MORPHOLOGICAL VARIATION IN SUBALPINE FIR AND ITS RELATIONSHIP TO BALSAM FIR IN WESTERN CANADA AND THE UNITED STATES

by

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

Lakehead University
School of Forestry
November 1988

ProQuest LLC.
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ISBN 0-315-48206-0

ABSTRACT

Palmer, C. L. 1988. Morphological variation in subalpine fir and its relationship to balsam fir in western Canada and the United States.

Keywords: balsam fir, morphological variation, subalpine fir, taxonomy

To help clarify the taxonomy of the two closely related North American firs subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and balsam fir (*Abies balsamea* (L.) Mill.) in western Canada and the United States, 10 populations of subalpine fir from Yukon Territory, northern British Columbia, and Alaska were compared on the basis of morphological traits to fir populations from Washington to northern Ontario. Principal components and discriminant analyses were carried out separately on cone and needle data for various subsets of these populations. Multiple regression analysis and analyses of variance were used to investigate which evolutionary processes may have been important in the recent development of subalpine fir at its northern extreme. The regression analyses and analyses of variance suggest that variation is expressed primarily within populations, throughout a single large genepool at the northern extreme of subalpine fir's range, and that selection due to local environmental pressures has produced the existing morphological variation among populations. The multivariate analyses of cone and needle data produced different results for several of the population subsets, indicating that vegetative and sexual features of these firs respond to different selection pressures at the various sites. Although the results are not entirely consistent, the combined cone and needle data indicate that 1) north coastal British Columbia and interior Rocky Mountain populations of subalpine fir are generally distinct with the exception of a Vancouver Island population; 2) northern subalpine fir populations exhibit an affinity to interior populations and are very distinct from coastal populations. Additional geographic trends are 1) two Washington Cascades subalpine fir populations are distinct from all other populations in needle morphology, but one of these populations (Mount Baker) is similar to the interior populations in cone morphology; 2) all balsam fir populations are indistinguishable from interior subalpine fir populations on the basis of needle morphology, but well-differentiated from these and coastal populations in cone morphology. These results support 1) continued recognition of subalpine and balsam fir as separate species and 2) recognition of coastal and interior subalpine fir as separate taxa, perhaps at varietal rank. The present results refute the theory that subalpine fir survived the Wisconsin glaciation in one or more northern refugia. Rather, the close affinity between northern and interior subalpine fir populations suggests that they originated from a common Rocky Mountain refugium.

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ACKNOWLEDGEMENTS

This research was supported in part by a National Science and Engineering Research Council of Canada operating grant. I wish to express my appreciation to Dr. William Parker for the inspiration that initiated this study and his continuing guidance and patience through to its completion. Special thanks are extended to Tim Dickinson and Kim Armstrong for consultation regarding botanical microtechnique procedures. I am indebted to my husband Paul Charrette for constant support and assistance throughout the duration of this study.

1. INTRODUCTION

The genus *Abies* Mill. is one of the largest in the family *Pinaceae*, and many of its species are distributed widely over the northern hemisphere. Eight species of true firs are native to North America, with ranges throughout much of Canada and the United States. In spite of its ubiquitous nature, the taxonomy of *Abies* is problematic due to the great morphological variability within and among populations and species (Liu, 1971). Repeated glaciations in North America throughout the Pleistocene Epoch of the Quaternary Period, and their associated climatic changes have drastically affected the existence of firs, among other conifers, and have contributed to or modified the high levels of variability now evident in this genus. The impact of numerous glaciations has made it difficult to determine which evolutionary processes have given rise to this variability.

Within the genus *Abies*, three species with neighbouring ranges have been placed within the section *Balsameae* Engelm., subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), balsam fir (*Abies balsamea* (L.) Mill.), and Fraser fir (*Abies fraseri* (Pursh) Poir.). These firs are morphologically similar, causing complications in taxonomic differentiation (Bazukis and Hansen, 1965), and their taxonomic relationships have been the subject of considerable study (Boivin, 1959; Ramseur, 1961; Myers and Borman, 1963; Roller, 1966, 1967; Robinson and Thor, 1969; Clarkson and Fairbrothers, 1970; Zavarin and Snajberk, 1972; Thor and Barnett, 1974; Hunt and von Rudloff, 1974, Parker et al., 1981, 1984; Jacobs et al., 1984). These investigations have utilized morphological, chemical, and genetic characters as taxonomic evidence.

Geographical variation in such traits provides the basis for taxonomic and biogeographic studies, and for the development and testing of hypotheses of species evolution. This variation arises from the combined effects of gene mutation, migration, drift, selection and historical factors including founding events (Stebbins, 1950). Although the importance of the evolutionary and migratory history of a species in producing geographical variation is widely recognized, it has been difficult to relate the modern geographical variation of many species to any specific historical factor due to the lack of detailed species histories (Cwynar and MacDonald, 1987).

Reconstruction of the biogeographical history of a species such as subalpine fir, which grows in extremely varied topographical and climatic conditions throughout a range that extends both north and south of the limits of glaciation, and for which detailed fossil records are very limited (MacDonald, in litt., 25 February 1988), is particularly problematic. Although the taxonomy of subalpine fir has been studied throughout much of its range (Zavarin et al., 1970; Hunt and von Rudloff, 1979; Parker and Maze, 1984) the evolutionary history of this fir has not been well-investigated in the Yukon Territory at its northern extreme, which, although affected by numerous glacial cycles, is located near a region that completely escaped glaciation. In addition, although it is now well documented that subalpine and balsam fir hybridize extensivley in west-central Alberta (Hunt and von Rudloff, 1974; Parker et al., 1981, 1984) the extent to which gene flow occurs between these firs is still unclear.

This thesis utilizes morphological characters to investigate the taxonomy and evolution of subalpine fir throughout a large part of its range in western Canada and the United States in an attempt to further clarify the taxonomic relationship between subalpine and balsam firs.

TAXONOMIC STATUS OF THE *ABIES* SECTION *BALSAMEAE* IN WESTERN CANADA AND THE UNITED STATES

Abies lasiocarpa is a wide-ranging, high-elevation species of the western mountains of North America, extending along the Pacific coast from southeastern Alaska and central Yukon Territory south to the San Fransisco Mountains of northern Arizona and the Mogollan Mountains of western New Mexico. Between these two extreme localities, subalpine fir extends throughout the mountains of British Columbia and southeastern Alberta, western

Washington, Oregon, Idaho, Montana, Wyoming, Utah, and central Colorado. Longitudinally, the species spreads from 104° 59' to 145° west. The altitudinal variation exhibited by subalpine fir ranges from sea level in the Coast Range of southeastern Alaska to as high as 3,650 m in the southern Rocky Mountains. Figure 1.1 depicts the range of *Abies lasiocarpa.*

Abies balsamea is also a very wide-ranging true fir of the *Abies* section *Balsameae*, but occurs primarily in the boreal forests of Canada, extending from Newfoundland to Alberta. In the United States, balsam fir extends south into Minnesota, Wisconsin, and Michigan, as well as several northeastern states. Figure 1.2 depicts the range of *Abies balsamea.*

Early opinion was that the range of balsam fir adjoined that of subapine fir in central Alberta, but that these firs did not overlap (Halliday and Brown, 1943; Raup, 1946). The more recent point of view is that there is a region of sympatry in Alberta around the area of Lesser Slave Lake (Moss, 1959; Hosie, 1969; Hunt and von Rudloff, 1974; Parker et al., 1981), although the extent of this overlap has varied depending on the author.

The taxonomic status of the balsam firs in western Canada has been disputed for some time. Boivin (1959) proposed that subalpine and balsam fir be considered the two subspecies *A. balsamea* ssp. *balsamea* and *A. balsamea* ssp. *lasiocarpa* (Hook.) Boivin, due to a lack of morpholgical differentiation between the taxa. Matzenko (1963, 1968) also supported recognition of a single species. These firs have been distinguished mainly by cone scales, ranking and angle of needle attachment, and relative abundance of stomata, particularly on the adaxial needle surface (Moss, 1959; Bazukis and Hansen, 1965). Intermediate trees have been reported by a number of authors in the putative zone of sympatry in west-central Alberta, suggesting that the firs interbreed in this region (Moss, 1959; Roller, 1967; Hunt and von Rudloff, 1974; Achuff and LaRoi, 1977).

In a study of variaton in needle and cone characters of balsam firs from Saskatchewan to British Columbia, Parker et al. (1981) found that the designated species did not represent elements of two distinct taxa, but that

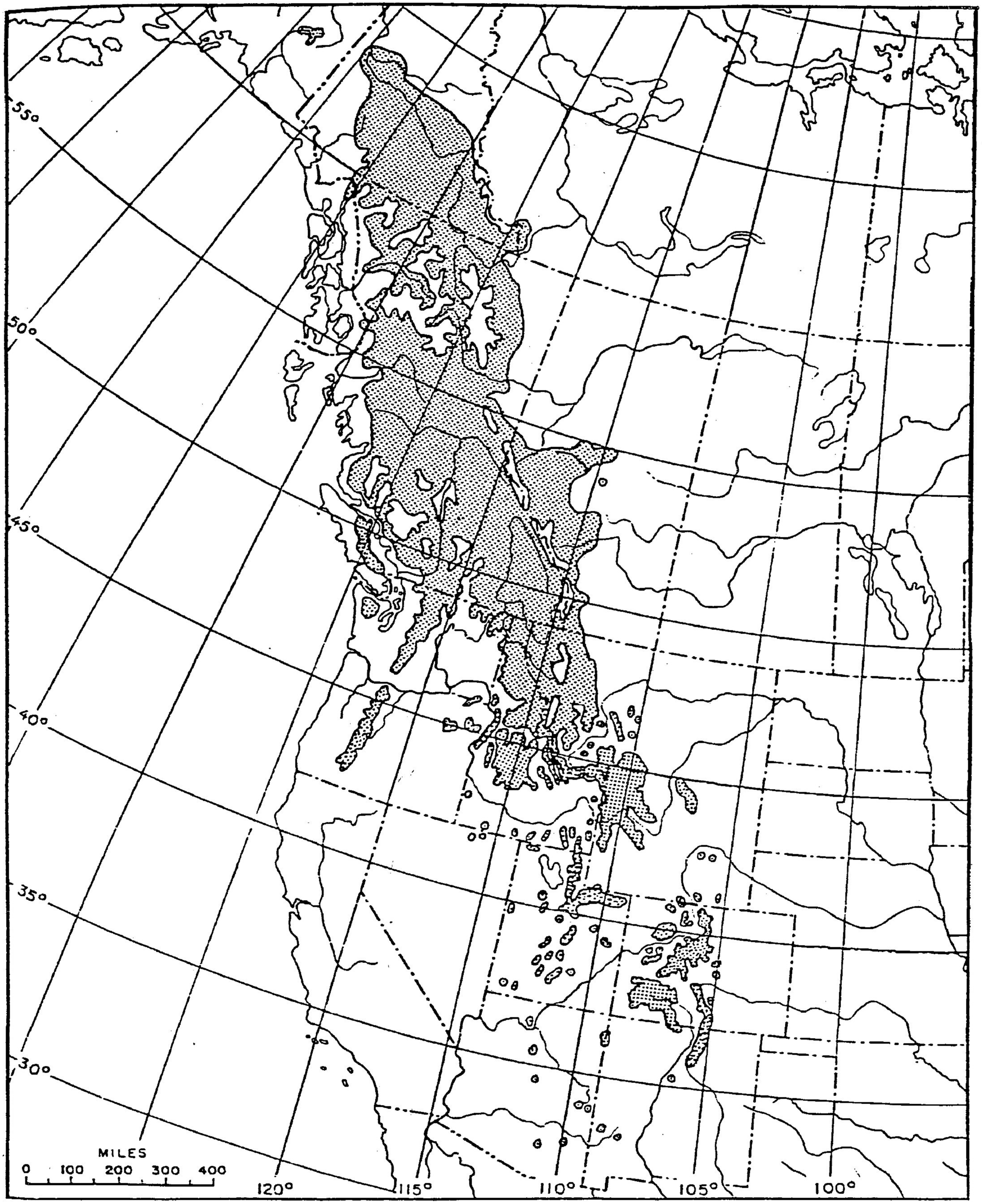

Fig. 1.1. The range of *Abies lasiocarpa* (Fowells, 1965).

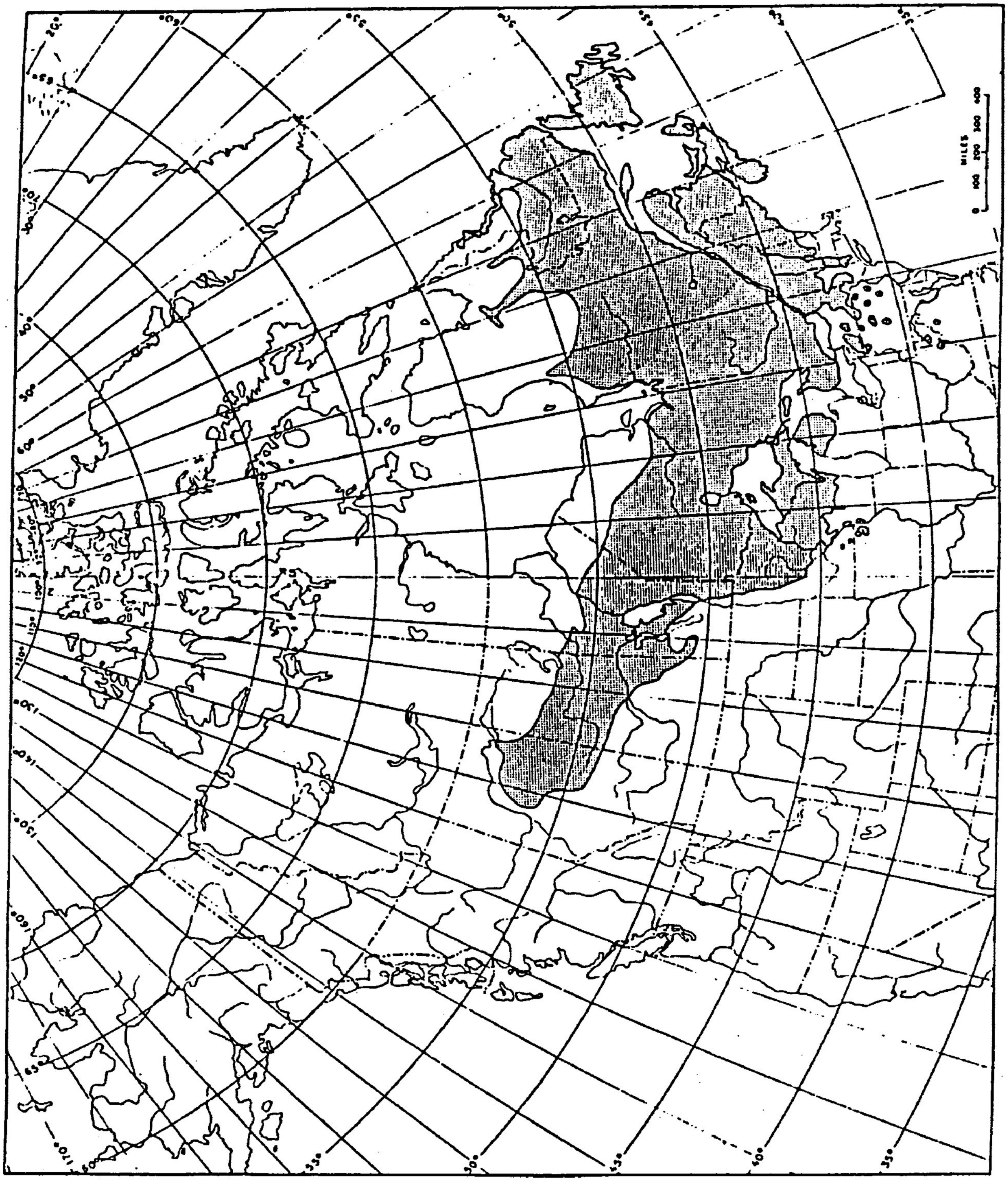

Fig. 1.2. The range of *Abies balsamea* (Fowells, 1965).

instead, population differentiation appeared to have occurred within a single variable complex in response to local selection pressures. However the study did indicate that there were minor differences in morphological characters from populations on either side of the Rocky Mountain crest that may reflect the existence of separate east and west refugia during glacial periods. The available fossil data also supports this conclusion (Lichti-Federovich, 1970; Ritchie, 1976; Kearney and Luckman, 1983).

A parallel study of variation in needle flavonoids (Parker et al., 1984) to the morphological investigation of Parker et al. (1981) indicated that westernmost (British Columbia) *A. lasiocarpa* and easternmost (Eastern Alberta and Saskatchewan) *A. balsamea* populations were distinct. However flavonoid patterns of geographically intermediate populations formed a continuum from east to west beginning in the lower foothills of the east slope of the Rocky Mountains in Alberta and extending to the interior of British Columbia. Although no sharp boundary separating the two species could be detected based on the flavonoid results, the observed clinal pattern was steepest at the Rocky Mountain crest, and populations on either side of the crest were more variable than populations to the east of the mountains. On the basis of the observed variation patterns, Parker et al. (1984) suggested that genetic interchange has occurred between *A. lasiocarpa* and *A. balsamea* to each side of the Rocky Mountain crest following post-glacial migration.

An earlier study of the terpenoids of subalpine and balsam fir in western Canada indicated that the two firs are different in their terpenoid patterns, but that intermediate populations exist in the Lesser Slave Lake and Battle lake regions of central Alberta (Hunt and von Rudloff, 1974). Based on their results, these authors suggested that extensive introgression has occurred between *A. lasiocarpa* and *A. balsamea* in central Alberta, and supported Moss'(1953, 1955) concept of intergrading populations between the two species. Hunt and von Rudloff (1974) further suggested that these two firs probably evolved from a common ancestor originating in western North America (a link across the Bering bridge is suspected by these authors on the basis of considerable similarity of the volatile leaf oils of Canadian *Abies* and *Abies sibirica*) as a result of isolation in separate refugia during periods of glaciation. They proposed that small stands of fir in Alberta that seem intermediate between subalpine and balsam fir may be progeny from hybrids between subalpine fir colonizing eastward from the Rocky Mountains and balsam fir colonizing westward from an eastern refugium.

Cortex monoterpene data of Zavarin et al. (1970), Zavarin and Snajberk (1972) and unpublished data presented by Critchfield (1984) also indicate that fir stands sampled in a transect across central Alberta are of hybrid origin. Critchfield(1984) suggests that the width of this zone of hybridization in central Alberta is approximately 500 to 800 km. This author concludes from the available data that neither fir has been genetically influenced by the other outside the zone of intergradation in Alberta, and if hybridization on the present scale has occurred in past interglacials, the introgressed populations must have been eliminated during the next glacial interval. However Parker and Maze (1984) observed the presence of *A. balsamea* -type flavonoids west of this species' range, suggesting that introgression with balsam fir may have played a role in the recent evolution of subalpine fir in the eastern interior of British Columbia, and perhaps also in the Washington Cascade mountains.

Further questions have arisen concerning variation in *A. lasiocarpa*. It was concluded by Hunt and von Rudloff (1979) based primarily on terpene data that the eastern elements of subalpine fir north of approximately 43^{o} latitude in Canada and the United States are distinct from the western more coastal elements with the exception of four north Cascades populations. These authors believe that the two elements should be recognized as separate species, and therefore reapplied the previously published name *Abies bifolia* A. Murr. (Murray, 1863) to the eastern segregate. Hunt and von Rudloff (1979) proposed that coastal and Rocky Mountain subalpine fir probably came from different glacial refugia and have since hybridized extensively. They also suggested that the existence of distinct coastal, Rocky Mountain, and intermediate forms of subalpine fir could explain why Kennedy et al. (1968) found crystals in the ray parenchyma of coastal but not in interior subalpine fir, and why Fraser and Swan (1972) found a log colour test to work on interior but not on coastal subalpine fir.

Support for Hunt and von Rudloff's (1979) hypothesis is generally provided by an earlier study of the cortical monoterpenes of subalpine fir throughout a large part of its range (Zavarin et al., 1970). In this study, subalpine fir populations in the Pacific coast area tended to have one group of cortical monoterpenes and those in the Rocky Mountain area had another.

In spite of the apparent differences between coastal and interior subalpine fir populations, Critchfield (1984) states that although the evidence indicates that subalpine fir has well-differentiated geographic races in the coastal and interior regions, the magnitude and character of the observed differences do not justify the recognition of separate species as proposed by Hunt and von Rudloff (1979). However, as Critchfield points out, the macrofossil record does support their conclusion that coastal and Rocky Mountain subalpine fir probably came from different refugia.

To clarify further the taxonomic status of *Abies lasiocarpa*, Parker and Maze (1984) undertook a study of its intraspecific variation in British Columbia and Washington, based on cone, needle, and flavonoid data. The results showed some inconsistencies among the measured characters suggesting that the evolution of each class of characters has been partly independent from the other two. As a result, the authors propsed the need to consider a variety of traits when drawing taxonomic conclusions. Analysis of cone data indicated no geographical patterning of the populations, although very few characters were evaluated. However eastern and western groups of populations were separated on the basis of needle morphology and flavonoids, with the exception that a Vancouver Island population was similar in needle morphology to interior British Columbia populations. Three geographic groups were generally discerned on the basis of the needle and flavonoid variation patterns: 1) coastal mountains of British Columbia 2) Cascade mountains of Washington and 3) eastern interior of British Columbia. Although there were some inconsistencies, the results of the study generally support the earlier recognition by Hunt and von Rudloff (1979) of separate coastal and interior taxa of subalpine fir. However Parker and Maze (1984) stated that in contrast to Hunt and von Rudloff's (1979) opinion, the evidence is not consistent enough to recognize separate species, and suggested instead the designation of separate varieties.

POTENTIAL GLACIAL REFUGIA IN NORTHERN, UNGLACIATED AREAS

St. Elias, Cordilleran and Laurentide ice affected various parts of the Yukon during at least two periods, once during early Wisconsin time 40,000 or more years before present (B.P.) and once during late Wisconsin time 13,000 to 14,000 years B.P. (Oswald and Senyk, 1977). Earlier ice advances were reported by Bostock (1966), Vernon and Hughes (1966), Hughes et. al. (1969) and Hughes (1972). The ice masses covered the southern and eastern parts of the Yukon Territory, and ice lobes extended westward to the vicinity of the present Tintina Valley, Bonnet Plume Basin, and Arctic Coastal Plain. However a large area in the western part of the Yukon Territory remained free of ice, because it laid in the rain and snow shadow of the St. Elias Mountains of Alaska and the Yukon (Prest, 1983). The unglaciated portion consists of most of the Klondike, Porcupine, and Arctic Plateaus, the Porcupine Plain, and portions of the Ogilvie, Wernecke, and British Mountains, as well as western slopes of the Richardson Mountains. Much of interior Alaska remained unglaciated throughout the Pleistocene. Figure 1.3 indicates ice sources, glacial limits, and flow patterns of ice that occurred in the Yukon Territory. Figure 1.4 illustrates the most recent glaciation (Wisconsin) in North America.

Plants in general, and conifers in particular, were surprisingly stable throughout the Pleistocene, since few species became extinct in spite of the numerous climatic changes throughout this period (Leopold, 1969). A species' survival was achieved either by migration south of the ice, or persistence in one or more glacial refugia. Subalpine fir's range is extremely wide, and

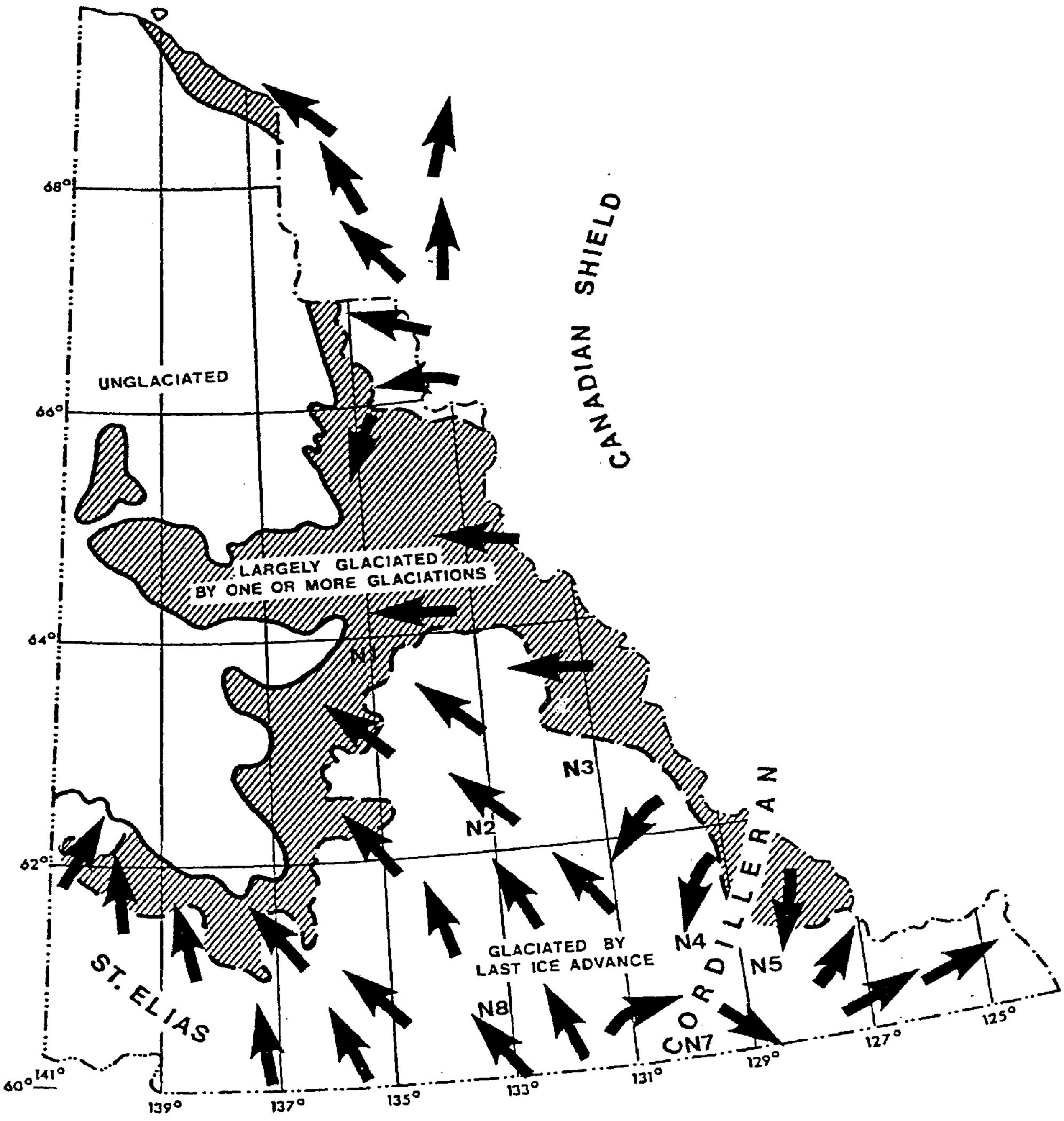

Fig. 1.3. Ice sources, glacial limits, and flow patterns in the Yukon Territory (Oswald and Senyk, 1977). *Abies lasiocarpa* collection site locations are indicated.

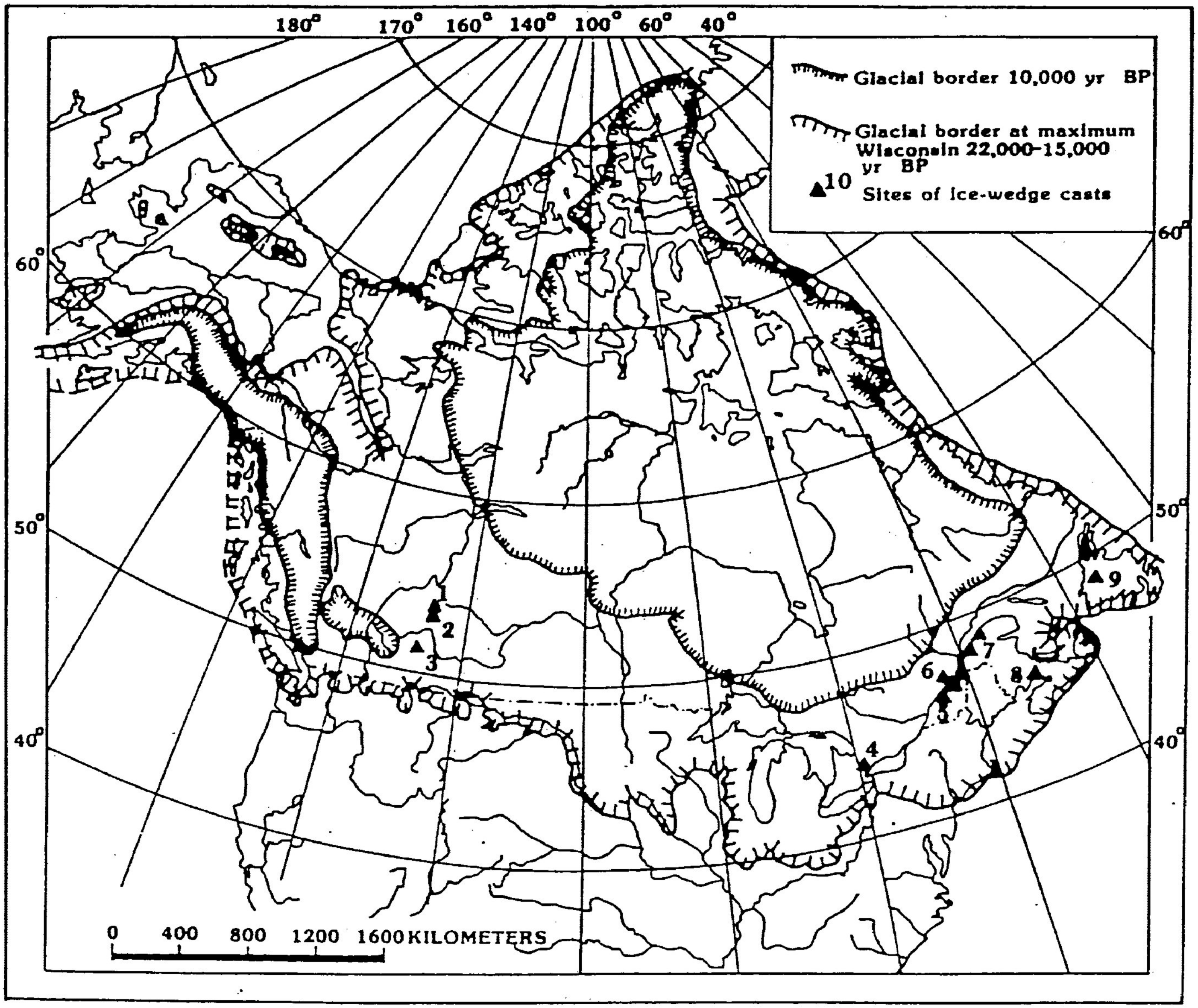

Fig. 1.4. Extent of the Wisconsin glaciation in North America (Pewe, 1983).

extends south of the limits of glaciation. Evidence for the persistence of this fir south of the Pleistocene ice sheets in both Pacific and Rocky Mountain regions appears in fossil pollen and plant macrofossil records from the late glacial and early postglacial periods, as summarized by Critchfield (1984). Although subalpine fir populations south of the glacial limit were not drastically affected by glaciation, there is evidence of some altitudinal displacement in these regions due to altered circulation patterns over the North American continent and general global cooling caused by glacial ice sheets. Betancourt (1984) reported the presence of this fir from a packrat midden site at 2195 m in the Abajo Mountains of southeastern Utah where it grew 11,300 yr. B.P. about 700 m below its present limits in these mountains. Similar altitudinal, geographical, and habitat displacements have been reported for a number of other plant species that existed throughout glaciation south of the ice limits (Spaulding, 1984).

The northernmost limit of the range of subalpine fir lies in central Yukon Territory, and extends westward down along the Alaska coast. In contrast to populations south of the glacial ice limits, the evolutionary history and biogeography of this fir is not well known in these northern, formerly glaciated areas, where fossil records are almost non-existent.

The possibility that certain plant species were able to survive in one or more northern refugia throughout glaciation, in areas of northwestern Canada and the United States, has been the subject of much controversy. It was first proposed by Hulten (1937) that a number of plant species including *Abies lasiocarpa* may have survived in small, isolated areas in the unglaciated Yukon Valley. Hulten suggested that in postglacial time, these elementary areas, which must have been situated very close to one another, joined up again to form one more-or-less continuous area.

Since Hulten's (1937) theory was first proposed, numerous attempts have been made to reconstruct the biogeographical history of a variety of tree species whose present ranges extend into northern unglaciated areas of the Canadian and American northwest. The reconstruction of a plant's biogeographical history may be done either through the use of the fossil record, to provide direct evidence of past distributions, or through indirect inference from the modern geographical distribution and patterns of variation in morphological, cytological, and genetic characteristics (Patterson, 1981; 1983). However, it is always preferable to reconstruct a species' history directly from the fossil record whenever possible, so that the modern distribution of variation in characters may be unambiguously related to the distributional and migrational history of the species. Unfortuately, fossil records often lack the sensitivity and completeness needed to provide detailed and reliable species histories (Patterson, 1983).

Pioneer research by Hansen (1949, 1950, 1953) provided a basic pollen stratigraphy for northern, unglaciated areas in western Alberta, the Yukon, and Alaska. Based on pollen analysis of peat sections in these studies, the author suggested that both subalpine fir and lodgepole pine probably persisted during late Wisconsin glaciation in refugia not far removed from the sampled sites, either in west-central Yukon, or from ice-free areas in western Alberta and/or northeastern British Columbia. Appreciable levels of pine pollen were observed in the lowest levels of sections from the Yukon, thus indicating that pine was prevalent in the region when the earliest pollen-bearing sediments were deposited. Subalpine fir was represented consistently in the pollen profiles from sections along the Alaska Highway from the Yukon-British Columbia border, west to Haines Junction, Alaska, although in low proportions with a maximum of only 10% near Whitehorse. Although this early work utilized fossil evidence, it was difficult to accurately establish a chronology of postglacial reforestation in these northern, unglaciated areas, since radiometric dates were not applied to the fossilized pollen, and mere speculation of the ages of the samples was attempted.

Because lodgepole pine has a similar distribution to that of subalpine fir, it is reasonable to assume these two species may have parallel biogeographical histories, particularly at the northern limits of their ranges. Thus, information on the biogeography of lodgepole pine could provide insight into subalpine fir's biogeography. Since the time of Hansen's (1949, 1959, 1953) early palynological work, other palaeoecologists have also suggested that lodgepole pine was able to persist in northern refugia during the last glaciation, despite a lack of complete late Pleistocene and Holocene fossil records from the potential refugia and postglacial migrational routes of this species in western Alberta, northeastern British Columbia, and the southern Yukon (Heusser, 1967; Anderson, 1970; 1971). Studies of the modern distribution of various characters of lodgepole pine have provided additional evidence to support the theory of a northern glacial refugium. Separate studies have indicated that northern British Columbia and Yukon populations of lodgepole pine differ morphologically (von Rudloff and Nyland, 1979; Critchfield, 1980), chemically (von Rudloff and Nyland, 1979; Forrest, 1980; 1981) and in genetic structure (Wheeler and Guries, 1982a; 1982b) from more southern populations.

A more recent reconstruction of the late Quaternary biogeographical history of lodgepole pine based upon fossil pollen evidence refutes the widely accepted hypothesis that relict populations were able to persist throughout the last glaciation in northern Canadian refugia (MacDonald and Cwynar, 1985). Based upon radiocarbon and tephrochronological dating of pollen profiles obtained from southern and central British Columbia, Alberta, and the Yukon, these authors provided substantial evidence to indicate that lodgepole pine survived the late Wisconsin glaciation south of the Laurentide and Cordilleran ice sheets and migrated northward following deglaciation. Apparently this pine was present in north central British Columbia and the southern Yukon by 4000 years B.P. and reached its northern extent in central Yukon less than 400 years ago. This study emphasizes the need to use caution when utilizing the indirect (i.e., non-fossil) approach to the biogeographical reconstruction of a species.

In a subsequent study, Cwynar and MacDonald (1987) proposed an alternative explanation for at least the observed genetic differences between northern and southern lodgepole pine populations. Based on a relation between genetic and morphological attributes of modern populations of lodgepole pine to their time since founding, these authors suggest that reduced allelic diversity toward the northern periphery of the range of this pine may result simply from the stochastic effects of repeated long-distance founding events during its continental-scale, postglacial spread. However they also state that because the migration of lodgepole pine has followed north-to-south macroenvironmental gradients, that the relative importance of selection along these gradients and the effects resulting from the migration process itself cannot be clearly distinguished.

Hopkins et al. (1981) synthesized the available macrofossil and palynological data for a number of tree and shrub species that are potential candidates for survival in northern refugia, and attempted to show the persistence of some, and total extinction of others during the last glaciation. As concluded by these authors, the macrofossil record remains so sparse and the pollen record so ambiguous that only tentative conclusions can be drawn concerning the possible persistence and former distribution of trees and large shrubs in northern, unglaciated areas. They speculate that balsam poplar (*Populus balsamifera* L.) is the best candidate for survival in this region during the last glaciation, on the basis of macrofossil and pollen evidence from a large number of sources. Larch (*Larix laricina* (Du Roi) K. Koch), aspen (*Populus tremuloides* Michx.), and alder (*Alnus* spp.)are also potential candidates, although the fossil evidence is less conclusive for the persistence of these species. Murray (1978) supports the theory that balsam poplar and aspen probably survived in northern refugia through full-glacial time. However Hopkins et al. (1981) point out that although these species may have been present in refugia during glaciation, that trees and large shrubs were certainly not abundant. Instead, they were probably scattered in isolated, local favourable sites, subsisting most of the time without producing pollen or fertile seeds.

The fossil records of white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.), as well as tree birch (*Betula* spp.) indicate that these species were probably exterminated in Beringia about 30,000 years ago and did not reappear until deglaciation permitted dispersal of a new population from refugia south of the continental ice. Speculation on the biogeography of white spruce by Hopkins et al. (1981) contradicts the earlier conclusions of Tsay and Taylor (1978) who compared the isoenzymes of populations in the Yukon, Alaska, and Ontario, and concluded that the Yukon is a centre of genetic diversity, with its unglaciated part having served as a refugium for white spruce during the last glaciation. However Critchfield (1984) does not accept the opinion of Tsay and Taylor (1978), stating that their data do not provide strong enough support for their conclusions.

The possibility that subalpine fir was able to survive in one or more northern refugia during the last glaciation, as initially proposed by Hulten (1937), is not well supported by fossil evidence. Other than the undated subalpine fir fossil pollen present in only trace amounts in Hansen's early studies (1949, 1950,1953), there is a lack of available fossil records for this species in or near the northern, unglaciated parts of Canada and the United States.

If subalpine fir was able to survive in northern unglaciated areas, the climatic conditions in such areas would likely have been very severe. However Heusser (1954) found subalpine fir growing on two sites at the northern end of the east ridge bordering Taku Glacier in Alaska (Figure 1.5), possibly indicating the ability of this species to withstand the type of adverse climatic conditions that would also have existed throughout glaciation. Fir occurs nine miles above the terminus of the glacier. Heusser (1954) agrees with the opinions of Hulten (1937) and Hansen (1949, 1950) that subalpine fir at this site migrated from an unglaciated northern refugium or refugia in either western Yukon Territory or western Alberta, during middle postglacial time. Heusser believes that this fir migrated from such a refugium to its present location near Taku Glacier during middle postglacial time.

It has also been conclusively documented that subalpine fir, among other species, survived during Wisconsin glaciation in a refugium along the Olympic Peninsula in Washington, within 6 kilometres of the ice mass (Heusser, 1972), although this location would have been moderated by the Pacific ocean, so that climatic conditions would not have been nearly so severe as in the arctic.

The subalpine fir trees found growing near the Taku Glacier in Alaska were of Krummholz form, and reproduction was observed to be by means of layering. This type of propagation has been described as common for subalpine fir at timberline (Cooper, 1911; Oosting and Reed, 1952) where climatic conditions

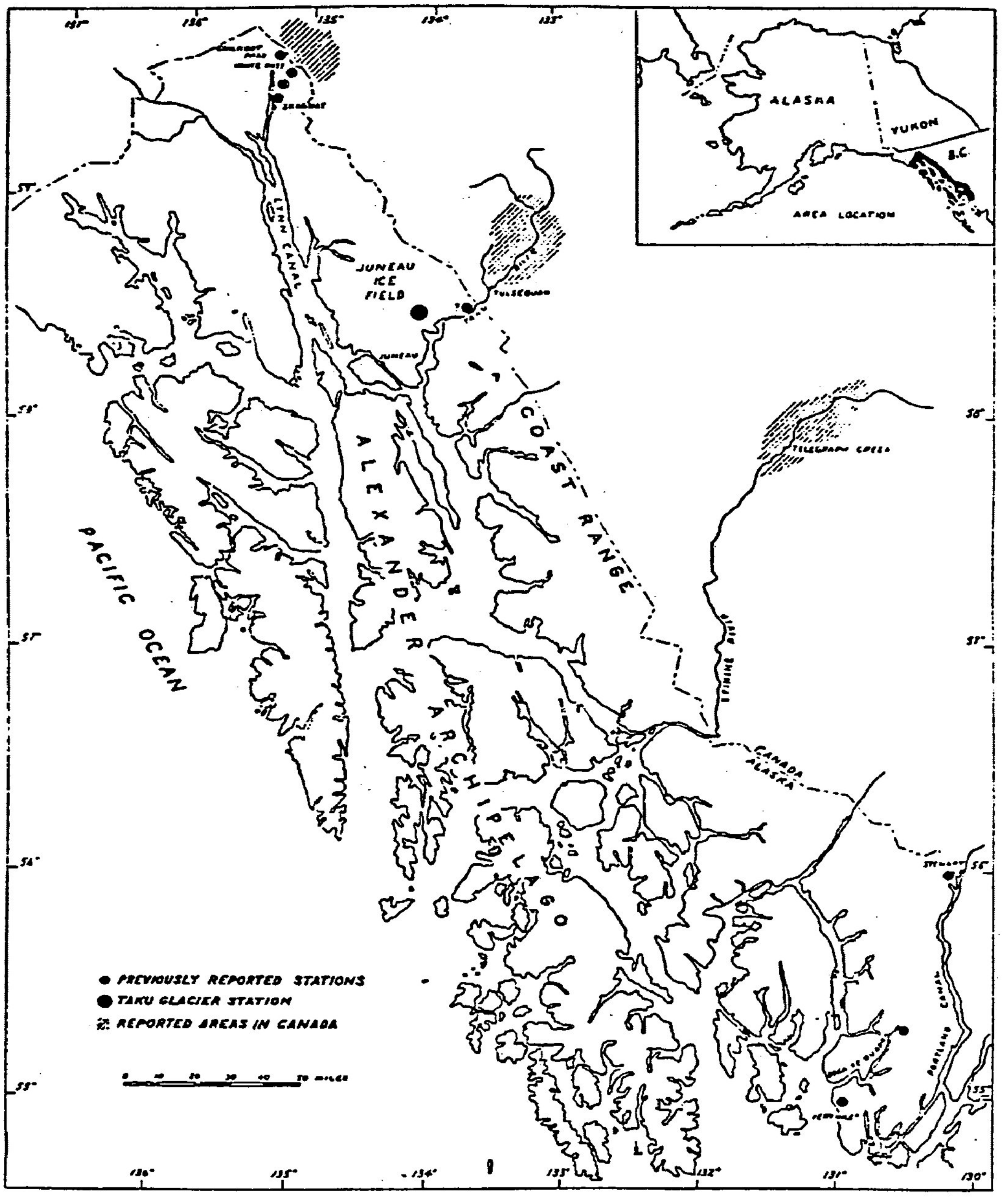

Fig. 1.5. Location of subalpine fir discovered growing near the Taku Glacier in southeastern Alaska. Locations of nearest known populations of subalpine fir in Alaska and British Columbia are also indicated. Map is from Heusser (1954).

are severe. If subalpine fir was able to survive throughout the most recent glaciation in isolated, northern refugia, reproduction may have been primarily by vegetative means, as has been suggested for aspen, larch, and alder under similar conditions (Hopkins et al.,1981). Such an occurrence could explain why only trace amounts of subalpine fir pollen were observed in peat sections sampled near potential refugium sites (Hansen, 1953). Even if subalpine fir trees surviving in one or more northern glacial refugia did produce pollen, it may not have been well preserved, since *Abies* pollen, including that of subalpine and balsam fir, is not well-represented even in modern pollen spectra (Lichti-Federovich and Ritchie, 1968; Webb and McAndrews, 1976; Mott, 1977; Mack et al., 1978). Similarly, the pollen of *Populus* and *Larix* are also not well preserved in modern pollen spectra even in areas where the trees are prominent in nearby vegetation, and their pollen is rarely reported from interglacial, interstadial, or full glacial pollen profiles, probably because of its fragility, although the evidence suggests that these species may have persisted in northern glacial refugia (Hopkins et al., 1981).

The only study of modern variation patterns in subalpine fir at the northern limits of its range was conducted by Zavarin et al. (1970). In this study, cortical monoterpenes were examined in populations from the Yukon to the southern limits of this fir in Arizona. On the basis of these characters, the Yukon populations were found to be similar to western Washington and Oregon populations. Critchfield (1984) interprets these results to indicate that the northernmost subalpine fir populations may have originated from a southern rather than a Yukon refugium, in which case the Yukon populations have migrated more than 2000 km in the past 13,000 years. However, additional characters need to be assessed, and the evolutionary processes that have been important in the recent development of the northernmost subalpine fir populations need to be investigated, in order to elucidate the evolutionary history of subalpine fir at its northern extreme.

