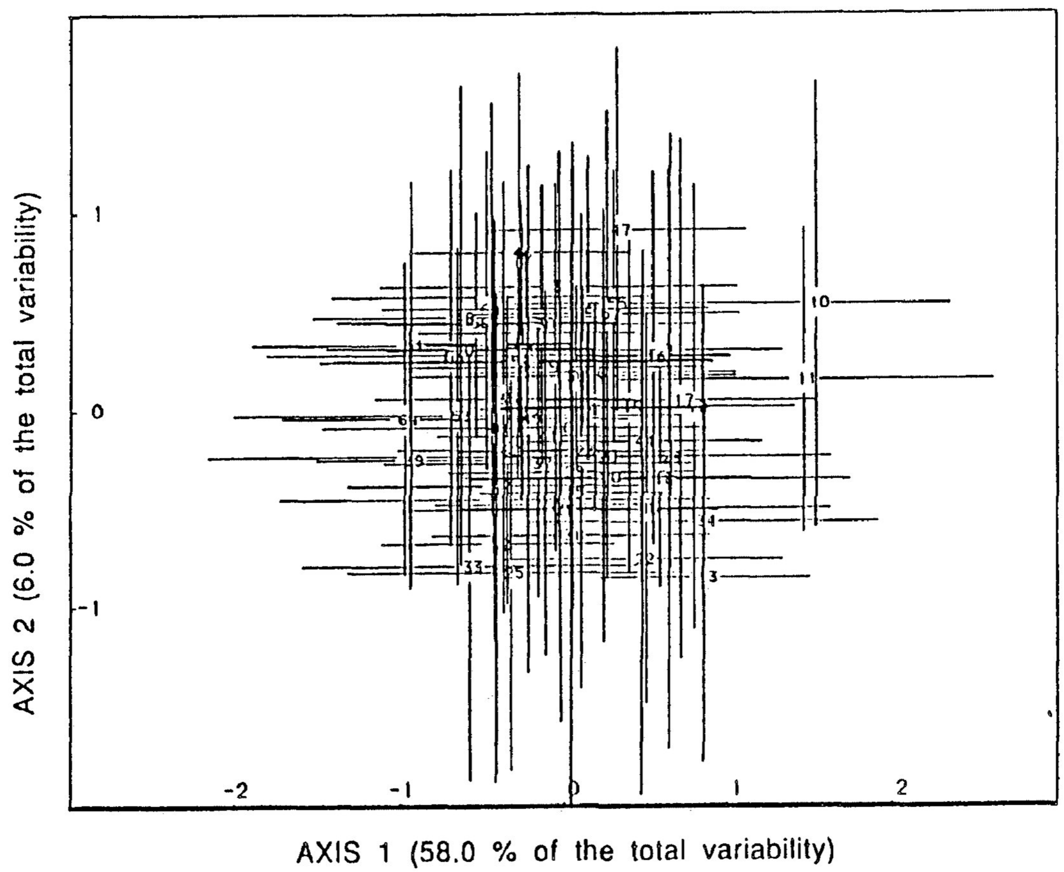
ORDINATION OF POPULATIONS BASED ON CONE PCA SCORES



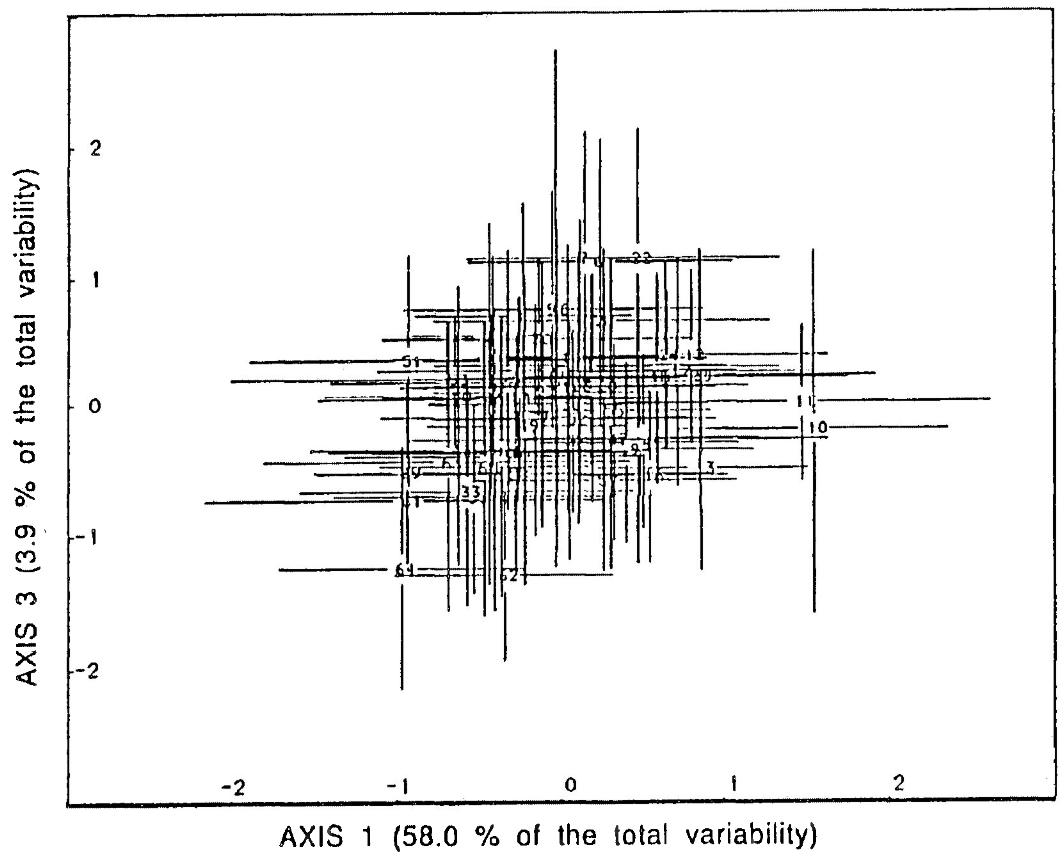
ORDINATION OF POPULATIONS BASED ON CONE PCA SCORES



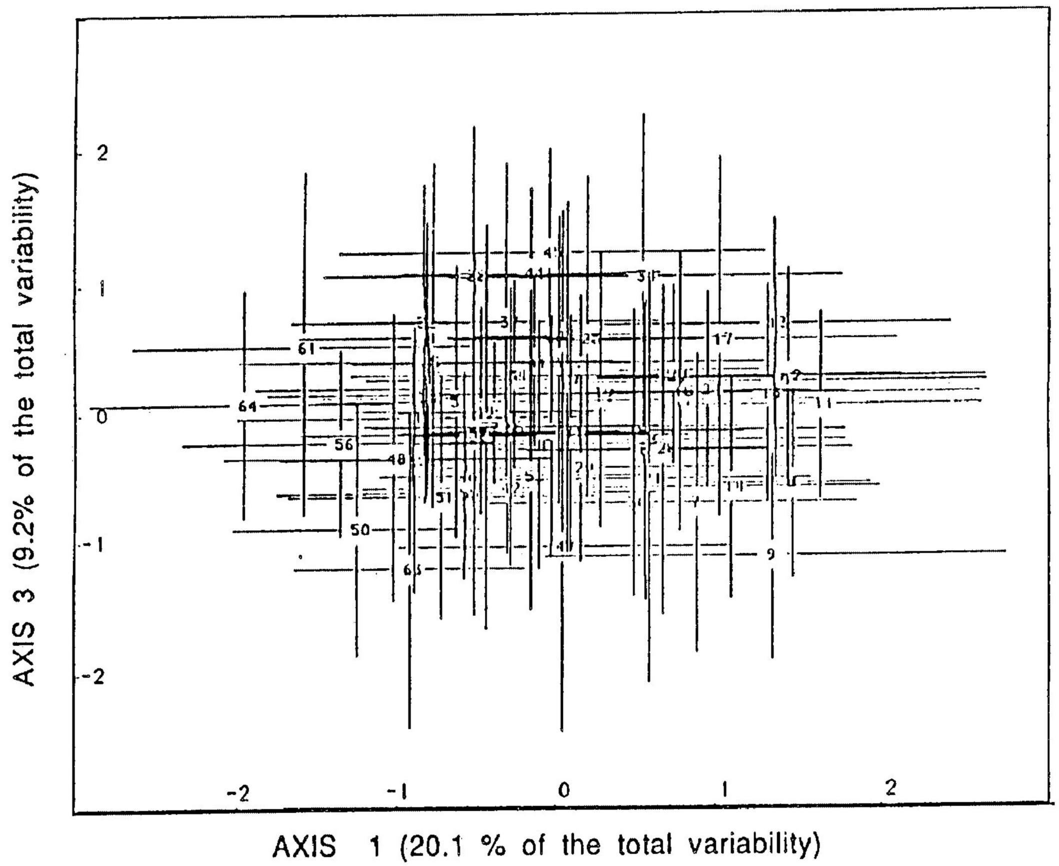
ORDINATION OF POPULATIONS BASED ON CONE DA SCORES



ORDINATION OF POPULATIONS BASED ON NEEDLE PCA SCORES



ORDINATION OF POPULATIONS BASED ON NEEDLE PCA SCORES



ORDINATION OF POPULATIONS BASED ON NEEDLE DA SCORES