Studies that attempt to correlate variation in specific morphological and physiological traits with variation in climatic factors have been carried out for a number of species, in order to determine which evolutionary processes have been important in the species' development. (Myers and Borman, 1963; Squillance, 1966, Lester, 1968; Morgenstern, 1978). Parker et al. (1979) found an indication that phenotypic divergence of subalpine fir populations was correlated with latitude and/or local environmental conditions in north coastal British Columbia.

Variation in such characteristics among populations of a species may be continuous or disjunct, and either gradual or abrupt. Any of the basic genetic processes of mutation, recombination, migration, isolation, genetic drift, and selection may operate either individually or jointly to change gene frequencies in natural populations (Stebbins, 1950). The operation of one or more of these processes ultimately results in phenotypic interpopulation variation, which may be the result of either direct plastic modification of the individual, genetic divergence due to selection pressures, or genetic divergence resulting at random (Heslop-Harrison, 1964). It is not possible to determine each component that contributes to the observed morphological variation among natural populations, since several sources may interact or have similar effects. Because random effects, such as those caused by genetic drift, do not follow a pattern, they cannot easily be identified. However, phenotypic plasticity is influenced greatly by changes in environmental conditions. Thus, differentiation resulting from selection pressures that are modified by a varying environment should show a detectable pattern. If phenotypic plasticity and/or adaptive genetic variation explain a significant amount of the variation observed among natural populations, population differentiation attributable to these sources should therefore correlate with environmental factors.

OBJECTIVES

The overall goals of this study were to clarify the taxonomy of *Abies lasiocarpa* throughout its range from Washington to the Yukon Territory and to gain a better understanding of the taxonomic relationship between subalpine fir in this region, and balsam fir from central Alberta to northern Ontario. Within this context, there were several specific objectives.

A major objective was to examine the patterns of variation in morphological characters among populations of subalpine fir at the northern limits of its range. The intent of this investigation was to help clarify the evolutionary history of subalpine fir in this region, and to provide an indication as to whether the species was able to survive the last glaciation in one or more northern refugia.

A second objective was to gain an understanding of the evolutionary processes that have been important in the recent development of subalpine fir at its northern extreme, by attempting to correlate the observed morphological variation among populations with specific environmental variables.

A third objective of the study was to expand the investigation of morphological variation in subalpine fir at the northern limits of its range, to include populations in more southerly locations, from British Columbia, Alberta, and Washington. These additional populations were previously used in studies of morphological and chemical variation in subalpine fir (Parker et al., 1979; Parker et al., 1981; Parker and Maze, 1984). Morphological data from these earlier studies was added to the more recent data from the northern limits of the species range to determine how the overall patterns of variation fit the hypothetical taxonomic framework of Coastal and Rocky Mountain forms of subalpine fir as proposed by Hunt and von Rudloff (1979). This expanded investigation would also provide further insight into the evolutionary history of subalpine fir at its northern extreme, by clarifying the relationship of the northernmost populations to those from further south.

The final main objective was to further clarify the relationship between the firs presently designated as *Abies lasiocarpa* and *Abies balsamea* by expanding the investigation to include populations from the sympatric zone of subalpine and balsam fir in west-central Alberta, and selected balsam fir populations from northwestern Ontario. Through this investigation, an attempt was made to determine, on the basis of morphological variation, the existence of either 1) two separate species, in which case the extent of introgression and gene flow that has occurred and that may now be occurring between these firs would be examined, or 2) a continuum in a single, variable species complex.

A subsidiary objective of the study was to examine whether or not the patterns of variation for mature *Abies lasiocarpa* from the northern limits of its range are similar to those of progeny from these populations grown in a common environment.

2.0 METHODS

SITES AND COLLECTIONS

Collections of cone and foliage samples were made from mature subalpine fir trees from ten sites in northwestern Canada and the United States in August of 1983. Seven of these sites are in the Yukon Territory, two are in northern British Columbia, and one is in Alaska near the Yukon border.

Foliage samples were collected from cone-bearing branches of ten trees at each site, and when they were available, current-season cones were collected from the same trees. These materials are presently stored in the Lakehead University herbarium.

Table 2.1 lists the location and elevation of the ten collection sites as well as mean height, age, and the range of these parameters for trees at each site. Table 2.2 provides additional detailed site information for each of these sites, including associated species. The vegetation associations are quite variable among sites, which is surprising for tree populations existing in such marginal situations. Figure 2.1 indicates the locations of the ten sites, as well as those from which samples were collected in previous studies (O'Reilly, 1981; Parker et al., 1981, 1984; Parker and Maze, 1984), and which have been used for morphological analyses in the present study. The shaded area contains populations in the tentative range of coastal subalpine fir, *Abies lasiocarpa,* as designated by Hunt and von Rudloff (1979). The hatched area contains populations in the tentative range of Rocky Mountain fir, *Abies bifolia.* Figure 2.2 indicates populations of balsam fir from northwestern Ontario used in this study. Table 2.3 lists all of the additional collection sites and their locations, as well as site elevation, tree size, and the number of trees samples at each site.

Table 2.1. Site and collection data for 10 northern populations of *Abies lasiocarpa.*

SITE	NAME	LATITUDE	LONGITUDE	ELEVATION (m)	NO. OF TREES SAMPLED	HEIGHT (m)		D.B.H. (cm)	
						MEAN	RANGE	MEAN	RANGE
N1	Keno Hill, Y.T.	63 55' N	135 16' W	1311	10	7.2	3.5-11.0	14.6	9.0-25.0
N2	Faro, Y.T.	62 17' N	133 15' W	1372	10	8.9	7.0-12.5	16.8	10.3-25.5
N3	Mt. Sheldon, Y.T.	62 40" N	131 14' W	1067	10	9.0	4.0-14.5	17.3	7.8-29.5
N4	Francis Lake, Y.T.	61 04' N	129 22' W	884	10	9.2	3.5-16.5	14.2	4.3-30.6
N5	Tuchitua, Y.T.	60 48' N	128 58' W	975	10	10.8	5.5-23.5	15.8	5.7-23.5
N6	Cassiar, B.C.	59 17' N	129 35' W	1006	10	9.1	2.5-14.5	15.0	4.0-22.0
N7	Rancheria, Y.T.	60 05' N	130 35' W	1036	10	14.9	8.5-20.5	22.3	10.0-40.8
N8	Johnson's Crossing, Y.T.	60 39' N	133 04' W	1219	10	7.2	4.0-14.5	15.1	9.3-32.3
N9	Atlin, B.C.	59 40' N	133 27' W	1372	10	6.6	3.5-9.0	16.3	8.5-21.0
N10	Skagway, Alaska	59 20' N	135 15' W	793	10	2.3	1.0-5.0	3.1	1.0-8.8

Table 2.2: Detailed location and site description for 10 northern *Abies lasiocarpa* sites.

SITE	DESCRIPTION	SITE	DESCRIPTION
N1	Northeast of Keno Hill, Y.T. Broken scrubby stand of white spruce and subalpine fir. Two species of shrubby willow and dwarf birch. Collecting site on NNW aspect of slope. Subalpine fir first encountered at 1100 m along a mining access road. Fir turns to Krumholz at approximately 1524 m.	N6	Sideroad to the north off of Stewart-Cassiar Road, 113 km south of Alaska Highway, 6 km north of turnoff. Between Boya Lake and Cassiar, just south of Fort Hope Lake Indian Reserve. Lodgepole pine stand with scattered individuals (10-15%) of subalpine fir and a very small element of trembling aspen. Very sandy soil.
N2	Road to a mine north of Faro, Y.T. Main cover on site is subalpine fir and black spruce. Shrubby willow, low shrub huckleberry and alder also present. Subalpine fir first encountered at approximately 1200 m (between 1070 and 1220 m). Individuals were stunted and without cones. Site is an abandoned gravel pit. Trees appear to be growing under marginal conditions. Layering is evident.	N7	Yukon Forest Service Transport tower access road to the south of Alaska Highway near Rancheria. Two stands are located on the site: 1) old growth (105 years) lodgepole pine with subalpine fir and some black spruce and birch coming up as lower tree stratum. 2) old growth white spruce and subalpine fir. Patches that apparently escaped an old burn are evident.
N3	Canol Road north of Ross River, 127 km north of Ferry. Collection site is a rocky knoll west of main road and due east of Mt. Sheldon. Cover is willow, trembling aspen, black spruce, white spruce, and subalpine fir.	N8	Canol Rd. 24 km north of Johnston's Crossing. Subalpine fir first encountered at 1067 m in a fairly dense lodgepole pine and white spruce stand. Collection site in an open subalpine fir stand with this tree the most frequent species. Lodgepole pine is the next most frequent tree species, and the site also contains willow and scattered black cottonwood.
N4	Yukon Highway # 4, 243 km south of Ross River Junction, between Francis Lake and Tuchitua. Site is a swampy black spruce stand with a few individuals of subalpine fir and tamarack. All but a few trees appear to have been produced by layering. Subsite (1 km south of collection area) has white and black spruce with some trembling aspen and is generally drier.	N9	Boulder Creek Mine Road approximately 20 km east of Atlin B.C. Lower elevations have stands of lodgepole pine changing to white spruce and finally subalpine fir at subalpine zone (ca. 1067 m). Close to treeline, subalpine fir is the only tree species present.
N5	Highway #10 east of Tuchitua, 24.6 km east to junction of Yukon Highways #4 and #10. Fairly steep sideslope of mountains. Old growth nearly pure stand of subalpine fir with a minor element of white spruce. Many of the trees were released by highway clearing right-of-way.	N10	Highway #2 near White Pass,approximately 10 km north of Skagway Alaska. Collection site is just off highway on edge of a gravel pit. Site is semi-Krumholz form of subalpine fir and Mountain hemlock. Most trees are stunted, rarely over 3 m, but cones are abundant. Nonetheless, layering appears to be most important for reproduction.

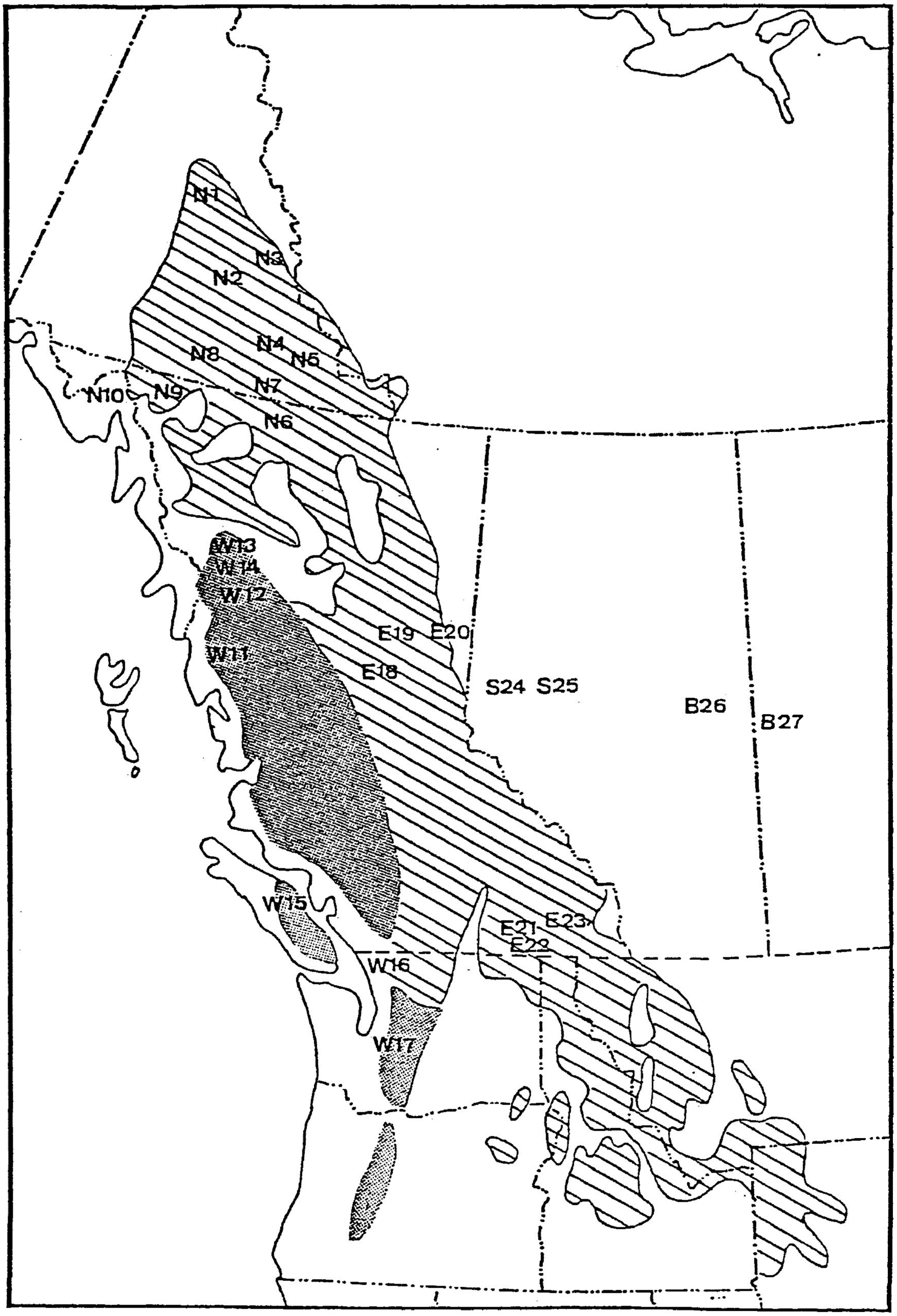

Fig. 2.1. Location of *Abies lasiocarpa* and *Abies balsamea* collection sites. The shaded area represents the tentative range of *A. lasiocarpa* (populations with a W) and the hatched area represents the tentative range of *A. bifolia* (populations with an E or N), as proposed by Hunt and von Rudloff (1979). Populations in the putative zone of sympatry between *A. lasiocarpa* and *A. balsamea* are designated with an S. *Abies balsamea* populations are designated with a B.

Fig. 2.2. Location of *Abies balsamea* populations in Northern Ontario.

Table 2.3: Site and collection data for 21 populations of *Abies lasiocarpa* and *Abies balsamea*.

SITE	NAME	LATITUDE	LONGITUDE	ELEVATION (m)	NO. OF TREES SAMPLED	D.B.H. (cm)	
						MEAN	RANGE
W11	Mayo Creek, B.C.	54 47' N	128 58' W	490	9	67.0	21.0-97.0
W12	Bonney Lake, B.C.	55 58' N	128 48' W	800	14	43.0	27.0-58.0
W13	North Bell-Irving, B.C.	56 45' N	129 48' W	580	14	45.0	31.0-75.0
W14	South Bell-Irving, B.C.	56 23' N	129 18' W	425	10	39.0	28.0-51.0
W15	Forbidden Plateau, B.C.	49 38' N	125 23' W	910	10	24.0	14.0-44.0
W16	Mt. Baker, Wash.	48 55' N	121 48' W	1220	10	25.0	12.0-43.0
W17	Corral/Mt. Rainier, Wash.	47 03' N	121 32' W	1770	10	17.0	6.0-31.0
E18	Carp Lake, B.C.	54 49' N	123 17' W	830	10	32.0	24.0-41.0
E19	Hart Highway, B.C.	55 31' N	122 47' W	800	10	27.0	17.0-45.0
E20	Puggins Mt., B.C.	55 40' N	120 48' W	1100	10	28.0	16.0-41.0
E21	Cayuse Creek, B.C.	49 25' N	117 57' W	1290	8	20.0	11.0-32.0
E22	Upper Sheep Creek, B.C.	49 08' N	117 07' W	1610	10	29.0	20.0-38.0
E23	Goat River, B.C.	49 19' N	116 23' W	900	6	31.0	27.0-33.0
S24	Pinto Creek, Alta.	54 38' N	118 55' W	920	10	28.0	16.0-41.0
S25	Hinton Forestry Rd. Alta.	54 40' N	118 30' W	900	10	22.4	17.0-28.0
B26	Touchwood Lake, Alta.	54 45' N	112 35' W	850	15	17.4	12.0-26.0
B27	Keeley Lake, Sask.	54 40' N	108 15' W	600	15	17.6	10.0-23.0
B28	Kenora, Ont.	49 50' N	94 58' W	380	10	14.1	9.3-21.2
B29	Mine Centre, Ont.	48 50' N	93 05' W	370	10	13.0	8.8-24.4
B30	Cameron Falls, Ont.	49 25' N	89 10' W	335	10	18.1	11.5-25.0
B31	Manitouwadge, Ont.	48 40' N	85 55' W	335	10	16.0	10.5-21.8
B32	Graham, Ont	49 20' N	92 25' W	460	10	17.1	11.8-23.7

PROGENY TEST

A progeny test from seed of five of the ten northern populations (N1, N3, N5, N6, N10) was initiated in October of 1983. Untreated seed from each of these sources was sown in Spencer-Lemaire Ferdinand containers in a randomized complete block design with ten replications. The flats of seedlings were then placed in a controlled greenhouse environment (natural photoperiod, 25^{o} C day, 15^{o}C night). After germination was complete, the seedlings were thinned and allowed to grow for six months in these greenhouse conditions. Evidently seed from population 10 was not viable, as no seedlings were obtained from this source, in spite of an abundant cone crop at this site.

In the spring following germination of the progeny, the seedlings were removed from the greenhouse and placed outside in a shade house. The seedlings were then grown for an additional four months before needles from individual seedlings were selected for measurement and analysis similar to that done for the parent needle material. Due to variable germination, progeny from only four or five of the parent trees at each site were available.

CHARACTERS

Similar needle and cone characters were used, whenever possible, in the present study, as those used in previous taxonomic studies of the variation in *Abies lasiocarpa* and *Abies balsamea* (Parker et al., 1979; Parker et al., 1981; Parker and Maze, 1984) where they have proven to be good discriminators of populations and descriptors of variation. Needle material parallel to that of the previous studies was also used. Needles were always selected randomly from the previous year's growth, and always from the mid portion of a lateral cone-bearing branch. In this way, a parallel could be drawn between the present and previous studies so that the results could be directly compared.

The needle characters (Figure 2.3) included 1) needle width (NW), 2) needle thickness (NT), 3) diameter of resin canal (RC), 4) distance from the resin canal to the adaxial needle surface (AD), 5) distance from the resin canal to the abaxial needle surface (AB), 6) distance from the resin canal to the needle margin (MD), 7) needle length (NL), and 8) number of rows of stomata on the adaxial surface at the midpoint of the needle (RS). An additional three characters were also used. These were 9) diameter of the vascular cylinder (VC), 10) distance from the vascular cylinder to the adaxial needle surface (VAD), and 11) distance from the vascular cylinder to the abaxial needle surface (VAB). For each tree, needle measurements were determined from the average of measurements made on five needles from each tree. For the progeny, needle measurements were determined from the average of measurements made on five needles of a single seedling from each tree. Each seedling was selected randomly from among the available progeny from each tree.

Because *Abies lasiocarpa* generally produces average or good seed crops only every three years (Fowells, 1965), it is often difficult to obtain seed cones from trees of this species. One of the populations (N2) examined had no cones available in 1983. In the remaining populations, one typical cone from each tree was used to obtain measurements of 1) cone length (CL), 2) diameter of cone axis at the base (ADB), and 3) diameter of cone axis at the midpoint (ADM). Additional cone characters measured were 4) cone-scale length (SL), 5) cone-scale width at the widest point (SW), 6) cone-scale bract length from the base of the awn to the fusion point (BL), 7) bract width at the widest point (BW) 8) bract awn length (AL), 9) angle of the apex of the scale bract excluding the awn (An), and 10) distance from the widest point of the bract to the fusion point (D). These characters (Figure 2.4) were determined as the average of five cone scales and associated bracts per tree from the mid-portion of the cone.

In addition to the cone and needle characters that have been described, 20 radial distances from the centres of the same needle cross-sections were also used as characters to describe needle cross-sectional shape. Leaf shape

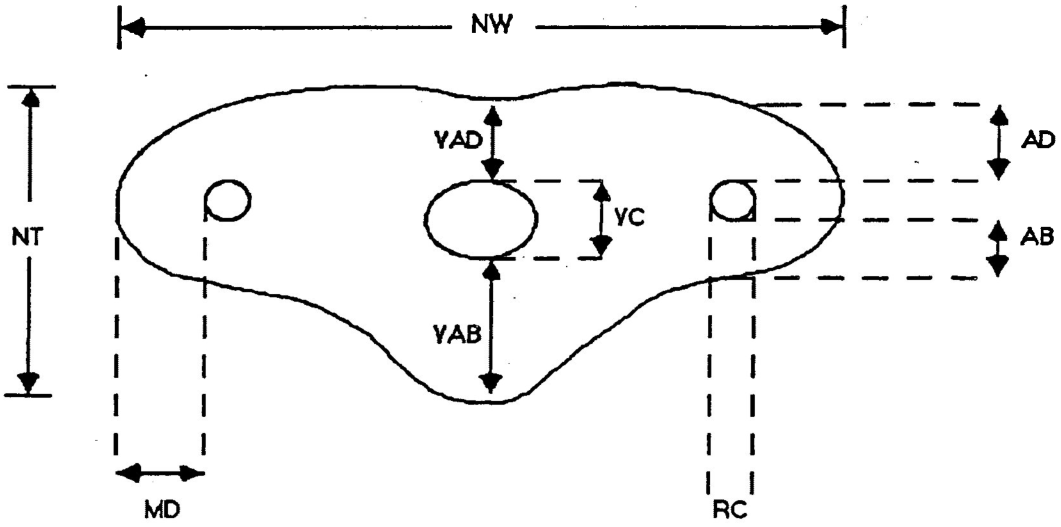

Fig. 2.3. Conventional needle characters.

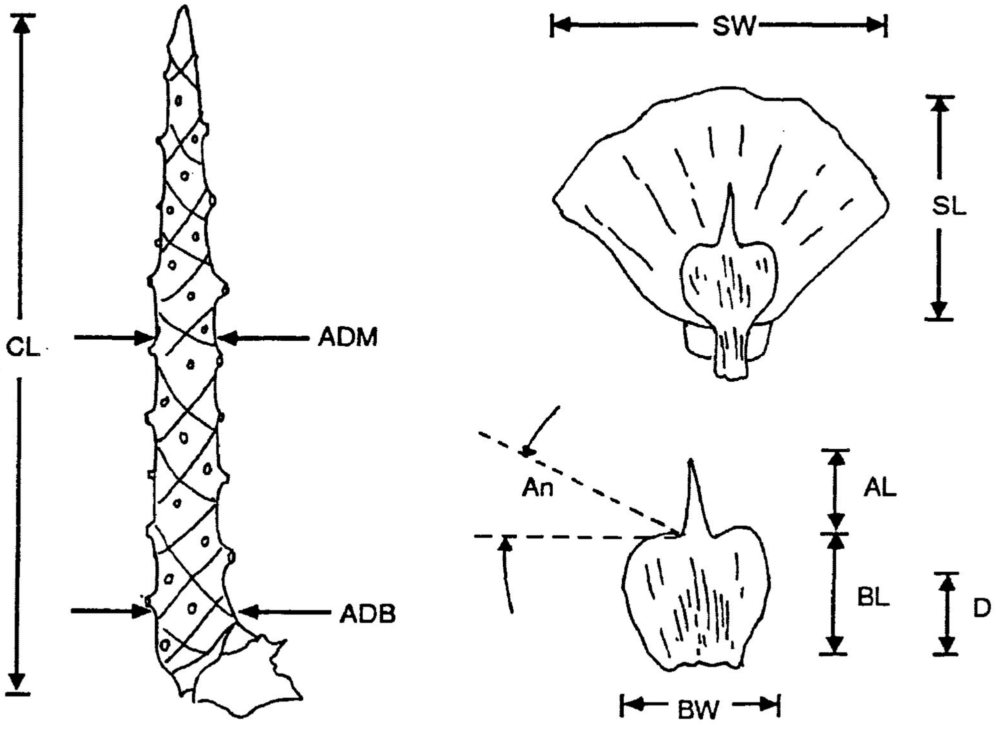

Fig 2.4. Cone characters.

is known to vary at every heirarchical level, within and between individuals, populations, and taxa, and it is considered to be a useful taxonomic character, since shape variation tends to be more independent of the environment, and more heritable than is the size of plant structures (Dickinson et al., 1987). Leaf shape in general has been a source of systematic data for as long as plants have been classified, due to the availability of leaves and the wide range of morphological variation that they exhibit (Linnaeus, 1751; Theophrastus, 1916). Variation in leaf shape has been studied in a number of deciduous and coniferous tree genera (Melville, 1937, 1960; Gathy, 1954; Dancik and Barnes, 1974; Dickinson and Phipps, 1984; Dickinson et al., 1987).

Strauss and Bookstein (1982) state that in principle, any measured distances between landmarks of a form may serve as characters for morphometric analyses. As these authors point out, many systematic studies have been based on very biased and repetitious characters to represent a form often with little regard for allometry or its variations among populations and growth forms. As noted by Dickinson et al. (1987), the approach to leaf shape measurement in many studies has been to measure only a few leaf dimensions, thus greatly oversimplifying leaf shape. In addition, ratios of leaf dimensions in many of these studies have been assumed to provide a summary of shape relationships that is independent of size differences; however, Atchley et al. (1976) have shown that ratio variables may be highly correlated with size variables and that they generally do not satisfy assumptions of normality. Because of these problems, Humphries et al. (1981), Strauss and Bookstein (1982), and Bookstein et al. (1985) recommend the use of a truss network or distances as characters to define the shape of an organism. A box truss consists of a series of contiguous quadrilaterals, each having both internal diagonals. Each quadrilateral shares one edge with the preceding quadrilateral and another with the succeeding one. Although several advantages of this geometric protocol for character selection are presented by Strauss and Bookstein (1982), including systematic coverage of the form and redundancy in archiving the landmark configuration, there is one main disadvantage of this method. For each quadrilateral of a truss network, there are six distances among four landmarks which may not be precisely coplanar when an average of measurements is taken among specimens. If this is the case, the truss network will not lie on a single plane and will therefore have to be flattened by adjusting the six distances until the landmarks become coplanar.

To avoid this problem, twenty radial distances were used as characters to describe needle shape (Figure 2.5). Distances were determined as the average of measurements of five needles per tree. By using this method, an average shape for the needles of each tree could be determined on a single plane. This approach to the measurement of leaf shape has also been used for *Crataegus* (Dickinson et al., 1987). For this system of measurement, leaf shape is defined, and distinguished from size, in terms of the covariances of multiple linear measurements of distances between corresponding points made on the leaf sample. Shape is the aspect of the spatial form of the sample described by covariances among these measurements that are both positive and negative.

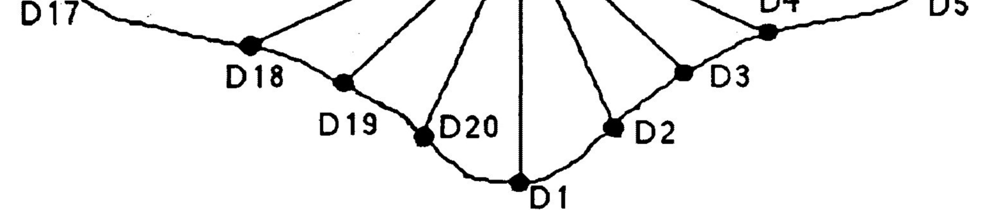

Fig. 2.5. 20 radial distances used as characters to describe needle cross-sectional shape. Each distance originates in a located centre point, and terminates where a designated line intersects the needle margin.

MEASUREMENT OF CHARACTERS

Cones

To soften the cone scales in order to make them easier to work with, they were soaked in a 1% solution of detergent (Tweed 80 polyoxyethylene (20) sorbiton monooleate) for 24 hours prior to measurement. By softening the scales in this way, they could be flattened, and the distance measures were considerably more accurate than they would have been if obtained on the unsoftened curved surfaces. Cone scales and bracts were measured under a dissecting microscope which contained an ocular micrometer in the eyepiece. Cone axis characters were measured directly with a vernier hand calliper.

Needles

Needle length was measured for each specimen using a vernier hand calliper before the needles were histologically prepared for subsequent measurement. The number of rows of stomata on the adaxial surface at the midpoint of the needle, a character that has commonly been used to separate *Abies lasiocarpa* and *Abies balsamea*, was determined on needles separate from those for which the other characters were measured, for both the parent and progeny populations. Due to the small size of the progeny, only a few needles were available from each seedling.Therefore, needles were not always available to measure the number of rows of stomata for all trees of a population once needles had been used for the measurement of the other needle characters. Needles were examined under a dissecting microscope after being soaked in water for several minutes to make the stomata more visible. For needles which had stomata that were not visible even after soaking in water, the needles were subsequently soaked for 2 to 3 days in a saturated solution of chlorohydrate. This procedure cleared the needle tissue and made the stomata easily visible.

Measurement of all other needle characters was made from histologically prepared needle cross sections on glass slides, using a Nikon light microscope with a camera lucida, and a digitizing tablet (Houston Instuments), attached to an Apple IIe microcomputer. By positioning the digitizing tablet beside the microscope and under the mirror of the camera lucida, it was possible to see the needle image superimposed on the face of the digitizing tablet. Basic computer programs on the Apple IIe microcomputer were used for the measurement of all cross-sectional needle characters, and to calibrate the size of the projected needle images for each series of measurements. These programs were written specifically for this purpose by W.H. Parker, and were designed such that sets of coordinates on each needle had to be measured on the digitizing tablet in a consistent order (Figure 2.6). The desired distances between appropriate coordinates were then directly calculated and stored on a diskette by the microcomputer.

Coordinates 1 to 6 and 7 to 12 were located by first finding the horizontal end points of the needle (coordinates 5 and 11/17) and then running a line perpendicular to that one through the centre point of each resin canal. Point 13 is the most extreme point on the abaxial needle surface, and point 14 was located by extending a vertical line from point 13, perpendicular to the line between points 5 and 11/17. Calculation of the distances AB, MD, and AD was made from the average of these measurements for each resin canal. When only one resin canal was present, these distances were measured twice on the single resin canal. Because of the occasional occurrence of this situation, a 17th point was always measured in the same location as point 11 so that needle width could still be determined.

For the distance characters that describe needle shape, Figure 2.7 indicates the order of measurement of each coordinate to calculate the 20 radial distances. A ray diagram was positioned over the image of each needle cross section on the digitizing tablet to locate these coordinates, as depicted in Figure 2.7. This diagram contained lines extending from a centre point at 20^{o} angles, except between points 6 and 7, 7 and 8, 16 and 17, and 17 and 18 which were 10 degree angles. The grid was positioned by locating the extreme points of the

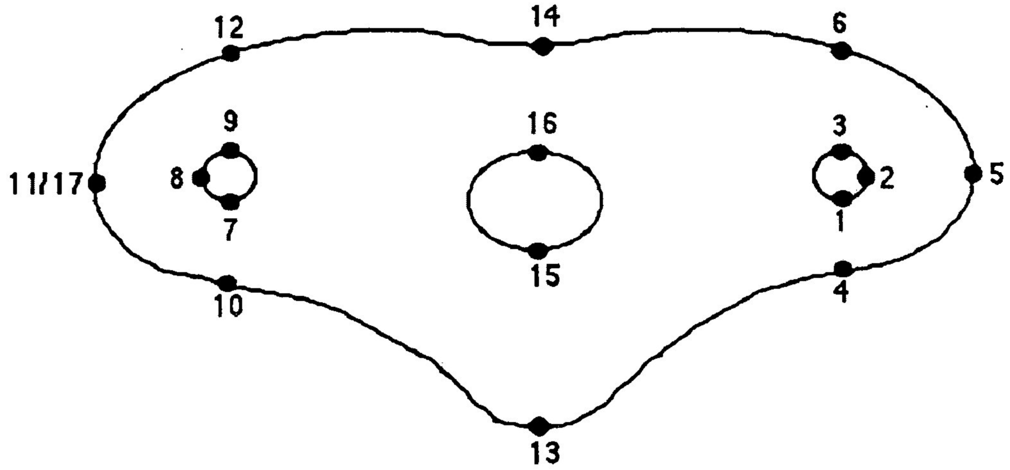

Fig. 2.6. Needle cross-section illustrating the order of measurement of coordinates for conventional needle characters.

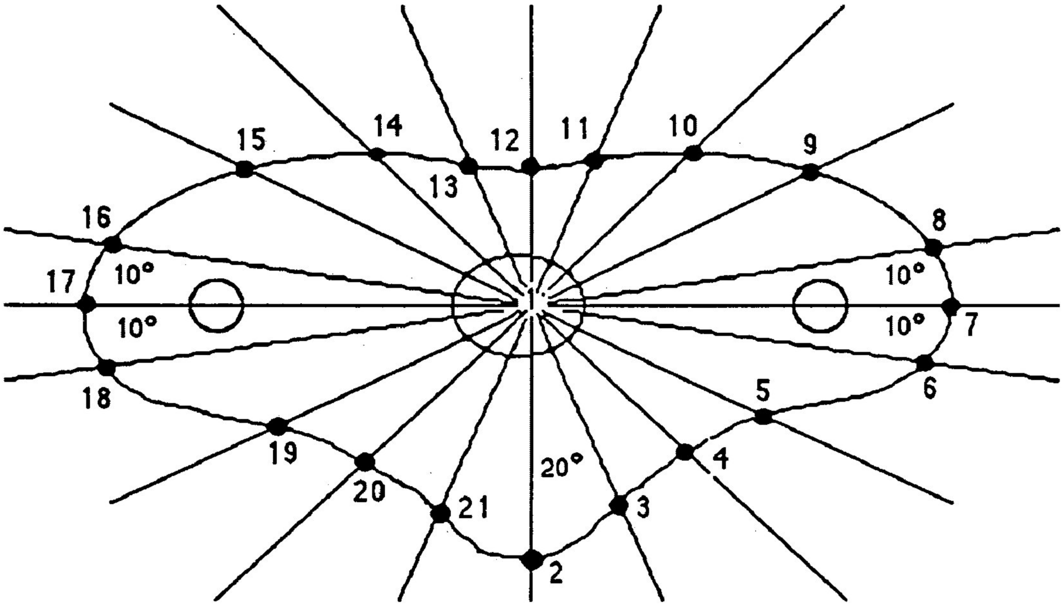

Fig. 2.7. Needle cross-section illustrating the order of measurement of each coordinate for radial distance characters. The ray diagram used to locate the coordinates is superimposed, with 10° and 20° angles indicated.

needle cross-section at each end of its width and on the abaxial surface. Once these points were located, two lines were drawn perpendicular to each other by connecting the points at each end of the needle's width, and drawing a line perpendicular to that line from the outermost point on the abaxial needle surface. The centre point was therefore at the intersection of the two lines and 0^o was at the outermost point of the abaxial needle surface.

HISTOLOGICAL PREPARATION OF NEEDLES

Because dried herbarium material was used, it was necessary to rehydrate the needles before further preparation of the needle cross-sections could be carried out. After rehydration, additional procedures required to prepare the needles were infiltration, embedding, sectioning, and staining. Similar procedures for the histological prepartion of various *Abies* species are described by Liu (1971). Berlyn and Miksche (1976) provide a detailed account of these botanical microtechnique procedures.

Rehydration

Three techniques for rehydration of needles were tested and compared for their effectiveness. The first involved immersion of the dried herbarium material overnight in a solution of 30% ethanol. The second technique involved immersion of the needles from one to several days in a 1% solution of detergent (Tweed 80 polyoxyethylene (20) sorbiton monooleate) followed by a thorough rinsing in water, 2 hours of soaking in a 15% solution of ethanol, and finally, 2 hours of soaking in 30% ethanol. The third technique simply involved boiling the needles for 20 minutes in water and then cooling them.

To test each of these rehydration techniques, two needles from each of six trees were rehydrated by each method. Each set of two needles was cut into a 5 mm section from the mid-portion of the needle and placed into a test tube. Sectioning the needles in this way allowed water and infiltrating materials to fully penetrate the needle tissues. These sets of needles were then rehydrated by the approriate methods and subsequently infiltrated, embedded, sectioned, and stained. No noticeable differences were detected among needle cross sections subjected to the different rehydration techniques. Thus the boiling rehydration method was selected for subsequent use since this method involves the least time and expense.

In order to make the process of rehydration more efficient, each sample of five needle sections per tree was placed in a plastic cassette designed for infiltration. Each needle section was taken from the midportion of the needle. The end of the needle closest to the point of attachment to the stem was sliced perpendicularly to it, and the other end was cut on an angle. In this way, the orientation of each needle was known for subsequent procedures. Because each cassette had holes that were small enough for a needle to pass through, a small section of cheesecloth was wrapped around each group of needles before they were placed into the cassette to prevent the escape of any needles. Groups of cassettes were then placed in glass jars filled with water and the needles were boiled by placing the jars on a hot plate.

Infiltration

The process of infiltration of needle tissue involved soaking the desired material in a series of alcohol solutions, and finally in paraffin. The purpose of this process was to allow the tissues to become completely infiltrated with paraffin so that when they were eventually embedded in paraffin blocks, the tissues would not be crushed when sectioned finely with a microtome blade. The alcohols used for infiltrating the needle tissues were ethanol and tertiary butyl alcohol which are recommended by Johansen (1940) for plant materials. The series of alcohols and paraffin that the needles were put through is known as the Johansen Series (Table 2.4). The length of time the needle material remained in each stage is outlined in Table 2.5.

Table 2.4. Johansen Series for the infiltration of needle tissues indicating the percentage of solution components in each Johansen Solution.

SOLUTION COMPONENTS	JOHANSEN SOLUTIONS (%)						
	J1	J2	J3	J4	J5	J6	J7
Distillled Water	50	30	15				
95% Ethanol	40	50	50	45			
Tertiary Butyl Alcohol	10	20	35	55	75	100	50
100% Ethanol					25		
Paraffin Oil (or Paraffin)							50

Table 2.5. Schedule for infiltration of needles.

SOLUTION	DURATION
Johansen 1	2 hours
Johansen 2	3 changes in 8 - 10 hours
Johansen 3,4,5	2 hours minimum each
Johansen 6	3 changes in 24 hours
Johansen 7	several hours with cork off
Pure Paraffin	infiltrate overnight (8 - 10 hours)

Embedding

This procedure involved putting the infiltrated needles into blocks of paraffin. A Fisher embedding machine with an attached cold plate was used for this process. Paraffin embedding medium was heated for several hours in the embedding machine until melted. When the paraffin was completely molten, individual needles were embedded into separate paraffin-filled metal embedding cassettes surrounded by plastic embedding rings. Needles were placed into partially filled cassettes so that the flat end of the section was face down, and the angled end of the needle was near the top of the plastic ring. This orientation was used so that needles would all be consistently in the same direction, and so that subsequent sectioning would take place on the flat cross-sectional surface of the needle. The cassettes were then filled with paraffin and allowed to cool on the adjoining cold plate. When the blocks had solidifed, they were removed from the metal embedding cassettes.

Sectioning

Before the embedded needles could be sectioned, it was necessary to trim the wax blocks down to a size small enough from which to cut a ribbon. This procedure was done with a razor blade. The wax blocks were trimmed so that enough paraffin remained around the needles so that they would not break off during the process of sectioning.

When each block was trimmed, it was sectioned to a thickness of 20μ on a rotary microtome. The sectioned wax ribbons containing the needle cross sections were then placed on slides which had been smeared with Haupt's adhesive and several drops of a 94% solution of formalin. The slides were then placed on a slide warmer so that the wax ribbons would spread out evenly. After this point, the excess solution on each slide was soaked off with paper towelling, and a rubber roller was pressed several times over each slide to ensure good adherence of the needle sections. The prepared slides were then left overnight on the slide warmer to dry.

Staining

Sections were stained with a 0.05% solution of Toludine Blue. This stain seemed to be absorbed well by the needle tissues. Slides were placed in glass staining dishes in groups of ten. Each group of slides was then put through a staining process which consisted of nine solutions and two washes at five minutes per stage (Table 2.6).

When the final stage of the staining process was complete, slides were immediately mounted with a cover slip using Permount as an adhesive. In order to ensure a proper distribution of Permount over the slide, and to prevent air bubbles from forming, the slides were placed on a slide warmer with metal weights on top of them. The slides were left in this position until the Permount was completely dried so that the cover slips would not move.

Table 2.6. Staining schedule for prepared slides
(5 minutes per stage).

STAGE	SOLUTION
1	Xylene 1
2	Xylene 2
3	Xylene and 100% Ethanol 1:1
4	100% Ethanol
5	95% Ethanol
6	70% Ethanol
7	Rinse with Distilled Water
8	Stain with .05% Toludine Blue O
9	Rinse with Distilled Water
10	Xylene 3
11	Xylene 4

DATA ANALYSIS

The various data sets were initially summarized by determining means and standard deviations for each population using the software program Statistical Processing System (SPS) (Buhyoff et al., 1983) on an Apple IIe microcomputer. These values were also calculated by site for cone and needle data from the northern subalpine fir populations. Possible trends in these data sets were assessed visually though the use of Hubb's diagrams.

To test the assumptions of the univariate and multivariate techniques that were subsequently applied, tests of univariate normality and homoscedasticity were carried out for the northern subalpine fir populations. Values of skewness and kurtosis of original variables were calculated using the Statistical Package for the Social Sciences (SPSS) (Nie et al., 1975) on the Vax 11/780. These values were also determined for tree means using the Sigma Soft software package Biostat (Pimentel and Smith, 1986) on a Macintosh Plus. The Kolmorov-Smirnov test of normality and Bartlett's test of homogeneity of population variances were carried out on tree means for all variables of the cone and needle data sets from the northern populations using Biostat. Examination of the data in this way provided insight into the nature of the variable distributions, and aided in the evaluation of potential outliers.

Although multivariate normality was not tested for the data matrices used in the study, it was assumed. Pimentel (1979) states that the departure of single variables from normality probably is insufficient to invalidate statistical analysis since both qualitative and quantitative biological data typically do not depart too far from normal to invalidate results; this also appears to be the case for multivariate data. All of the variables measured in this study are quantitative in nature, and thus, departures from normality would be unexpected, probably occurring only due to errors of sampling or measurement. In addition, because means rather than single observations were used in the multivariate analyses, the data should theoretically be normal. This assumption follows from the Central Limit Theorem, which states that both the sum and mean of independent observations having any distribution whatsoever approach normality as the number of observations increases (Stevens, 1986). Most statistical textbooks present as accepted fact that normality is approximated by the average of a very few variates.

As noted by Pimentel (1979), although it is possible to transform data to approximate normality for the purpose of drawing statistical conclusions, such transformations must be used with extreme caution, since they make the interpretation of results very difficult. Consequently, Pimentel suggests avoiding the use of transformations whenever possible. A loss of information is also possible when transformations are used. In an investigation of morpholgical variation in *Crataegus*, Dickinson (1983) found that the use of log-transformed ratios of leaf dimensions as descriptors in canonical variates analyses resulted in a loss of discrimination, when compared with analyses using the original measurements.

Nested Analysis of Variance

Nested analyses of variance were carried out using SPSS for each needle character of both parent and progeny data sets from the ten northern populations. From these results, variance components were calculated to determine the percent of variation for the various characters among sites, among trees within sites, and within individual trees. Because of the limited number of cones available from the trees of several of the ten populations, nested analyses of variance were not carried out for the cone parameters.

Multivariate Analysis

In order to examine the quantitative affinities among various taxa or groups of taxa, and to gain insight into which variables contribute most to the separation of taxa, several multivariate statistical techniques were employed. This classifactory method, known as numerical taxonomy, is described in detail by Sokal and Sneath (1963) and Sneath and Sokal (1973). Using this empirical approach, which allows for repeatability and objectivity, taxonomic relationships between taxa are evaluated on the basis of the resemblance existing in the material, thus producing a phenetic classification. Once a basic phenetic classification has been made, the classification may then be interpreted in evolutionary, or phylogenetic terms.

It is the convention in numerical taxonomy to analyse as many characters together as possible, since one of the underlying hypotheses of this technique (the hypothesis of nonspecificity) assumes that all kinds of characters are of equal taxonomic merit (Mayr et al., 1953; Michener, 1953). This theory has generally been accepted although it may hold only in part, since certain genes may affect the characters of one organ only (Sokal and Sneath, 1963). It is the opinion of Stebbins (1950) that the vegetative organs of a plant respond to a different subset of selection pressures than do the sexual organs. As well, Clegg, Kahler and Allard (1978) have reported that selection in viability components (a subset of vegetative features) and in fecundity components (a subset of reproductive features) often oppose each other. In the taxonomic investigations of *Abies* by Parker et al. (1981, 1984) and Parker and Maze (1984), separate analyses performed on cone, needle, and flavonoid characters, indicated that they may respond to different selection pressures. Therefore this approach was also taken for the multivariate analyses carried out in the present study, where the same species (and even many of the same populations) and similar characters were utilized.

Principal Components Analysis

Principal components analysis (PCA) was used to identify the major components of variation in each data set. Green (1978) describes the technique in detail. The purpose of PCA is to initially investigate the correlations between a number of variables measured for a number of entities, which in the present study are defined as operational taxonomic units (Sokal and Sneath, 1963). Transformations of these variables are then made during the analysis in such a way that they are linear on an arithmetic or logarithmic scale, in order to find a number of components which is smaller than the original number of variables.

These "principal" components are extracted by the use of a particular mathematical transformation so that they are independent of each other, and so that the first component accounts for a maximum of the variation described by the original variables, the second component a maximum of the variation remaining after the removal of the first component, and so forth, until all of the variation is accounted for. In this way, a principal component analysis generates new variables so that the variance in the sample will be explained in reduced dimensions. At the same time, the loss of information is minimized.

As stated by Jeffers (1964), the selection of preliminary variables for a PCA is very important. The variables should be quantitative characters and preferably measured on a continuous scale, although many discrete variables adequately approximate continuous variables. All of the variables in the data sets used in PCA were continuous, with the exception of number of rows of stomata, which should approximate a continuous variable adequately.

In the analyses of this study, PCA was based upon the coefficients of correlation between every pair of the original variables. Pimentel (1979) recommends the use of a correlation matrix whenever the initial data matrix is composed of data drawn from different kinds of measurements or different scales. The use of a variance-covariance matrix is recommended instead if variables are of a similar kind of measurement, and of the same scale, so that absolute changes in morphology may be studied. However a correlation matrix is still recommended to interpret changes relative to standardized data. Since several of the cone and needle variables used in this study were either different kinds of measurements, or of different magnitudes of scale, correlation matrices were used for all PCA's.

From the correlation matrices, the latent roots, or eigenvalues, and eigenvectors of the entire set of correlation coefficients were calculated. The calculated eigenvalues represent the amount of variation accounted for by each principal component. Lawley (1956) showed that the degree of difference between eigenvalues can be measured by the ratio of the geometric mean of the eigenvalues to the arithmetic mean, which is distributed as χ^2. However, Jeffers

(1964) recommended that eigenvalues of 1.0 or greater be considered significant as an arbitrary rule of thumb for biological data. This approach was used in the present study.

All PCA's were carried out on the Apple IIe using SPS. The data matrices used in these analyses consisted of the mean values of trees within populations. Analyses were carried out for each of the sets of needle data from the ten northern populations, as well as for needle data sets for the progeny populations. Because of the variable number of trees for which the character number of rows of stomata was available for the progeny, this variable was excluded from PCA of the conventional progeny needle data. In order to make the results of PCA for the progeny needle data comparable with that of the parent trees, a second PCA for the parent conventional needle data was also done eliminating the character number of rows of stomata.

A PCA was carried out for the cone data from nine of the northern populations for which cones were available. Within these nine populations, not all of the ten sampled trees had available cones, and therefore PCA was carried out using a variable number of trees for each population (Table 2.7).

In order to examine the variation patterns of these northern populations of subalpine fir in conjunction with those of previously studied subalpine fir populations to the south, PCA of all needle and cone data was carried out using these additional populations, with data from the studies of Parker et al. (1981) and Parker and Maze (1984). Because there were no shape needle data available for the additional populations, PCA was carried out using only conventional needle characters that had been measured for both the northern and the additional populations. These characters were NL, RC, AB, AD, MD, NW, and NT.

A PCA was initially carried out using the seven needle characters for the ten northern subalpine fir populations and eleven additional populations (W11-13, W15-17, E18-19, E21-23 in Figure 2.1) located in areas that have tentatively been classified as either *Abies lasiocarpa* or *Abies bifolia* by Hunt and von Rudloff (1979), in order to examine population variation in subalpine fir

Table 2.7. Number of trees with available cones for 22 populations of *Abies lasiocarpa* and *Abies balsamea.*

SITE	NUMBER OF TREES WITH AVAILABLE CONES
N1	10
N2	5
N4	10
N5	10
N6	10
N7	10
N8	3
N9	6
N10	10
W11	9
W12	14
W13	15
W14	10
W16	10
E21	8
E22	8
E23	5
B28	10
B29	10
B30	10
B31	10
B32	10

throughout diverse regions of its range, including the northern extreme. A total of 208 trees were used in this analysis.

To expand the analysis further, an additional ten populations (E20, S1-2, B26-32 in Figure 2.1) were included in a subsequent PCA. One of these populations (E20) is in the tentative *Abies bifolia* range, two (S1-2) are located in the putative zone of sympatry between *Abies lasiocarpa* and *Abies balsamea*, and five (B28-32) are populations of balsam fir from Alberta, Saskatchewan, and northern Ontario. The intent of this analysis was to gain information about the patterns of variation in subalpine fir over a large part of its range, and to observe how balsam fir variation patterns relate to those of subalpine fir. A total of 316 trees were used in this analysis.

A final PCA of cone characters was carried out for the nine northern populations in addition to 12 of the additional subalpine and balsam fir populations used in the expanded needle character PCA's for which cone data were available (W11-13, W16, E21-23, B28-32 in Figure 2.1). One additional subalpine fir population (W14) for which cones were available was also included in the analysis. All ten of the previously described cone characters were used in this analysis. Since all trees in each of the additional populations did not have available cones, the number of trees within each population varied within this analysis, similar to the PCA of cone characters for the ten northern populations. The number of trees used for the additional 13 populations is included in Table 2.7.

Discriminant Analysis

Multiple discriminant analysis (MDA), which is appropriate for three or more pre-established groups, was used to examine the variation between each of the populations for which PCA was carried out. Green (1978) provides a detailed description of this multivariate technique and its objectives, which are outlined below.

The first objective of discriminant analysis is to find linear composites of the predictor variables with the property of maximizing among-group to within-group variability in such a way that each linear composite (or discriminant function) is uncorrelated with all previously obtained composites. The discriminant functions are computed so that the accounted-for variation appears in decreasing order of magnitude. When there are three or more groups, one axis will generally not exhaust the discriminating potential. The second objective of discriminant analysis is to test whether the centroids of the pre-established groups are different, and if so, to determine the number of discriminant axes for which this is the case. The final objective of discriminant analysis is to determine which predictor variables contribute most to discrimination among the groups. This technique also provides a measure of the discriminating power of the analysis and of the reliability of its classification by providing the percentage of cases that are placed into the groups to which they actually belong.

An underlying assumption of discriminant analysis is that group covariance matrices are equal. Box's M statistic, a modification of Bartlett's test of homogeneity of variances for univarite data, is used to test this assumption, and was examined for all MDA's.

MDA's were carried out for various data sets on the Vax 11/780 using SPSS. The data sets and characters used were similar to those for which PCA was carried out, with several exceptions for the needle shape data. Because 20 distances were used as characters expressing needle shape in an initial MDA, and there were only 10 observations per group, singular data matrices were produced for these data sets. A singular data matrix is one where the number of variables is equal to or exceeds the number of observations for each group. In order to test whether group covariance matrices are equal, it is necessary to have non-singular data matrices. An attempt was made to alleviate this problem by reducing the number of variables used in the MDA's of needle shape characters. For both the parent and progeny needle shape data sets, ten new variables were calculated from the original 20. Each of the distance measurements from the centre point of each needle was added to the distance measure at 180° from it, to produce ten composite variables, designated sequentially as V1 to V10. However, even with ten variables and ten observations per group, the resultant data matrix was still singular, and a test of the equality of group covariance matrices could not be performed. A solution to this problem was attempted by altering the criteria by which independent variables were selected for inclusion in the MDA.

The SPSS discriminant procedure has available both direct and stepwise procedures for discriminant analysis. In the direct procedure, all independent variables are entered into the analysis concurrently, and the discriminant functions are created directly from the entire set of independent variables. The stepwise selection method chooses variables for entry into the analysis on the basis of their discriminating power. This method may be useful when the full set of variables contains excess information about the group differences, or when one or more of the variables are not very useful in discriminating among the groups. At each step of the analysis, the "next best" discriminator is sequentially selected, and a reduced set of variables is found which may be as good or better than the original set. Because singular data matrices existed for many of the data sets, the stepwise selection procedure was utilized so that all variables were not entered concurrently into the MDA's. Where data matrices were non-singular, this procedure was still used to make all of the discriminant analyses comparable.

The Wilks stepwise selection criterion was used for selection of variables to be included in the MDA's. In this procedure, the selection criterion is the overall multivariate F ratio for the test of differences among group centroids. The variable which maximizes the F ratio also minimizes Wilks lamda, which is a measure of group discrimination. This test takes into consideration the differences between all the centroids and the cohesion, or homogeneity, within the groups.

Multiple Regression Analysis

Multiple regressions were used to determine whether any of the variation in cone and needle characters among the ten northern populations may be correlated with environmental variation among these sites. The summary variables from the first three PCA axes for the relevant data sets were used as dependent variables in the analyses, since they efficiently summarize each set of variables. Independent variables were meteorological data from selected weather stations as close as possible to the sites (Table 2.8, 2.9, Figure 2.8). This type of analysis indicated the amount of variation in the summary variables (PCA axes) for the cone and needle data that can be explained by linear dependence upon the meteorological variables operating jointly. The resultant coefficient of determination (r^2) yielded this information.

The data sets used for these multiple regression analyses included the conventional and shape needle data as well as the cone data from nine of the ten northern populations. Data from Skagway, Alaska was not included because meteorological data could not be obtained from a weather station in that vicinity. Similar analyses were also carried out for conventional and needle shape data for the progeny populations. Summary variables for individual trees rather than

Table 2.8. Locations of weather stations and corresponding sites for multiple regression of weather data and subalpine fir populations.

WEATHER STATION	ELEVATION (m)	LATITUDE	LONGITUDE	SITE	ELEVATION (m)	LATITUDE	LONGITUDE
Keno Hill, Y.T	1472	63 56' N	135 12' W	N1	1311	63 55 'N	135 16' W
Faro, Y.T.	694	62 14' N	133 21' W	N2	1372	62 17' N	133 15' W
Sheldon Lake, Y.T.	884	62 37' N	131 17' W	N3	1067	62 40' N	131 14' W
Ross River, Y.T.	698	61 59' N	132 27' W		1067	62 40' N	131 14' W
Tuchitua, Y.T.	724	60 56' N	129 15' W	N4	884	61 04' N	129 22' W
Tuchitua, Y.T.	724	60 56' N	129 15' W	N5	975	60 48' N	128 58' W
Cassiar, B.C.	1077	59 17' N	129 50' W	N6	1006	59 17' N	129 35' W
Swift River, Y.T.	891	60 00' N	131 11' W	N7	1036	60 05' N	130 35' W
Johnson's Crossing, Y.T.	690	60 29' N	133 18' W	N8	1219	60 39' N	133 04' W
Atlin, B.C.	674	59 34' N	133 42' W	N9	1372	59 40' N	133 27' W

Table 2.9. Meteorological data (from Environment Canada, 1982abc) from 9 weather stations in Yukon Territory and British Columbia.

WEATHER STATION	ADT (C)	AJANT (C)	AJULT (C)	EMINT (C)	EMAXT (C)	RAIN (mm)	SNOW (mm)	RDAYS	SDAYS	FFREE
Keno Hill, Y.T	-5.0	-19.6	10.0	-44.0	27.2	241.3	356.7	----	----	55
Faro, Y.T.	-2.8	-24.5	14.9	-55.0	32.8	120.9	125.9	52	62	90
Sheldon Lake, Y.T.			11.7		30.6					16
Ross River, Y.T	-5.7	-28.6		-56.4		152.1	105.8	46	41	
Tuchitua, Y.T.	-4.2	-26.7	13.6	-55.6	32.8	243.8	337.4	61	77	59
Cassiar, B.C.	-3.2	-19.2	11.2	-47.3	29.4	305.2	395.0	69	90	37
Swift River, Y.T.	-3.1	-20.9	11.7	-52.2	31.1	235.6	332.6	62	77	19
Johnson's Crossing, Y.T	-2.0	-22.3	13.1	-52.2	32.2	195.4	152.4	52	63	45
Atlin, B.C.	-0.6	-19.2	12.0	-50.0	30.6	192.2	134.9	55	55	87

ADT: average daily temperature

AJANT: average January temperature

AJULT: average July temperature

EMINT: extreme minimum temperature

EMAXT: extreme maximum temperture

RAIN: total amount of rain per year

SNOW: total amount of snow per year

RDAYS: number of rain days per year

SDAYS: number of snow days per year

FFREE: number of frost free days per year

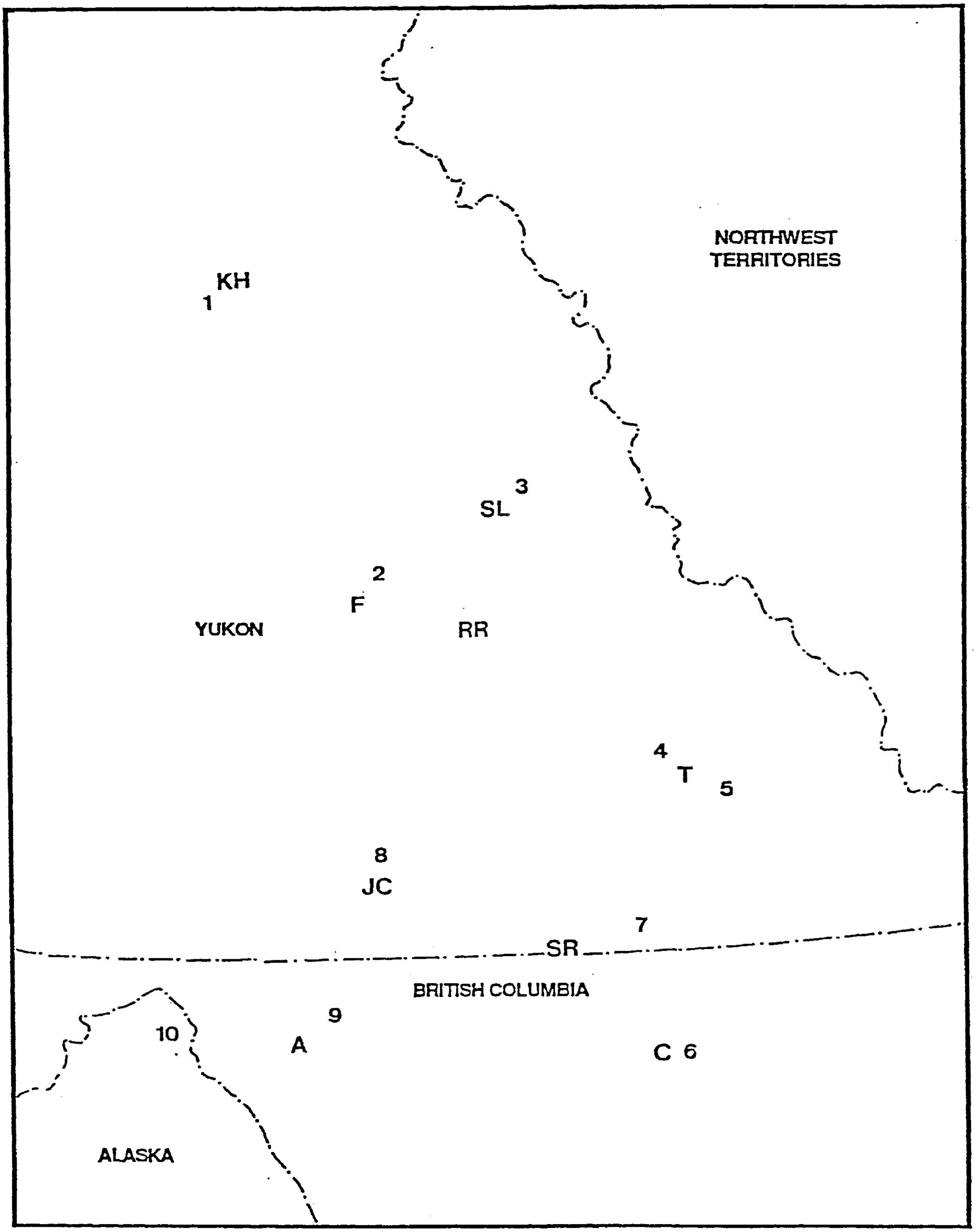

Fig. 2.8. Location of weather stations at Keno Hill (KH), Sheldon Lake (SL), Ross River (RR), Faro (F), Tuchitua (T), Johnson's Crossing (JC), Swift River (SR), Cassiar (C), and Atlin (A) relative to 10 subalpine fir sites which are indicated with population numbers.

means for each site were were used in the analyses. This approach was taken since trees at each site have been subjected to the same climatic conditions, and by using individual tree data, the variation within each site could be incorporated into the analyses.

Although a number of methods are available for multiple regression analysis, the stepwise selection method is recommended by most statisticians (Stevens, 1986). Draper and Smith (1966) consider the stepwise procedure to be the most practical regression method since it avoids working with more independent variables than are necessary while it improves the regression equation at every stage of the analysis. Thus, it was the stepwise method that was chosen for the multiple regression analyses in this study.

In the stepwise regression procedure, independent variables are inserted sequentially until the regression equation is satisfactory. The order of insertion of variables is determined by using the partial correlation coefficient as a measure of the importance of variables not yet in the equation. At every stage of the stepwise procedure, the least useful predictor currently in the equation is tested. A variable that may have been the best candidate at an earlier stage may be removed at a subsequent stage if it provides a nonsignificant contribution to the model, because of the relationships between the variable and the current variables in the equation. The process stops when no further variables in the equation can be removed and the next best candidate variable cannot hold its place in the equation.

After the initial analyses using the stepwise regression procedure, it was found that several of the environmental variables were highly correlated with each other. In an attempt to increase the correlation coefficient of the regressions, one of each pair of highly correlated variables was arbitrarily removed. Variables that remained in the subsequent analyses of parent data sets were elevation, latitude, average daily temperature, average January temperature, average July temperature, snowfall per year, number of days of snow per year, and number of frost free days per year. For the progeny data sets, only four variables, elevation, average daily temperature, average July temperature, and extreme minimum temperature remained in the subsequent analyses, since these were highly correlated with all other variables.

After each analysis was completed, the obtained regression model was tested to ensure that the assumptions of multiple regression were not breached. Bonferroni's t-test was used to test for outliers, and scatterplots of predicted versus residual values were examined to ensure that the residuals showed a random distribution.

One-Way Analysis of Variance

In order to examine the variation in the summary variables within and among nine of the northern populations, one-way analyses of variance were carried out for each of the PCA axes used in the multiple regressions. Variance components were then calculated from the results of each analysis of variance, in order to determine the percent of variation that is expressed among and within sites for these summary variables. Only the between-population variance would be expected to correlate with environmental differences corresponding to the different sites.

Once the amount of variation among populations was determined for each of the PCA axes, the ratio of r^2 (from each regression analysis) to values of among-population variation was calculated. This ratio provided an approximation of the total amount of variation among the populations that is due to environmental selection pressures, for each summary variable.

3. RESULTS

MEANS AND STANDARD DEVIATIONS

The means and standard deviations for characters from the various data sets for the northern populations are presented in Tables 3.1 to 3.5. For all additional populations, the means of conventional needle data are presented in Parker et al. (1981), and Parker and Maze (1984). The individual tree means for all data sets from all populations used in this study, are presented in Appendices I to VII.

Trees from populations 3, 4, 5, and 10 have needles that are shorter and narrower, with smaller-diameter vascular cylinders, shorter distances from the vascular cyclinder to the abaxial and adaxial needle surfaces, and shorter distances from the resin canals to the adaxial needle surface, than needles from trees of the other populations (Table 3.1). Populations 7 and 8 have trees whose needles are generally largest in these dimensions, with the exception that population 9 has needles with larger VAD. The large-needled populations also tend to have more rows of stomata on their adaxial surfaces. This observation was also made by Parker et al. (1981) for subalpine fir populations in the central Rocky Mountains. In general, the population values of the conventional needle characters appear to be closest to the values determined for Rocky Mountain populations (tentatively *Abies bifolia*) by Parker and Maze (1984), when similar needle characters from northern, eastern, and coastal populations from the present and previous studies are compared.

The general trend in needle dimensions for the conventional needle characters are also evident in the needle shape characters, with populations 3, 5, and 10 being smallest in all distance characters and population 7 having the largest distances (Table 3.2). These similar trends in the two types of needle characters illustrate that certain of the conventional and shape characters

Table 3.1. Mean and standard deviation (in parentheses) values for conventional needle data from 10 northern populations of *Abies lasiocarpa.*

	NEEDLE CHARACTER										
	RC	AB	MD	AD	NT	NW	VC	VAB	VAD	NL	RS
Population					(mm x .01)					(mm)	
N1	16.39	22.15	30.11	22.43	90.17	206.69	34.12	30.80	25.43	17.79	11.62
	(2.98)	(3.74)	(7.90)	(1.77)	(9.81)	(26.56)	(3.02)	(5.24)	(3.54)	(2.22)	(2.17)
N2	15.66	23.08	30.24	21.60	88.84	201.44	34.40	31.19	23.40	15.36	13.68
	(2.09)	(2.35)	(3.05)	(2.63)	(11.09)	(28.41)	(4.17)	(5.80)	(4.44)	(2.34)	(1.59)
N3	13.58	23.48	27.71	20.15	80.47	177.87	29.83	29.98	20.82	14.46	11.76
	(2.50)	(2.97)	(3.05)	(2.23)	(9.83)	(16.55)	(1.90)	(4.75)	(4.38)	(1.17)	(1.61)
N4	13.23	23.82	26.35	20.72	79.23	185.51	30.27	28.65	20.33	18.02	10.82
	(2.73)	(4.76)	(4.20)	(4.56)	(14.92)	(19.59)	(3.67)	(6.64)	(7.19)	(3.36)	(1.47)
N5	12.15	21.87	25.48	18.12	73.60	170.80	29.29	25.91	18.43	16.46	10.64
	(3.44)	(2.49)	(4.95)	(3.06)	(10.23)	(25.66)	(4.50)	(3.36)	(3.28)	(1.66)	(1.16)
N6	13.99	24.38	31.83	21.96	88.86	202.26	33.80	32.83	22.25	17.59	12.32
	(2.56)	(3.97)	(4.75)	(2.82)	(15.01)	(27.42)	(4.78)	(7.16)	(3.98)	(2.57)	(1.41)
N7	14.76	19.71	31.26	21.61	96.79	221.29	34.72	35.86	26.22	15.84	12.64
	(2.82)	(2.77)	(3.70)	(3.93)	(13.49)	(20.53)	(3.91)	(5.26)	(7.03)	(1.32)	(1.66)
N8	14.99	23.47	29.60	22.73	94.45	204.55	35.47	33.06	25.92	15.92	13.22
	(1.80)	(3.11)	(5.93)	(1.90)	(8.54)	(21.58)	(4.39)	(3.66)	(3.62)	(1.66)	(2.11)
N9	15.48	22.18	25.27	21.39	93.42	197.77	34.47	31.59	27.37	15.31	12.82
	(3.09)	(2.56)	(3.38)	(3.50)	(12.87)	(18.30)	(3.53)	(5.09)	(6.48)	(2.05)	(1.39)
N10	15.88	21.54	30.76	20.35	71.97	170.61	28.52	23.18	20.28	16.85	11.90
	(2.33)	(4.51)	(4.31)	(3.31)	(8.41)	(24.82)	(4.47)	(3.06)	(3.56)	(2.15)	(1.61)

describe similar needle dimensions.

An average needle cross section from each site, based on the means of conventional and shape needle characters was produced by a basic computer program written for the Apple IIe microcomputer by W.H. Parker (Figure 3.1). Although the described trends are evident, there does not appear to be any geographical pattern to them.

Populations 5, 9, and 10 have cones with shorter, narrower cone axes, and cone scale bracts that are narrower with shorter awns than cones from the other

Table 3.2. Mean and standard deviation (in parentheses) values for shape needle data from 10 northern populations of *Abies lasiocarpa*.

	NEEDLE CHARACTER (mm x .01)																			
Population	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20
N1	55.17 (5.70)	54.65 (4.90)	54.82 (4.28)	61.76 (5.44)	93.24 (10.83)	101.40 (13.46)	94.42 (11.66)	66.97 (7.16)	49.83 (6.59)	39.86 (5.86)	36.58 (5.83)	40.25 (5.59)	50.02 (5.59)	68.38 (6.54)	97.40 (10.97)	106.43 (13.30)	98.52 (11.22)	62.95 (5.10)	55.93 (4.94)	55.37 (5.33)
N2	55.69 (8.31)	53.17 (8.22)	52.39 (7.82)	57.97 (7.70)	87.47 (11.16)	99.53 (14.18)	94.01 (12.79)	68.02 (7.71)	50.70 (6.10)	39.39 (6.21)	35.49 (6.51)	39.74 (6.96)	50.21 (7.83)	67.98 (8.70)	93.60 (12.12)	100.52 (12.67)	89.87 (11.73)	57.89 (7.91)	52.51 (7.08)	53.82 (7.00)
N3	52.67 (4.80)	50.01 (4.47)	48.25 (5.00)	53.21 (6.13)	77.33 (6.87)	85.21 (8.80)	80.10 (8.21)	59.03 (6.41)	43.30 (5.92)	34.01 (5.93)	29.96 (6.18)	32.15 (7.43)	41.38 (7.56)	59.02 (7.16)	84.70 (9.49)	91.28 (9.97)	85.09 (8.84)	57.75 (7.18)	51.65 (6.04)	51.40 (5.08)
N4	51.01 (8.40)	49.24 (7.75)	49.42 (7.40)	56.42 (8.27)	83.92 (10.47)	91.13 (8.30)	84.83 (8.10)	60.61 (8.98)	42.94 (11.01)	34.10 (11.00)	30.02 (10.12)	31.87 (10.37)	41.26 (9.92)	60.64 (9.79)	85.83 (12.31)	93.07 (13.12)	86.77 (11.74)	57.41 (8.05)	50.67 (7.45)	49.97 (7.88)
N5	50.72 (6.57)	49.08 (5.92)	49.15 (6.66)	55.33 (7.45)	80.36 (10.57)	88.82 (14.22)	82.79 (12.42)	55.32 (6.54)	38.27 (6.64)	28.67 (6.06)	26.32 (5.63)	29.71 (6.01)	38.11 (7.35)	54.17 (9.60)	79.93 (12.83)	87.13 (15.71)	78.82 (11.38)	53.87 (8.44)	48.21 (7.83)	48.78 (7.06)
N6	59.48 (10.21)	57.07 (9.69)	55.88 (8.32)	61.01 (8.27)	90.07 (12.73)	102.07 (15.40)	92.93 (12.93)	63.36 (10.94)	46.02 (9.46)	36.44 (10.47)	33.53 (9.30)	36.98 (9.38)	47.64 (9.08)	65.90 (7.87)	91.48 (10.95)	99.78 (13.70)	88.19 (12.53)	59.53 (7.62)	54.68 (7.68)	56.70 (8.87)
N7	55.62 (4.63)	53.91 (4.22)	53.42 (4.13)	58.50 (5.06)	93.22 (9.89)	111.28 (13.00)	101.92 (12.50)	68.76 (11.62)	51.83 (10.66)	43.38 (10.12)	41.17 (10.09)	44.78 (10.76)	51.99 (11.36)	66.94 (12.42)	96.03 (8.56)	106.62 (8.51)	91.20 (6.68)	56.21 (6.40)	51.32 (4.86)	53.64 (5.01)
N8	57.84 (7.65)	53.03 (7.32)	53.87 (7.55)	58.89 (7.33)	91.79 (10.39)	102.96 (12.55)	97.91 (12.55)	71.98 (9.06)	52.40 (6.41)	41.40 (4.57)	37.01 (2.94)	40.37 (3.94)	50.00 (5.50)	68.07 (7.67)	93.87 (11.26)	99.52 (12.96)	90.45 (10.06)	59.65 (7.78)	54.11 (7.43)	55.82 (7.40)
N9	54.70 (5.28)	53.51 (5.54)	54.15 (5.28)	61.28 (5.21)	89.07 (8.81)	99.04 (10.72)	92.46 (10.10)	67.89 (9.03)	52.73 (9.00)	44.02 (9.12)	40.68 (9.02)	43.31 (7.83)	51.49 (6.33)	67.18 (6.03)	92.03 (6.24)	98.72 (7.35)	98.52 (5.16)	61.05 (4.31)	53.39 (4.26)	52.93 (4.94)
N10	45.28 (7.14)	43.49 (7.35)	43.69 (7.25)	51.60 (8.66)	77.70 (10.85)	85.08 (12.96)	79.42 (11.51)	56.58 (9.41)	41.86 (8.49)	32.56 (6.96)	29.14 (6.24)	31.44 (6.61)	39.67 (8.15)	56.53 (10.11)	80.12 (11.00)	86.86 (12.30)	79.42 (8.86)	52.78 (6.79)	44.72 (5.86)	44.01 (6.35)

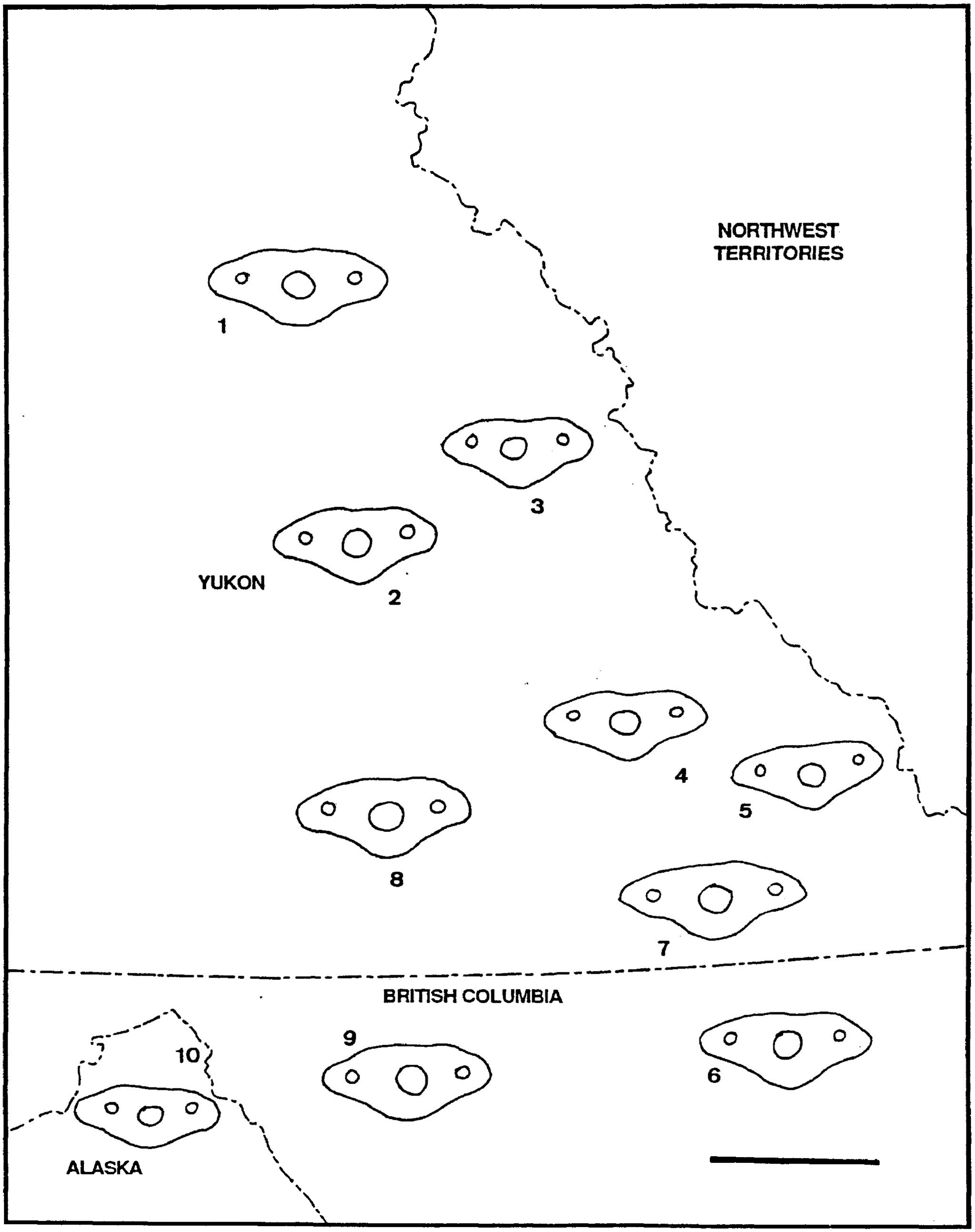

Fig. 3.1. Average needle cross section from 10 northern populations of *Abies lasiocarpa*. Scale bar = 2 mm.

populations (Table 3.3). However population 4 also has cones with narrow cone axes at the axis midpoint, and both populations 4 and 5 are smallest in cone scale bract length. Population 5 is also the smallest in distance from the base of the bract to its widest point.

Table 3.3. Mean and standard deviation (in parentheses) values for cone data from nine northern populations of *Abies lasiocarpa*.

	CONE CHARACTER									
Population	ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
N1	3.27	3.69	46.48	3.50	3.96	4.80	2.85	6.63	17.82	13.13
	(0.27)	(0.35)	(7.02)	(0.80)	(1.13)	(0.33)	(0.96)	(0.68)	(2.41)	(1.74)
N3	3.17	3.72	46.43	2.88	3.65	4.79	2.56	6.86	16.30	10.30
	(0.50)	(0.36)	(4.30)	(0.28)	(0.21)	(0.29)	(0.50)	(0.40)	(2.17)	(2.09)
N4	3.22	3.25	48.38	3.43	3.31	4.86	1.83	7.16	19.69	13.73
	(0.38)	(0.40)	(6.02)	(0.60)	(0.46)	(0.95)	(0.37)	(1.02)	(3.61)	(2.79)
N5	3.07	3.38	41.28	2.95	3.12	4.67	1.67	7.46	17.15	11.72
	(0.56)	(0.56)	(5.70)	(0.56)	(0.33)	(0.65)	(0.32)	(0.93)	(2.36)	(1.75)
N6	3.52	3.57	50.22	3.71	3.3.7	4.89	1.77	7.48	18.51	12.80
	(0.40)	(0.35)	(5.73)	(0.88)	(0.48)	(0.56)	(0.36)	(0.72)	(1.66)	(1.57)
N7	3.13	3.50	51.78	3.40	3.57	5.15	1.81	7.53	17.92	11.55
	(0.53)	(0.48)	(10.11)	(0.71)	(0.37)	(0.38)	(0.28)	(0.86)	(2.24)	(1.98)
N8	3.28	3.55	49.10	3.41	3.37	5.40	2.02	6.70	14.34	9.79
	(0.30)	(0.43)	(3.01)	(0.19)	(0.39)	(0.62)	(0.20)	(0.82)	(0.88)	(1.14)
N9	2.76	2.96	33.41	2.68	3.89	4.68	2.11	7.85	13.22	8.62
	(0.38)	(0.45)	(9.34)	(0.44)	(0.38)	(0.28)	(0.19)	(0.70)	(1.86)	(1.26)
N10	2.94	3.37	36.71	2.62	3.57	4.45	1.83	7.57	16.02	10.81
	(0.39)	(0.46)	(3.60)	(0.31)	(0.47)	(0.40)	(0.55)	(0.82)	(2.10)	(1.07)

Latitudinal trends are evident in several of the conventional needle characters among the four examined populations of progeny (Table 3.4). The characters RC, NW, VC, and NL all increase in size from population 1 to 6, which are located from north to south geographically. In contrast, the character VAD decreases from population 1 to 6.

The characters D1 to D5 and D17 to D20, all of which describe the shape of the curved portion of the abaxial needle surface, are larger for populations 1 and 6 than for populations 3 and 5 (Table 3.5). The distances D6 and D16, which together describe needle width, tend to become larger in the southernmost populations, similar to the observation for needle width in the conventional needle data. However, the characters D9, D10, D11, D12, and D13, which describe shape of the adaxial needle surface and needle thickness from the needle centre to the adaxial needle surface, are all smaller for population 6 than the other populations.

Table 3.4. Mean and standard deviation (in parentheses) values for conventional needle data from 4 populations of *Abies lasiocarpa* progeny.

	NEEDLE CHARACTER									
Population	RC	AB	MD	AD	NT (mm x .01)	NW	VC	VAB	VAD	NL (mm)
1	3.97	4.35	5.05	14.49	50.65	138.17	15.24	13.85	21.60	14.28
	(2.07)	(1.03)	(1.62)	(6.46)	(2.51)	(8.43)	(2.52)	(1.71)	(2.86)	(5.25)
3	4.53	2.76	9.60	17.27	45.64	151.77	15.56	12.42	17.67	15.94
	(2.43)	(0.44)	(4.75)	(3.55)	(4.60)	(23.44)	(2.91)	(2.18)	(3.95)	(7.09)
5	4.59	2.46	11.04	15.41	40.49	153.29	15.94	10.39	14.17	21.52
	(0.75)	(0.72)	(3.97)	(3.07)	(5.54)	(14.47)	(1.18)	(1.05)	(3.41)	(2.53)
6	6.24	2.44	8.03	17.56	44.00	161.78	18.06	12.27	13.71	23.02
	(1.10)	(0.17)	(2.14)	(3.35)	(3.31)	(7.73)	(1.40)	(1.98)	(2.64)	(2.22)

Table 3.5. Mean and standard deviation (in parentheses) values for shape needle data from four northern populations of *Abies lasiocarpa*.

	NEEDLE CHARACTER (mm x .01)																			
Population	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20
1	27.91 (5.07)	28.56 (4.55)	31.52 (4.81)	39.86 (5.33)	61.53 (7.52)	73.37 (3.81)	66.01 (6.68)	42.77 (4.79)	30.72 (3.39)	25.64 (4.25)	24.19 (4.08)	25.00 (2.82)	28.85 (2.79)	39.51 (4.56)	58.85 (8.31)	65.18 (8.78)	58.64 (10.35)	36.49 (10.06)	30.96 (5.47)	27.91 (4.90)
3	22.12 (7.26)	22.52 (7.37)	24.90 (8.03)	30.86 (9.31)	51.21 (9.97)	74.58 (14.03)	69.94 (12.78)	42.68 (5.68)	29.99 (7.83)	25.14 (9.44)	24.18 (10.96)	25.78 (10.85)	29.89 (9.74)	41.67 (8.17)	68.92 (11.85)	74.93 (9.79)	53.97 (14.30)	29.22 (6.86)	23.59 (6.49)	21.93 (6.93)
5	19.29 (8.55)	19.36 (8.12)	20.56 (8.56)	24.92 (9.77)	46.43 (9.99)	73.79 (7.04)	68.53 (4.01)	43.60 (5.62)	29.65 (5.96)	23.35 (5.26)	21.34 (5.28)	23.15 (6.19)	28.78 (7.22)	42.85 (7.18)	70.09 (5.41)	75.93 (8.44)	48.28 (10.62)	25.78 (11.42)	21.08 (9.53)	19.60 (8.77)
6	29.78 (1.41)	28.98 (1.06)	29.74 (1.07)	33.81 (1.34)	59.33 (3.52)	78.77 (4.51)	72.59 (4.04)	41.31 (4.36)	22.05 (4.76)	16.86 (3.79)	15.68 (3.49)	17.04 (3.53)	22.58 (4.34)	38.11 (5.43)	74.10 (3.83)	81.83 (3.36)	66.80 (7.81)	35.10 (2.29)	30.20 (1.94)	29.11 (1.32)

A visual comparison of the variation patterns in conventional needle and cone characters is provided in the Hubbs Diagrams in Appendix VIII and IX. These diagrams illustrate the means, ranges, and standard deviations of characters in the data sets, for each population. Although the described trends are evident, it is also clear that there is a great deal of overlap for most of the needle and cone characters, with none of them completely separating any of the 10 populations. There is instead a pattern of gradual overlap among populations for each of the characters.

DATA ASSUMPTIONS

It was found that of the needle and cone variables tested for univariate skewness and kurtosis, several were not distributed normally. However, the tree means of the majority of these characters were not skewed or kurtotic, and all passed the Kolmogorov-Smirnov test of normality which is more sensitive to departures from normality than are tests of skewness or kurtosis (Pimentel and Smith, 1986). Thus, the Central Limit Theorem was illustrated, and it was not necessary to transform any of the variables for subsequent analyses.

Bartlett's tests of homogeneity of variance of population variances indicated that variances were equal for all but one shape needle character of both the parent and progeny data sets, and four cone characters relating to cone scale bract dimensions. Thus, transformations were not carried out, since the assumption of homogeneous variances was met for the majority of variables. Furthermore, as noted by Pimentel (1979), departures from homoscedasticity will generally not be too serious to invalidate either analysis of variance or multivariate analyses.

NESTED ANALYSIS OF VARIANCE

Results of the nested analyses of variance for parent and progeny needle data are presented in Tables 3.6 to 3.9. These tables indicate both the significance and the per cent of variation accounted for among sites and among trees within sites for the individual variables in each data set. The within-tree variance component is also presented, although there is no test of significance for this effect.

The results indicate that for the parent conventional needle data, the largest amount of variation is expressed among trees at a site, for all but RC and RS. However for the parent shape and progeny data sets, the largest component of variation is generally expressed within trees at each site, with the next largest component of variation being accounted for by trees within sites. The smallest component of variation is accounted for among populations for all characters of both parent data sets, although there are generally highly significant differences at all levels except among sites for two of the conventional needle characters.

For the progeny shape characters, variation among sites is consistently non-significant and the smallest component of variation. However for the conventional characters, there are significant differences among sites for five characters, of which four have a greater component of variation than is expressed among trees within sites.

Table 3.6. Summary of nested analysis of variance of parent conventional needle characters from 10 northern populations of *Abies lasiocarpa*.

Variable	% Variation Among Sites	% Variation Among Trees Within Sites	% Variation Among Needles Within Trees
RC	8.60 *	45.66 **	45.74
AB	3.70 ns	50.42 **	45.85
MD	9.90 *	59.64 **	30.45
AD	5.65 ns	50.25 **	44.09
NT	25.61 **	49.18 **	25.24
NW	25.78 **	56.44 **	17.78
VC	19.02 **	45.15 **	34.82
VAB	21.23 **	46.25 **	32.52
VAD	14.86 **	44.90 **	40.21
NL	13.64 **	57.39 **	29.00
RS	13.22 **	40.41 **	46.37

Table 3.7. Summary of nested analysis of variance of progeny conventional needle characters from 10 northern populations of *Abies lasiocarpa*.

Variable	% Variation Among Sites	% Variation Among Trees Within Sites	% Variation Among Needles Within Trees
RC	5.60 ns	69.33 **	25.07
AB	38.10 **	17.26 **	44.64
MD	10.79 **	27.13 **	62.08
AD	0.00 ns	52.84 **	47.16
NT	27.66 **	25.28 **	47.05
NW	9.00 ns	37.87 **	53.13
VC	6.86 ns	36.96 **	56.18
VAB	14.44 ns	21.50 **	64.05
VAD	37.91 *	37.97 **	31.11
NL	0.27 ns	16.05 **	83.68
RS	42.66 **	5.16 ns	52.18

* Significant at the .05 level of alpha
** Significant at the .01 level of alpha
ns Not significant

Table 3.8. Summary of nested analysis of variance of parent shape needle characters from 10 northern populations of *Abies lasiocarpa.*

Variable	% Variation Among Sites	% Variation Among Trees Within Sites	% Variation Among Needles Within Trees
D1	12.28**	40.90 **	47.20
D2	12.99**	42.76 **	44.24
D3	12.07**	41.45 **	46.48
D4	6.85*	41.67 **	51.47
D5	13.31 **	44.18 **	42.52
D6	10.75**	18.71 **	70.54
D7	18.03**	41.80 **	40.17
D8	10.30**	22.82 **	66.87
D9	12.30**	29.43 **	58.27
D10	13.25**	32.29 **	54.45
D11	15.60**	35.36 **	49.03
D12	16.33**	32.91 **	50.76
D13	14.45**	31.33 **	54.21
D14	12.31 **	36.01 **	51.68
D15	13.70**	47.10 **	39.19
D16	13.46**	50.33 **	36.21
D17	11.79**	40.87 **	47.35
D18	4.86*	40.64 **	54.50
D19	8.50**	40.60 **	50.90
D20	11.98**	40.38 **	47.64

Table 3.9. Summary of nested analysis of variance of progeny shape needle characters from 4 northern populations of *Abies lasiocarpa.*

Variable	% Variation Among Sites	% Variation Among Trees Within Sites	% Variation Among Needles Within Trees
D1	18.55 ns	38.41 **	43.04
D2	0.00 ns	18.28 **	81.12
D3	17.21 ns	38.37 **	44.41
D4	20.55 ns	34.35 **	45.10
D5	13.36 ns	12.71 ns	73.93
D6	0.00 ns	32.22 **	67.83
D7	0.00 ns	33.72 **	66.28
D8	0.00 ns	11.79 ns	82.77
D9	10.77 ns	26.34 **	62.89
D10	9.51 ns	32.30 **	55.65
D11	7.01 ns	42.26 **	50.72
D12	6.75 ns	41.35 **	51.90
D13	1.60 ns	39.70 **	58.70
D14	0.00 ns	23.50 **	76.50
D15	21.64 ns	35.75 **	42.60
D16	22.46 ns	28.52 **	49.01
D17	12.07 ns	34.86 **	53.06
D18	16.99 ns	43.74 **	39.27
D19	16.86 ns	42.48 **	40.66
D20	16.21 ns	41.64 **	42.16

*Significant at the .05 level of alpha   ns Not significant

**Significant at the .01 level of alpha

PRINCIPAL COMPONENTS ANALYSIS

For each of the relevant data sets, the first three principal components from the results of PCA are presented in tabular form (Tables 3.10 to 3.18). All three of these components are significant for each analysis, since their eigenvalues are equal to or greater than 1.0. The PCA summary tables indicate the characters that make the greatest contributions to each of the three axes of variation for each data set, and whether or not the contributions are significant. The contribution of any character to a component of variation is considered significant when its coefficient in an eigenvector is greater than 0.75 (Jeffers and Black, 1963). The results of each of these PCA's are also presented as two-dimensional ordinations of the sampled populations (Figures 3.2 to 3.10). Only the first two PCA axes have been illustrated in each figure since these axes constitute the major portions of the variability. To simplify the interpretation of these ordinations, only the mean values for each site have been plotted with their corresponding population numbers. Population numbers are similar to those in Figures 2.1 and 2.2, excluding the associated letters. Standard deviation scores on each axis are represented as horizontal and vertical lines on each side of the population mean values. In this way, a visual comparison of variation existing in each sampled population can be made among the total number of populations.

Conventional Needle Data: 10 Northern Populations

The first three axes for PCA of 11 conventional needle characters of individual trees from the 10 northern populations accounted for 72% of the total variation, with the first axis accounting for 48% of the total variance (Table 3.10). The characters NT, NW, VAB, VAD, VC and AD make significant contributions to this major axis of variation. All character loadings have similar and positive polarity, except for needle length, indicating that the first component may be interpreted as a general size axis (Jolicoeur and Mosimann, 1960; Rao, 1964).

Table 3.10. Results of principal components analysis of conventional needle data for 10 northern populations of *Abies lasiocarpa*.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	48	61	72
Needle Characters	Eigenvectors		
RC	0.56	0.37	-0.36
AB	0.35	0.30	0.75
MD	0.55	0.47	0.19
AD	0.78	-0.06	0.37
NT	0.96	-0.18	-0.007
NW	0.85	0.16	-0.27
VC	0.79	0.06	-0.26
VAB	0.87	-0.15	0.09
VAD	0.82	-0.33	0.09
NL	-0.06	0.85	-0.12
RC	0.54	-0.12	-0.33

The second axis accounts primarily for needle length, which is the only character that makes a significant contribution. Coefficients in the second eigenvector have mixed polarity. Similarly, AB is the only character making a large and significant contribution to the third axis of variation, and coefficients of this eigenvector have mixed polarity. Thus, the third PCA axis accounts mainly for distance of the resin canal from the abaxial needle surface.

The ordination of the first two PCA axes for the 10 populations indicates that all ten populations overlap extensively in these needle characters, and that all are nearly equally variable (Figure 3.2). Populations 3, 4, 5, and 10 are somewhat separated from the others. However there is no apparent geographical trend to the ordination of populations. Variation among the populations is primarily due to the combination of NT,NW,VAB,VAD,VD and AD, as indicated by the spread of populations along the first axis, with needle length primarily separating populations along the second axis. The trends in variation among populations in conventional needle characters evident from this PCA reflect those observed in the Hubb's diagrams of Appendix VIII.

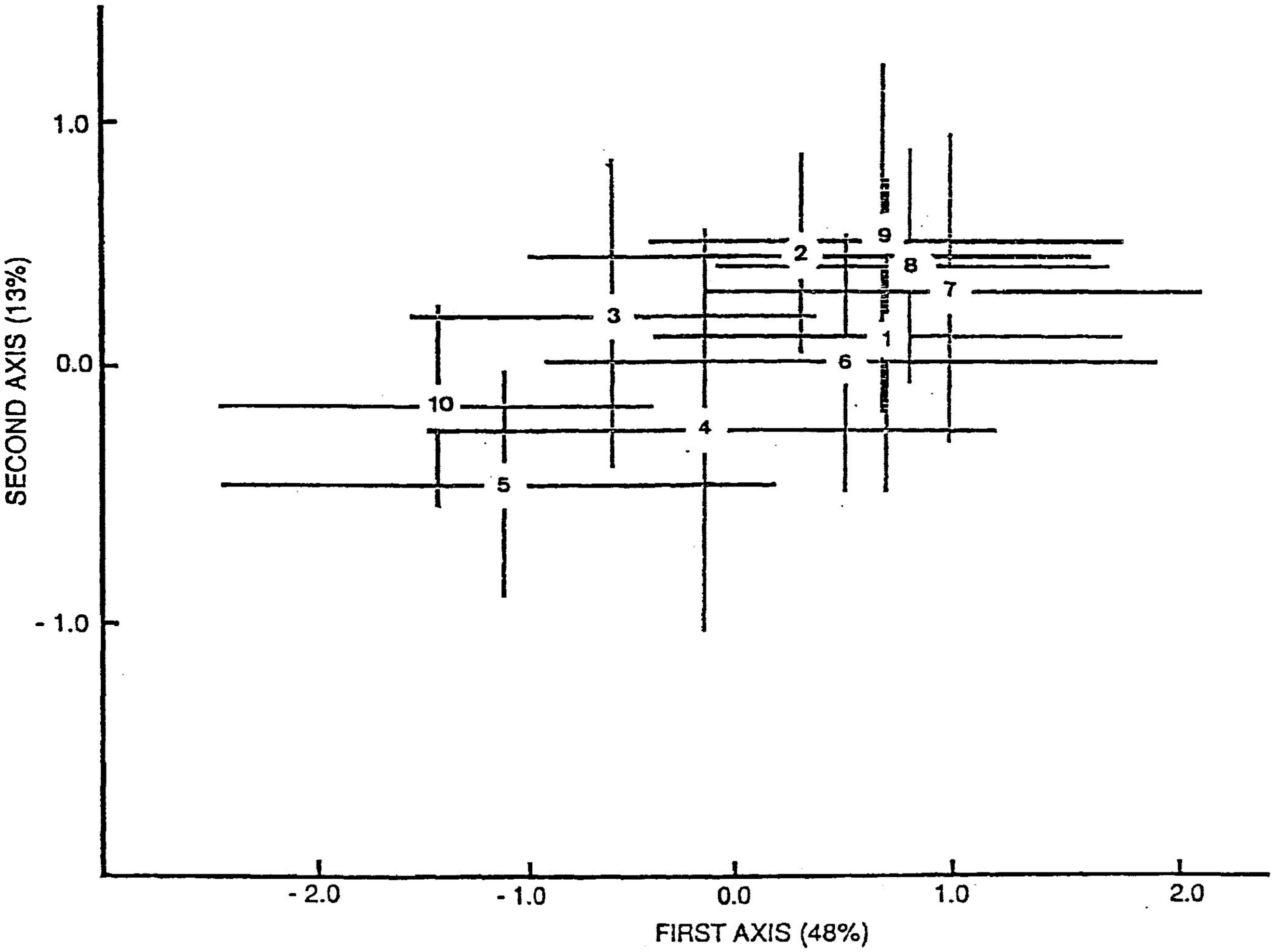

Fig. 3.2. Two-dimensional ordination of 10 northern populations of *Abies lasiocarpa* based on principal components analysis of conventional needle data.

Conventional Needle Data (Excluding RS): 10 Northern Populations

For PCA of parent conventional needle data from the 10 northern populations, excluding RS, the first three principal components account for 76% of the total variation (Table 3.11). Thus slightly more variation was accounted for by the first three PCA axes than when RS was included in the analysis. The first axis accounts for 50% of this total, and the characters NT,VAB,NW,VAD,AD and VC make significant contributions to this axis. As for the PCA of this data set including RS, all of the characters have similar polarity on this axis, which again indicates that this axis expresses variation in size of needles among populations. Needle length makes the only significant contribution to the second axis of variation, as does AB to the third axis. Coefficients of both the second and third eigenvectors have mixed polarity. These results are similar to those of the same data set with the character RS included in the analysis, indicating that the character RS does not contribute a large degree to the variation.

Table 3.11. Results of principal components analysis of conventional needle data (excluding RS) from 10 northern populations of *Abies lasiocarpa.*

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	50	64	76
Needle Characters	Eigenvectors		
RC	-0.55	-0.39	0.32
AB	-0.37	-0.25	-0.90
MD	-0.56	-0.45	-0.23
AD	-0.79	0.10	-0.34
NT	-0.96	0.20	0.07
NW	-0.84	-0.17	0.30
VC	-0.78	-0.06	0.31
VAB	-0.88	0.18	-0.01
VAD	-0.82	0.35	-0.05
NL	0.05	-0.85	0.08

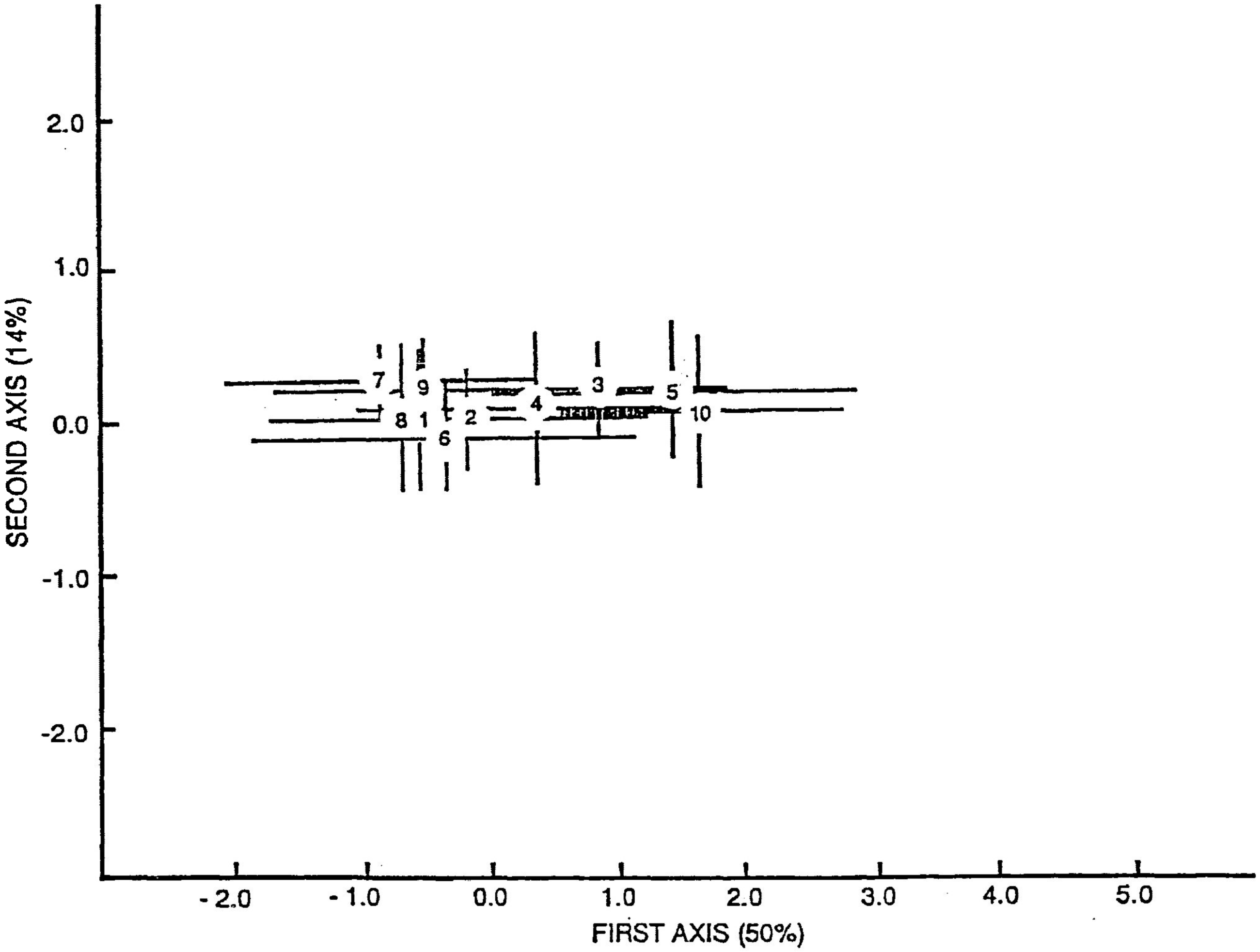

Fig. 3.3. Two-dimensional ordination of 10 northern populations of *Abies lasiocarpa* based on principal components analysis of conventional needle data (excluding the character RS).

The populations overlap to an even greater degree than for the same data set with the character RS included, although the positioning of each population relative to the others is very similar in both ordinations (Figure 3.3). Once again there are no apparent geographical trends in the ordination of populations which appear to be equally variable along both axes. Variation is again due primarily to the combination of NT,VAB,NW,VAD,AD and VC as indicated by the spread of populations on the first axis. Although needle length accounts for most of the variation on the second axis, it is evident from Figure 3.3 that it does not separate the populations as much as when the character RS is included in the PCA. As in Figure 3.2, and in the Hubb's diagrams of Appendix VIII, it is evident that similar to the previous PCA ordination, populations 3, 4, 5, and 10 are somewhat distinct from the others, due mainly to needle size.

Progeny Conventional Needle Data

The first three principal component axes for PCA of conventional needle characters for the progeny populations accounted for 83% of the total variation (Table 3.12). The first axis accounted for 49% of this total. The characters NL and VAD are the only ones that make significant contributions to this axis of variation, although the contribution of VAB is quite substantial. This axis has mixed polarity, indicating that it does not account primarily for needle size, as was the case for the first PCA axis of the parent conventional needle data, but instead accounts mainly for needle length and distance from the vascular cylinder to each needle surface. Needle thickness is the only character that makes a significant contribution to the second PCA axis, which accounts for 22% of the total variance. All characters except MD have the same polarity on this axis. Thus, this axis primarily accounts for thickness of needles. The character AD is the only one that makes a significant contribution to the third axis, which accounts for 12% of the total variation. Coefficients of this eigenvector have mixed polarity.

Figure 3.4 indicates that there is overlap among populations 1, 3 and 5, and that population 6 is somewhat separated from the others. The variability of

Table 3.12. Results of principal components analysis of progeny conventional needle data from four northern populations of *Abies lasiocarpa*.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	49	71	83
Needle Characters	Eigenvectors		
RC	0.71	0.56	-0.14
AB	-0.60	0.40	0.27
MD	0.56	-0.41	0.54
AD	0.50	0.35	-0.72
NT	-0.67	0.70	-0.14
NW	0.73	0.45	0.10
VC	0.71	0.58	0.25
VAB	-0.74	0.42	-0.22
VAD	-0.83	0.36	-0.20
NL	0.86	0.27	0.28

populations 1 and 3 is greater than that of populations 5 and 6, especially along the second axis, which accounts for needle thickness. A geographical pattern is apparent along this axis. The populations are ordered from south to north from the top to the bottom of the ordination, with population 1 having the thickest needles, as illustrated in Table 3.4. The same geographical pattern is evident along the first axis, although there is much less separation. Populations have needles that increase in length, and decrease in distance from the vascular cylinder to the adaxial needle surface from population 1 to 6. These trends are similar to those observed in Table 3.4. There is not a great deal of similarity between this ordination, and that of the parent conventional needle data, where populations 1 and 6 tended to be more similar, with wider, thicker needles than those of populations 3 and 5.

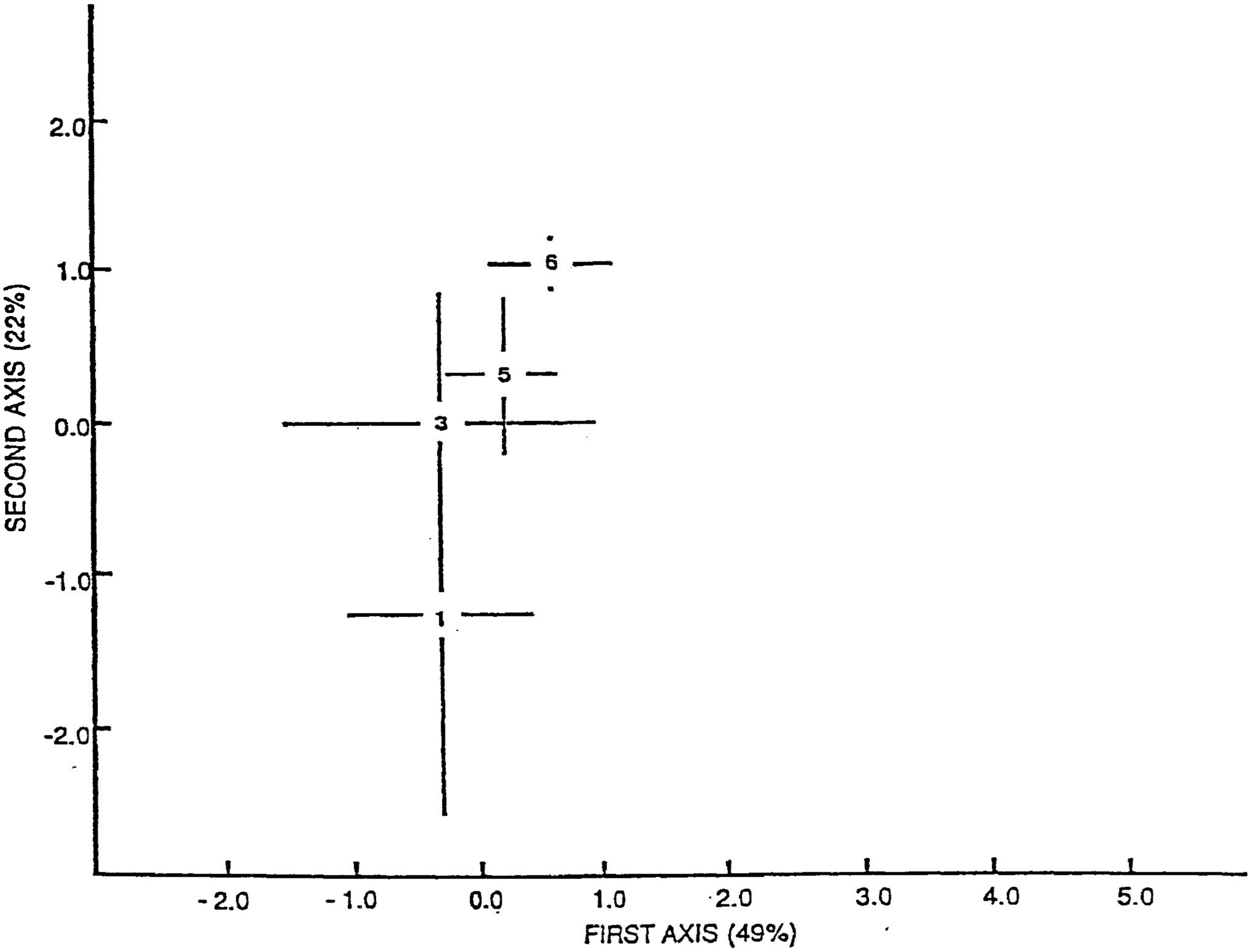

Fig. 3.4. Two-dimensional ordination of four northern populations of *Abies lasiocarpa* progeny based on principal components analysis of conventional needle data.

Needle Shape Data: 10 Northern Populations

The first three axes of variation accounted for 89% of the total variation for PCA of 20 radial needle distances for the ten northern populations (Table 3.13). The first axis accounted for 66% of this total. All characters except D18 make a significant contribution to the first axis of variation. All coefficients of this eigenvector have the same polarity, indicating that the second axis accounts for needle size, similar to the first PCA axis of the conventional needle data from these same populations. The second and third axes account for 17% and 5% of the total variation, respectively. None of the characters of either of these axes are considered to be significant as defined by Jeffers and Black (1963),

Table 3.13. Results of principal components analysis of shape needle data from 10 northern populations of *Abies lasiocarpa.*

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	66	83	89
Needle Characters	Eigenvectors		
D1	-0.79	-0.55	-0.01
D2	-0.81	-0.53	-0.15
D3	-0.79	-0.47	-0.31
D4	-0.76	-0.43	-0.31
D5	-0.86	-0.08	-0.40
D6	-0.86	0.07	-0.38
D7	-0.87	0.14	-0.36
D8	-0.85	0.41	-0.06
D9	-0.81	0.49	0.11
D10	-0.78	0.50	0.17
D11	-0.78	0.50	0.08
D12	-0.80	0.49	-0.04
D13	-0.84	0.47	-0.009
D14	-0.85	0.37	0.10
D15	-0.87	0.11	0.24
D16	-0.86	-0.002	0.21
D17	-0.84	-0.12	0.34
D18	-0.68	-0.49	0.46
D19	-0.75	-0.53	0.34
D20	-0.78	-0.57	0.11

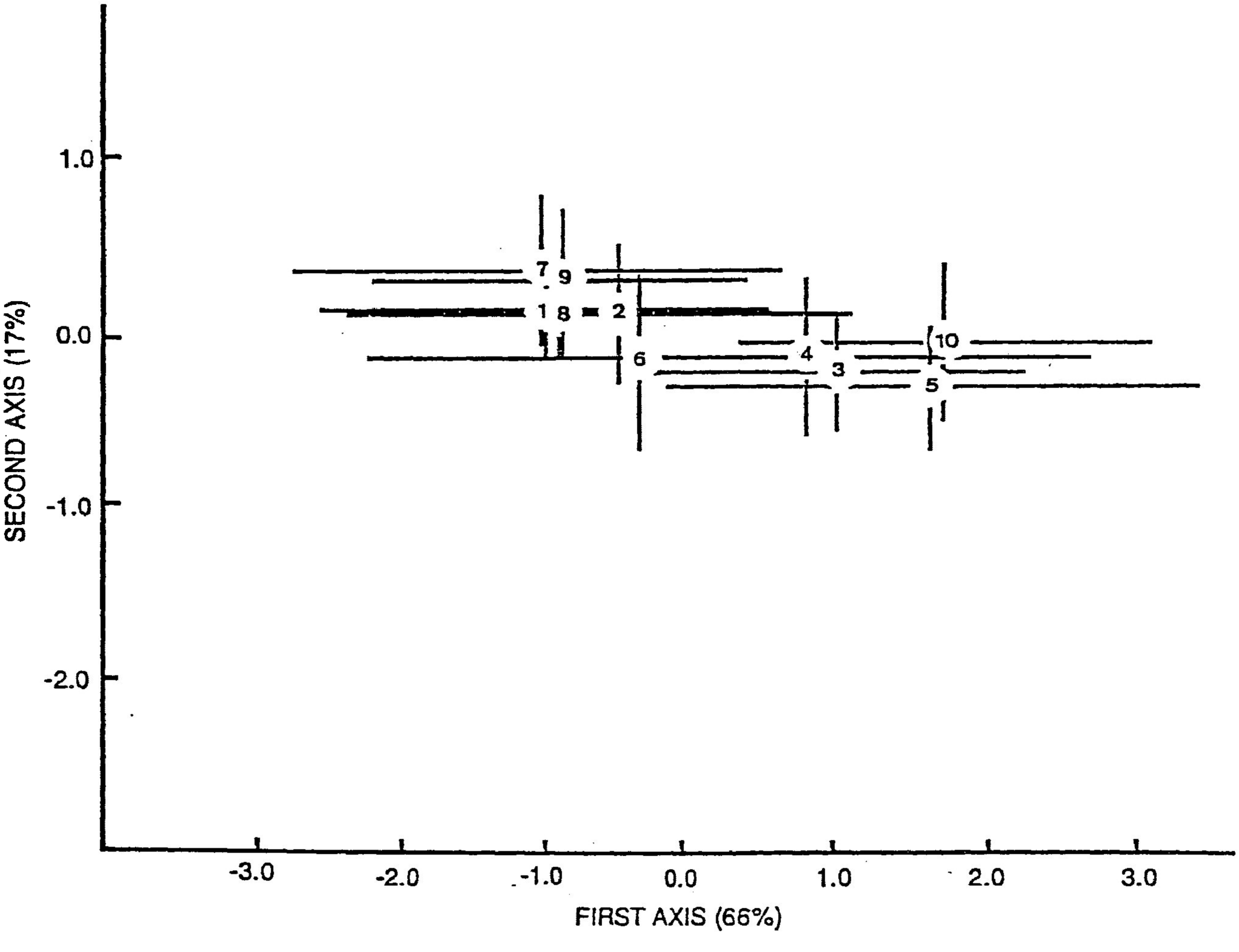

Fig. 3.5. Two-dimensional ordination of 10 northern populations of *Abies lasiocarpa* based on principal components analysis of shape needle data.

although there are differences in the degree of contribution to the variation that specific characters make for each axis. Characters making the greatest contribution to the second axis of variation are those which relate more to thickness of the needle and shape of the abaxial and adaxial needle surfaces (D1-D4, D8-D14, D18-D20), whereas characters contributing most to the third axis relate primarily to needle width (D5-D7, D15-D17). The polarity of the eigenvectors of each of these axes is mixed.

The ordination of the first two PCA axes indicates that the populations overlap extensively and that, as for the parent conventional needle data, there is no apparent geographical pattern to their ordination (Figure 3.5). The distribution of the populations is almost identical to that of the conventional needle data PCA ordinations. Variability appears to be equal along both axes for all populations, with the greatest amount of variation being along the first axis, due to needle size, as indicated by the spread of the populations in that direction. These results indicate that both the conventional and shape needle characters generally account for the same patterns of variation among the 10 populations, since they express many of the same needle dimensions that relate to needle size.

Progeny Needle Shape Data

The first three principal component axes account for 93% of the total variation, with the first axis accounting for 61% of this total, for PCA of needle shape data from the progeny populations (Table 3.14). Coefficients of the first eigenvector have mixed polarity, in contrast to the first PCA axis of variation of the parent needle shape data set, which represented needle size. Instead, the first PCA axis of the progeny needle shape data is comprised primarily by characters that relate to needle thickness, and shape of the adaxial and abaxial needle surfaces (D1-D5, D9-D13, D17-D20). These are the same characters that were evident in separating the populations in Table 3.5.

The second and third axes of variation account for 18 and 14% of the total variance, respectively. As for the parent needle shape data set, none of the characters of either of these axes make a significant contribution, except the

Table 3.14. Results of principal components analysis of shape needle data from the progeny of four northern populations of *Abies lasiocarpa*.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	61	79	93
Needle Characters	Eigenvectors		
D1	-0.95	-0.23	0.15
D2	-0.93	-0.27	0.19
D3	-0.89	-0.35	0.27
D4	-0.80	-0.44	0.36
D5	-0.84	-0.45	0.18
D6	-0.70	-0.21	-0.55
D7	-0.56	-0.27	-0.70
D8	0.40	-0.74	-0.41
D9	0.78	-0.60	0.03
D10	0.83	-0.49	0.12
D11	0.83	-0.47	0.13
D12	0.83	-0.51	0.08
D13	0.80	-0.58	-0.02
D14	0.58	-0.64	-0.34
D15	-0.40	-0.05	-0.89
D16	-0.52	0.09	-0.77
D17	-0.90	-0.16	-0.14
D18	-0.84	-0.40	0.29
D19	-0.91	-0.34	0.21
D20	-0.94	-0.27	0.15

characters D15 and D16 in the third principal component. However, as for the parent needle data set, there are some characters which make much higher contributions than do others, for both axes of variation. The second axis accounts mainly for thickness of the needle from the centre to the adaxial needle surface, and shape of the adaxial needle surface, since the characters D8-D14 account for most of the variation. Polarity is similar for all coefficients of the second eigenvector, indicating differences are due to size of the distance characters, in contrast to the second axis of the parent data set, which does not have coefficients of the same polarity. The coefficients of the third eigenvector have mixed polarity, as do those of the third eigenvector of the parent data set.

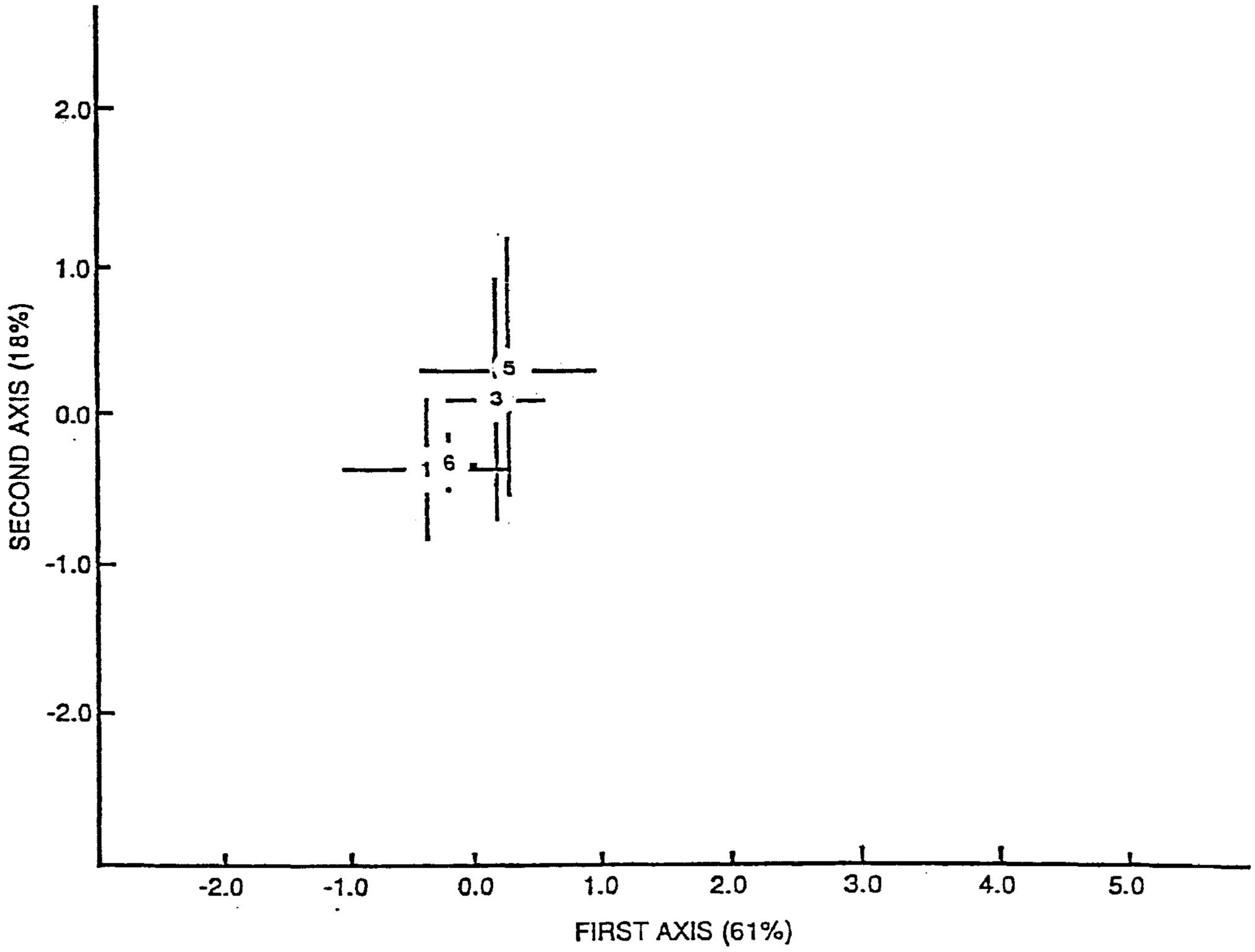

Fig. 3.6. Two-dimensional ordination of four northern populations of *Abies lasiocarpa* progeny based on principal components analysis of shape needle data.

Table 3.15. Results of principal components analysis of cone data from nine northern populations of *Abies lasiocarpa*.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	36	54	67
Cone Characters	Eigenvectors		
CL	-0.60	-0.35	-0.60
AL	-0.63	-0.19	-0.61
BL	-0.60	-0.34	0.17
BW	-0.54	-0.46	0.19
D	-0.43	0.78	-0.26
AN	-0.75	-0.09	0.02
SW	-0.47	-0.80	-0.04
SL	0.32	-0.17	-0.44
ADB	-0.80	-0.02	0.29
ADM	-0.73	-0.05	0.38

contributions than any of the others. The coefficients in both the second and third eigenvectors are mixed in polarity.

As presented in Figure 3.7, there is a large degree of overlap among all nine populations. As for the needle data ordinations, there is no apparent geographical trend in the distribution of populations. However there is little similarity between the patterns of distribution of the populations for the needle and cone data ordinations. All populations are equally variable along the first axis. Populations 1, 5, 6 and 7 are slightly more variable along the second axis than are the others.

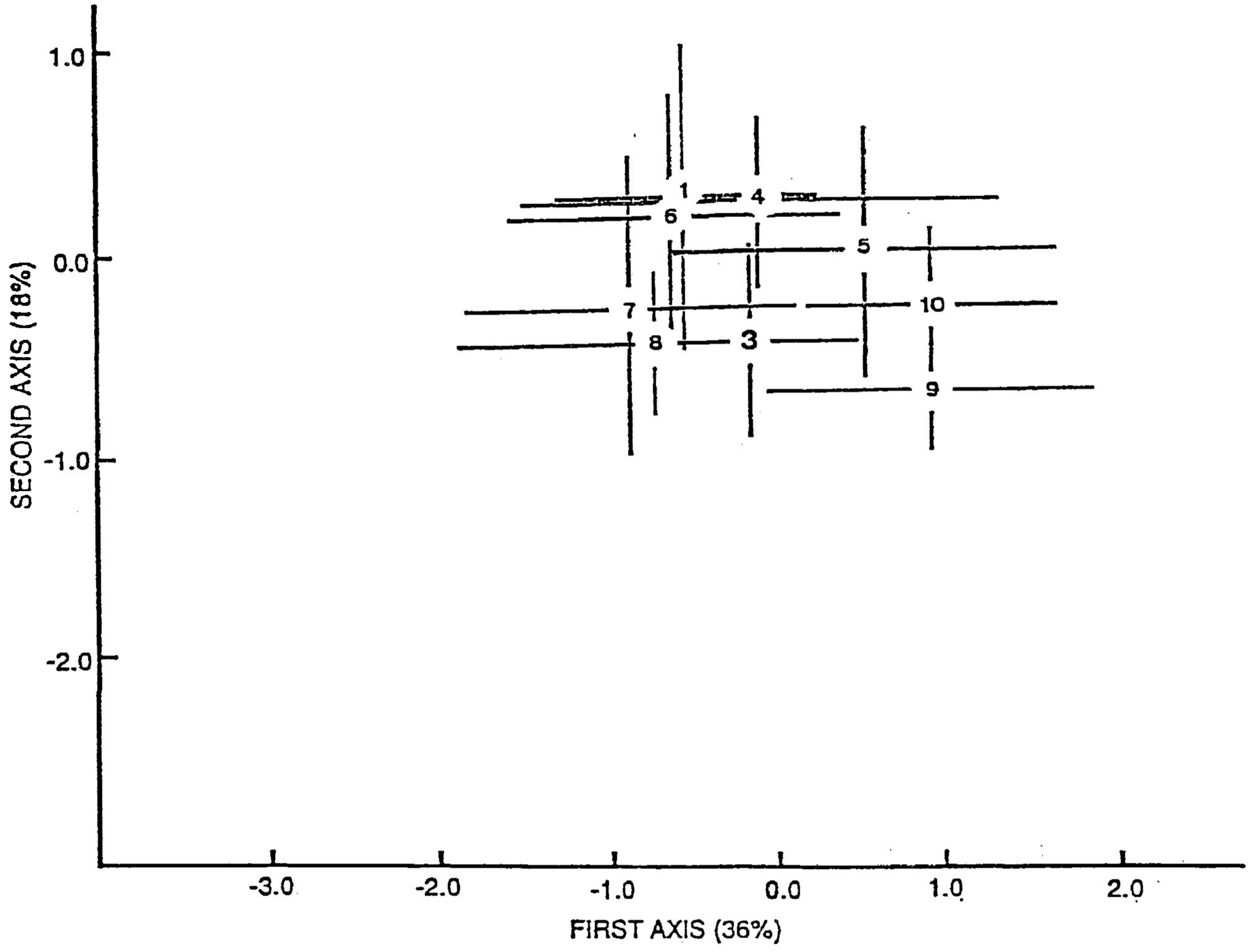

Fig. 3.7. Two-dimensional ordination of nine northern populations of *Abies lasiocarpa* based on principal components analysis of cone data.

Conventional Needle Data: 21 Populations

Table 3.16 and Figure 3.8 present the results of PCA of 21 populations of *Abies lasiocarpa* from the Yukon, Alaska, British Columbia, and Washington, where seven conventional needle characters from 208 individual trees were used. The first three principal component axes account for 79% of the total variation. The first of these axes accounts for 47% of this total, which is similar to the amount of variation accounted for by the first axis of the PCA's of needle data sets for the northern populations. The four characters NT, AD, MD, and NW make the largest and only significant contributions to this axis of variation, although both RC and AB also make relatively large contributions. All coefficients in the first eigenvector have the same polarity, indicating that this axis expresses variation in needle size, as well as position of the resin canal with respect to the adaxial needle surface and needle margin. The characters contributing most to this axis are the same ones that contributed to the first axis of the PCA for conventional needle data for the northern populations (excluding

Table 3.16. Results of principal components analysis of needle data from 21 populations of *Abies lasiocarpa* in Yukon Territory, Alaska, British Columbia, and Washington.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	47	67	79
Needle Characters	Eigenvectors		
NL	-0.12	-0.86	-0.31
MD	-0.78	-0.12	0.04
AB	-0.59	0.22	-0.72
AD	-0.76	0.41	-0.03
RC	-0.64	-0.56	0.13
NW	-0.76	-0.20	0.34
NT	-0.86	0.29	0.16

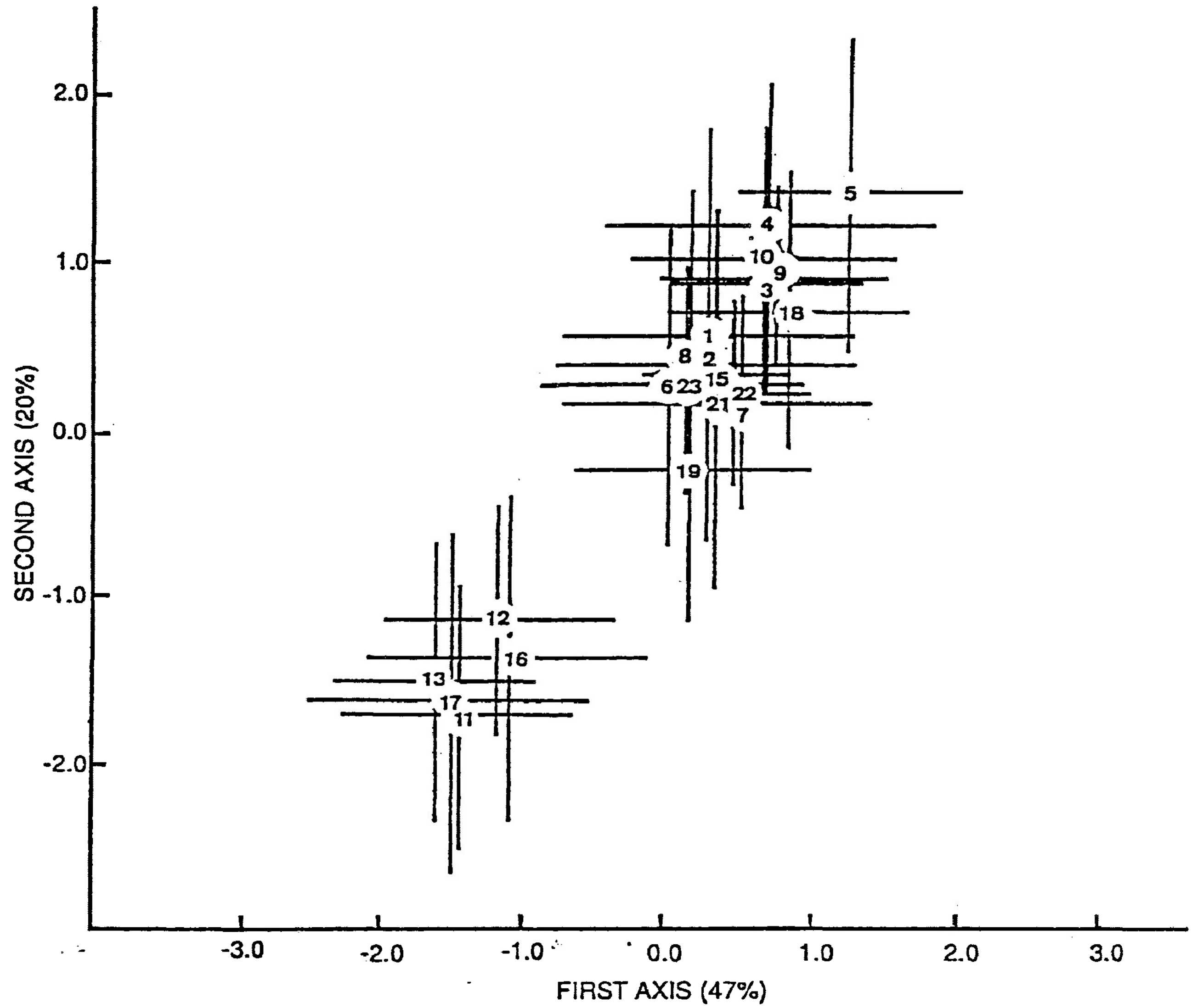

Fig. 3.8. Two-dimensional ordination of 21 populations of *Abies lasiocarpa* based on principal components analysis of conventional needle data.

the characters VC, VAB, and VAD which were not measured for the more southern populations). The second and third axes account for 20 and 11%, respectively, of the total variance.

The only character to make a significant contribution to the second axis is needle length, and the coefficients in the second eigenvector have mixed polarity. None of the coefficients in the third eigenvector make a significant contribution, although the character AB makes the largest contribution. Coefficients in the third eigenvector have mixed polarity. Again, these results are nearly identical to those for the second and third axes of the conventional needle PCA's for the 10 northern populations.

In the PCA ordination of the 21 populations, several very clear geographical trends are apparent (Figure 3.8). All of the northern populations (N1-10), as well as the interior eastern populations (E18-19, E21-23), form a tight cluster in the upper right part of the ordination. The Vancouver Island population (W19) is the only coastal population included among the northern and interior subalpine fir population grouping. The three north-coastal B.C. populations (W1-13), as well as the Washington populations (W16-17), form a completely separate group at the lower left part of the graph. All of the populations of both groups tend to be equally variable along both axes.

Conventional Needle Data: 31 Populations

Table 3.17 and Figure 3.9 present the results of PCA of the needle characters of individual trees of *Abies lasiocarpa* and *Abies balsamea* from 31 populations in the Yukon, Alaska, British Columbia, Washington, Alberta, Saskatchewan, and Ontario. The first three principal components account for 78% of the total variation. The first axis accounts for 51% of the total variance, and the characters NW, NT, MD and AD make the greatest contributions to this major axis of variation. All coefficients have similar polarity in this eigenvector, indicating the first axis accounts mainly for differences in needle size. This result is almost identical to that of the PCA for 21 populations of subalpine fir, with the first principal component accounting for only slightly more of the total variation in

Table 3.17. Results of principal components analysis of needle data from 31 populations of *Abies lasiocarpa* and *Abies balsamea* in Yukon Territory, Alaska, British Columbia, Washington, Alberta, Saskatchewan, and Ontario.

	PRINCIPAL COMPONENT 1	2	3
Cumulative Variance (%)	51	67	78
Needle Character	**Eigenvectors**		
NL	-0.40	-0.73	0.51
MD	-0.79	-0.04	-0.26
AB	-0.61	0.34	0.53
AD	-0.75	0.39	0.16
RC	-0.69	-0.44	-0.37
NW	-0.84	-0.16	-0.05
NT	-0.82	0.31	-0.17

the analysis of 31 populations. The second and third axes account for 16 and 11%, respectively, of the total variance. None of the coefficients in either of these eigenvectors make significant contributions to the total variance. However, the character NL makes quite a large contribution to the second axis. The characters NL and AB make the largest contributions to the third axis of variation. Polarity is mixed for the coefficients of both the second and third eigenvectors. Again, these results are very similar to those of the PCA for 21 populations, with the second and third axes of both analyses accounting for very similar amounts of variation, and similar characters making contributions to each of these components.

The ordination of populations in Figure 3.9 is similar to that of Figure 3.8, in that there are two distinct population groupings. However in the present ordination, the two Washington populations (W16-17), which are located very close geographically, form a separate group from the cluster of all remaining populations. In contrast to the results of the PCA for 21 populations of subalpine fir, the three north-coastal B.C. populations (W11-13) are now included with all of the other subalpine and balsam fir populations from further east. This cluster

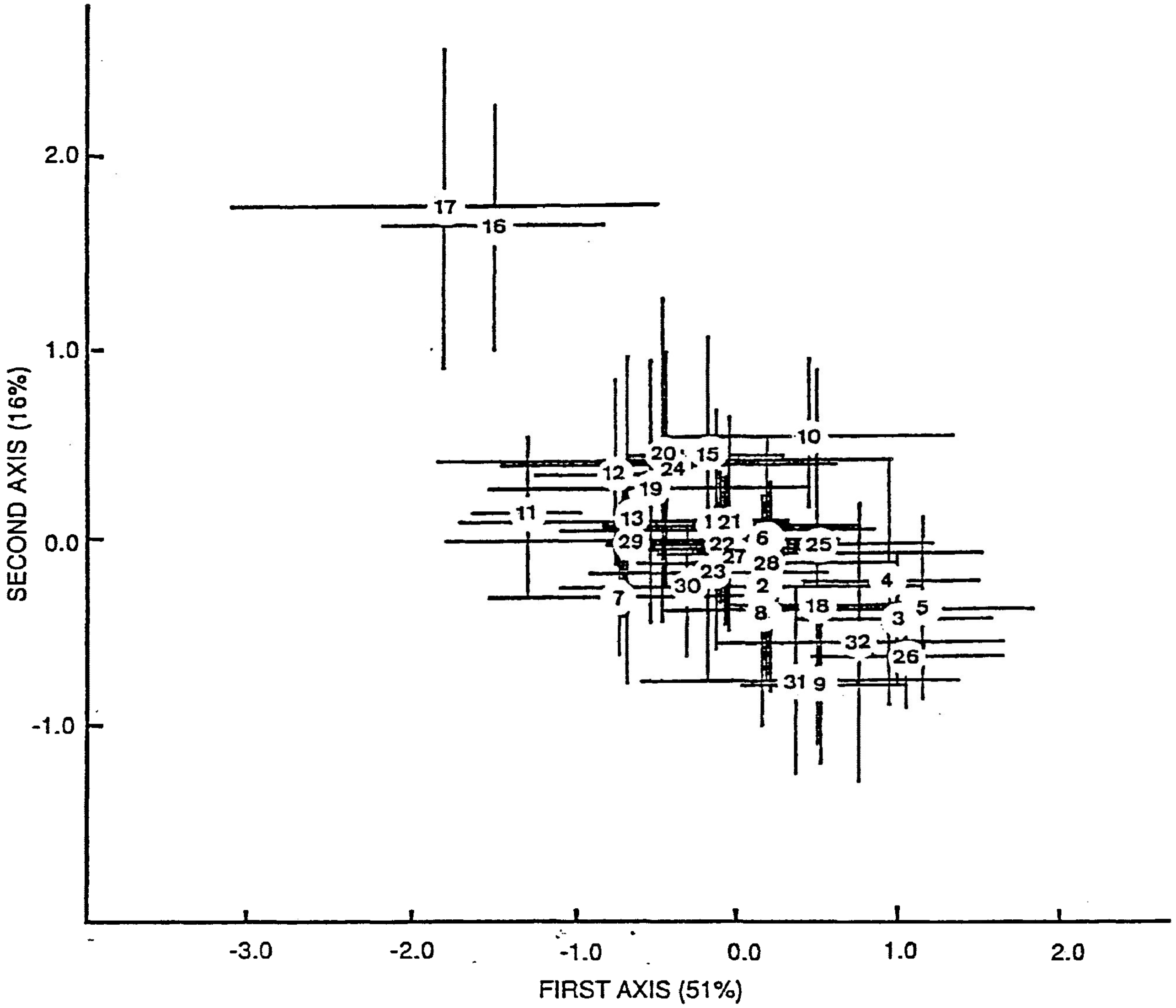

Fig. 3.9. Two-dimensional ordination of 31 populations of *Abies lasiocarpa* and *Abies balsamea* based on principal components analysis of conventional needle data.

of remaining populations includes all of the 10 northern populations (N1-10), the interior subalpine fir populations, (E18-23), the populations from the putative balsam-subalpine fir sympatric zone (S24-25), and the balsam fir populations from northern Ontario (B28-32). Although they are now separated from the Washington coastal populations, the three north-coastal B.C. populations in the large population cluster are situated at the cluster's upper left extremity closest to the two separated populations. All of the populations appear to have relatively equal variability along both major PCA axes.

Cone Data: 22 Populations

The first three principal components account for 70% of the total variation for PCA of cone characters for the 22 sampled populations (Table 3.18). The first axis accounts for 40% of this total. The characters SW, BL and ADB make large significant contributions to this axis of variation; however, CL also makes a large, nearly significant contribution. The coefficients of the first eigenvector, except that of the character AN, are all of equal polarity. Therefore, the first axis expresses variation in size of the cone axis, cone scale, and scale bract. The second and third axes contribute 12 and 8%, respectively, to the total variation. Only ADM makes a significant contribution to the second axis, although AN makes a nearly significant contribution. The character AL makes the greatest contribution to the third axis, although none of the characters of this axis make significant contributions to the total variation. The coefficients of both the second and third eigenvectors have mixed polarity. The characters contributing most to each PCA axis are generally different than those that contributed most to the PCA axes of cone data from only the nine northern populations.

Certain geographical trends are illustrated in the ordination of the 22 populations (Figure 3.10). The nine northern populations (N1, N3-N10) are situated in a cluster to the lower left part of the graph. The remaining populations, composed of the north-coastal B.C. (W11-W14) and eastern subalpine fir (E21-23) populations, as well as the balsam fir populations from northern Ontario (B28-32), are clustered together in the upper part of the graph.

Table 3.18. Results of principal components analysis of cone data from 22 populations of *Abies lasiocarpa* and *Abies balsamea* in Yukon Territory, Alaska, British Columbia, Washington, and Ontario.

	PRINCIPAL COMPONENT		
	1	2	3
Cumulative Variance (%)	40	62	70
Cone Characters	Eigenvectors		
CL	-0.74	-0.44	-0.12
AL	-0.48	0.26	-0.67
BL	-0.81	-0.01	0.44
BW	-0.52	0.23	-0.04
D	-0.57	-0.56	0.32
AN	-0.04	0.72	0.03
SW	-0.88	-0.01	-0.05
SL	0.66	-0.42	-0.32
ADB	-0.75	0.48	0.11
ADM	-0.47	0.75	0.13

Although there is some distinction between these two clusters, there is also a degree of overlap, between the northern subalpine fir populations, and the eastern subalpine fir and balsam fir populations. Interestingly, the most northern population (N1) is situated most closely to the cluster of eastern and coastal subalpine fir and balsam fir populations.

DISCRIMINANT ANALYSIS

For each of the relevant data sets, the results of discriminant analysis are presented in tabular form (Tables 3.19 to 3.25). These tables present the standardized canonical discriminant function coefficients and the cumulative percent of variation for each significant canonical discriminant function of the analyses. Significance of functions is based on a chi-square test. The standardized canonical discriminant function coefficients indicate which characters make the greatest contribution to each discriminant function. Only variables which make a significant contribution to the discriminant functions are

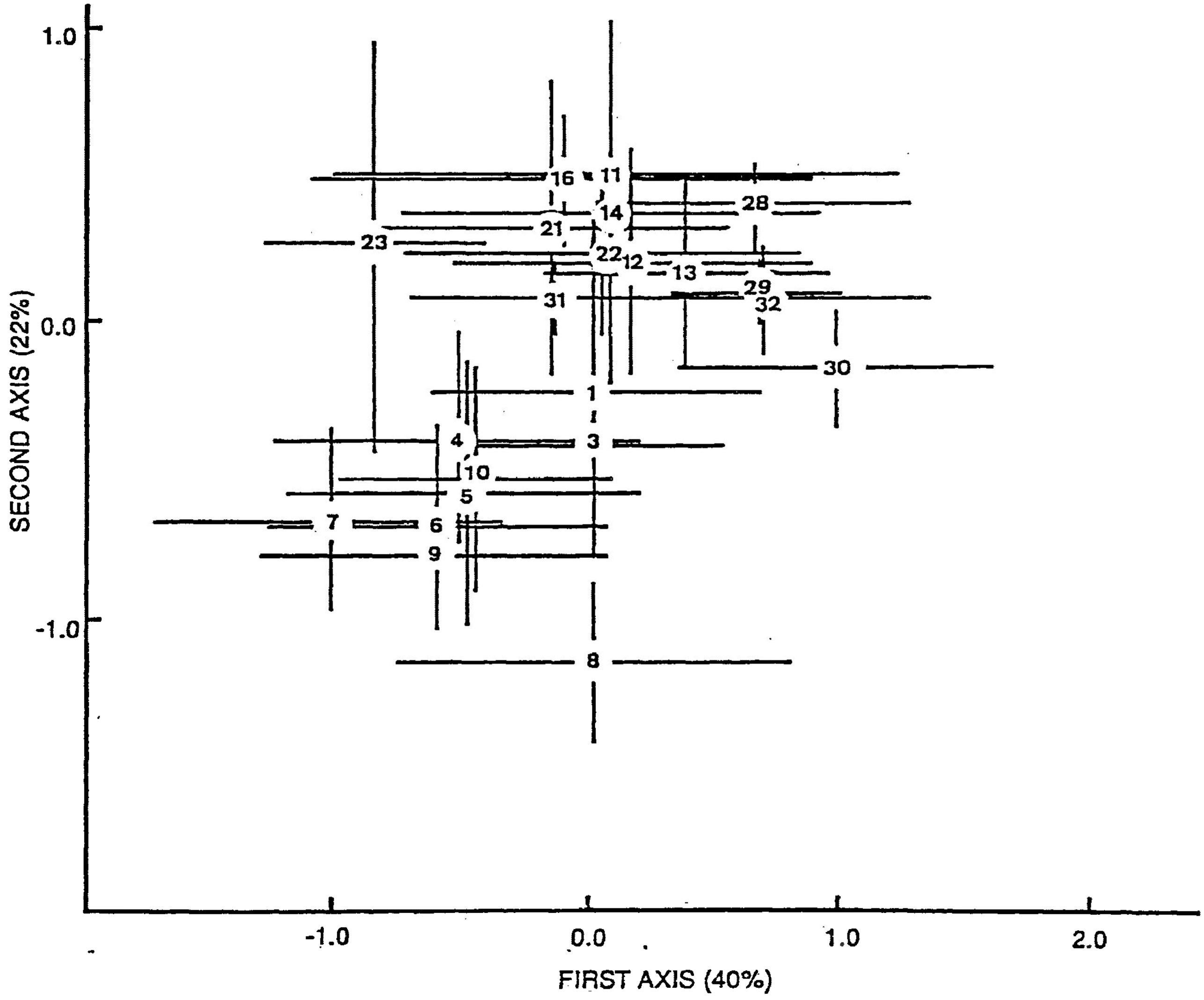

Fig. 3.10. Two-dimensional ordination of 22 populations of *Abies lasiocarpa* and *Abies balsamea* based on principal components analysis of cone data.

included. The results of each discriminant analysis are also presented as two-dimensional ordinations of the first two discriminant functions of the sampled populations (Figures 3.11 to 3.18). As for the ordination of PCA results, only the mean values for each population have been plotted, with their corresponding population numbers. Standard deviation scores on each axis are also represented in the same way as for the PCA ordinations.

For several of the discriminant analyses, the assumption of equality of variance-covariance matrices as indicated by Box's M test was not met. However many of these analyses still indicate very interesting trends, from which interpretations of population variation have been made. In addition, according to Nie et al. (1975), the SPSS subprogram DISCRIMINANT, which was used in this study for all discriminant analyses, is very robust, so that the assumptions of both equality of variance-covariance matrices among groups, and multivariate normality need not be adhered to strongly.

Conventional Needle Data: 10 Northern Populations

The MDA results for conventional needle data from the 10 northern populations indicate that only the first three discriminant functions significantly discriminate among the 10 populations (Table 3.19). The first axis contributes 33% to the overall variance, and the greatest contribution to this function is made by NW. The second axis accounts for almost 26% of the variation, primarily due to NT and VAB. The third axis accounts for 20% of the variation, with the characters NT, VC and VAB making the greatest contributions to this axis.

In the ordination of the first two discriminant functions, the 10 populations are generally arranged in a similar manner with respect to each other as they were in the parallel PCA ordination (Figure 3.32). However there are more distinct groupings than were evident from the PCA results. Populations 1, 2, 7, 8 and 9 are most similar, and these populations are somewhat distinct from populations 3, 4 and 5, which are also most similar. Population 6 is intermediate between these two groups, which are separated by the second

Table 3.19. Results of discriminant analysis of conventional needle data from 10 northern populations of *Abies lasiocarpa*.

	CANONICAL DISCRIMINANT FUNCTIONS		
	1	2	3
Cumulative Variance (%)	33	59	80
Needle Characters	Standardized CDF* Coefficients		
RC	-0.60	0.35	0.09
AB	0.01	-0.76	0.35
MD	-0.79	0.68	-0.05
NT	0.08	1.66	-2.14
NW	1.01	-0.39	-0.57
VC	0.06	-0.16	1.05
VAB	0.49	-1.14	1.64
NL	0.22	-0.13	-0.77
RS	-0.13	0.30	0.65

* Canonical discriminant function

discriminant function. However there is still a fair degree of overlap among these 9 populations. Unlike the parallel PCA ordination, population 10 is distinct from the other populations, due primarily to the first discriminant function, to which needle width contributes most. The degree of overlap among all of the populations except population 10 explains why only 56% of the individual trees were correctly identified as members of the groups to which they actually belong.

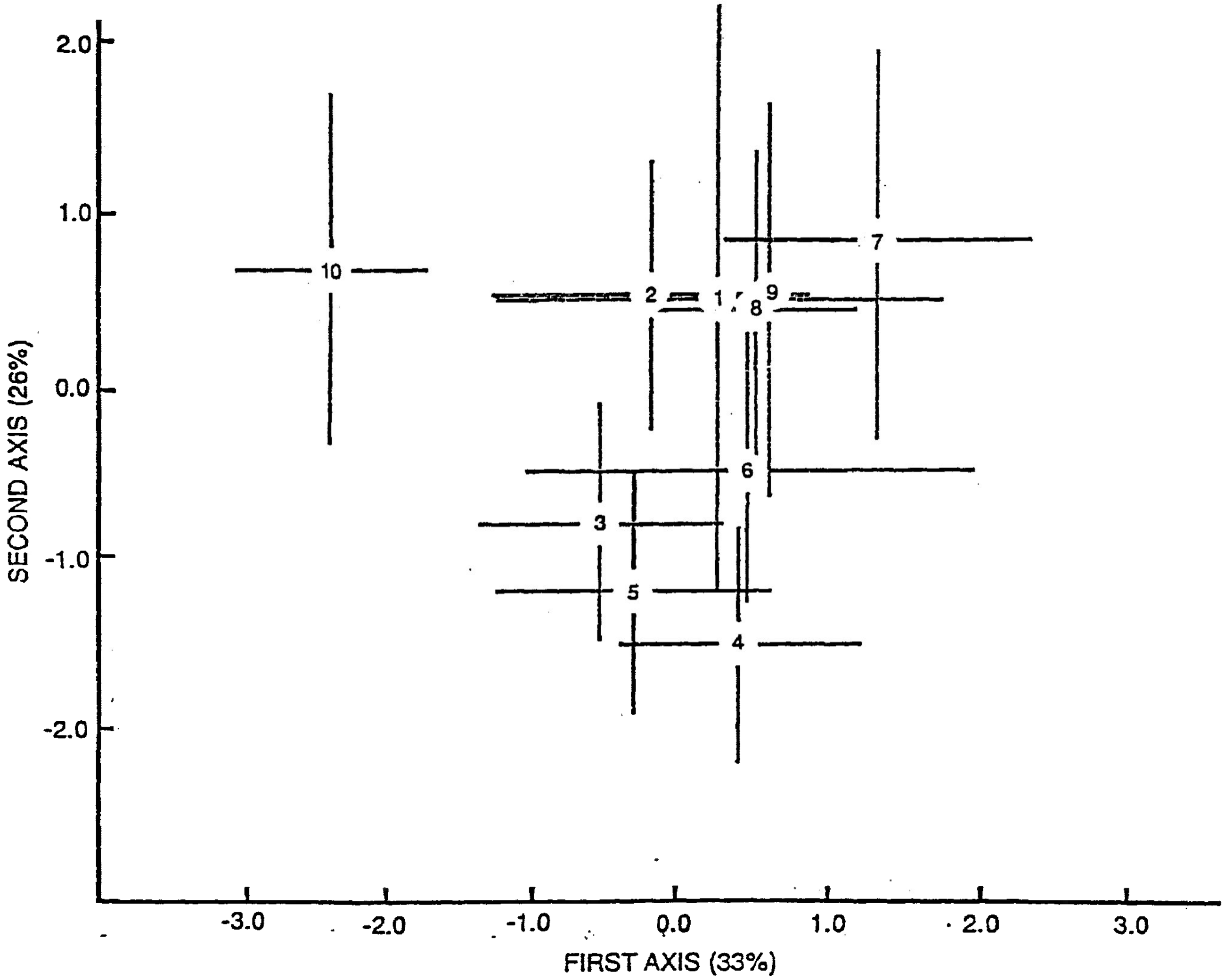

Fig. 3.11. Two-dimensional ordination of 10 northern populations of *Abies lasiocarpa* based on discriminant analysis of conventional needle data.

Progeny Conventional Needle Data

Only the first discriminant function is significant in discriminating among the four progeny populations for MDA of conventional needle data; however, this function accounts for 87% of the total variation. The characters VAD, VAB and AB make the largest contributions to this axis. These results are quite different than those of the MDA for the parent conventional needle data, where different needle characters contributed most to the largest axis of variation.

Table 3.20. Results of discriminant analysis of conventional needle data from four northern populations of *Abies lasiocarpa* progeny.

	CANONICAL DISCRIMINANT FUNCTION 1
Cumulative Variance (%)	87
Needle Characters	Standardized CDF Coefficients
RC	-0.97
AB	1.44
MD	0.91
VAB	-1.84
VAD	1.97

The ordination of populations indicates a degree of overlap between populations 1 and 3, as well as between populations 5 and 6 (Fig. 3.12). There is a slight separation between these two groupings. The arrangement of populations in this ordination is basically similar to that for PCA of the same data, although the populations are more separated in the discriminant analysis ordination. More than 82% of the individual trees were classified correctly to the groups to which they actually belong in the discriminant analysis.

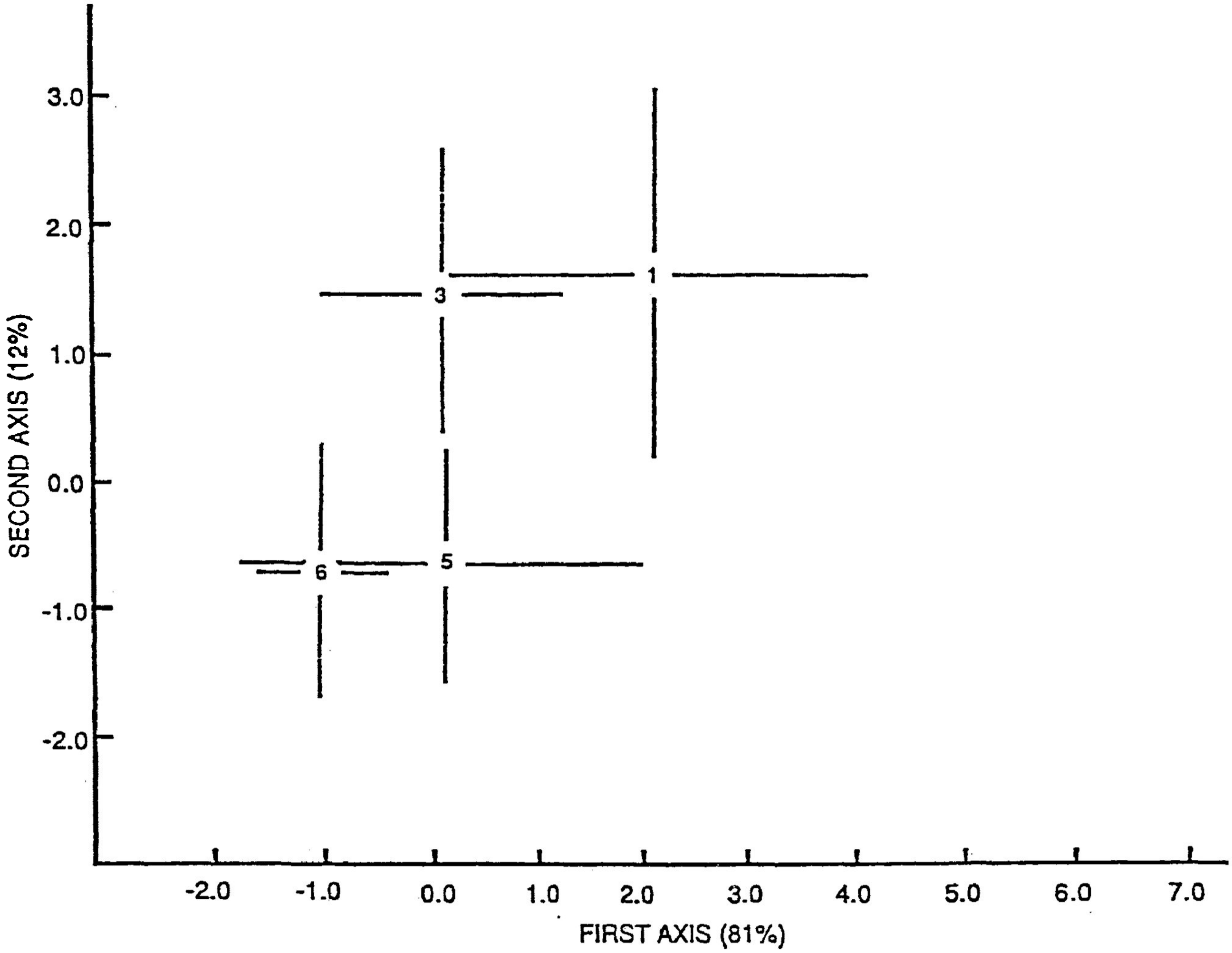

Fig. 3.12. Two-dimensional ordination of four northern populations of *Abies lasiocarpa* progeny based on discriminant analysis of conventional needle data.

Needle Shape Data: 10 Northern Populations

For MDA of needle shape data for the 10 northern populations, the first two discriminant functions, accounting for 75% of the total variation, are significant in discriminating among the 10 populations (Table 3.21). The first of these axes accounts for 47% of the variance. The characters V3, V4, V6 (which is similar to needle width) and V7 make large contributions to this function. The second discriminant function accounts for 28% of the total variation, with V2, V3, V6 and V7 accounting for most of this variation.

Table 3.21. Results of discriminant analysis of shape needle data from 10 northern populations of *Abies lasiocarpa.*

	CANONICAL DISCRIMINANT FUNCTIONS	
	1	2
Cumulative Variance (%)	47	75
Needle Characters	Standardized CDF Coefficients	
V1	0.32	1.28
V2	-0.14	-3.28
V3	2.06	2.83
V4	-1.98	-0.42
V6	2.16	-3.41
V7	-1.59	3.53

In the MDA ordination, the ten populations are generally arranged in a similar way to that of the PCA ordination for this data set, although the populations are more separated on the basis of discriminant analysis (Figure 3.13). However there is still a continuous overlapping among all populations, as in the PCA ordination. Population 7 is much more segregated and in a somewhat different location with respect to the other populations in the discriminant analysis ordination than in the PCA ordination. Only 49% of the individual trees were correctly classified into the groups to which they actually belong in the discriminant analysis, due to the overlap among populations.

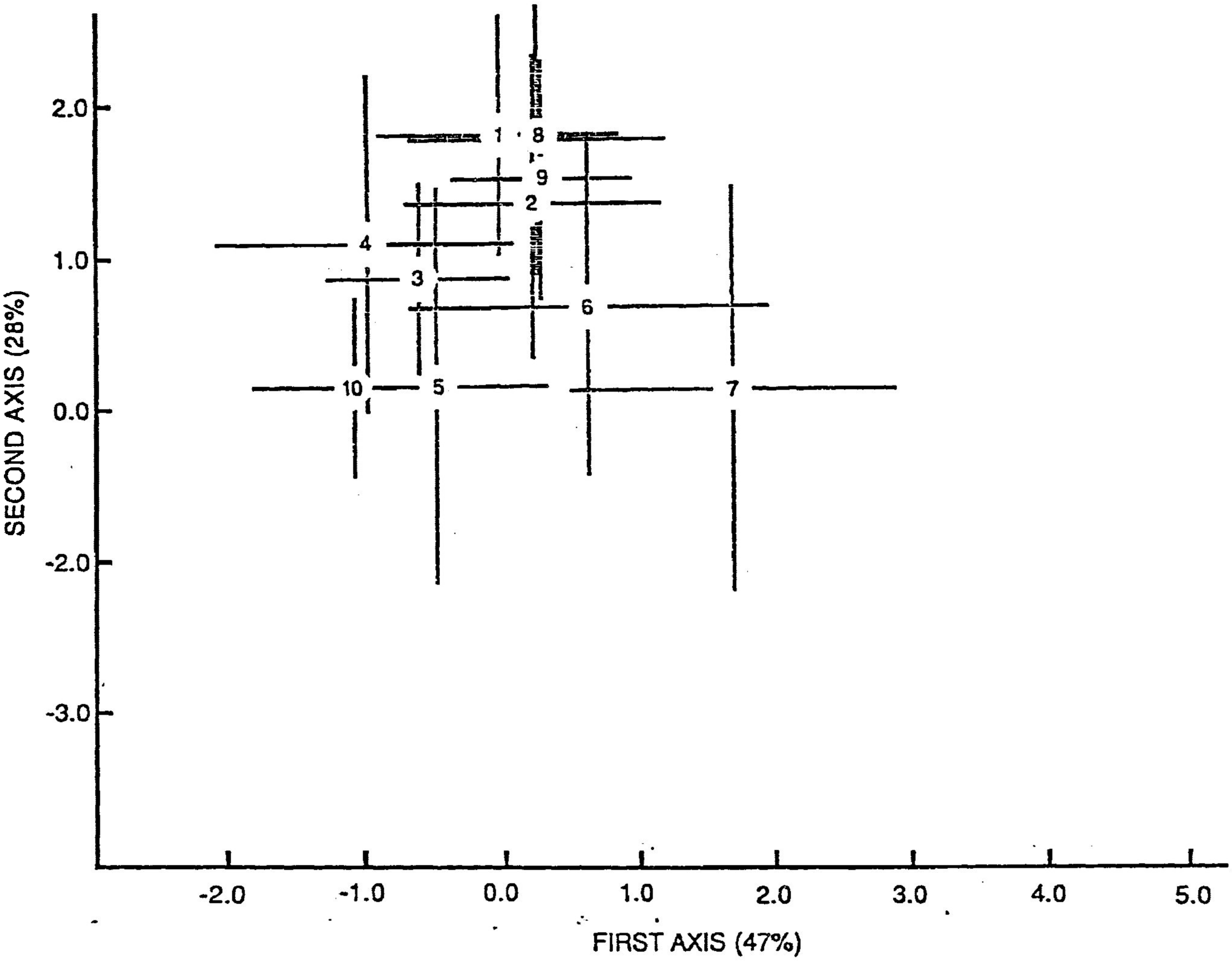

Fig. 3.13. Two-dimensional ordination of 10 northern populations of *Abies lasiocarpa* based on discriminant analysis of shape needle data.

Progeny Needle Shape Data

Although only the first discriminant function is significant in discriminating among groups for MDA of the progeny needle shape data, which was also the case for the progeny conventional needle data, this function accounts for 73% of the total variation. The character V9 makes the greatest contribution to this function. The next highest contributions are made by V7 and V10.

Table 3.22. Results of discriminant analysis of shape needle data from four northern populations of *Abies lasiocarpa* progeny.

	CANONICAL DISCRIMINANT FUNCTION 1
Cumulative Variance (%)	73
Needle Characters	Standardized CDF Coefficients
V1	1.19
V6	-2.85
V7	3.61
V9	-4.53
V10	3.13

The arrangement of populations in Figure 3.14 is generally similar to that of the PCA for this data set, with populations forming a continuously overlapping cluster. However, the populations in the discriminant analysis ordination are more separated that in that of the PCA ordination, where all 20 radial distances were used. Populations 1 and 6 are much more distinct from each other, and population 1 is intermediate between 6 and populations 3 and 5, which are grouped together. Populations 1 and 6 are also more variable than populations 3 and 5, primarily along the second axis, which is the reverse of the situation in the PCA ordination. More than 88% of the individual trees were classified into the actual groups to which they belong.

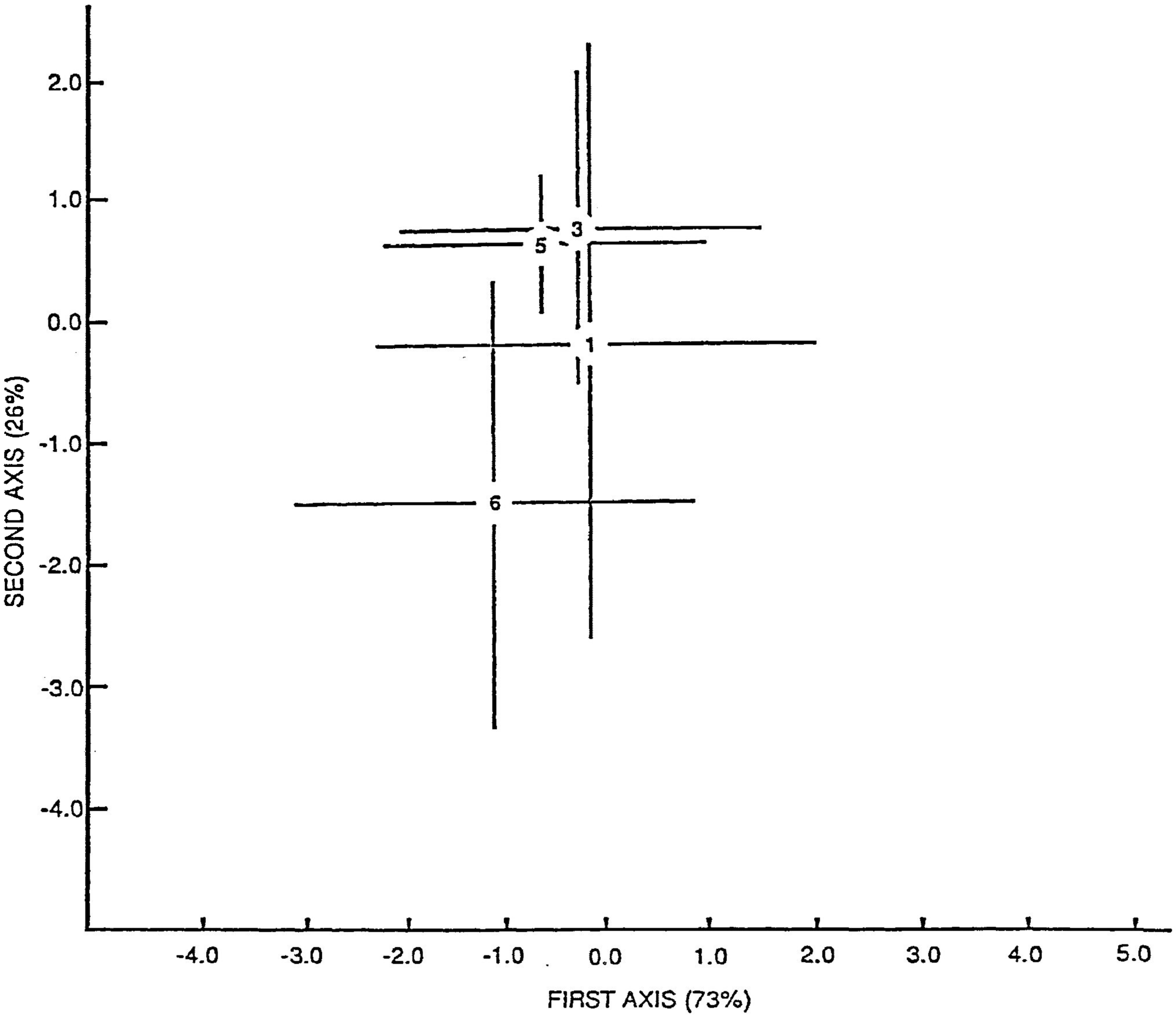

Fig. 3.14. Two-dimensional ordination of four northern populations of *Abies lasiocarpa* progeny based on discriminant analysis of shape needle data.

Cone Data: 9 Northern Populations

The first three discriminant functions are significant in discriminating among groups for MDA of cone data for the northern populations (Table 3.23). These functions account for approximatley 87% of the total variation. The characters SW, D, and ADM make large contributions to the first discriminant function which accounts for 38% of the variation. The second and third functions account for 32 and 16% of the variation, respectively.

Table 3.23. Results of discriminant analysis of cone data from nine northern populations of *Abies lasiocarpa*.

	CANONICAL DISCRIMINANT FUNCTIONS		
	1	2	3
Cumulative Variance (%)	38	71	87
Cone Characters	Standardized CDF Coefficients		
CL	0.43	-0.34	0.88
AL	0.03	0.29	0.21
BL	0.16	-0.29	-0.76
B	-0.10	-1.08	0.66
D	-1.04	0.59	0.80
AN	0.14	-0.63	0.33
SW	1.18	0.12	-0.20
SL	-0.30	0.84	-0.50
ADB	0.30	0.79	-0.16
ADM	-0.74	0.03	-0.05

The arrangement of the nine populations in the ordination of the first two discriminant functions indicates that there is a greater distinction among populations than in the PCA for this data set (Figure 3.15). Population 1 and to a lesser extent population 3, the two northernmost populations, are somewhat distinct from the others. There is some overlap among the remaining populations, although three population groupings (populations 8 and 9, populations 5, 7, and 10, and populations 4 and 6) are apparent. Population 8 is much less variable along the first axis than

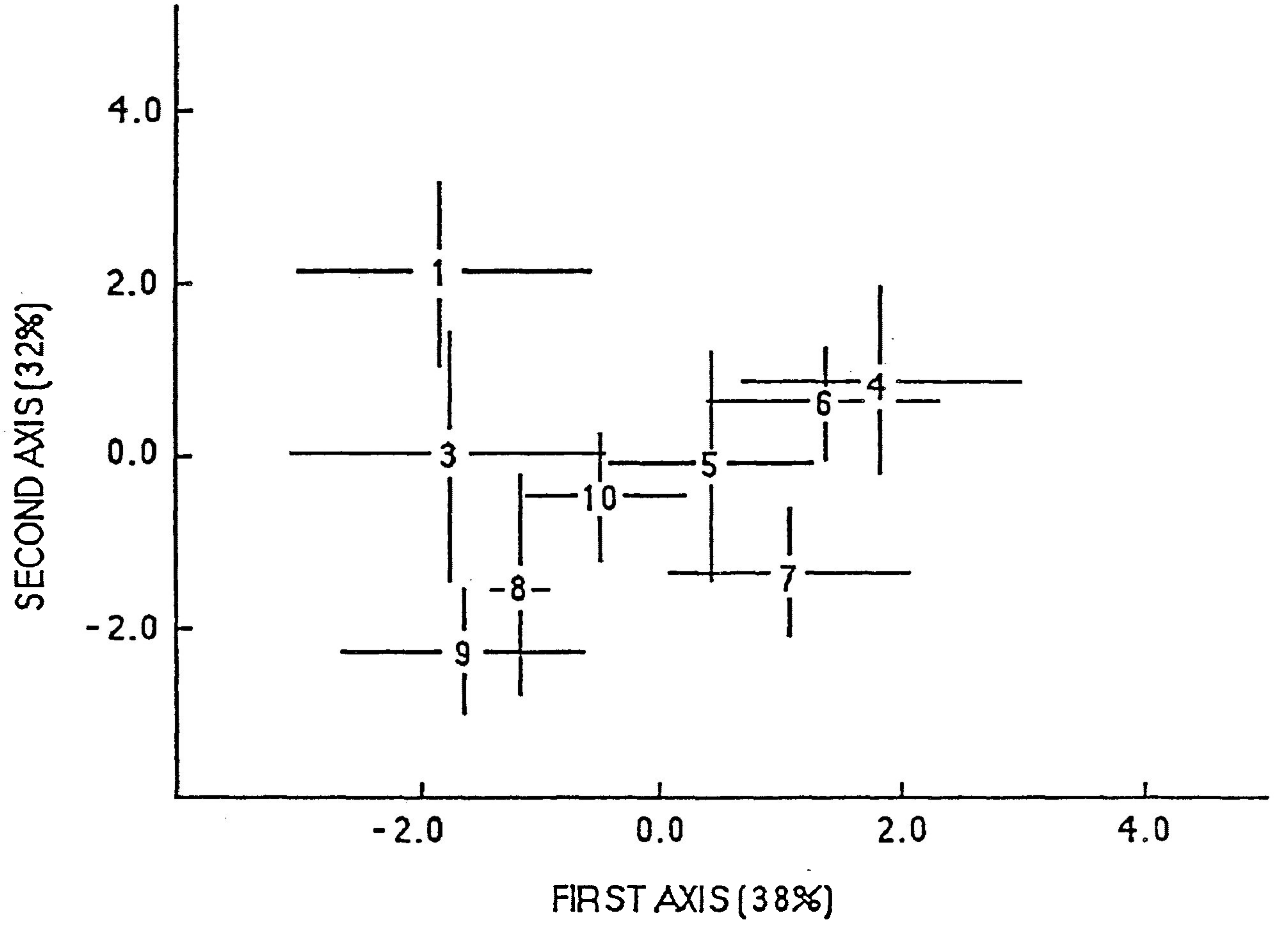

Fig. 3.15. Two-dimensional ordination of nine northern populations of *Abies lasiocarpa* based on discriminant analysis of cone data.

the other populations, due to a smaller sample size. The arrangement of populations does not indicate any geographical patterning, other than the separation of the two northernmost populations from the others, and is quite different from the MDA ordinations of needle data for the same populations. Nearly 74% of the individual trees were classified into the actual groups to which they belong.

Conventional Needle Data: 31 Populations

For MDA of conventional needle data from 31 populations, the first five discriminant functions are significant in discriminating among the groups with these axes accounting for nearly 97% of the variation (Table 3.24). The first function accounts for only 33% of the total variance, with large contributions being made by MD, NW, and NL. The second function, which accounts for approximately 28% of the variation, has the greatest contribution made by MD. The other three functions account for 18, 9, and 9% of the total variation, respectively.

Table 3.24. Results of discriminant analysis of conventional needle data from 31 populations of *Abies lasiocarpa* and *Abies balsamea*.

	CANONICAL DISCRIMINANT FUNCTIONS				
	1	2	3	4	5
Cumulative Variance (%)	33	61	79	88	97
Needle Characters	Standardized CDF Coefficients				
NL	0.61	0.29	-0.18	0.44	-0.51
MD	-0.90	0.62	0.12	-0.06	-0.70
AB	0.52	0.24	0.10	0.83	0.28
AD	0.03	0.02	0.12	0.38	-0.34
RC	-0.11	0.17	-0.96	0.24	0.71
NW	0.75	0.02	0.26	0.01	0.30
NT	-0.22	0.11	0.60	-0.90	0.45

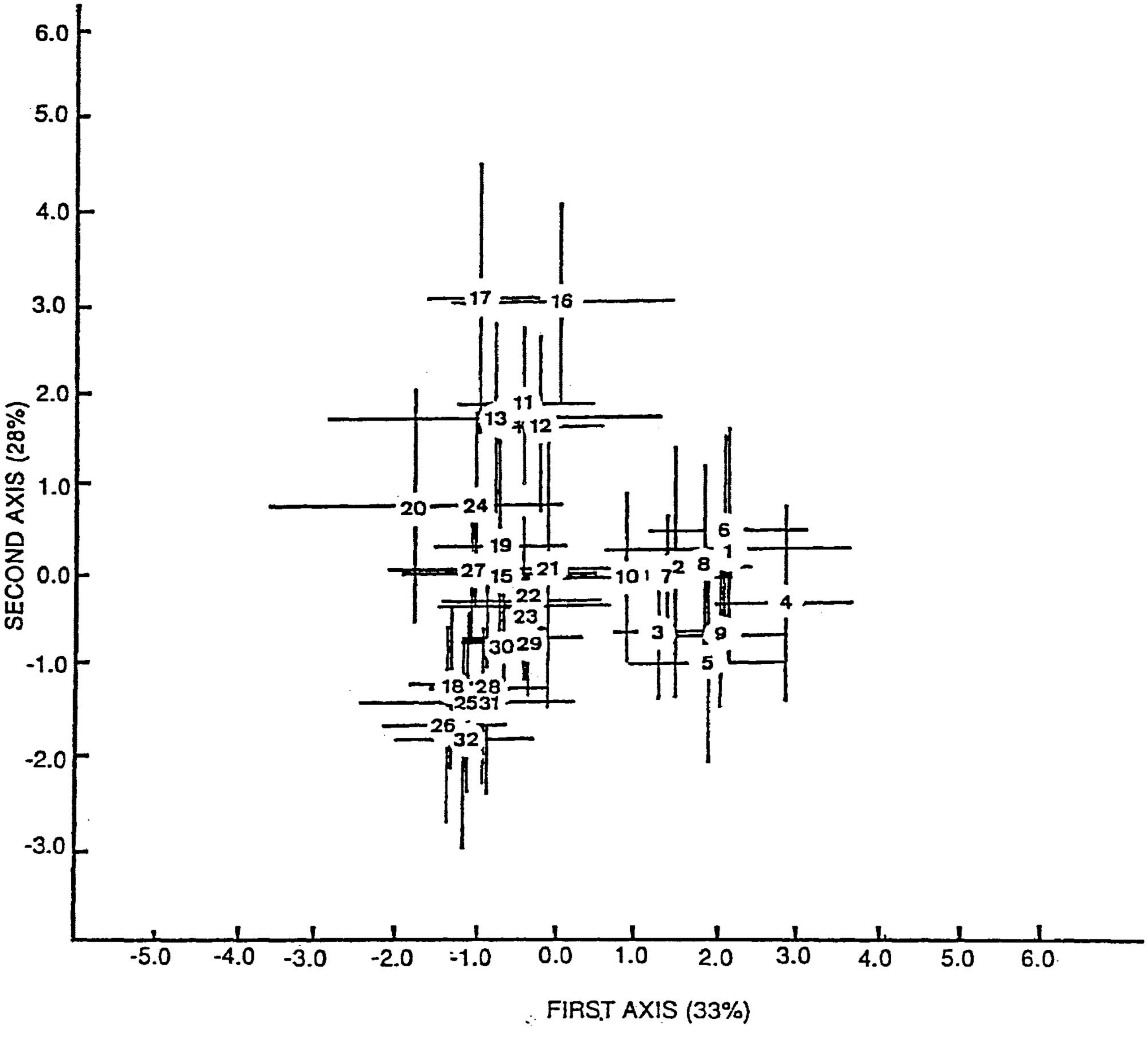

Fig. 3.16. Two-dimensional ordination of 31 populations of *Abies lasiocarpa* and *Abies balsamea* based on discriminant analysis of conventional needle data.

The ordination of the first two discriminant functions indicates that although there is a continuous overlap among all populations, there are obvious distinctions between certain groups of populations (Figure 3.16). These groups are generally arranged in a geographical pattern. The 10 northern populations form a cluster to the right of the graph. Immediately to the left of this group of populations, there is a cluster of all of the eastern segregate of subalpine fir from B.C. and Alberta, as well as the balsam fir populations from Ontario. Also included in this cluster is the population of coastal subalpine fir from Vancouver Island (W19). The extreme populations (E21 and N10) of each of these groups overlap. Interestingly, the most northern subalpine fir population overlaps with the Rocky Mountain subalpine fir and balsam fir group of populations.

Two other groupings of populations are 1) the north coast subalpine fir populations (W11-13) and 2) the Cascades subalpine fir populations (W16-17). Populations W11-13 intergrade between the cluster of eastern subalpine and balsam fir populations, and the Cascades populations. In the cluster of Rocky Mountain subalpine fir and balsam fir populations, the balsam fir populations are located at the bottom part of the graph, furthest from the coastal subalpine fir populations (excluding the Vancouver Island population), and Rocky Mountain subalpine fir populations are closest and overlapping with the coastal populations. Thus, this clustering of populations indicates a degree of geographical patterning, although there is a distinct overlap among eastern subalpine fir and balsam fir populations, as well as with one coastal subalpine fir population from Vancouver.

The relative arrangement of populations in this MDA ordination are generally comparable to the ordination of the same data set based on PCA. However, the differences between groups of populations are much more pronounced in this discriminant analysis. The similarities in ordinations based on both types of analyses indicate that the main components of variation in the sampled trees are generally also the components which best distinguish the populations. Only 44% of the individual trees were classified into the actual groups to which they belong in this MDA, reflecting the great degree of overlap among many of the populations.

Cone Data: 22 Populations

For MDA of cone data from 22 populations of subalpine and balsam fir, the first eight discriminant functions are significant in discriminating among the groups, and they account for 99% of the variation. (Table 3.25). However the first function accounts for 59% of the total variation, and the first two axes together account for 84% of this total. The remaining six functions, although significant, contribute much less to the total variation.The characters BL, SW, D, and SL make large contributions to the first axis of variation. The second axis accounts for an additional 25% of the variation, with the characters CL and ADM contributing most to this discriminant function.

Table 3.25. Results of discriminant analysis of cone data from 22 populations of *Abies lasiocarpa* and *Abies balsamea*.

	CANONICAL DISCRIMINANT FUNCTIONS							
	1	2	3	4	5	6	7	8
Cumulative Variance (%)	59	84	88	92	94	96	98	99
Cone Characters	Standardized CDF Coefficients							
CL	-0.13	-0.93	-0.05	0.02	0.22	0.81	0.26	-0.48
AL	-0.00	0.19	0.01	0.32	-0.14	-0.02	-0.96	-0.19
BL	-1.49	-0.26	-0.58	-0.15	0.07	0.79	-0.80	0.88
B	0.62	0.06	0.72	0.12	0.05	-0.67	0.32	0.01
D	1.28	0.03	0.85	-0.33	0.47	-1.08	0.36	-0.18
An	0.41	0.30	0.51	0.10	-0.37	0.11	0.40	0.29
SW	-1.32	-0.06	0.42	-0.11	-0.48	-0.93	0.79	-0.58
SL	-1.17	0.07	-0.76	0.88	0.17	0.16	-0.34	0.94
ADB	0.00	-0.00	0.63	0.18	-0.35	-0.65	-0.18	-0.03
ADM	-0.19	0.84	-0.54	0.06	0.86	0.18	0.19	-0.16

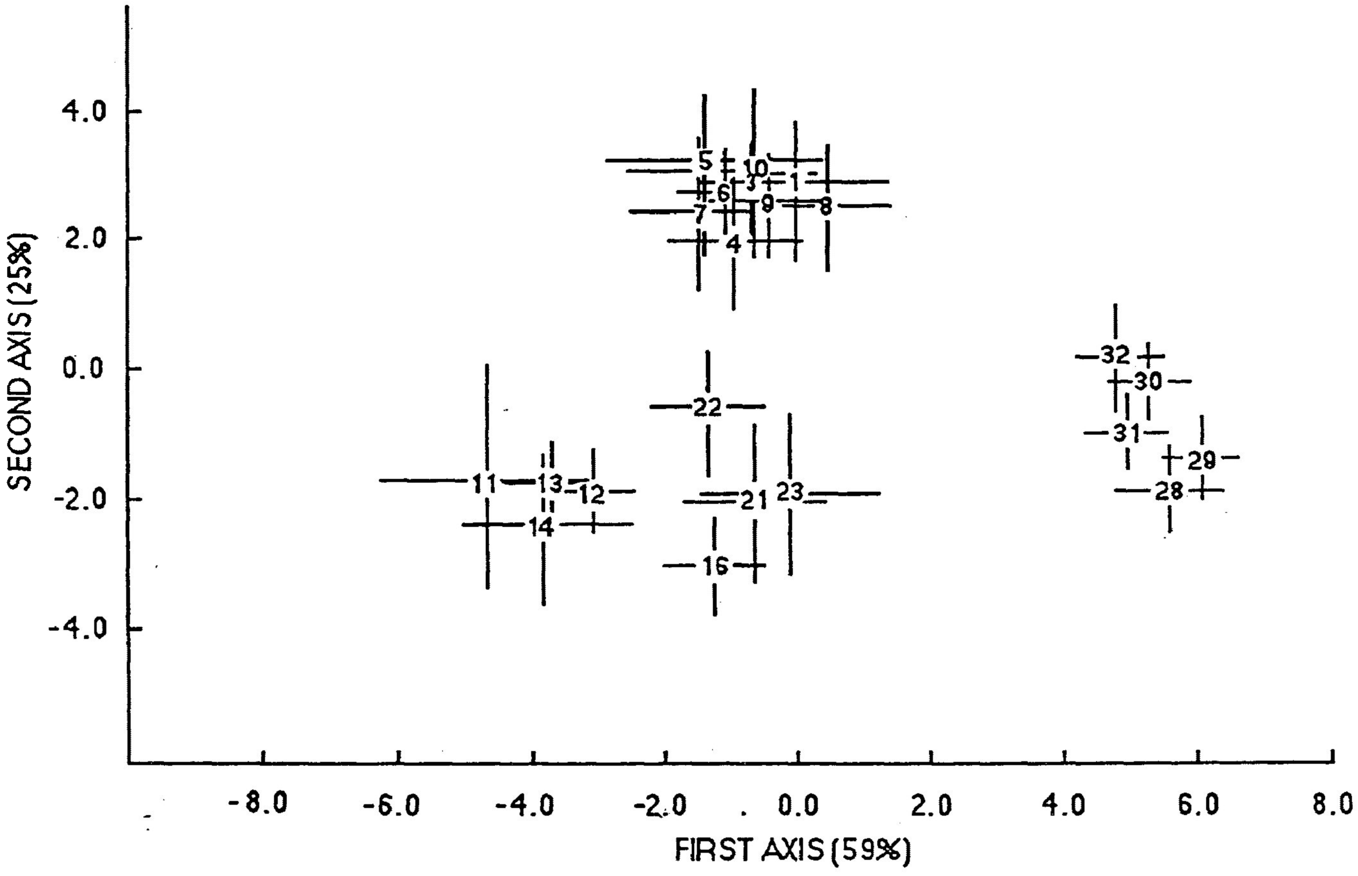

Fig. 3.17. Two-dimensional ordination of 22 populations of *Abies lasiocarpa* and *Abies balsamea* based on discriminant analysis of cone data.

The ordination of the first two discriminant functions indicates several very strong geographical trends (Figure 3.17). Four completely distinct groups of populations have been separated, and the respective arrangement of groups is similar to their geographical locations. Along the first discriminant axis, three major groups are separated, due primarily to the characters BL, SW, D, and SL. These groups are 1) the north coast subalpine fir populations (W11-14), 2) the Rocky Mountain (E21-23), Mount Baker (W16), and northern (N1-10) subalpine fir populations, and 3) the northern Ontario balsam fir populations. These population groupings reflect their geographical affinities. Thus, the first discriminant function reflects longitude. The balsam fir popluations tend to be less variable along the first two discriminant axes than are the other populations. The second discriminant function separates the northern subalpine fir populations from the cluster of Rocky Mountain subalpine fir population, thus reflecting a latitudinal trend. Both of these groups of populations lie within the tentative range of *Abies bifolia* as designated by Hunt and von Rudloff (1979).

This ordination of populations indicates much more pronounced differences among groups of populations than did the ordination of populations based on PCA, where similar trends were indicated, although there was a degree of overlap among all populations. This discriminant analysis correctly classified 71% of the individual trees into the groups to which they actually belong.

SUMMARY OF MULTIVARIATE ANALYSIS RESULTS

For the principal components analyses of the cone and needle data sets in this study, a substantial proportion of the variability in the data sets has been accounted for by the first two principal components. All analyses of conventional needle data for the various data subsets from natural populations produced comparable results, with 61 to 67% of the total variability accounted for by the first two PCA axes. The first two principal components of the conventional progeny needle data from four of the northern populations accounted for slightly more of the variation (71%). Even greater proportions of the total variability were accounted for by the first two principal components for both parent (83%) and progeny (79%) needle shape data sets. The results for the two PCA's of cone data were comparable to those of the needle data sets, although the total amount of variability accounted for by the first two principal components tended to be lower, with 54% being accounted for in the PCA of the northern populations, and 62% accounted for in the PCA of all 22 populations.

These results are comparable to those for previous taxonomic studies of cone and needle morphology and flavonoids in *Abies lasiocarpa* and *Abies balsamea* (O'Reilly, 1981; Parker et al., 1981; Parker and Maze, 1984; Parker et al., 1984) where the proportion of the variability accounted for by the first two principal components ranged from 52% for cone morphology to 74% for needle morphology. A much lower percentage (34%) of the total variability was accounted for by the first two principal components in a study of flavonoid variation of *Abies* in the section *Nobilis* (Bennet Sutton, 1986).

A substantial proportion of the variability among populations was also accounted for by the canonical discriminant functions for both cone and needle morphology, with a range of from 59 to 87% of the total variability being accounted for by the first two functions. In contrast to the results of principal components, the discriminant functions based on analysis of cone data accounted for more variability than those based on needle data for the analyses of trees from natural stands. Although only the first discriminant function was significant for the analyses based on both needle data sets of the progeny populations, these functions accounted for more of the variability than those produced by any other data set.

These results of MDA from the present study are generally comparable to the results of canonical variates analyses (CVA, a comparable multivariate technique) in the previous studies of morphological and chemical variation in *Abies lasiocarpa* and *Abies balsamea*, although the first two discriminant functions based on analyses of cone characters in the present study tended to account for higher proportions of the total variability. O'Reilly (1981) found that, for similar needle and cone characters of *Abies balsamea*, 69% and 56% of the total variability for respective characters was accounted for by the first two CVA axes. Similarly, Parker et al. (1981) found that 72% and 57% of the total variability for needle and cone characters of subalpine and balsam firs, respectively, was accounted for by the first two CVA axes. In a comparable study, Parker et al. (1984) found that an even greater proportion of the total variability among populations was accounted for by CVA of flavonoids, with 89% of this variation accounted for by the first two CVA axes. However, in their study of flavonoid variation among coastal and interior populations of subalpine fir, Parker and Maze (1984) found that only 72% of the total variation among populations was explained by the first two CVA axes.

For the discriminant analyses of the present study, the percentage of correctly classified cases ranged from 44 to 88 percent. These values reflect the degree of similarity among populations in the examined morphological characters, since misclassification of one population to another occurs when there is little distinction between the populations in these characters. The lowest percentage of correctly classified cases (44%) was obtained for discriminant analysis of all populations using needle data, since so many populations were used in this analysis. Conversely, the highest percentages were obtained for discriminant analyses of the four populations of progeny, for both types of needle data. For both the MDA's of the northernmost populations, and those including all populations, substantially higher percentages of correctly classified cases were obtained for cone data than for needle data. These classification values numerically illustrate what is apparent in the MDA ordinations, that the northernmost subalpine fir populations are more distinct in cone morphology than in needle morphology, and the four populations of progeny are well differentiated in both types of needle characters. Similarly, there is a greater overall distinction among all populations on the basis of cone data than needle data.

The results of both multivariate techniques indicate a lack of distinction in needle morphology between subalpine and balsam fir populations from the British Columbia Rocky Mountains to northwestern Ontario. However in an earlier investigation, Parker et al. (1981) found that the number of rows of stomata on the adaxial needle surface, proved relatively diagnostic for similar fir populations from British Columbia to Saskatchewan. This character was not included in the analyses of all populations in the present study, since it had not previously been measured for the northern Ontario balsam fir populations. However, for studies on intermediacy between two species it is reasonable to focus on diagnostic characters.

In order to investigate whether the character RS might prove diagnostic for fir populations across a large part of central and western Canada, it was determined for the northern Ontario balsam fir populations using similar procedures as those used for the ten northern (Yukon, British Columbia, Alaska) populations. Means and standard deviations were then determined for each population for which this character was assessed in either the present study, or in the earlier study of Parker et al. (1981). These populations included the ten northern subalpine fir populations (N1-10), three of the eastern subalpine fir populations (E18-20), the populations from the putative zone of sympatry between subalpine and balsam fir (S24-25), and the balsam fir populations from Alberta and Saskatchewan (B26-27). Also included were three additional populations from central Alberta, Calling Lake (CL), Eastern Lesser Slave Lake (EL), and Southern Lesser Slave Lake (SL), all of which were part of Parker et al.'s (1981) investigation. A Hubb's diagram was produced from the calculated means and standard deviations to allow a visual comparison of the variation patterns in this needle character among the 25 populations (Figure 3.18).

The Hubb's diagram in Figure 3.18 indicates that although the ten northern subalpine fir populations (1-10) tend to have needles with more rows of stomata than the subalpine and balsam fir populations to the south and east, there is a great deal of overlap among all of the populations in this needle character. Both the northern subalpine fir populations and the balsam fir

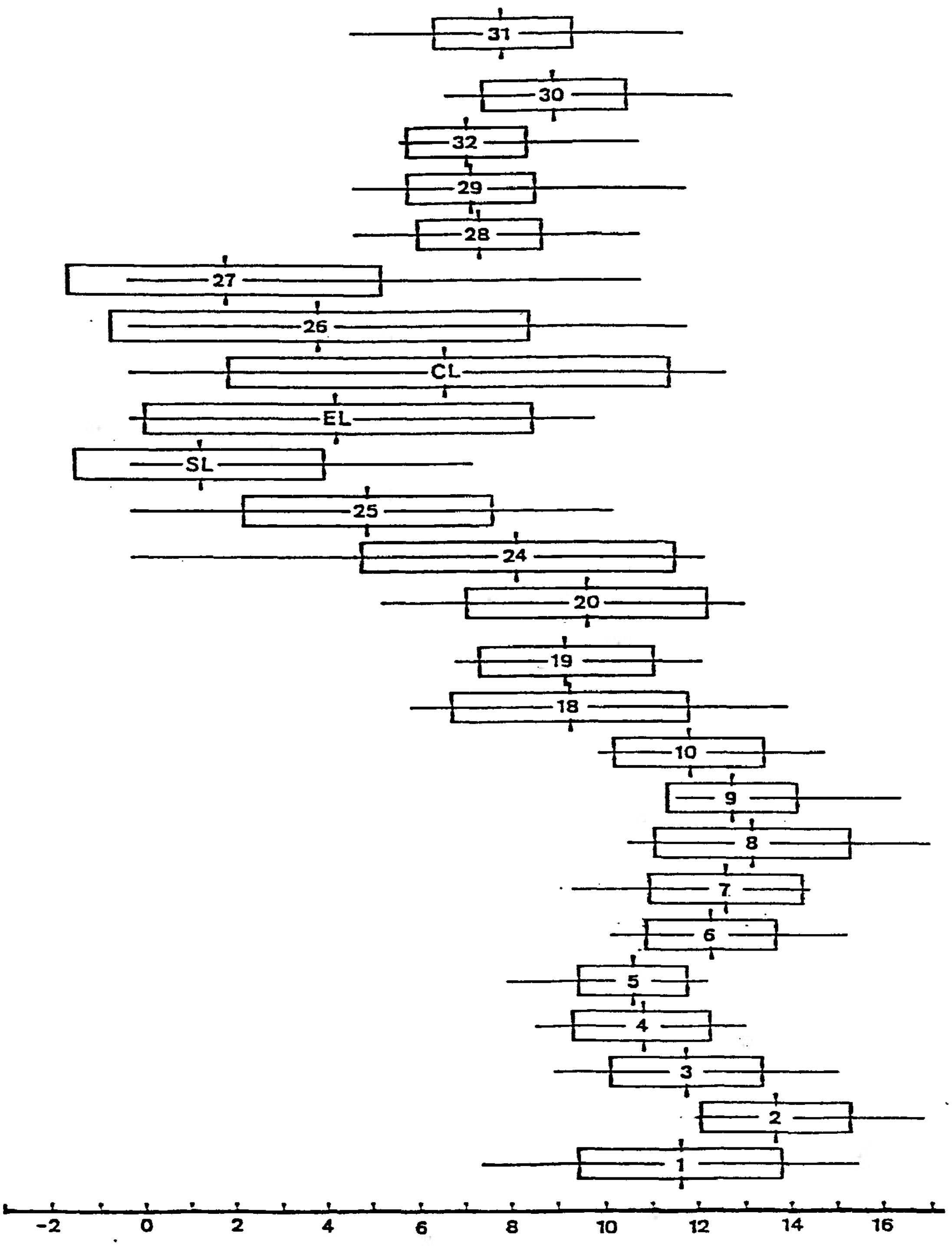

Fig. 3.18. Means, ranges and standard deviations of number of rows of stomata on the adaxial needle surface for 25 populations of fir from Alaska to northern Ontario. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean. Population numbers correspond with those used throughout the study. The three additional populations from central Alberta are designated with letters: Calling Lake (CL), Eastern Lesser Slave Lake (EL), and Southern Lesser Slave Lake (SL).

populations from northern Ontario are much less variable in this character than the fir populations from the Rocky Mountains and the Prairies. The apparently clinal trend of decreasing numbers of rows of stomata in fir populations from the Rocky Mountains eastward observed by Parker et al. (1981) does not hold for the northern Ontario balsam fir populations which have more rows of stomata than the fir populations from the Prairies. Thus, on the basis of this character, the populations in central Alberta could not be considered intermediate between western and intermediate groups. However the northern subalpine fir populations do tend to have more rows of stomata than any of the balsam fir populations, based on population means, although this character could not be considered diagnostic, due to the large amount of variation among all populations.

MULTIPLE REGRESSION

Table 3.26 presents the correlation matrix for all independent variables that were initially used in the multiple regressions for the nine parent populations. The highly correlated variables that were deleted for the final regressions are underlined. The results of multiple regression analysis for the various conventional and shape needle data and cone data sets for the nine parent populations are presented in Table 3.27 Similar results for the various progeny data sets are presented in Table 3.28.

The independent variables included in each regression model explain the amount of variation among sites in the summary variables as indicated by the coefficients of determination (r^2). All regressions for the parent and progeny populations were significant (Tables 3.27 and 3.28). For each of the regression models, the assumptions that there are no outliers and that the residuals are randomly distributed were met.

As the multiple regression results indicate, there is generally not a great amount of variation explained by the environmental variables operating jointly, for most of the data sets, even though the regression models themselves are

Table 3.26. Correlation matrix of environmental variables used as independent variables in multiple regression analyses for nine northern subalpine fir populations. Highly correlated pairs of variables are underlined.

Variable	Elev	Lat	Long	ADT	AJanT	AJulT	EMinT	EMaxT	Rain	Snow	RDays	SDays	FFree
ELEV	1.00	0.28	0.91	0.52	0.43	0.05	0.33	-0.27	-0.56	-0.55	-0.41	-0.47	0.62
LAT		1.00	0.56	-0.61	-0.33	-0.17	-0.08	-0.32	-0.44	-0.15	-0.72	-0.75	0.07
LONG			1.00	0.24	0.42	-0.17	0.42	-0.44	-0.47	-0.43	-0.67	-0.72	0.41
ADT				1.00	0.45	0.41	0.12	0.29	-0.23	-0.44	0.43	0.41	0.55
AJANT					1.00	-0.45	0.90	-0.55	0.42	0.31	-0.32	-0.28	0.11
AJULT						1.00	-0.54	0.87	-0.43	-0.38	0.54	0.54	0.59
EMINT							1.00	-0.73	0.57	0.52	-0.59	-0.53	0.12
EMAXT								1.00	-0.34	-0.31	0.74	0.74	0.16
RAIN									1.00	0.90	-0.06	0.03	-0.36
SNOW										1.00	-0.23	-0.12	-0.29
RDAYS											1.00	0.99	-0.08
SDAYS												1.00	-0.08
FFREE													1.00

significant. For the parent populations, the greatest amount of variation (25%) has been explained by elevation for the second PCA axis of the cone data. Of the multiple regression analyses for the progeny data sets, the only dependent variable which showed any correlation with any of the independent variables was the second PCA axis for the conventional needle data set. A correlation coefficient of 0.47 was obtained for this analysis, which is a much higher amount of variation that was explained than that explained in the analysis of any of the parent data sets. For the other regression analyses of the progeny data sets, none of the environmental variables were significant in influencing the dependent variables, and therefore none of the independent variables were entered into a model.

Table 3.27. Results of multiple regression analyses, one-way analyses of variance, and fraction of coefficients of determination (r^2) from multiple regression analysis to percent variation among groups from one-way analysis of variance for PCA axis scores for cone and needle data sets of nine northern populations.

Dependent Variable	Independent Variables Included in Regression Model	r^2	% Variation Among Among Groups From One-Way ANOVA	r^2/ % Variation Among Groups
PCA Axis1 Cone Data	ELEV	.14 **	10.94 *	1.28
PCA Axis 2 Cone Data	ELEV	.25 **	38.17 **	0.66
PCA Axis 3 Cone Data	AJANT, FFREE	.19 **	18.89 **	1.00
PCA Axis 1 Conventional Needle Data	AJANT	.18 **	20.74 **	0.87
PCA Axis 2 Conventional Needle Data	ELEV	.14 **	17.85 **	0.78
PCA Axis 3 Conventional Needle Data	AJANT	.07 *	0.57 ns	0.12
PCA Axis 1 Shape Needle Data	AJANT	.20 **	23.13 **	0.87
PCA Axis 2 Shape Needle Data	AJANT, SNOW	.18**	22.27 **	0.81
PCA Axis 3 Shape Needle Data	AJANT	.18**	27.30 **	0.81

* = Significant at the .05 level of alpha
* * = Significant at the .01 level of alpha
ns = Not significant

Table 3.28. Results of multiple regression analyses, one-way analyses of variance, and fraction of coefficients of determination (r^2) from multiple regression analysis to percent variation among groups from one-way analysis of variance for PCA axis scores of cone and needle data sets for four progeny populations.

Dependent Variable	Independent Variables Included in Regression Model	r^2	% Variation Among Among Groups From One-Way ANOVA	r^2/ % Variation Among Groups
PCA Axis 1 Conventional Needle Data			4.47 ns	
PCA Axis 2 Conventional Needle Data	ELEV	.47**	46.00**	1.02
PCA Axis 3 Conventional Needle Data			55.90 **	
PCA Axis 1 Shape Needle Data			18.95 ns	
PCA Axis 2 Shape Needle Data			4.78 ns	
PCA Axis 3 Shape Needle Data			11.14 ns	

* = Significant at the .05 level of alpha
* * = Significant at the .01 level of alpha
ns = Not significant

ONE-WAY ANALYSIS OF VARIANCE

The among-group variance components from the one-way analyses of variance of principal component axes scores are presented for each of the parent needle and cone data sets (Table 3.27) as well as the progeny needle data sets (Table 3.28). These results indicate that for the parent data sets, the majority of variation in the summary variables (PCA scores) is expressed within rather than among sites. However, there is still a significant amount of variation expressed among sites for all summary variables except the third PCA axis for conventional needle data from the 10 parent populations. Similarly, for the progeny data sets, there is generally a greater amount of variation expressed within sites rather than among sites. For all PCA scores except that for axis 2 and 3 of the progeny conventional needle data, the amount of variation expressed among sites is not significant. These results correspond well with those obtained by nested analysis of variance of individual variables, where for most variables and data sets there was little variation expressed among sites.

Tables 3.27 and 3.28 also present the fraction of r^2 values (from regression analysis) to the values of percent variation among groups (from one-way analysis of variance) for each data set. These results generally indicate that the amount of variation which is expressed among populations for each data set is similar to that expressed by the environmental variables in the relevant regression models, since the ratios tend to be large. An exception is PCA axis 3 for conventional needle data, in which case the ratio of the coefficient of determination to the percent of variation among groups is very low.

Although it is not theoretically possible to obtain a ratio larger than one, this has occurred for the first PCA axis of the cone data. This result indicates the potential drawbacks to using this method, since inflated ratios may be obtained. This occurrence is most likely due to inflated r^2 values being obtained from the multiple regression models.

4. DISCUSSION

VARIATION IN SUBALPINE FIR AT THE NORTHERN LIMITS OF THE SPECIES RANGE

The results of univariate and multivariate analyses of both reproductive and vegetative characters for the 10 northern subalpine fir populations indicate that variation is expressed primarily within rather than among the populations. However there are greater distinctions among the populations on the basis of cone characters than needle characters, as indicated by discriminant analyses. No geographical trends are evident in the patterning of morphological variation in the multivariate ordinations based on either type of morphological character. These results are consistent with those obtained by Parker (1984) for chemical taxonomic characters from the same trees of these populations. Parker found that needle flavonoid variation was expressed mainly within rather than among populations, and that multivariate analysis (PCA) similarly showed no geographical patterning of the observed variation.

These ten subalpine fir populations are located throughout extremely heterogeneous environments, in a number of different ecoregions as described by Oswald and Senyk (1977), with changes in elevation of up to approximately 600 m. Species adapt to spatial and temporal environmental variations (a process known as microevolution) according to contrasting modes, which are viewed as alternative strategies (Lerner, 1954; Levins, 1966; Roughgarden, 1979). One alternative involves specialization, where natural selection by dissimilar environments alters gene frequencies to produce differentiated populations. The other alternative involves generalization, where genetic homeostasis is maintained through phenotypic plasticity or genetic flexibility. For some species, either specialization or flexibility has been sacrificed in favour of the opposite mode, and in still other species, intermediate levels of both modes are exhibited. Rehfeldt (1984) discusses the contrasting modes used by a number of western, montane conifers in order to adapt to the extremely heterogeneous environments of the Northern Rocky Mountains. On the basis of the morphological and chemical variation patterns among subalpine fir populations in the northern part of the species range, this fir apparently tends toward a generalist mode of adaption, where population differentiation occurs across broad environmental gradients, and selection enhances within-population variability.

The relationships among populations evident in the PCA and discriminant analysis ordinations of needle data are different from those based on cone data. Such differences in clusters of populations between cone and needle data suggest that the two types of characters have evolved in different directions. This result has been observed in other studies of population differentiation among and between subalpine and balsam firs (Parker et al. 1981, 1984; O'Reilly, 1981) and supports the opinion of Stebbins (1950) that the vegetative organs of a plant respond to a different subset of selection pressures than do the sexual organs. Thus, the results of the present study indicate that needle and cone characters of subalpine fir populations at the northern extemes of the species range may have reacted to different local selection pressures and/or that the two types of structures may vary in the degree of phenotypic plasticity that they exhibit from site to site.

The relationship among the populations made evident by PCA of conventional needle characters can also be seen in the Hubbs diagrams of individual conventional needle characters. Populations 3,4,5, and 10 have thinner narrower needles, resin canals placed closer to the adaxial surface of the needle, smaller vascular cylinders, and shorter distances from the vascular cylinder to both needle surfaces, than do the other populations. These are the characters that are primarily responsible for the relationship among the populations observed in the PCA and discriminant analysis ordinations of conventional needle characters. Similar trends in the PCA and Hubbs diagrams are evident for the cone data.

Both the conventional and shape needle characters show similar patterns of variation among the 10 populations, which indicates that the conventional characters and needle shape characters are well correlated. Such a correlation is not surprising since the conventional character NL is the same as the shape characters D1 and D11 combined, and NW is the same as D6 and D16 combined. Generally, the ordinations based on the results of discriminant analyses for both needle data sets are very similar to those obtained by PCA, except that discriminant analysis separates the populations to a greater degree as expected. These similarities in ordinations from the two methods indicate that the main components of variation in the examined characters are generally also the components which best distinguish the populations. In contrast, the degree of similarity between PCA and discriminant analysis ordinations is not as great for the cone data. Thus, the main components of variation in the sampled trees do not necessarily best distinguish the populations.

The general lack of extensive variation expressed among northern subalpine fir populations for needle characters of parent trees is also expressed in the progeny of these trees, although it is much more apparent on the basis of the shape characters. Little variation is present among the four progeny populations based on univariate analyses of variance of all shape characters, and whatever variance component is expressed among populations is not significant. Additionally, a great degree of overlap among the populations is illustrated in both multivariate ordinations. In the analyses of variance of conventional needle data, a number of the characters do exhibit a significant amount of among-population variation, and less overlap is apparent in the multivariate ordinations. For the conventional needle data set, both multivariate ordinations show a latitudinal trend along the second axis. This apparent latitudinal trend may reflect genetic differences between populations from northern and more southern sites. However, this trend is not evident for the conventional needle data from the ten parent populations, nor is it apparent for either the parent or progeny data sets for needle shape data. There are, however, greater similarities between the parent and progeny variation patterns in the multivariate analysis ordinations based on shape needle data, which could reflect the existence of genetic variation among the populations, although no geographical trend is apparent.

The observed differences in among-population variation patterns for the four comparable parent and progeny populations could be explained by a number of reasons. Firstly, the needles of the progeny were obtained from seedlings that were less than a year old. In contrast, needles of the parent trees were obtained from the previous year's growth, on developmentally mature individuals. Differences in morphology between the parent and progeny needles were evident, particularly in location of the resin canals with respect to the needle margin, as well as overall cross-sectional needle shape. Therefore optimally, a more reliable progeny test would utilize needles from trees that are developmentally mature, although such a test would be long-term in nature.

Secondly, although the seedling progeny used in this study were produced by parents that have undergone selection in natural conditions, the seedlings themselves have not been subjected to this process. As Heslop-Harrison (1964) has pointed out, in extreme situations, where the local selection pressures on a population are very high, so that gene-flow from nearby populations in unlike habitats is outbalanced, adaptation may occur from generation to generation. In such a case, essentially random dispersal of genotypes occurs each year, with subsequent stringent selection for adapted genotypes in the particular habitat "sub-population". Thus, the use of seed samples for tests such as the progeny test of the present study, may not provide an accurate representation of what the actual surviving population at each site would be like. Consequently, a wider range of variation may be present in the progeny populations than the parent populations, due to the presence of seedlings that would not normally have survived in the wild, so that the variation patterns of the two generations may not be truly comparable. This effect may be especially appreciable for a species such as subalpine fir, in which, as the present study has shown for morphological traits, a large percentage of the variation is expressed within populations. In other species such as Douglas-fir (*Pseudotsuga menziesii* var *glauca*) and lodgepole pine (*Pinus contorta*), adaptation is of the specialist mode for certain highly adaptive characteristics including growth potential, phenology, and cold hardiness (Rehfeldt, 1984). Consequently, a high proportion of the total variability in these traits is expressed among populations, and thus, the use of seed to assess variation between generations may present less of a problem.

Finally, an additional problem inherent in the progeny study, as discussed by Heslop-Harrison (1964), is that the greenhouse conditions, in which the progeny populations have been propagated, do not approximate the natural environments of the respective sites. In contrast, all environmentally imposed variation has purposely been eliminated, in an attempt to observe potentially genetic differences among the populations. As a consequence of this approach, the genetically determined differences in the capacity of the seedling progeny to react to the particular environments of the actual sites may have been obscured. Furthermore, while suppressing some environmentally induced characteristics, the progeny test environment may have evoked others that would not normally be expressed in the natural habitats, thereby prejudicing the evaluation of genetic differentiation among the populations. To avoid these problems, the methods of varied-environment, or reciprocal transplanting, may be used, as exemplified by the classical work of Clausen et al. (1940). However such an approach was much beyond the limits of the present study.

If possible, a progeny test that considers the discussed concerns would allow a much more reliable assessment of the relationship between parent and progeny variation patterns in subalpine fir populations, and would, as a result, provide a better perspective on the recent evolution of this species near its northern extreme. In addition, to better observe possible geographic trends, such a test should contain progeny from all ten of the populations, as well as from a greater number of trees at each site. However such a test would be difficult to carry out, because of the irregular production of cones in subalpine fir, and the inherent germination problems in this species due to low seed viability. It may be difficult in any particular year to obtain viable seed from more individuals and populations than was already done in this study.

The results of analysis of variance of needle and cone PCA axes further confirm that little morphological variation is expressed among these northern subalpine fir populations. Table 3.28 illustrates that, for the natural populations, only 0.5 to 22 % of the total variation exists among sites in both types of needle characters, as summarized by the various PCA axes. The amount of variation expressed among sites is slightly higher for cone characters as summarized by PCA axes, ranging from nearly 11 to 38%. This difference in population variation for the two types of characters has already been discussed, with regard to the multivariate analyses.

These results suggest that although the populations are in some cases separated by large distances (up to 600 km) and elevational differences (up to 600 m), perhaps the selection pressures due to climatic forces have not differed greatly among the various sites, so that a great deal of variation in cone and needle morphology has not occurred among the subalpine fir populations. In addition, the multiple regressions of needle and cone PCA axes with selected environmental variables generally showed very low correlations for the examined data sets, thus indicating that these environmental variables do not account for a great deal of the variation in cone and needle morphology that is present in these northern populations. However, since the among-population variance components are small for all of the data sets, the variation that is expressed among the populations is almost totally accounted for by the environmental variables in each regression model, as indicated by the ratios of r^2 values from the regressions to values of among-group variation from the one-way analyses of variance (Tables 3.27 and 3.28). These results therefore suggest that although the among-population variance component is small, selection due to local environmental pressures at the various sites has in fact been an important force in producing the among-population variation that is present in the cone and needle morphology of these subalpine fir populations.

The most distinct population, as determined by discriminant analysis of conventional needle characters, is located at White Pass, near Skagway, Alaska. This population contains trees that are very stunted and of semi-Krumholz form, rarely over 3 m in height, whereas trees from the other populations are generally much taller, and of a more normal form. Evidently the local environmental selection pressures at this site have caused greater differentiation in internal needle morphology and overall tree form, as compared to the other sites. Interestingly, the local selection pressures at this site have not affected cone morphology to the same degree, whereas population 1, the most northerly population from Keno Hill, has cones that are much more distinct from those of the other populations.

Of the environmental variables examined, elevation generally accounts for the greatest amount of variation in cone morphology among the nine natural subalpine fir populations (Table 3.27). However longitude is highly correlated to elevation, which probably reflects that the effect of longitude on cone and needle morphology may actually be due to elevation. This correlation seems logical since the mountain chains in western North America tend to run from north to south. Since temperature and moisture are the two factors that most directly affect plant growth, it is likely that elevation has influenced one or both of these factors, which have therefore had some degree of influence on the evolution of the examined cone characters of these populations. Temperature does in fact appear to be a force that may have influenced cone morphology, since average January temperature, as well as the number of frost free days per year account for the greatest amount of variation in the third PCA component of variability in cone characters. O'Reilly (1981) similarly observed that a significant correlation existed between a canonical variates analysis component of variability in cone characters of balsam fir in northern Ontario and extreme minimum temperature. O'Reilly (1981) therefore suggested that the observed pattern of variation in cone morphology might be due to the selection pressure of minimum temperature. Grant (1967) discovered a strong linkage between genes controlling morphology of reproductive organs with genes responsible for seedling vitality. Extreme winter temperature seems to have had the most important influence on the needle morphology of the trees in these populations, possibly indicating that the same selection forces have most greatly affected both cone and needle morphology of subalpine fir at its northern extreme, since extreme winter temperature is comparable to average January temperature.

Wind exposure, which may also be affected by elevation, is suggested by Schmidt (1957) as being the primary limiting climatic factor for subalpine fir at tree-line habitats. Thus the effect of increased wind exposure may have influenced the cone and needle morphology of subalpine fir populations at higher elevations, compared with those at lower-elevation sites. Direct evidence that wind forms of plants are adaptive is available from the work of Whitehead and Luti (1962) and Whitehead (1962, 1963a,b), who have shown that in maize and sunflower, exposure to windspeeds approximating those found in mountainous regions induced anatomical and morphological changes that were demonstrably advantageous with respect to overall water economy. In these studies, the phenotype became more xeromorphic with increased windspeed, and the change was directly related to the incidence of adverse conditions.

The various analyses of the northern subalpine fir populations provide evidence that they have probably all originated from one large gene pool, since they do not show extensive morphological distinctions. Local selection pressures have most likely caused the variation patterns that are now evident among the populations. The present results indicate that the environmental variables included in the examined regression models are likely the major evolutionary forces (selection pressures) responsible for the amount of variation that has developed in the examined characters among these populations at the northern limits of the species range. However, it must be realized that the multiple regression analyses carried out in this study utilized climatic data as independent variables from weather stations as close to the study sites as possible, but not right at the sites themselves. Because of this disparity, the climatic data are not an exact representation of the climates right at the sites. It is therefore possible that better correlations between components of variation for the cone and needle characteristics and environmental variables might be obtained if climatic data could be obtained at the sites themselves, although it is not theoreticaly possible to increase these correlations for the data sets in which the r^2 values are already equal to the among-population variance components. It is also probable that consideration of additional variables concerning the nature of the sites (i.e., soil moisture, etc.) would provide a better insight into the causes of morphological variation among the populations.

VARIATION IN SUBALPINE FIR IN WESTERN CANADA AND THE UNITED STATES

Insight into the nature of variation in cone and needle morphology over a large part of the range of subalpine fir has been provided by the present study. It is evident that in the part of the range investigated (Yukon Territory to Washington, and Alberta to British Columbia), subalpine fir exhibits considerable geographic variation in cone and needle morphology. This extensive variation is not surprising, considering that this fir has been subjected to extremely diverse and changing habitats throughout the Pleistocene Epoch. Stebbins (1950) notes that most western North American fir species are extremely variable, due to survival and reproduction under the long-term stressful conditions caused by repeated glaciations during this period.

Several general patterns can be observed on the basis of the ordinations of multivariate analysis of cone and needle characters from populations at the northern limits of the fir's range that included populations from more southerly locations: 1) Coastal and interior populations tend to be distinct on the basis of both cone and needle characters, with the exception of the Vancouver Island population which is most similar to the interior populations. 2) The two Washington Cascades populations are very distinct from all other populations in needle morphology, although the Mt. Baker trees are most similar to the interior Rocky Mountain populations in cone morphology. 3) The northern populations exhibit an affinity to the interior Rocky Mountain populations, and are very distinct from the coastal populations for both types of morphological characters.

The general distinction in cone and needle morphology between north coastal and interior Rocky Mountain populations confirms the earlier observations of Parker and Maze (1984) for needle characters of these populations. In the present study, coastal and interior elements were clearly separated on the basis of discriminant analysis of cone characters, with the exception of the Mount Baker population, whereas Parker and Maze (1984) did not observe distinct coastal and interior groupings on the basis of cone characters. They did however observe very clear distinctions between the groups on the basis of needle flavonoids. The present results therefore provide additional support for Hunt and von Rudloff's (1979) proposed theory of segregate coastal and Rocky Mountain elements of subalpine fir. However, both the present study and the previous work of Parker and Maze (1984) indicate inconsistencies in the distinction of the two groups, with the Vancouver Island population being included in the eastern group. In the earlier study, it was suggested that this inconsistency was likely a reflection of a response to drier conditions in the area of Vancouver Island (Forbidden Plateau) where the trees were sampled, compared to other western collection sites, since flavonoid data from the same study and terpenoid data from Hunt and von Rudloff's (1979) study both indicated that samples from Vancouver Island were similar to other western populations. However the possibility was also suggested that the difference in needle morphology of the Vancouver Island trees from other coastal populations may be the result of long-term isolation of subalpine fir in a separate Vancouver Island glacial refugium.

The results of needle data for the Mount Baker and Mount Rainier populations are similar to those already presented by Parker and Maze (1984). In both studies, these Cascade Mountain populations have been separated very distinctly from all other populations in terms of their larger diameter resin canals and longer needles than all other samples. However, although cones from only the Mount Baker population were available for evaluation of variation in cone morphology in the present study, this population is most similar to the southernmost Rocky Mountain populations to the east of the Mount Baker population. Thus, the distinction of the Cascades populations is apparently only on the basis of needle morphology.

Hunt and von Rudloff (1979) observed that populations from the Mount Baker area had terpenoids different from those in the more southern Cascades of Washington and Oregon, but similar to those from the more easterly sites in the Rockies. However some of the trees sampled from four populations in the Mount Baker area also had terpenoids considered to be of an intermediate nature between coastal and interior forms of subalpine fir on the basis of a "terpene hybridization index". Trees from a population at Fort St. James in central British Columbia also contained terpenoids of an intermediate nature. These authors concluded that coastal and Rocky Mountain subalpine fir probably came from different glacial refugia and have since hybridized extensively.

Parker and Maze (1984) found *Abies balsamea* type flavonoids present in interior Rocky Mountain populations as well as in Mount Baker and Mount Rainier populations and suggested that gene flow from balsam fir from the east may have occurred into the Cascades of Washington. As these authors have pointed out, this theory would help explain why Hunt and von Rudloff (1979) observed similarities in terpenes between trees in the Mount Baker area and those of populations to the east in the Rockies. On the basis of an earlier study of morphological variation among populations of interior subalpine fir and balsam fir east of the Rocky Mountains, Parker et. al. (1981) also suggested that east-west gene flow has probably occured on each side of the Rocky Mountain crest. The present study also indicates similar trends on the basis of needle morphology, with interior subalpine fir populations in the Rockies not being well-differentiated from balsam fir populations from the Prairies and as far east as Northern Ontario. However if gene-flow from balsam fir to the east of the Rocky Mountains has influenced the Cascades populations, it is not reflected in the needle variation patterns, where the Cascades populations are very distinct from the Rocky Mountain subalpine fir and balsam fir populations to the east. On the basis of discriminant analysis of cone data, although the Mount Baker population is similar to the southern Rocky Mountain subalpine fir populations, this group is very distinct from the balsam fir populations in northern Ontario. The relationship in cone morphology between the Cascades populations and the putative sympatric zone populations in central Alberta, as well as balsam fir populations from further east on the prairies could not be assessed due to missing cone data for these populations. However, if gene migration from balsam fir populations on the prairies and further eastward has occurred into the Cascades populations, it is not reflected in the relationship between the northern Ontario balsam fir populations and the Mount Baker population. It seems more reasonable that the similarity in cone morphology between the Mount Baker and interior subalpine fir populations in southern British Columbia is due to gene-flow between these populations, which are relatively near each other geographically, perhaps as the result of hybridization between separate coastal and interior taxa, as suggested by Hunt and von Rudloff (1979). Parker (1984) has also suggested the occurrence of such hybridization between these two taxa, based on the intermediate nature of flavonoids in the Mount Baker and Mount Rainier region. The implications of these flavonoid results are discussed in more detail below, with respect to all of the sampled subalpine fir populations.

The possibility that the Cascades populations are from an entirely separate glacial refugium than those from which other coastal and interior populations presumably arose must also be considered given the large distinction in needle morphology between these and other subalpine fir popuations. Unfortunately, due to the lack of extensive fossil records throughout the Cascades region of the Pacific northwest, it is only possible to speculate on the existence of such a refugium. In addition, pollen records of subalpine fir are not as reliable in this region as in the northern Rocky Mountains where this is the only prevalent fir. Pollen identification is much more difficult where it must be identified to the species level. However, the available fossil records indicate that subalpine fir had a refugium south of the glacial limits, at a low elevation on the west side of the Cascades in Oregon (Gottesfeld et al., 1981). Fossil needles and pollen from a deposit at this site are dated at more than 35,000 years before present (BP). Heusser (1972) has presented conclusive evidence for the survival of subalpine fir for 70,000 years in a separate refugium that was closely surrounded by Wisconsin glacial ice along the coast of the Olympic Peninsula in Washington. Perhaps the north coastal British Columbia populations and the Cascades populations originated from separate glacial refugia such as these, so that isolation during glacial periods has created the observed divergence in morphological characters. It would be interesting to examine the fossil needles that have been obtained from the two refugia to compare their morphology to that of modern needles from the north coastal British Columbia and Cascades populations, in order to further explore this hypothesis. However there is no evidence of any distinction in subalpine fir populations between these two locations, on the basis of Hunt and von Rudloff's (1979) terpenoid data. Thus, the sharp distinction in needle morphology between the north Cascades populations, and other coastal and interior populations warrants further investigation. In particular, additional paleobotanical studies throughout the Cascades region, in conjunction with a more extensive sampling of subalpine fir populations, are required to determine whether the north Cascades populations have in fact originated from a separate glacial refugium. Despite their origin, the difference in relationship between at least the Mount Baker and other subalpine fir populations on the basis of the present cone and needle variation patterns, apparently reflects differential responses to selection pressures between these characters.

The patterns of variation in both cone and needle morphology between the northern and interior subalpine fir populations could be accounted for by two hypotheses. The first of these is that we could be seeing a very sharp clinal pattern of variation between interior and northern populations along a latitudinal gradient, due to strong selection pressures encountered by this fir during migration to the northern extremes of the species range. Under this hypothesis, both the northern and eastern subalpine fir populations would have originated from the same southern glacial refugium, and migration to the northern limits of the species range occurred following retreat of the most recent glaciers. The alternate hypothesis is that subalpine fir survived in one or more northern refugia during the last glaciaton, and the present patterns of variation in cone and needle morphology are the result of gene flow between the northern and interior populations as the these populations spread northward and the northern populations spread southward following glacial retreat. For the latter hypothesis, it is also possible that the effects of both gene flow and selection during migration of the populations from both directions may have (or still may be) operating simultaneously.

On the basis of the existing morphological evidence alone, it would be difficult to choose between the two contrasting hypotheses. Sampling gaps between the northern and more southern Rocky Mountain populations may make distinctions between these populations more exaggerated than they actually are, especially in the case of cone morphology, since cones from interior populations in the central B.C. Rockies (E18-19) were not available for use in this study, so that the available sites are fairly scattered.

Parker's (1984) study of needle flavonoid variation in subalpine fir parallels the present study of morphological variation in populations from Washington to the Yukon and Alaska, and has indicated similar trends to those observed in the present study. The combined morpholgical and flavonoid data provide a good basis for speculation on the evolution of subalpine fir throughout its range. Based on PCA of flavonoids, the same general distinction between coastal and interior subalpine fir populations was observed, with the exception of Mount Baker, Mount Rainier and Cassiar populations, all of which appeared to be intermediate between the two major groups.The Mount Baker and Cassiar populatons are geographically located very near populations previously observed to be of an intermediate nature between coastal and subalpine fir taxa by Hunt and von Rudloff (1979). In addition to the distinction between coastal and interior populations, Parker observed that the northernmost Yukon and Alaskan subalpine fir populations were most closely associated with the interior subalpine fir populations, and that an apparently clinal, north-south variation pattern was evident among these populations.

From these findings, Parker (1984) has suggested that there were likely two major southern refugia for subalpine fir during Wisconsin glaciation, one being in the Cascades from which the coastal populations have originated, and the other in the Rocky Mountains from which the northern and Rocky Mountain populations have originated. Parker further suggested that following northward migration from these refugia, barriers to gene exchange were not perfect, so that genetic interchange has occurred at the region around Mount Baker and along the system of valleys where the Stewart Cassiar highway is located. On the basis of the combined morphological and flavonoid data from his study as well as the present study, this theory is appealing, since it also supports Hunt and von Rudloff's (1979) findings. As presented by Critchfield (1984) in a review of the geographic variation of subalpine fir, the macrofossil record supports the conclusion that coastal and Rocky Mountain subalpine fir likely came from separate glacial refugia, therefore adding strength to the hypothesis.

The theory that subalpine fir populations at the northern limits of the species range originated from a southern refugium, as opposed to a northern Yukon or Alaskan refugium, is supported by the monoterpene data of Zavarin et. al. (1970). However, there are contradictions between the implications of the present morphological data and Parker's (1984) flavonoid data, in comparison with the data of Zavarin et. al. (1970). Critchfield's (1984) taxonomic interpretation of this study, was that the nearly identical levels of 3-carene, B-phellandrene, and linonene in the Yukon and in western Washington and Oregon populations point to a southern origin for the northern populations, probably in western Washington. However the flavonoid data of Parker (1984) and the present morphological data indicate that the northern populations probably originated from a refugium in the Rocky Mountains, along with the interior Rocky Mountain populations of subalpine fir, due to the close association of northern and interior subalpine fir populations and the lack of similarity between coastal and northern populations evident in the various multivariate analyses. If the latter interpretation is true, then the northern populations are merely an extension of the interior subalpine fir taxon.

Although the contradiction between the studies cannot be resolved on the basis of the present data, the modern variation patterns in a number of characters from these studies all suggest that the northern populations originated from a southern refugium, rather than from a northern refugium as was initially proposed by Hulten (1937) and supported by Hansen (1949, 1950) and Heusser (1954). Unpublished palynological data for subalpine fir near its northern extreme (Cwynar, in litt., 23 March 1988), along with fossil records from a number of additional sources, provide direct evidence to support the theory of a southern glacial refugium. Fossil pollen records identified as *Abies lasiocarpa* were obtained at Kettlehole Pond, Yukon Territory, and those identified as *Abies* were obtained from Fir Lake, Yukon Territory and Waterdevil Pond, British Columbia (Cwynar, in litt., 23 March 1988). The location of these sampled sites is indicated in Figure 4.1. Among these sites, the earliest time for the consistent sample-to-sample presence of subalpine fir pollen is 5000 years BP for Kettlehole Pond. At Waterdevil Pond, fir pollen becomes consistently present at about 4300 years BP. At Fir Lake, the pollen analysis is incomplete and preliminary, but fir pollen appears sometime between 5700 and 3700 years BP. At these sites, the amounts of pollen present in the samples increased to a maximum of 10 to 16% at around the 3000 year BP point, and the percentages subsequently decreased to from 4 to 6% at present. Based on these results, it is Cwynar's opinion that one can conservatively conclude that there is no evidence for the presence of subalpine fir in the region of these three sites prior to 5700 years BP, although 5000 years BP is probably a more accurate date. Thus, subalpine fir was probably not present in this region until sometime between 4000 and 5000 years after the retreat of the Wisconsin glacial ice sheets.

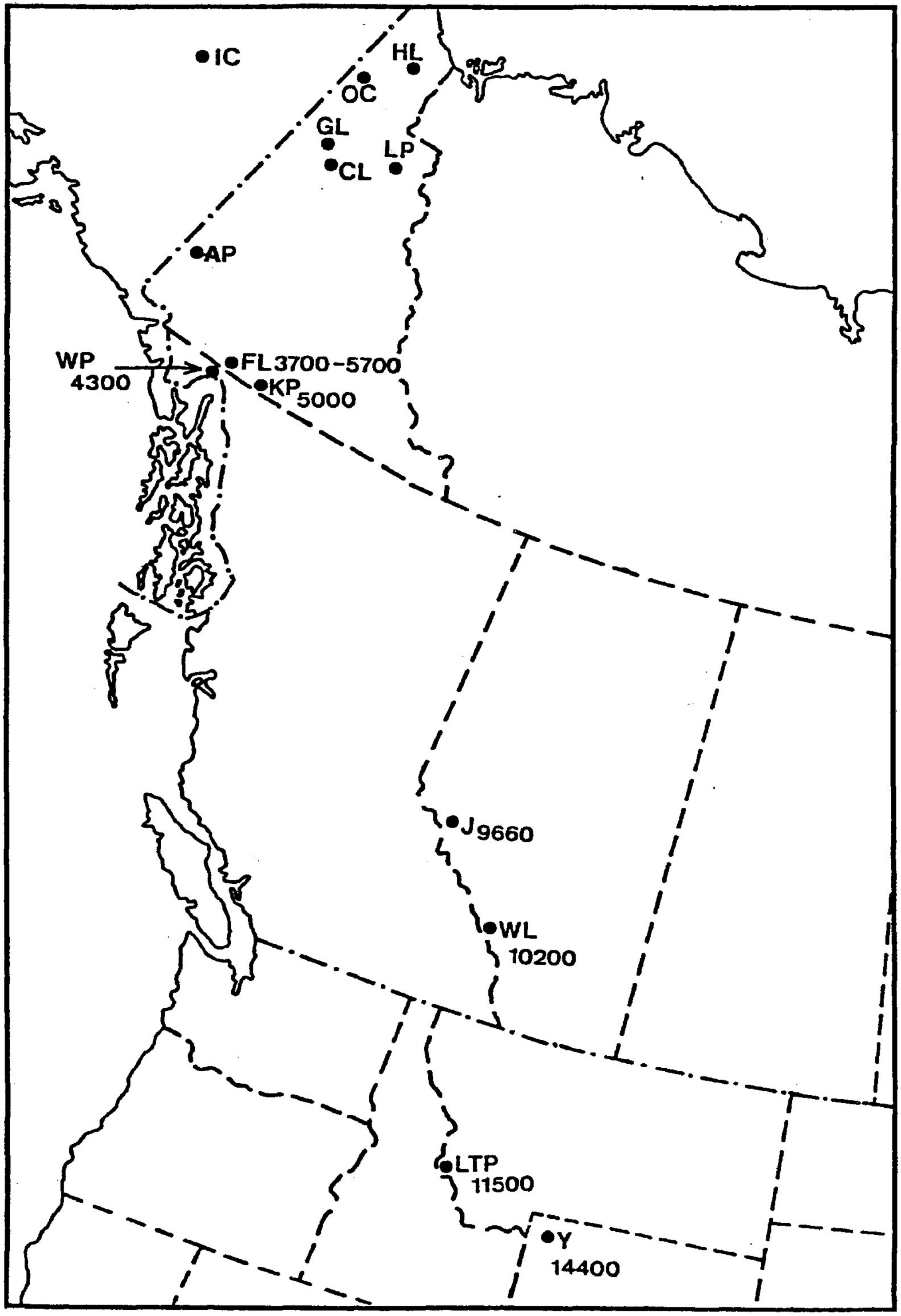

Fig. 4.1. Location of fossil pollen sites at or near (see text) Isabella Creek, Alaska (IC), Hanging Lake, Yukon (HL), Old Crow, Yukon (OC), Lateral Pond, Yukon (LP), Gill Lake, Yukon (GL), Chapman Lake, Yukon (CL), Antifreeze Pond, Yukon (AP), Fir Lake, Yukon (FL), Kettlehole Pond, Yukon (KP), Waterdevil Pond, British Columbia (WP), Jasper, Alberta (J), Wedge Lake, Alberta (WL), Lost Trail Pass, Montana (LTP), and Yellowstone, Wyoming (Y). The arrival date of *Abies* (in some cases identified as *Abies lasiocarpa*) is indicated at each site in radiocarbon years before present.

As pointed out by Cwynar, and as summarized by Mosiman and Greenstreet (1971), there are limitations to the pollen method for the reconstruction of a species history, since absence from the pollen record does not necessarily mean that the species was absent from the surrounding vegetation.Thus, the absence of subalpine fir pollen at these sites before 5700 years BP does not preclude the possibility that this fir was present at low densities; however, Cwynar believes that such a possibility is very unlikely, considering the fact that no samples at Kettlehole Pond older than 5000 years BP contain even a trace of fir pollen.

Although Cwynar's sampled sites are not actually located in the unglaciated portions of the Yukon Territory or Alaska, they are relatively near (within 250 km) the southern part of this region. Palynological records from a number of sites in the unglaciated parts of the Yukon and Alaska that lie beyond the modern limits of subalpine fir's range, indicate a total lack of *Abies* pollen from any period throughout the last glaciation and the Holocene. In the Yukon these sites include Antifreeze Pond (Rampton, 1971), Chapman Lake (Terasmae and Hughes, 1966), Gill Lake (Terasmae and Hughes, 1966), Lateral Pond (Ritchie, 1982), and Hanging Lake (Chapman, 1982), as well as five sites near Old Crow, in the Old Crow and Porcupine River valleys (Lichti-Federovich, 1973,1974). In Alaska, such a site is located at Isabella Creek near Fairbanks (Matthews, 1974). At two sites in the Old Crow River valley of the northern Yukon, *Abies* pollen was present very sporadically in only trace amounts (less than 2%) before 42,000 years BP (Lichti-Federovich, 1973). The location of these sites is indicated in Figure 4.1. On the basis of these fossil records, it appears unlikely that subalpine fir was present during the Wisconsin glaciation at any of the described locations, unless it existed in very small, scattered, and vegetatively reproducing populations.

Fossil records of subalpine fir from several locations in the Rocky Mountains of Canada and the United States are also presented in Figure 4.1. Under the hypothesis of a Rocky Mountain refugium south of the glacial limits for the interior subalpine fir populations, these records imply that subalpine fir migrated northward through the Rocky Mountains from south of the glacial limits in the region of Yellowstone Park, Wyoming, to Jasper, Alberta, a distance of approximately 1,100 km, in 4,400 years. Assuming that the northernmost subalpine fir populations also migrated through the Rocky Mountains from a similar refugium, as the variation patterns from the present study suggest, it would have taken this fir 4660 and 5300 years to reach the sites at Kettlehole Pond and Waterdevil Pond respectively, from the Jasper area. This time period is very comparable to that for the apparent migration of subalpine fir from the Yellowstone region to Jasper, for a comparable distance, therefore supporting the theory of subalpine fir's migration from a southern Rocky Mountain refugium to the Yukon. If subalpine fir did survive in a northern glacial refugium (or refugia), it seems unlikely that it would take approximately 5000 years subsequent to Wisconsin glacial retreat for this fir to reach the sites sampled by Cwynar (which are only several hundred km from the southern border of the unglaciated Yukon Valley) considering its apparent migration rate through the Rocky Mountains from Wyoming to Alberta, Thus, although fossil records for subalpine fir are not extensive, the available palynological evidence does suggest a southern origin for the northernmost subalpine fir populations.

The theory of a southern glacial refugium for interior subalpine fir, and northward migration through the Rocky Mountains to the present northern limits of the species, is comparable to that for lodgepole pine, *Pinus contorta* ssp. *latifolia* (MacDonald and Cwynar, 1985), which was also initially believed to have survived in a northern glacial refugium based on its modern variation patterns in a number of characters (von Rudloff and Nyland, 1979; Critchfield, 1980; Forest, 1980, 1981; Wheeler and Guries, 1982a, 1982b). Using fossil pollen records, MacDonald and Cwynar (1985) showed that this subspecies of lodgepole pine migrated a distance of approximately 2,200 km to its present northern limit in the Yukon in a period of approximatley 12,000 years. Under the present hypothesis, subalpine fir apparently migrated along a comparable route through the Rocky Mountains to the southern part of the Yukon, a distance of approximately 2,400 km, in between 9,000 and 10,000 years, which is a comparable, although slightly faster, migration rate to that of lodgepole pine. However subalpine fir arrived at least in southern Yukon Territory at Kettlehole Pond and in northwestern British Columbia at Waterdevil Pond, 2,500 and 1,100 years earlier, respectively, than lodgepole pine arrived at these same sites, based on the fossil records of Cwynar (personal communication) and MacDonald and Cwynar (1985). Unfortunately, no palynological data is available to indicate the arrival times of subalpine fir at its northern limit in the Yukon, in the Keno Hill area.

Although the modern variation patterns from the present and previous (Parker, 1984) studies along with the available palynological evidence suggest that the northern subalpine fir populations are probably an extension of the interior subalpine fir taxon to the south, some differences in cone and needle morphology are nevertheless evident between populations from these locations. It is possible, as already suggested, that these differences are the result of selection along a latitudinal gradient, during the post-glacial northward migration of populations. However, perhaps an alternative explanation of founding effects that occurred during such long-distance migration, as suggested for the observed genetic differences between northern and southern lodgepole pine (*Pinus contorta* ssp. *latifolia*) populations (Cwynar and MacDonald, 1987), would also explain the variation patterns among the northern and interior subalpine fir populations. Both subalpine fir and lodgepole pine have similar ranges in Western Canada and parts of the United States, with separate coastal and interior races, and both species have been subjected to the same kinds of glacial impacts throughout the Pleistocene Epoch. It would not be surprising that both species respond in a similar manner to long-distance founding events during a similar continental-scale, postglacial spread.

As Cwynar and MacDonald (1987) have suggested, it is possible that a combination of such founding events and selection have produced the variation patterns presently evident among northern and southern lodgepole pine populations, and that to distinguish between the two effects would be difficult.

Such a distinction might also be difficult if both of these processes have operated on the interior subalpine fir taxon. However, because the northernmost lodgepole pine populations, which have the lowest allelic diversity, have been in existence for only a short time (probably less than 100 years according to these authors), Cwynar and MacDonald (1987) believe that founding events due to migration have probably been more important than selection pressures, since there has been so little time for selection to operate on them. In the case of subalpine fir, selection may have played a more important role in producing the modern variation patterns. Since this species arrived in southern Yukon Territory substantially earlier than lodgepole pine, the northernmost populations in central Yukon likely also arrived much earlier, so that there has probably been more time for selection to have since taken place.

It would be useful to conduct a study of the genetic variation patterns throughout the range of subalpine fir, using isoenzymes or other genetic markers, in order to examine whether genetic characters support the present designation of separate coastal and interior taxa, with the northern populations being an extension of the latter group. Such a study would also indicate whether the populations at the northern extreme of the species limit have the lowest allelic diversity, as has been observed for lodgepole pine (*Pinus contorta* ssp. *latifolia*). Additionally, if more extensive fossil records could be obtained throughout subalpine fir's range, and particularly at its northern limits in central Yukon Territory, the approaches used by MacDonald and Cwynar (1985) and Cwynar and MacDonald (1987) could be used to relate more accurately the modern patterns of variation in this species to historical factors, thus confirming which evolutionary processes have produced this variation. A more intensive sampling of subalpine fir populations than has been carried out in the present study, as well as more uniform samples, would be preferable for such a study. However subalpine fir is a species that generally grows in very inaccessable, high-elevation locations, and the production of cones is very irregular, making the possibility of more intensive and uniform sampling difficult and therefore unlikely.

VARIATION IN THE SUBALPINE/BALSAM FIR COMPLEX

The multivariate analysis ordinations of both cone and needle data from this study indicate a geographical trend, where the populations of fir from east of the Rocky Mountains exhibit an affinity with the interior subalpine fir taxon to the west. In terms of the needle characters included in these multivariate analyses, the subalpine fir populations from the Rocky Mountains are not a distinct group from either the fir populations in the putative zone of sympatry between subalpine and balsam fir, or the balsam fir populations from either the Prairies or northern Ontario. No strong east-west pattern of potentially clinal variation among these indistinct populations is evident in the ordinations of the multivariate analyses of needle data; nor is there any indication that the populations in the putative sympatric zone are hybrids between two separate species, since the populations from this region are not more variable than those from any of the other sampled locations further east or west. It is generally accepted that where hybridization has occurred between two distinct species, the hybrids exhibit greater variation than either of the parent species (Anderson, 1949).

These results are very similar to those obtained by Parker et al. (1981) for needle morphology of trees in the same populations from British Columbia to Saskatchewan. However the present results indicate that the indistinction among subalpine and balsam fir populations is even more extensive than was evident from the earlier study. Parker et al. (1981) observed that although no sharp boundary was apparent delineating eastern and western fir populations, gradual morphological differences were evident among these firs to either side of the Rocky Mountain crest. However, such a variation pattern is not apparent from the present analysis, which has included a greater number of subalpine and balsam fir populations from more extensive parts of their ranges.

Although the fir populations investigated by Parker et al. (1981) could not be separated through multivariate analyses using the examined morpholgical variables, the needle character number of rows of stomata on the adaxial needle surface proved relatively diagnostic for the two firs, even though this single character would be unreliable for identifying individuals from central Alberta. However in the present study, this needle character did not prove to be diagnostic for subalpine and balsam fir populations from the entire range sampled, although a trend toward more rows of stomata in subalpine fir populations than balsam fir populations at the extremes of the sampled ranges was apparent. This result was somewhat surprising since this needle character has been considered diagnostic for the two firs in a number of identification manuals (Moss, 1959; Hosie, 1969; Liu, 1971; Scoggan, 1978). However, the possibility exists that inconsistencies may be present in the data for this character used in the present analysis, since its determination was made using different methodologies in the present and previous study (Parker et al., 1981) from which data were obtained. Therefore the character needs to be reassessed using similar, reliable methodology for all of these fir populations, before final conclusions can be drawn about its usefulness as a diagnostic character for subalpine and balsam fir.

In contrast to the lack of differentiation among the subalpine and balsam fir populations from British Columbia to northern Ontario in terms of needle morphology, the northern Ontario balsam fir populations are very distinct from the subalpine fir populations in the Rocky Mountains in cone morphology, as is apparent in the MDA ordination of Figure 3.38. Because cone data were not available from the Alberta and Saskatchewan populations, the possibility of hybridization between the firs in the putative sympatric region could not be investigated on the basis of cone characters. However, the cone data of Parker et al. (1981) indicated that, as for the needle characters, populations from the Rocky Mountains to Saskatchewan were not elements of two distinct taxa, nor was there any evidence of hybridization in the supposed zone of intergradation in Alberta. However, gradual morphological differences were also apparent on the basis of cone morphology, to either side of the Rocky Mountian crest. Parker et al. (1981) utilized similar cone characters as in the present study, although several characters were used as ratios.

Parker et al. (1981) speculated that the variation patterns in their study reflect that the sampled populations do not represent elements of two morphologcially distinct taxa, but that instead, population differentiation has occurred within a single, regionally variable complex in response to local selection pressures following east-west gene flow among populations originating from separate eastern and western glacial refugia. These authors suggested that any isolation between these firs has probably not been long term, since during interglacial periods from 200,000 to 300,000 years throughout the Quaternary (Ericson and Wollin, 1968), these firs could probably have intermingled and exchanged genes in western Canada, thus creating the present lack of morphological difference in this region. Parker et al. (1981) further speculated that natural selection has already eliminated much of the variation in morphological traits that would normally be present as the by-product of introgression between two species. This conclusion also appears to be applicable on the basis of the present results for needle morphology, although it extends the complex as far east as northern Ontario.

The conclusion that genetic interchange has been extensive throughout a single, widely distributed gene pool from British Columbia to northern Ontario is consistent with the evidence of Hawley and DeHayes (1985) who found that balsam fir from eastern North America crossed readily with subalpine fir from British Columbia through artificial pollination. These authors concluded that there are few, if any genetic crossability barriers between these *Balsameae* taxa, and that geographic rather than genetic isolation has been primarily responsible for their taxonomic separation.

The difference in variation patterns among the sampled populations in needle and cone morphology suggests that vegetative and sexual characters have evolved in different directions from each other, most likely due to differential responses to local selection pressures, as was apparent for the Cascades subalpine fir populations. Parker et al. (1984) also observed that the pattern of flavonoid variation among fir populations from British Columbia to Saskatchewan was not the same as the variation patterns among these same populations based on morphology as determined in the earlier study (Parker et al.,1981). Parker et al. (1984) found that although no sharp boundary separating the two firs could be detected based on flavonoid results, an east-west clinal pattern of variation that was also steepest at the Rocky Mountain crest was evident, which apparently reflects hybridization between the two firs. On the basis of the flavonoid data, these authors concluded that introgression is still in progress between two separate species, and thus, that the flavonoids and morphological features of these firs appear to be evolving at least partially independently.

The implications of the present analyses based on cone data are not the same as those of the needle data. Since the fir populations from central Canada were missing for these analyses, one can only speculate on the relationship of the firs in that area. Although the interior subalpine fir populations in southern British Columbia are sharply distinct from the balsam fir populations in northern Ontario, the possibility of a cline that occurs across a single gene pool cannot be ruled out, considering the geographic nature of the MDA ordination in Figure 3.38. Heslop-Harrison (1969) stresses the point that where such a continuity in variation exists, and populations are only examined at either end of the cline, it is possible to mistake these populations for separate species, since the populations will be quite distinct. However, Parker et al. (1981) did not observe a cline in subalpine and balsam fir populations from the Rocky Mountains to Saskatchewan, using similar cone characters and many of the same populations used in the present study; instead, as previously discussed, these authors observed gradual morphological differences reflecting introgression between separate eastern and western taxa. Thus, if the present cone data are considered together with that of Parker et al. (1981), the combined studies imply the existence of separate taxa that are well differentiated in cone morphology, but which have introgressed near where their ranges come together, and as a result are not as distinct in cone characters in this region.

Other authors, including Hunt and von Rudloff (1974) on the basis of terpenoid data, and Roller (1967) and Achuff and LaRoi (1977) on the basis of morphological data, have concluded that introgression has occurred between two separate species of fir, but that hybridization has occurred in the Prairie forest regions in Alberta, rather than near the Rocky Mountain crest as is evident in the studies of Parker et al. (1981, 1984). Although noting that the two firs are poorly differentiated morphologically, Critchfield (1984) presents monoterpene data from unpublished and published (Zavarin et al., 1970; Zavarin and Snajberk, 1972) sources, which also indicate that the northern interior race of subalpine fir and balsam fir from the Prairie provinces are sharply distinct. Critchfield supports the view that hybridization between two separate species has occurred in a zone in central Alberta that is approximatley 500 to 800 km wide, where they came together approximately 8500 years ago. Palynological evidence indicate that the two firs probably arrived near the extremes of their ranges in Alberta from separate eastern and western glacial refugia between 9 and 10 thousand years ago (Kearney and Luckman, 1983; Lichti-Federovich, 1970). It is Critchfield's (1984) opinion that, based primarily on summarized subalpine and balsam fir monoterpene data, neither the interior race of subalpine fir nor balsam fir from the western limits of its range have genetically influenced the other ouside the zone of intergradation in Alberta. However there has been no study to date of genetic variation among subalpine and balsam firs, in the suggested zone of intergradation, or to the east or west of this region. Such an investigation would help to clarify whether or not these two firs are in fact genetically distinct, as Critchfield (1984) has suggested. It would also be useful to examine additional characters which have been considered diagnostic for the two firs, throughout a large part of their range, in order to elucidate whether their variation patterns might indicate gene flow outside of Critchfield's (1984) designated zone of intergradation. Such characters include wood odour, leaf arrangement on the lower branches, pollen-cone colour, branchlet pubescense colour, and bark thickness and degree of fissuring (Moss, 1959; Hosie, 1969; Liu, 1971; Scoggan, 1978). Because many of these characters must be subjectively assessed, it is difficult to include them in a quantitative analysis, and as a result they were not included in either the present study or the earlier morphological investigation of Parker et al. (1981).

If the morphological evidence of the present study is combined with morphological and chemical evidence from previous studies, it seems appropriate to consider subalpine and balsam fir separate taxa which have introgressed in western Canada due to repeated contact in this region. Unfortunately, the present study does not provide additional information to that already obtained in previous studies, to clarify the limits of the zone of intergradation between the taxa, over which there is some dispute. The present conclusion of separate subalpine and balsam fir taxa is supported by the cone data of the present study, as well as chemical data (Hunt and von Rudloff, 1974; Zavarin et al., 1970; Zavarin and Snajberk, 1972; Parker et al., 1984), and to a more limited extent, morphological data (Roller, 1967; Achuff and LaRoi, 1977) from previous investigations.

Because the needle data of the present study do not suggest a distinction between subalpine and balsam fir populations from a large region across western and central Canada (excluding the character rows of stomata on the adaxial needle surface, which warrants further investigation), it is likely that the two taxa have simply not diverged in the examined needle characters, since these firs had one common ancestor, due to repeated contact during interglacials throughout the Pleistocene. In contrast subalpine and balsam fir populations originating from separate glacial refugia east and west of the Rocky Mountains have apparently diverged in the cone characters investigated in the present study, and to a greater extent, the chemical characters used in previous studies. Thus, as already discussed, these characters seem to have responded differently to local selection pressures than have the needle characters, during isolation of the taxa in separate refugia, and subsequent to glacial retreat.

The present results indicate that the examined needle characters are not very useful in separating the two firs from the Rocky Mountains to northern Ontario. Whether or not balsam fir populations from further east than northern Ontario might be distinct in these needle characters from subalpine fir populations in the British Columbia Rocky Mountains remains to be seen. Such a distinction is likely, since fossil data and modern variation patterns in chemical characters among balsam fir populations, as summarized by Critchfield (1984), indicate the existence of separate eastern and western races of balsam fir, which originated from separate glacial refugia east and west of the Appalachian Mountains. Populations from the western refugium ultimately occupied or reoccupied most of the Great Lakes region and the western interior of Canada, and those from the eastern refugium migrated into the northeastern United States and Canada.

TAXONOMIC IMPLICATIONS

As the present study has shown, subalpine fir is very geographically variable with regard to a number of characters. The present study has confirmed that the most recent, or Wisconsin, glaciation has created distinct geographic races in this fir, already noted by a number of authors. Most notably, there appear to be separate coastal and Rocky Mountain taxa of subalpine fir, as evidenced by chemical and morphological features. These segregate taxa have apparently arisen because of the climatically diverse regions of the refugia in which this fir was able to survive throughout glaciation.

Hunt and von Rudloff (1979) have suggested that these two taxonomic entities be designated as the separate species *Abies lasiocarpa* and *Abies bifolia* for respective coastal and interior taxa. Their decision was based primarily on chemical (terpenoid) characters, although they also investigated a limited number of morphological characters as well. In contrast, Parker and Maze (1984) feel that although these taxa should be designated as separate taxonomic entities, they favour recognition of two varieties of *Abies lasiocarpa* on the basis of their analysis of morphology and flavonoids for the following reasons: 1) Eastern and western entities were indistinguishable by their cone morphology. 2) The eastern and western entities were not wholly discrete even in needle morphology and needle flavonoids, perhaps as a result of interbreeding and blending between eastern and western entities where their ranges are contiguous, including perhaps the north Cascades of Washington. 3) Separation into eastern and western varieties parallels closely analogous situations in other conifers including *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus contorta* Dougl., two species which consist of eastern and western varieties in much the same areas of British Columbia and Washington (Hosie, 1969) as those noted here for subalpine fir. 4) Earlier studies investigating the relationships between pairs of *Abies* species have shown much higher levels of data set congruence than those observed in their study (Maze, 1983). In accordance with this designation, Critchfield's (1984) view is that, although the chemical data of Hunt and von Rudloff (1979) and Zavarin et al. (1970) indicate that subalpine fir has well differentiated geographic races, and the paleobotanical evidence supports the conclusion that these races arose from different glacial refugia, the drastic separation of the coastal and interior subalpine fir elements into species is not fully justified based on the magnitude and character of the differences.

Various definitions of a species have been attempted, although none may be completely adequate. However, it is generally accepted that to be considered a discrete species, a taxon should be either consistently distinguishable from all other species in the genus, or reproductively isolated from closely related species (Davis and Heywood, 1963; Sneath and Sokal, 1973). Taxonomic principles also dictate that the best taxonomic classifications are achieved by consideration of more than one type of evidence. The present study utilized similar populations and morphological characters as those used in Parker and Maze's (1984) earlier work, and therefore as would be expected, similar results have been obtained with regard to separation of coastal and interior subalpine fir populations. Therefore, given the combined evidence of the present and previous studies, and considering the generally accepted species concept, the designation of eastern and western varieties of coastal and interior subalpine fir seems most appropriate, in contrast to Hunt and von Rudloff's (1979) suggestion. The rationale for this designation is similar to that of Parker and Maze (1984), since the taxa are not entirely discrete in needle and cone morphology, and the third and fourth reasons these authors presented are applicable here. Intermediate populations such as those near Mount Baker and Cassiar, may be the products of interbreeding between the two varieties, as Parker and Maze (1984) have suggested. However the precise relationship of at least the Cascades populations to either variety still warrants further investigation, due to the large differences between these and other populations on the basis of needle morphology. In particular, the possibility that these, and perhaps other Cascades populations are from an entirely separate glacial refugia, requires additional investigation. Similarly, although Hunt and von Rudloff (1979) found that several Vancouver Island populations were similar in terpenoids to other coastal populations, the relationship between Vancouver Island and other coastal and interior populations requires further investigation, since the Vancouver Island population used in this study does not fit into the suggested taxonomic framework, at least on the basis of needle morphology. As for the north Cascades region, the possiblility that all or part of Vancouver Island served as a glacial refugium for subalpine fir needs to be explored in conjunction with the fossil record.

The proposed classification would separate coastal and interior elements of subalpine fir at the same taxonomic level that presently separates cork bark fir, *Abies lasiocarpa* var *Arizonica*, from the typical *Abies lasiocarpa* var *lasiocarpa.* Cork bark fir, which grows mostly scattered over mountains in central and southwestern Colorado, northern, western, and southwestern New Mexico, and northern Arizona, is nearly identical in morphology to subalpine fir, with the exception that it has a thick, highly elastic, corky bark. It is this trait that separates cork bark fir from populations to the north (Liu, 1971). As Hunt and von Rudloff (1979) have pointed out, cork bark fir is widely separated geographically from the coastal subalpine fir taxon, and is therefore more likely to be related to interior subalpine. These authors suggest that the true relationship of cork bark fir to subalpine fir needs to be clarified, since they agree with Doren (1977) that the distribution of cork bark fir deserves the status of a form rather than a variety. The present study did not include subalpine fir populations from far enough south to help clarify this relationship.

On the basis of the affinity between the northern and interior subalpine fir populations, both in the morphological data of the present study and Parker's (1984) flavonoid data, and considering the available fossil record, it seems appropriate to consider the northern populations an extension of the interior Rocky Mountain variety of subalpine fir. However, the monoterpene data of Zavarin et al. (1970) is not entirely consistent with the hypothesis, pointing instead to a southern origin similar to that for the north coastal British Columbia populations, possibly in western Washington. Because of this inconsistency, the present taxonomic designation of an interior variety of subalpine fir that extends to the northern limits of the species range must be considered tentative until more conclusive evidence for its support is available.

Given the indistinction in needle morphology among the interior subalpine and balsam fir populations across Canada from the Rocky Mountains to northern Ontario, reflecting the existence of only one widely distributed gene pool, it would seem logical to classify the firs as a single species, according to the generally accepted species concept (Davis and Heywood, 1963). Such a classification would support Boivin's (1959) earlier opinion that these firs should be considered a single species due to similar morphology. However, the distinct nature of balsam fir populations in northern Ontario from interior subalpine fir populations in the Rockies based on cone morphology, as well as the sharp differentiation of these firs in chemical characters outside central Alberta, conflicts with such a taxonomic framework. Although they observed similarities between these firs in cone and needle morphology as well as flavonoid composition from British Columbia to Saskatchewan, Parker et al. (1981, 1984) favoured the retention of the two species designations *Abies* *lasiocarpa* and *Abies balsamea*, to reflect the gradual morphological and flavonoid differences that exist between the groups on either side of the Rocky Mountain Crest, and their origins from separate eastern and western glacial refugia. Both Hunt and von Rudloff (1979) and Critchfield (1984) have also designated these firs as separate species that are sharply differentiated on the basis of terpenoids, but which hybridize in central Alberta. The cone data of the present study support the recommendation of the separate species *Abies lasiocarpa* and *Abies balsamea*, whereas the needle data have been interpreted to reflect a lack of divergence in these characters between the two species. This designation takes into consideration as many types of taxonomic evidence as are available.

In summary, the present study has provided taxonomically significant results regarding the morphological variation of subalpine and balsam firs throughout a large part of their ranges. Additional studies which investigate the modern variation patterns in morphological and other characters throughout the ranges of these species, in conjunction with the fossil record would aid in substantiating or refuting the taxonomic classifications presented in this study and would allow further insight into both the evolutionary history of these firs, and the direction in which they are presently evolving. In particular, a thorough genetic analysis of populations throughout at least the ranges of *Abies lasiocarpa* and *Abies balsamea* sampled in the present study, would help resolve the inconsistencies that are apparent among the various types of taxonomic evidence that have already been investigated. A study of this nature would also help in the assessment of the phenotypic plasticity of these morphological and chemical characters.

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APPENDICES

APPENDIX I

TREE MEANS FOR CONVENTIONAL NEEDLE CHARACTERS FROM 10 NORTHERN POPULATIONS OF *Abies lasiocarpa*

		Needle Character										
Pop.	Tree	RC (mm)	AB (mm)	MD (mm)	AD (mm)	NT (mm)	NW (mm)	VC (mm)	VAB (mm)	VAD (mm)	NL (mm)	RS
N1	1	0.17	0.26	0.31	0.21	0.80	2.14	0.29	0.30	0.22	20.64	11.00
	2	0.20	0.22	0.29	0.24	0.99	2.23	0.39	0.33	0.28	19.92	12.60
	3	0.21	0.19	0.33	0.21	0.83	2.11	0.32	0.25	0.26	18.52	15.40
	4	0.18	0.18	0.28	0.24	1.00	2.47	0.37	0.35	0.29	15.80	11.80
	5	0.13	0.19	0.21	0.24	0.88	1.82	0.32	0.28	0.28	16.46	10.00
	6	0.16	0.24	0.33	0.23	0.93	2.07	0.35	0.31	0.27	15.16	12.60
	7	0.12	0.21	0.21	0.19	0.70	1.51	0.33	0.20	0.17	18.82	7.40
	8	0.12	0.29	0.28	0.21	0.99	2.10	0.36	0.37	0.25	20.88	10.40
	9	0.17	0.26	0.49	0.25	0.97	2.29	0.36	0.36	0.24	15.70	11.40
	10	0.18	0.19	0.26	0.22	0.92	1.92	0.32	0.33	0.28	15.96	13.60
N2	11	0.14	0.19	0.20	0.19	0.78	1.67	0.35	0.22	0.21	14.62	12.60
	12	0.13	0.19	0.23	0.21	0.88	2.02	0.31	0.33	0.26	12.46	16.20
	13	0.14	0.24	0.28	0.21	0.83	1.69	0.35	0.27	0.21	13.92	13.00
	14	0.18	0.23	0.32	0.24	1.02	2.41	0.39	0.34	0.29	18.38	16.80
	15	0.15	0.27	0.37	0.24	0.95	2.11	0.34	0.36	0.25	13.86	12.60
	16	0.18	0.24	0.40	0.25	1.04	2.31	0.32	0.40	0.33	19.24	14.20
	17	0.15	0.24	0.32	0.19	0.79	2.02	0.32	0.27	0.20	13.72	13.20
	18	0.15	0.24	0.29	0.19	0.77	1.66	0.30	0.25	0.21	14.96	12.00
	19	0.20	0.24	0.36	0.25	1.02	2.35	0.43	0.38	0.21	18.16	13.00
	20	0.16	0.23	0.26	0.19	0.80	1.91	0.31	0.30	0.19	14.26	13.20
N3	21	0.12	0.19	0.23	0.19	0.76	1.81	0.28	0.28	0.20	14.14	11.40
	22	0.13	0.24	0.26	0.20	0.76	1.54	0.27	0.29	0.20	14.66	11.00
	23	0.11	0.22	0.31	0.20	0.68	1.72	0.29	0.24	0.15	14.02	11.80
	24	0.20	0.27	0.31	0.23	1.01	1.99	0.33	0.39	0.29	13.52	15.00
	25	0.11	0.22	0.27	0.20	0.86	1.82	0.29	0.35	0.22	13.48	11.40
	26	0.12	0.24	0.25	0.16	0.68	1.65	0.29	0.25	0.14	15.78	13.60
	27	0.14	0.19	0.31	0.18	0.81	1.97	0.29	0.32	0.20	13.74	11.80
	28	0.15	0.26	0.31	0.20	0.89	1.99	0.33	0.32	0.25	15.06	9.00
	29	0.14	0.26	0.25	0.23	0.82	1.70	0.32	0.29	0.21	13.26	10.80
	30	0.14	0.27	0.28	0.23	0.78	1.59	0.29	0.26	0.23	16.92	11.80
N4	31	0.13	0.24	0.25	0.26	0.89	1.78	0.36	0.31	0.22	17.80	10.20
	32	0.14	0.17	0.26	0.16	0.58	1.69	0.28	0.21	0.10	20.88	8.60
	33	0.16	0.19	0.25	0.18	0.66	1.84	0.28	0.23	0.15	18.28	10.40
	34	0.16	0.25	0.30	0.20	0.76	2.03	0.29	0.31	0.16	24.46	11.00
	35	0.14	0.26	0.26	0.23	0.84	1.95	0.27	0.31	0.26	14.08	9.60
	36	0.14	0.28	0.28	0.29	1.12	2.06	0.32	0.43	0.36	13.72	12.40
	37	0.13	0.32	0.35	0.24	0.84	2.16	0.35	0.31	0.18	17.04	13.00
	38	0.14	0.17	0.20	0.16	0.84	1.83	0.34	0.31	0.19	15.66	9.40
	39	0.08	0.23	0.22	0.17	0.70	1.53	0.26	0.22	0.22	17.02	11.00
	40	0.10	0.27	0.26	0.18	0.71	1.69	0.28	0.23	0.19	21.26	12.60
N5	41	0.11	0.20	0.23	0.19	0.70	1.58	0.30	0.26	0.15	16.80	10.40
	42	0.06	0.21	0.28	0.19	0.79	1.68	0.31	0.28	0.20	16.56	12.20
	43	0.15	0.21	0.22	0.23	0.74	1.74	0.30	0.26	0.18	15.78	11.40
	44	0.12	0.22	0.23	0.22	0.81	1.69	0.34	0.27	0.20	17.72	10.60
	45	0.10	0.21	0.21	0.16	0.65	1.46	0.25	0.22	0.18	15.02	10.40
	46	0.10	0.17	0.22	0.13	0.53	1.30	0.21	0.21	0.11	14.74	8.00
	47	0.19	0.24	0.37	0.18	0.84	2.24	0.33	0.31	0.20	18.90	11.20
	48	0.11	0.24	0.28	0.19	0.69	1.65	0.26	0.25	0.18	15.46	10.80
	49	0.15	0.26	0.22	0.15	0.88	1.92	0.36	0.30	0.22	19.08	9.80
	50	0.13	0.24	0.28	0.18	0.73	1.82	0.29	0.23	0.21	14.52	11.60

		Needle Character										
Pop.	Tree	RC (mm)	AB (mm)	MD (mm)	AD (mm)	NT (mm)	NW (mm)	VC (mm)	VAB (mm)	VAD (mm)	NL (mm)	RS
N6	51	0.17	0.23	0.31	0.21	0.73	1.69	0.27	0.26	0.20	19.38	11.60
	52	0.18	0.25	0.33	0.22	0.95	2.19	0.36	0.35	0.24	19.06	11.40
	53	0.14	0.24	0.39	0.28	1.16	2.49	0.42	0.47	0.27	20.90	15.20
	54	0.14	0.24	0.27	0.25	1.04	2.14	0.39	0.40	0.26	15.56	11.60
	55	0.12	0.22	0.29	0.23	0.81	1.85	0.28	0.29	0.24	16.50	13.40
	56	0.15	0.26	0.30	0.21	0.92	2.21	0.36	0.32	0.24	14.76	13.40
	57	0.13	0.24	0.39	0.20	0.94	2.19	0.36	0.35	0.23	13.36	11.40
	58	0.09	0.17	0.30	0.19	0.70	2.00	0.30	0.26	0.14	17.20	12.60
	59	0.15	0.26	0.25	0.18	0.71	1.59	0.31	0.23	0.18	20.94	10.20
	60	0.13	0.33	0.35	0.23	0.91	1.87	0.33	0.34	0.24	18.26	12.40
N7	61	0.13	0.16	0.35	0.27	1.11	2.44	0.34	0.41	0.35	16.64	12.40
	62	0.16	0.20	0.30	0.20	0.92	2.07	0.39	0.30	0.22	17.18	13.00
	63	0.11	0.16	0.31	0.19	0.95	2.22	0.36	0.34	0.25	15.16	11.00
	64	0.16	0.20	0.26	0.16	0.73	1.97	0.29	0.26	0.18	18.34	14.00
	65	0.14	0.22	0.33	0.25	1.02	2.28	0.34	0.41	0.26	14.80	14.20
	66	0.18	0.22	0.29	0.28	1.17	2.13	0.36	0.40	0.41	14.24	14.40
	67	0.16	0.17	0.25	0.18	0.98	2.10	0.39	0.35	0.24	15.96	14.00
	68	0.13	0.23	0.34	0.24	0.97	2.18	0.33	0.38	0.27	15.40	12.80
	69	0.20	0.21	0.36	0.21	1.06	2.67	0.39	0.41	0.26	16.40	11.20
	70	0.12	0.19	0.34	0.19	0.78	2.08	0.28	0.32	0.18	14.32	9.40
N8	71	0.14	0.20	0.24	0.20	0.93	1.95	0.32	0.37	0.23	16.10	13.40
	72	0.14	0.22	0.28	0.22	0.85	1.90	0.33	0.32	0.20	17.38	11.00
	73	0.14	0.28	0.28	0.24	1.04	2.05	0.38	0.32	0.34	12.48	17.00
	74	0.17	0.21	0.26	0.23	0.89	2.05	0.35	0.30	0.24	16.14	15.80
	75	0.18	0.28	0.41	0.26	1.03	2.37	0.38	0.39	0.27	18.38	14.20
	76	0.17	0.24	0.32	0.22	1.10	2.44	0.45	0.36	0.29	15.38	14.20
	77	0.12	0.25	0.31	0.20	0.95	1.94	0.32	0.35	0.28	14.16	12.40
	78	0.15	0.20	0.29	0.24	0.87	1.89	0.36	0.28	0.24	15.76	11.20
	79	0.13	0.21	0.21	0.20	0.85	1.75	0.30	0.29	0.26	16.52	10.60
	80	0.15	0.26	0.36	0.24	0.94	2.12	0.35	0.34	0.25	16.94	12.40
N9	81	0.19	0.25	0.26	0.26	1.10	1.96	0.34	0.39	0.36	12.36	12.60
	82	0.16	0.26	0.29	0.23	0.90	2.11	0.31	0.33	0.26	15.54	13.00
	83	0.12	0.19	0.25	0.22	0.92	1.91	0.33	0.31	0.27	11.96	11.60
	84	0.21	0.24	0.22	0.22	1.09	1.82	0.38	0.36	0.36	14.68	13.20
	85	0.14	0.21	0.25	0.19	0.92	2.25	0.39	0.25	0.28	16.16	16.40
	86	0.13	0.19	0.19	0.15	0.71	1.67	0.31	0.22	0.17	17.44	11.80
	87	0.16	0.23	0.27	0.27	1.07	2.11	0.39	0.34	0.33	17.08	12.20
	88	0.13	0.24	0.31	0.20	0.78	1.87	0.29	0.28	0.21	17.06	11.60
	89	0.19	0.20	0.25	0.18	0.97	2.19	0.36	0.32	0.29	17.22	12.80
	90	0.12	0.21	0.23	0.20	0.88	1.90	0.34	0.34	0.20	13.68	13.00
N10	91	0.18	0.21	0.33	0.21	0.73	1.87	0.35	0.20	0.18	20.50	14.80
	92	0.19	0.26	0.33	0.20	0.85	2.13	0.36	0.25	0.24	18.36	11.00
	93	0.13	0.19	0.21	0.17	0.57	1.29	0.24	0.18	0.14	16.40	11.40
	94	0.15	0.21	0.29	0.19	0.66	1.52	0.24	0.23	0.19	17.88	11.80
	95	0.15	0.26	0.33	0.21	0.70	1.54	0.27	0.21	0.21	19.14	11.20
	96	0.15	0.30	0.29	0.28	0.83	1.47	0.27	0.28	0.28	15.32	10.00
	97	0.17	0.16	0.29	0.17	0.37	1.75	0.23	0.25	0.18	15.78	14.20
	98	0.12	0.19	0.37	0.22	0.69	1.78	0.26	0.22	0.21	13.28	10.00
	99	0.19	0.15	0.31	0.19	0.75	1.89	0.30	0.25	0.20	17.10	11.80
	100	0.16	0.22	0.33	0.19	0.76	1.83	0.31	0.25	0.20	14.22	12.80

APPENDIX II

TREE MEANS FOR PROGENY CONVENTIONAL NEEDLE CHARACTERS FROM 4 NORTHERN POPULATIONS OF *Abies lasiocarpa*

						Needle	Character	(mm)			
Pop.	Tree	RC	AB	MD	AD	NT	NW	VC	VAB	VAD	NL
N1	2	0.02	0.04	0.03	0.06	0.47	1.31	0.15	0.13	0.19	13.33
	5	0.03	0.05	0.06	0.14	0.51	1.33	0.13	0.16	0.21	9.06
	6	0.06	0.05	0.05	0.20	0.52	1.49	0.19	0.13	0.20	21.58
	8	0.05	0.03	0.06	0.19	0.53	1.40	0.14	0.13	0.26	13.16
N3	24	0.02	0.03	0.04	0.12	0.51	1.35	0.13	0.15	0.23	9.32
	25	0.03	0.02	0.12	0.19	0.41	1.30	0.13	0.11	0.17	13.06
	26	0.05	0.03	0.14	0.20	0.48	1.65	0.17	0.14	0.17	15.52
	27	0.08	0.03	0.08	0.18	0.43	1.78	0.19	0.10	0.14	25.86
N5	42	0.05	0.03	0.14	0.15	0.41	1.68	0.17	0.10	0.14	22.16
	46	0.04	0.02	0.10	0.20	0.41	1.37	0.16	0.10	0.14	23.72
	47	0.05	0.02	0.14	0.14	0.34	1.46	0.14	0.09	0.10	17.88
	48	0.04	0.03	0.06	0.13	0.47	1.62	0.17	0.12	0.18	22.32
	50	0.07	0.03	0.07	0.18	0.48	1.56	0.17	0.11	0.20	21.22
N6	52	0.06	0.02	0.06	0.15	0.39	1.60	0.20	0.09	0.10	25.62
	55	0.06	0.03	0.07	0.14	0.46	1.63	0.16	0.14	0.16	24.02
	56	0.05	0.02	0.11	0.20	0.44	1.71	0.18	0.13	0.13	21.76
	58	0.08	0.02	0.09	0.20	0.47	1.53	0.18	0.13	0.16	20.68

APPENDIX III

TREE MEANS FOR SHAPE NEEDLE CHARACTERS FROM 10 NORTHERN POPULATIONS OF *Abies lasiocarpa*

		Needle Character (mm)									
Pop.	Tree	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
N1	1	0.52	0.53	0.57	0.66	0.99	1.06	0.99	0.70	0.51	0.34
	2	0.59	0.58	0.57	0.65	0.98	1.05	0.99	0.76	0.58	0.45
	3	0.50	0.51	0.53	0.63	0.93	1.03	0.94	0.68	0.46	0.35
	4	0.61	0.60	0.60	0.67	1.11	1.24	1.14	0.71	0.54	0.44
	5	0.51	0.51	0.49	0.52	0.87	0.93	0.91	0.70	0.54	0.44
	6	0.59	0.57	0.57	0.64	0.96	1.01	0.94	0.66	0.50	0.43
	7	0.46	0.44	0.46	0.52	0.68	0.72	0.68	0.51	0.36	0.29
	8	0.62	0.59	0.58	0.64	0.92	0.99	0.92	0.65	0.50	0.43
	9	0.59	0.56	0.55	0.60	0.98	1.14	1.04	0.72	0.56	0.46
	10	0.59	0.57	0.55	0.64	0.91	0.96	0.89	0.61	0.42	0.36
N2	11	0.56	0.55	0.55	0.61	0.81	0.86	0.82	0.57	0.41	0.31
	12	0.54	0.52	0.51	0.56	0.81	1.01	0.95	0.69	0.53	0.42
	13	0.50	0.48	0.47	0.53	0.76	0.82	0.79	0.58	0.45	0.34
	14	0.67	0.66	0.67	0.73	1.11	1.27	1.18	0.76	0.52	0.42
	15	0.56	0.51	0.49	0.57	0.86	0.97	0.91	0.69	0.56	0.48
	16	0.59	0.57	0.57	0.66	0.98	1.11	1.03	0.74	0.57	0.46
	17	0.41	0.40	0.41	0.46	0.81	1.00	0.98	0.75	0.58	0.46
	18	0.49	0.47	0.46	0.50	0.78	0.84	0.79	0.59	0.44	0.34
	19	0.69	0.66	0.61	0.63	0.97	1.14	1.07	0.77	0.55	0.39
	20	0.56	0.52	0.50	0.55	0.85	0.93	0.88	0.65	0.47	0.32
N3	21	0.47	0.45	0.42	0.45	0.76	0.85	0.82	0.62	0.47	0.38
	22	0.54	0.51	0.52	0.56	0.74	0.79	0.72	0.52	0.37	0.29
	23	0.46	0.43	0.41	0.46	0.71	0.78	0.74	0.54	0.39	0.28
	24	0.61	0.57	0.54	0.61	0.83	0.89	0.84	0.66	0.51	0.45
	25	0.59	0.54	0.50	0.52	0.82	0.90	0.83	0.57	0.40	0.32
	26	0.54	0.49	0.46	0.48	0.67	0.73	0.68	0.50	0.36	0.26
	27	0.53	0.50	0.48	0.53	0.82	0.91	0.84	0.55	0.39	0.32
	28	0.54	0.54	0.55	0.62	0.90	1.04	0.98	0.68	0.50	0.39
	29	0.49	0.46	0.44	0.50	0.73	0.80	0.78	0.66	0.50	0.38
	30	0.50	0.50	0.51	0.58	0.76	0.83	0.78	0.59	0.43	0.32
N4	31	0.55	0.53	0.53	0.58	0.81	0.87	0.82	0.65	0.53	0.44
	32	0.41	0.41	0.42	0.48	0.82	0.90	0.85	0.51	0.24	0.16
	33	0.42	0.43	0.46	0.54	0.81	0.90	0.83	0.60	0.40	0.28
	34	0.54	0.49	0.45	0.53	0.84	0.91	0.86	0.66	0.49	0.39
	35	0.50	0.48	0.49	0.58	0.85	0.91	0.86	0.67	0.52	0.42
	36	0.62	0.60	0.60	0.69	1.01	1.04	1.01	0.76	0.61	0.54
	37	0.62	0.61	0.61	0.69	0.98	1.03	0.94	0.64	0.35	0.26
	38	0.57	0.54	0.53	0.59	0.89	0.96	0.80	0.44	0.33	0.27
	39	0.38	0.38	0.40	0.44	0.66	0.81	0.77	0.58	0.44	0.37
	40	0.48	0.45	0.43	0.51	0.73	0.78	0.73	0.54	0.38	0.28
N5	41	0.52	0.49	0.47	0.53	0.75	0.79	0.73	0.49	0.30	0.21
	42	0.55	0.50	0.46	0.50	0.71	0.79	0.73	0.46	0.35	0.29
	43	0.48	0.49	0.52	0.62	0.85	0.89	0.86	0.62	0.43	0.31
	44	0.54	0.53	0.54	0.60	0.82	0.88	0.81	0.58	0.42	0.34
	45	0.45	0.44	0.45	0.49	0.72	0.77	0.73	0.49	0.32	0.22
	46	0.39	0.37	0.36	0.42	0.65	0.75	0.71	0.52	0.34	0.60
	47	0.60	0.55	0.52	0.58	0.95	1.21	1.10	0.67	0.52	0.40
	48	0.49	0.50	0.51	0.56	0.78	0.85	0.79	0.54	0.36	0.25
	49	0.59	0.58	0.61	0.69	0.98	1.04	0.97	0.59	0.42	0.33
	50	0.47	0.46	0.46	0.53	0.84	0.91	0.85	0.56	0.37	0.30

		Needle Character (mm)									
Pop.	Tree	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
N6	51	0.50	0.48	0.47	0.54	0.76	0.83	0.78	0.60	0.43	0.33
	52	0.57	0.55	0.53	0.58	0.91	1.08	0.99	0.76	0.58	0.51
	53	0.83	0.79	0.72	0.74	1.11	1.30	1.17	0.75	0.52	0.38
	54	0.64	0.62	0.64	0.70	1.03	1.13	0.99	0.71	0.52	0.44
	55	0.59	0.57	0.58	0.65	0.95	1.02	0.94	0.57	0.36	0.27
	56	0.55	0.52	0.52	0.59	1.02	1.12	1.04	0.75	0.55	0.46
	57	0.58	0.52	0.47	0.49	0.77	0.98	0.90	0.68	0.53	0.46
	58	0.45	0.44	0.47	0.52	0.87	1.08	0.96	0.54	0.38	0.31
	59	0.59	0.58	0.57	0.60	0.74	0.79	0.75	0.44	0.30	0.17
	60	0.64	0.62	0.62	0.68	0.85	0.88	0.79	0.55	0.42	0.32
N7	61	0.57	0.58	0.59	0.64	0.94	1.29	1.18	0.80	0.63	0.55
	62	0.57	0.55	0.52	0.55	0.83	1.02	0.96	0.68	0.51	0.39
	63	0.56	0.53	0.51	0.54	0.83	1.05	0.96	0.58	0.45	0.39
	64	0.46	0.46	0.50	0.57	0.93	1.03	0.94	0.60	0.38	0.29
	65	0.58	0.57	0.58	0.64	1.02	1.12	1.05	0.73	0.56	0.47
	66	0.60	0.56	0.53	0.61	0.99	1.07	1.01	0.77	0.62	0.55
	67	0.53	0.52	0.50	0.52	0.86	1.05	0.95	0.66	0.53	0.47
	68	0.53	0.52	0.53	0.56	0.94	1.11	1.03	0.76	0.58	0.48
	69	0.63	0.61	0.60	0.67	1.14	1.39	1.27	0.83	0.61	0.48
	70	0.54	0.50	0.49	0.55	0.84	1.00	0.85	0.46	0.31	0.25
N8	71	0.55	0.53	0.52	0.57	0.87	1.03	0.97	0.70	0.52	0.42
	72	0.53	0.52	0.52	0.55	0.96	1.01	0.97	0.71	0.47	0.35
	73	0.65	0.60	0.60	0.69	0.95	1.01	0.95	0.66	0.50	0.43
	74	0.52	0.47	0.46	0.52	0.84	0.92	0.88	0.71	0.56	0.46
	75	0.66	0.62	0.61	0.65	0.98	1.24	1.19	0.90	0.65	0.50
	76	0.71	0.70	0.69	0.68	1.09	1.22	1.17	0.85	0.61	0.44
	77	0.60	0.52	0.44	0.47	0.76	0.88	0.83	0.62	0.46	0.39
	78	0.50	0.50	0.50	0.54	0.85	0.96	0.90	0.68	0.51	0.42
	79	0.48	0.47	0.49	0.57	0.84	0.92	0.87	0.62	0.46	0.37
	80	0.60	0.58	0.57	0.61	1.05	1.11	1.07	0.74	0.49	0.37
N9	81	0.58	0.57	0.58	0.69	1.01	1.05	0.99	0.79	0.65	0.57
	82	0.51	0.51	0.53	0.60	0.87	1.03	0.97	0.77	0.61	0.49
	83	0.48	0.45	0.46	0.51	0.79	0.91	0.84	0.62	0.50	0.44
	84	0.60	0.58	0.57	0.64	0.86	0.92	0.87	0.70	0.59	0.53
	85	0.53	0.53	0.53	0.59	0.97	1.13	1.06	0.77	0.59	0.47
	86	0.51	0.49	0.50	0.57	0.80	0.87	0.82	0.54	0.37	0.27
	87	0.66	0.65	0.64	0.69	0.92	1.01	0.95	0.69	0.53	0.43
	88	0.51	0.50	0.49	0.54	0.78	0.86	0.80	0.58	0.42	0.33
	89	0.53	0.52	0.56	0.67	1.02	1.17	1.07	0.73	0.58	0.49
	90	0.57	0.56	0.56	0.62	0.90	0.95	0.86	0.59	0.45	0.37
N10	91	0.43	0.41	0.42	0.47	0.77	0.92	0.87	0.66	0.50	0.37
	92	0.54	0.54	0.55	0.67	0.98	1.05	0.97	0.68	0.49	0.38
	93	0.39	0.36	0.36	0.44	0.59	0.62	0.59	0.43	0.32	0.24
	94	0.43	0.41	0.42	0.50	0.73	0.79	0.76	0.56	0.39	0.30
	95	0.43	0.40	0.41	0.51	0.68	0.72	0.67	0.53	0.42	0.32
	96	0.48	0.46	0.47	0.57	0.73	0.76	0.72	0.60	0.49	0.40
	97	0.39	0.37	0.36	0.42	0.76	0.85	0.80	0.59	0.44	0.34
	98	0.41	0.39	0.39	0.48	0.83	0.88	0.82	0.57	0.41	0.33
	99	0.42	0.41	0.41	0.46	0.84	0.98	0.93	0.65	0.49	0.39
	100	0.61	0.59	0.57	0.65	0.87	0.93	0.81	0.39	0.24	0.19

		Needle Character (mm)									
Pop.	Tree	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20
N1	1	0.29	0.34	0.49	0.68	0.97	1.05	0.98	0.64	0.57	0.54
	2	0.42	0.47	0.57	0.78	1.08	1.16	1.10	0.69	0.61	0.54
	3	0.33	0.38	0.48	0.68	0.98	1.07	0.98	0.60	0.51	0.50
	4	0.41	0.44	0.53	0.72	1.10	1.23	1.11	0.67	0.59	0.60
	5	0.40	0.43	0.49	0.66	0.87	0.91	0.87	0.57	0.51	0.50
	6	0.39	0.44	0.52	0.68	0.97	1.07	0.99	0.63	0.58	0.58
	7	0.25	0.28	0.37	0.54	0.73	0.79	0.74	0.53	0.47	0.46
	8	0.40	0.44	0.54	0.74	1.07	1.14	1.03	0.69	0.63	0.61
	9	0.40	0.41	0.55	0.72	1.03	1.19	1.07	0.64	0.57	0.60
	10	0.36	0.39	0.46	0.64	0.94	1.03	0.97	0.63	0.55	0.57
N2	11	0.29	0.34	0.44	0.59	0.82	0.88	0.81	0.58	0.53	0.55
	12	0.38	0.40	0.50	0.68	0.95	1.03	0.81	0.60	0.55	0.54
	13	0.31	0.37	0.46	0.56	0.75	0.80	0.75	0.50	0.46	0.48
	14	0.40	0.47	0.59	0.75	1.03	1.12	1.01	0.64	0.60	0.63
	15	0.41	0.41	0.50	0.69	1.04	1.12	1.05	0.68	0.57	0.56
	16	0.47	0.51	0.60	0.76	1.06	1.16	1.00	0.56	0.51	0.53
	17	0.41	0.47	0.61	0.78	0.97	1.00	0.85	0.42	0.38	0.39
	18	0.30	0.32	0.39	0.55	0.75	0.80	0.76	0.53	0.48	0.48
	19	0.31	0.37	0.52	0.77	1.05	1.13	1.03	0.65	0.61	0.66
	20	0.27	0.30	0.41	0.66	0.94	1.01	0.91	0.63	0.56	0.56
N3	21	0.33	0.35	0.45	0.64	0.90	0.95	0.87	0.50	0.45	0.46
	22	0.25	0.27	0.33	0.47	0.68	0.77	0.75	0.60	0.54	0.53
	23	0.24	0.26	0.37	0.59	0.86	0.90	0.80	0.52	0.46	0.45
	24	0.42	0.44	0.54	0.71	1.00	1.09	1.03	0.76	0.67	0.62
	25	0.29	0.30	0.39	0.56	0.82	0.89	0.83	0.55	0.51	0.55
	26	0.20	0.18	0.28	0.51	0.83	0.89	0.85	0.60	0.54	0.53
	27	0.30	0.33	0.42	0.59	0.92	1.02	0.94	0.54	0.49	0.50
	28	0.35	0.39	0.48	0.63	0.86	0.92	0.84	0.56	0.51	0.52
	29	0.33	0.37	0.47	0.66	0.90	0.94	0.88	0.58	0.49	0.48
	30	0.29	0.33	0.41	0.55	0.71	0.76	0.73	0.57	0.51	0.49
N4	31	0.38	0.39	0.48	0.63	0.84	0.89	0.85	0.59	0.53	0.53
	32	0.15	0.18	0.27	0.46	0.72	0.78	0.73	0.47	0.40	0.40
	33	0.25	0.32	0.46	0.66	0.89	0.94	0.83	0.49	0.42	0.41
	34	0.31	0.27	0.37	0.68	1.03	1.11	1.03	0.66	0.58	0.54
	35	0.36	0.38	0.48	0.66	0.95	1.03	0.93	0.62	0.54	0.50
	36	0.52	0.55	0.62	0.76	0.95	0.99	0.94	0.68	0.60	0.60
	37	0.23	0.26	0.39	0.65	0.98	1.11	1.03	0.61	0.56	0.60
	38	0.25	0.27	0.33	0.47	0.72	0.84	0.81	0.58	0.52	0.55
	39	0.31	0.33	0.39	0.51	0.67	0.72	0.67	0.45	0.40	0.39
	40	0.25	0.24	0.35	0.58	0.83	0.90	0.86	0.61	0.51	0.48
N5	41	0.19	0.21	0.30	0.43	0.74	0.80	0.76	0.53	0.49	0.51
	42	0.26	0.28	0.34	0.50	0.83	0.91	0.75	0.53	0.51	0.52
	43	0.31	0.37	0.48	0.64	0.82	0.86	0.80	0.53	0.45	0.45
	44	0.29	0.30	0.36	0.48	0.74	0.82	0.80	0.62	0.58	0.55
	45	0.18	0.19	0.26	0.44	0.64	0.70	0.66	0.47	0.42	0.43
	46	0.21	0.27	0.35	0.46	0.65	0.68	0.60	0.38	0.33	0.36
	47	0.34	0.36	0.48	0.73	1.09	1.25	1.02	0.69	0.60	0.60
	48	0.24	0.31	0.41	0.58	0.78	0.84	0.78	0.51	0.44	0.46
	49	0.32	0.36	0.44	0.60	0.86	0.94	0.86	0.58	0.53	0.55
	50	0.29	0.31	0.39	0.56	0.85	0.92	0.85	0.53	0.46	0.45

						Needle Character (mm)					
Pop.	Tree	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20
N6	51	0.28	0.29	0.38	0.57	0.80	0.86	0.82	0.57	0.48	0.49
	52	0.43	0.43	0.56	0.76	1.03	1.12	1.00	0.62	0.55	0.55
	53	0.33	0.37	0.49	0.71	1.08	1.22	1.06	0.72	0.69	0.77
	54	0.40	0.46	0.56	0.71	0.91	0.99	0.86	0.58	0.56	0.60
	55	0.27	0.33	0.44	0.61	0.86	0.93	0.86	0.55	0.50	0.54
	56	0.46	0.51	0.60	0.74	0.96	1.04	0.93	0.58	0.52	0.53
	57	0.40	0.41	0.50	0.68	1.03	1.15	1.00	0.63	0.58	0.57
	58	0.29	0.36	0.47	0.68	0.86	0.90	0.67	0.44	0.41	0.43
	59	0.15	0.18	0.30	0.52	0.74	0.79	0.73	0.58	0.54	0.57
	60	0.32	0.36	0.46	0.61	0.88	0.96	0.89	0.68	0.62	0.62
N7	61	0.51	0.52	0.54	0.65	0.97	1.09	0.95	0.56	0.52	0.55
	62	0.37	0.41	0.51	0.72	0.98	1.04	0.89	0.54	0.53	0.57
	63	0.37	0.40	0.48	0.61	1.02	1.13	0.90	0.58	0.55	0.55
	64	0.28	0.32	0.41	0.61	0.85	0.92	0.81	0.48	0.42	0.43
	65	0.45	0.54	0.63	0.75	1.03	1.14	0.98	0.62	0.54	0.55
	66	0.54	0.55	0.61	0.75	0.97	1.01	0.96	0.65	0.58	0.59
	67	0.47	0.52	0.61	0.76	0.95	1.02	0.79	0.46	0.45	0.49
	68	0.46	0.49	0.57	0.71	0.94	1.02	0.90	0.52	0.49	0.51
	69	0.46	0.51	0.59	0.77	1.09	1.23	0.98	0.57	0.54	0.59
	70	0.22	0.22	0.26	0.36	0.79	1.04	0.94	0.63	0.53	0.55
N8	71	0.37	0.40	0.46	0.61	0.83	0.86	0.79	0.55	0.49	0.52
	72	0.32	0.37	0.45	0.60	0.81	0.85	0.79	0.50	0.45	0.50
	73	0.36	0.37	0.44	0.61	0.93	0.99	0.95	0.73	0.64	0.64
	74	0.40	0.41	0.54	0.76	1.06	1.13	1.04	0.66	0.57	0.53
	75	0.43	0.48	0.59	0.77	1.03	1.09	0.95	0.62	0.58	0.63
	76	0.37	0.46	0.58	0.79	1.13	1.22	1.03	0.68	0.67	0.69
	77	0.36	0.37	0.49	0.69	0.99	1.06	0.97	0.61	0.56	0.57
	78	0.39	0.42	0.50	0.67	0.89	0.92	0.82	0.53	0.48	0.48
	79	0.35	0.37	0.45	0.59	0.79	0.84	0.78	0.52	0.46	0.46
	80	0.35	0.38	0.50	0.72	0.94	1.00	0.91	0.55	0.50	0.55
N9	81	0.54	0.53	0.59	0.71	0.87	0.90	0.86	0.63	0.53	0.54
	82	0.42	0.46	0.57	0.74	0.97	1.04	0.97	0.61	0.52	0.51
	83	0.44	0.45	0.52	0.67	0.93	1.00	0.89	0.57	0.51	0.48
	84	0.51	0.52	0.57	0.70	0.87	0.91	0.87	0.66	0.58	0.58
	85	0.42	0.43	0.53	0.69	1.02	1.10	0.96	0.57	0.51	0.51
	86	0.24	0.28	0.39	0.55	0.82	0.88	0.82	0.57	0.49	0.49
	87	0.40	0.44	0.54	0.74	0.98	1.06	0.96	0.69	0.63	0.65
	88	0.30	0.34	0.44	0.63	0.95	1.00	0.94	0.63	0.55	0.52
	89	0.46	0.48	0.53	0.65	0.93	1.01	0.91	0.60	0.51	0.50
	90	0.35	0.39	0.48	0.63	0.86	0.96	0.88	0.57	0.50	0.53
N10	91	0.32	0.37	0.48	0.67	0.90	0.96	0.86	0.52	0.44	0.42
	92	0.36	0.40	0.51	0.72	1.00	1.08	0.92	0.57	0.50	0.51
	93	0.20	0.21	0.26	0.41	0.64	0.67	0.65	0.48	0.41	0.39
	94	0.25	0.27	0.35	0.49	0.69	0.75	0.70	0.50	0.41	0.41
	95	0.29	0.30	0.38	0.56	0.81	0.86	0.83	0.62	0.49	0.43
	96	0.36	0.36	0.42	0.53	0.69	0.72	0.70	0.59	0.51	0.48
	97	0.29	0.32	0.44	0.63	0.84	0.90	0.76	0.43	0.37	0.37
	98	0.30	0.33	0.42	0.60	0.85	0.92	0.86	0.48	0.40	0.40
	99	0.35	0.36	0.43	0.61	0.84	0.91	0.82	0.47	0.40	0.41
	100	0.19	0.22	0.27	0.43	0.77	0.91	0.86	0.62	0.55	0.58

APPENDIX IV

TREE MEANS FOR PROGENY SHAPE NEEDLE CHARACTERS FROM 4 NORTHERN POPULATIONS OF *Abies lasiocarpa*

		Needle Character (mm)									
Pop.	Tree	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10
N1	2	0.22	0.23	0.25	0.33	0.54	0.69	0.56	0.36	0.29	0.27
	5	0.26	0.27	0.31	0.39	0.57	0.72	0.67	0.47	0.35	0.31
	6	0.31	0.31	0.35	0.45	0.69	0.75	0.70	0.46	0.31	0.24
	8	0.32	0.33	0.36	0.43	0.67	0.77	0.70	0.42	0.27	0.21
N3	24	0.11	0.12	0.13	0.17	0.37	0.63	0.61	0.48	0.41	0.39
	25	0.24	0.24	0.27	0.34	0.52	0.62	0.57	0.35	0.23	0.18
	26	0.27	0.28	0.31	0.38	0.57	0.86	0.80	0.44	0.30	0.23
	27	0.25	0.26	0.28	0.34	0.59	0.87	0.82	0.45	0.26	0.20
N5	42	0.25	0.25	0.25	0.28	0.46	0.82	0.74	0.37	0.24	0.19
	46	0.11	0.12	0.13	0.17	0.40	0.66	0.64	0.51	0.38	0.31
	47	0.13	0.13	0.14	0.17	0.39	0.70	0.67	0.43	0.29	0.22
	48	0.29	0.28	0.31	0.38	0.61	0.77	0.70	0.43	0.28	0.21
	50	0.25	0.25	0.28	0.34	0.57	0.78	0.75	0.52	0.34	0.26
N6	52	0.30	0.29	0.29	0.33	0.55	0.77	0.73	0.35	0.15	0.12
	55	0.30	0.30	0.30	0.32	0.60	0.78	0.73	0.41	0.23	0.19
	56	0.31	0.30	0.31	0.35	0.63	0.85	0.77	0.46	0.22	0.16
	58	0.28	0.27	0.29	0.35	0.59	0.75	0.67	0.43	0.27	0.21

		Needle Character (mm)									
Pop.	Tree	D11	D12	D13	D14	D15	D16	D17	D18	D19	D20
N1	2	0.26	0.25	0.26	0.33	0.54	0.62	0.51	0.29	0.24	0.22
	5	0.29	0.29	0.32	0.41	0.55	0.59	0.53	0.27	0.30	0.26
	6	0.22	0.23	0.28	0.42	0.71	0.78	0.74	0.48	0.37	0.32
	8	0.20	0.23	0.29	0.42	0.56	0.62	0.57	0.41	0.34	0.32
N3	24	0.40	0.42	0.44	0.51	0.65	0.70	0.36	0.19	0.14	0.12
	25	0.16	0.18	0.22	0.32	0.55	0.65	0.55	0.34	0.26	0.24
	26	0.22	0.24	0.30	0.44	0.72	0.77	0.53	0.31	0.27	0.27
	27	0.18	0.20	0.24	0.40	0.83	0.88	0.71	0.33	0.27	0.25
N5	42	0.17	0.18	0.22	0.34	0.74	0.84	0.52	0.31	0.26	0.25
	46	0.29	0.32	0.39	0.51	0.65	0.68	0.39	0.16	0.13	0.12
	47	0.20	0.21	0.27	0.42	0.65	0.69	0.41	0.17	0.13	0.13
	48	0.19	0.21	0.27	0.44	0.75	0.83	0.62	0.39	0.32	0.29
	50	0.24	0.27	0.33	0.48	0.73	0.75	0.56	0.35	0.29	0.26
N6	52	0.11	0.12	0.17	0.31	0.73	0.81	0.64	0.34	0.30	0.29
	55	0.17	0.18	0.23	0.40	0.76	0.84	0.71	0.35	0.30	0.29
	56	0.16	0.17	0.22	0.37	0.78	0.85	0.75	0.38	0.33	0.31
	58	0.19	0.21	0.28	0.44	0.69	0.78	0.57	0.33	0.28	0.27

APPENDIX V

TREE MEANS FOR CONE CHARACTERS FROM 9 NORTHERN POPULATIONS OF *Abies lasiocarpa*

		Cone Character									
Pop.	Tree	ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
N1	1	2.85	3.20	40.25	2.14	6.54	5.04	5.04	6.70	21.38	14.80
	2	3.45	4.50	58.35	4.14	3.78	4.70	2.92	7.40	18.48	14.48
	3	3.00	3.80	48.65	2.72	5.16	5.16	3.80	6.50	20.32	13.66
	4	3.40	3.65	52.40	3.64	2.96	4.54	2.14	6.60	19.58	12.16
	5	3.15	3.55	47.15	3.18	3.98	5.26	2.36	5.40	18.00	14.92
	6	3.10	3.45	37.00	2.78	2.86	4.36	1.70	7.30	14.24	11.04
	7	3.25	3.65	54.00	4.58	4.20	4.86	2.86	6.60	17.58	12.76
	8	3.45	3.85	46.35	4.48	3.46	4.50	2.90	6.90	18.56	14.90
	9	3.25	3.40	39.45	3.84	3.54	4.46	2.56	7.30	15.46	12.74
	10	3.80	3.85	41.15	3.46	3.12	5.16	2.22	5.60	14.56	9.88
N3	24	3.65	3.95	50.30	2.72	3.66	4.42	2.30	7.10	13.30	8.60
	25	3.10	3.10	43.50	2.90	3.42	4.72	1.88	6.40	15.78	8.52
	26	2.35	3.75	41.00	3.36	3.50	5.18	2.54	6.60	16.42	9.80
	27	3.35	4.00	51.00	2.76	3.74	4.94	2.98	6.80	19.36	13.58
	28	3.40	3.80	46.35	2.68	3.94	4.68	3.10	7.40	16.64	10.98
N4	31	3.00	3.05	45.20	3.36	3.18	4.10	1.94	6.70	16.66	10.50
	32	3.50	3.35	55.85	2.96	3.02	5.74	2.06	5.50	22.56	15.60
	33	2.65	2.80	46.25	3.00	3.00	3.78	1.74	7.90	17.12	15.60
	34	3.85	4.05	53.10	4.54	4.40	6.56	2.70	6.70	27.58	19.22
	35	3.40	3.55	56.05	3.12	3.70	5.14	1.84	8.00	21.56	15.04
	36	2.90	2.90	51.15	3.48	2.90	4.16	1.76	7.30	16.26	10.96
	37	3.70	3.20	50.45	4.06	3.62	5.86	1.46	7.80	21.74	14.96
	38	3.15	3.20	40.90	4.06	3.16	5.04	1.52	5.50	18.60	11.68
	39	3.10	3.60	38.20	2.90	3.16	3.98	1.44	8.30	17.16	12.16
	40	2.90	2.80	46.60	2.78	3.00	4.24	1.82	7.90	17.62	11.54
N5	41	2.55	3.15	36.25	2.94	2.98	3.88	1.44	7.60	14.40	9.78
	42	2.40	2.60	35.80	2.58	3.10	4.72	1.42	7.20	17.46	11.24
	43	4.40	4.60	48.60	3.80	3.34	5.12	1.64	7.80	15.70	9.74
	44	2.75	2.90	36.15	2.22	3.40	4.90	1.60	7.50	13.32	9.58
	45	2.90	3.05	35.95	3.14	2.70	3.84	1.54	8.10	17.76	13.18
	46	2.90	3.10	42.05	2.64	2.90	4.76	1.78	6.60	16.50	11.48
	47	3.50	3.70	51.05	2.54	3.86	5.92	2.46	5.40	21.16	14.84
	48	2.95	3.50	39.60	3.52	2.92	4.06	1.28	8.70	17.58	12.74
	49	3.10	3.45	40.65	3.70	3.06	5.10	1.80	7.40	17.52	11.48
	50	3.25	3.80	46.75	2.42	2.96	4.42	1.70	8.30	20.08	13.16
N6	51	3.10	3.40	45.35	4.08	3.78	5.34	2.20	7.80	20.26	14.00
	52	3.20	3.10	54.65	4.04	3.16	4.44	1.64	8.50	18.20	14.12
	53	4.25	3.75	46.10	4.54	4.44	5.14	2.46	7.80	16.60	10.58
	54	3.75	4.00	45.50	2.48	3.30	4.54	1.48	7.50	15.96	10.50
	55	3.65	3.55	44.50	3.50	3.06	4.10	1.50	8.00	16.90	11.36
	56	3.30	3.20	48.30	3.30	2.58	4.36	1.38	6.40	18.08	11.78
	57	3.50	3.85	54.40	3.18	3.24	5.02	2.08	6.70	20.62	14.00
	58	4.05	4.15	61.35	3.16	3.48	5.48	1.52	8.10	20.22	14.30
	59	3.25	3.40	55.10	5.56	3.28	5.84	1.76	6.50	19.60	14.12
	60	3.15	3.30	46.90	3.22	3.34	4.62	1.72	7.50	18.68	13.24
N7	61	2.55	2.95	30.80	2.42	3.08	4.94	1.56	7.10	14.66	9.00
	62	2.35	2.70		3.74	3.22	4.84	1.40	7.20	15.58	10.06
	63	3.20	3.25	48.00	3.14	4.08	5.16	2.06	8.90	19.82	12.44
	64	3.70	4.30	45.15	2.90	3.50	5.52	1.64	7.60	19.06	10.62
	65	3.75	3.35	50.40	3.62	3.88	4.68	1.54	9.10	17.62	11.72
	66	3.90	3.90	59.55	3.70	3.74	5.58	2.12	7.40	17.74	10.74
	67	2.85	3.80	55.05	4.16	3.76	5.82	2.12	7.40	21.82	15.48
	68	2.85	3.30	56.95	3.80	3.40	5.20	1.74	6.40	19.30	14.02
	69	2.80	3.85	53.65	4.30	3.04	5.02	1.74	6.70	18.26	11.48
	70	3.35	3.60	66.50	2.20	3.96	4.74	2.16	7.50	15.32	9.92

Pop.	Tree	Cone Character									
		ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
N8	76	3.25	3.95	48.90	3.60	3.62	5.56	2.02	7.40	14.80	8.98
	79	3.00	3.10	46.20	3.42	2.92	4.72	1.82	5.80	13.32	9.30
	80	3.60	3.60	52.20	3.22	3.56	5.92	2.22	6.90	14.90	11.10
N9	85	2.25	2.30	20.70	2.58	3.84	4.42	2.16	8.00	11.52	7.26
	86	2.90	3.05	28.85	2.78	3.80	4.86	2.30	7.80	11.66	7.28
	87	2.70	2.80	39.00	2.98	3.48	4.28	1.88	7.22	13.52	8.84
	88	2.85	2.75	32.50	1.90	3.54	4.58	1.88	8.50	13.30	8.84
	89	3.35	3.60	48.15	3.16	4.26	5.00	2.30	6.90	12.72	8.82
	90	2.50	3.25	31.25	2.66	4.42	4.94	2.14	8.70	16.62	10.66
N10	91	3.20	3.80	30.55	2.80	2.98	4.16	0.72	9.20	12.42	9.32
	92	3.50	3.85	36.25	2.42	3.10	4.06	1.08	7.60	15.04	11.14
	93	2.55	2.90	35.75	2.32	3.74	4.46	2.48	7.50	15.92	11.46
	94	2.85	3.20	42.65	2.84	3.74	5.00	2.34	7.00	16.40	11.42
	95	2.45	2.80	34.80	2.88	3.42	4.12	1.90	7.80	16.56	12.18
	96	2.65	2.95	35.53	2.44	3.42	4.56	1.86	6.80	15.66	10.36
	97	3.35	3.85	37.70	2.24	4.42	4.62	1.94	8.50	19.86	11.74
	98	2.70	2.90	35.65	2.90	3.12	3.80	1.64	7.00	13.46	9.10
	99	3.45	3.85	42.55	3.08	4.20	4.86	2.22	7.80	17.46	9.88
	100	2.75	3.60	35.85	2.28	3.56	4.82	2.10	6.50	17.38	11.52

APPENDIX VI

TREE MEANS FOR CONVENTIONAL NEEDLE CHARACTERS FROM 21 POPULATIONS OF *Abies lasiocarpa* AND *Abies balsamea*

				Needle	Character	(mm)		
Pop.	Tree	NL	MD	AB	AD	RC	NW	NT
W11	1	11.6	0.47	0.28	0.27	0.20	2.37	1.16
	2	14.6	0.44	0.27	0.28	0.16	2.39	1.21
	3	13.1	0.44	0.27	0.26	0.15	2.13	1.18
	4	15.5	0.37	0.25	0.26	0.14	2.39	1.12
	5	13.0	0.41	0.23	0.21	0.19	2.39	0.97
	6	13.1	0.37	0.24	0.28	0.19	2.32	1.35
	7	12.7	0.50	0.29	0.27	0.16	2.31	1.15
	8	16.1	0.43	0.21	0.24	0.19	2.35	1.06
	9	13.2	0.36	0.21	0.25	0.14	2.06	1.01
W12	1	15.9	0.50	0.29	0.28	0.15	2.24	1.12
	2	16.1	0.45	0.32	0.28	0.15	2.18	1.11
	3	13.9	0.45	0.26	0.27	0.18	2.19	1.04
	4	12.6	0.34	0.23	0.27	0.17	2.07	1.10
	5	11.5	0.38	0.21	0.23	0.18	2.13	1.10
	6	16.3	0.41	0.25	0.25	0.18	2.01	0.95
	7	14.5	0.39	0.26	0.27	0.14	2.00	0.96
	8	13.5	0.43	0.27	0.23	0.19	2.18	0.95
	9	14.3	0.39	0.30	0.26	0.17	2.15	1.13
	10	17.5	0.40	0.29	0.26	0.18	2.12	1.10
	11	13.8	0.38	0.27	0.22	0.16	2.00	0.96
	12	15.9	0.43	0.21	0.21	0.18	2.03	0.85
	13	14.9	0.34	0.33	0.25	0.16	2.02	1.07
	14	13.9	0.34	0.18	0.24	0.17	2.15	1.05
W13	1	13.3	0.42	0.24	0.30	0.14	2.25	1.15
	2	13.4	0.37	0.27	0.23	0.15	2.02	0.90
	3	11.4	0.45	0.27	0.23	0.16	2.28	1.08
	4	10.9	0.41	0.34	0.22	0.17	2.30	1.15
	5	10.4	0.36	0.25	0.27	0.13	2.10	1.03
	6	11.9	0.44	0.27	0.29	0.17	2.26	1.15
	7	14.5	0.36	0.25	0.24	0.15	2.16	0.99
	8	11.1	0.41	0.27	0.31	0.12	2.12	1.08
	9	15.2	0.56	0.26	0.30	0.19	2.61	1.19
	10	13.6	0.41	0.32	0.27	0.17	2.16	1.21
	11	14.2	0.39	0.27	0.29	0.15	2.17	1.11
	12	14.3	0.45	0.31	0.24	0.14	2.16	1.06
	13	15.2	0.49	0.26	0.27	0.21	2.25	1.18
	14	10.4	0.39	0.28	0.26	0.12	1.94	1.04
	15	11.4	0.35	0.20	0.30	0.16	2.49	1.40
W15	1	10.3	0.36	0.23	0.27	0.07	1.57	0.92
	2	12.3	0.40	0.21	0.23	0.08	1.79	0.81
	3	24.3	0.37	0.17	0.20	0.13	1.77	0.72
	4	9.3	0.34	0.19	0.17	0.12	1.66	0.74
	5	13.2	0.32	0.21	0.25	0.08	1.72	0.87
	6	17.4	0.33	0.22	0.19	0.11	1.62	0.82
	7	14.5	0.35	0.21	0.26	0.12	1.70	0.85
	8	16.9	0.38	0.19	0.14	0.12	1.73	0.74
W16	1	13.8	0.44	0.23	0.22	0.26	2.14	1.10
	2	24.6	0.40	0.16	0.20	0.18	1.87	0.69
	3	19.2	0.49	0.33	0.29	0.27	2.20	1.19
	4	20.9	0.53	0.20	0.20	0.21	2.45	0.90
	5	28.1	0.46	0.24	0.20	0.29	2.33	0.89
	6	15.0	0.43	0.21	0.22	0.22	2.06	0.93
	7	21.9	0.43	0.25	0.20	0.21	1.87	0.89
	8	17.3	0.45	0.21	0.16	0.25	2.23	0.90
	9	19.8	0.41	0.24	0.23	0.22	2.16	0.85

				Needle	Character	(mm)		
Pop.	Tree	NL	MD	AB	AD	RC	NW	NT
W17	1	17.6	0.49	0.28	0.23	0.27	2.35	1.17
	2	15.0	0.39	0.21	0.22	0.18	1.94	0.91
	3	18.1	0.53	0.22	0.28	0.21	2.24	0.86
	4	17.2	0.45	0.24	0.26	0.21	2.12	0.92
	5	22.2	0.55	0.25	0.31	0.22	2.55	1.15
	6	19.9	0.51	0.22	0.24	0.23	2.03	0.86
	7	14.1	0.37	0.22	0.19	0.18	1.56	0.76
	8	16.4	0.45	0.22	0.22	0.16	1.81	0.81
	9	21.1	0.57	0.20	0.26	0.25	2.58	1.14
	10	19.3	0.46	0.26	0.21	0.23	2.12	1.04
E18	1	9.4	0.34	0.21	0.20	0.14	1.78	0.78
	2	11.2	0.26	0.18	0.19	0.17	1.66	0.80
	3	9.3	0.37	0.22	0.23	0.13	1.85	0.92
	4	9.1	0.26	0.20	0.22	0.10	1.51	0.74
	5	11.0	0.37	0.27	0.23	0.12	1.72	0.87
	6	7.7	0.32	0.23	0.19	0.09	1.49	0.70
	7	9.7	0.30	0.22	0.19	0.10	1.47	0.79
	8	10.8	0.22	0.13	0.20	0.11	1.54	0.81
	9	11.5	0.32	0.20	0.21	0.13	1.73	0.77
	10	9.4	0.30	0.17	0.23	0.13	1.59	0.82
E19	1	18.3	0.37	0.25	0.22	0.14	1.87	0.95
	2	12.8	0.43	0.20	0.29	0.15	2.45	1.18
	3	10.4	0.30	0.16	0.19	0.13	1.72	0.79
	4	17.6	0.42	0.19	0.21	0.18	1.94	0.70
	5	10.1	0.31	0.20	0.19	0.12	1.86	0.80
	6	16.7	0.38	0.21	0.17	0.16	1.94	0.80
	7	13.9	0.42	0.18	0.15	0.20	2.18	0.88
	8	15.0	0.30	0.23	0.20	0.11	1.52	0.77
	9	10.4	0.38	0.25	0.22	0.16	1.92	1.00
	10	11.9	0.32	0.19	0.24	0.12	1.85	0.86
E20	1	15.0	0.37	0.18	0.22	0.24	2.15	1.07
	2	12.8	0.44	0.23	0.18	0.18	2.03	0.91
	3	18.4	0.27	0.21	0.18	0.15	1.41	0.75
	4	10.7	0.52	0.20	0.22	0.23	2.01	0.92
	5	10.6	0.52	0.20	0.24	0.24	2.07	0.97
	6	11.5	0.31	0.20	0.18	0.17	1.72	0.88
	7	9.5	0.33	0.27	0.23	0.17	1.88	0.97
	8	11.2	0.31	0.24	0.17	0.15	1.51	0.71
	9	10.4	0.44	0.23	0.27	0.22	1.91	1.03
	10	12.2	0.35	0.20	0.16	0.15	1.78	0.78
E21	1	15.8	0.34	0.23	0.20	0.15	1.77	0.86
	2	13.5	0.21	0.14	0.21	0.12	1.61	0.79
	3	17.8	0.39	0.21	0.22	0.16	1.98	0.85
	4	13.4	0.32	0.26	0.21	0.12	1.73	0.86
	5	11.0	0.30	0.20	0.18	0.12	1.47	0.80
	6	18.9	0.43	0.25	0.24	0.17	2.18	1.05
	7	12.3	0.37	0.23	0.22	0.19	2.06	0.97
	8	14.2	0.33	0.19	0.17	0.13	1.74	0.80
E22	1	15.5	0.39	0.21	0.22	0.17	2.08	0.88
	2	15.2	0.33	0.19	0.15	0.14	1.91	0.83
	3	13.0	0.35	0.19	0.21	0.16	1.88	0.89
	4	13.3	0.30	0.19	0.19	0.15	1.85	0.86
	5	12.7	0.32	0.21	0.17	0.11	1.17	0.82
	6	14.9	0.37	0.23	0.23	0.18	2.05	1.05
	7	16.3	0.31	0.22	0.23	0.14	1.77	0.97
	8	14.8	0.29	0.19	0.23	0.13	1.70	0.88

				Needle	Character	(mm)		
Pop.	Tree	NL	MD	AB	AD	RC	NW	NT
E22	9	13.6	0.34	0.18	0.21	0.15	1.91	0.89
	10	8.0	0.30	0.23	0.21	0.14	1.48	0.80
E23	1	10.3	0.34	0.25	0.25	0.12	1.71	0.94
	2	13.1	0.33	0.17	0.23	0.14	2.17	0.94
	3	16.4	0.28	0.19	0.22	0.11	1.73	0.85
	4	13.2	0.37	0.21	0.25	0.18	1.83	0.89
	5	10.6	0.33	0.25	0.27	0.10	1.74	1.05
S24	1	12.1	0.31	0.20	0.21	0.19	1.67	0.92
	2	13.5	0.36	0.19	0.19	0.19	1.75	0.74
	3	14.8	0.38	0.18	0.17	0.23	1.93	0.86
	4	13.3	0.38	0.17	0.17	0.25	2.07	0.82
	5	13.5	0.44	0.19	0.20	0.25	2.19	0.91
	6	16.4	0.34	0.22	0.16	0.18	1.81	0.83
	7	13.7	0.37	0.29	0.22	0.21	1.81	0.89
	8	10.0	0.30	0.23	0.17	0.16	1.58	0.85
	9	13.8	0.32	0.24	0.24	0.18	1.91	1.09
	10	14.5	0.46	0.24	0.24	0.23	2.33	1.11
S25	1	8.2	0.29	0.21	0.17	0.14	1.50	0.67
	2	11.1	0.27	0.16	0.12	0.15	1.46	0.72
	3	13.6	0.28	0.18	0.17	0.12	1.42	0.68
	4	14.3	0.36	0.18	0.20	0.18	1.92	0.92
	5	10.3	0.30	0.19	0.18	0.14	1.38	0.70
	6	8.1	0.33	0.21	0.22	0.13	1.61	0.86
	7	9.3	0.24	0.15	0.14	0.13	1.43	0.68
	8	15.9	0.24	0.21	0.57	0.22	1.98	0.93
	9	10.7	0.25	0.20	0.16	0.10	1.45	0.71
	10	9.9	0.26	0.17	0.15	0.09	1.41	0.65
B26	1	13.4	0.29	0.22	0.15	0.14	1.61	0.75
	2	12.5	0.28	0.20	0.17	0.14	1.51	0.77
	3	9.4	0.30	0.21	0.16	0.14	1.45	0.72
	4	11.7	0.30	0.18	0.17	0.15	1.58	0.82
	5	12.7	0.34	0.29	0.25	0.14	1.71	1.01
	6	8.4	0.22	0.19	0.17	0.07	1.21	0.64
	7	8.9	0.29	0.20	0.18	0.14	1.52	0.77
	8	12.1	0.32	0.20	0.19	0.16	1.93	0.94
	9	9.4	0.28	0.16	0.17	0.15	1.48	0.77
	10	7.2	0.24	0.18	0.17	0.08	1.27	0.71
	11	10.4	0.24	0.19	0.16	0.12	1.28	0.63
	12	8.6	0.28	0.17	0.14	0.16	1.53	0.74
	13	7.1	0.23	0.18	0.18	0.11	1.28	0.72
	14	9.4	0.27	0.18	0.17	0.13	1.47	0.78
	15	8.0	0.25	0.20	0.18	0.10	1.34	0.74
B27	1	13.6	0.28	0.22	0.20	0.01	1.52	0.89
	2	12.1	0.28	0.21	0.21	0.11	1.55	0.78
	3	14.1	0.36	0.23	0.21	0.14	1.76	0.83
	4	12.1	0.34	0.22	0.22	0.16	1.90	0.97
	5	15.3	0.35	0.21	0.18	0.16	1.76	0.78
	6	12.3	0.33	0.21	0.20	0.19	1.78	1.02
	7	12.4	0.40	0.21	0.26	0.22	1.71	1.11
	8	10.3	0.42	0.22	0.27	0.22	1.97	1.07
	9	10.4	0.36	0.22	0.22	0.16	1.79	0.95
	10	14.7	0.30	0.19	0.19	0.17	1.77	0.92
	11	9.1	0.36	0.23	0.26	0.13	1.70	0.93
	12	13.3	0.35	0.20	0.18	0.16	1.99	0.97
	13	15.1	0.33	0.22	0.20	0.17	1.92	1.03
	14	14.7	0.31	0.20	0.18	0.16	1.76	0.97

				Needle	Character	(mm)		
Pop.	Tree	NL	MD	AB	AD	RC	NW	NT
B27	15	11.7	0.31	0.19	0.16	0.18	1.55	0.77
B28	1	10.4	0.25	0.15	0.16	0.11	1.35	0.67
	2	14.7	0.26	0.16	0.16	0.12	1.50	0.64
	3	10.1	0.24	0.14	0.14	0.11	1.53	0.70
	4	17.1	0.29	0.17	0.16	0.16	1.52	0.64
	5	11.8	0.32	0.18	0.19	0.15	1.84	0.93
	6	10.3	0.29	0.20	0.20	0.12	1.56	0.91
	7	13.4	0.25	0.18	0.16	0.11	1.52	0.71
	8	10.8	0.29	0.17	0.20	0.13	1.60	0.89
	9	19.8	0.38	0.17	0.20	0.16	1.98	0.99
	10	15.2	0.33	0.15	0.17	0.16	1.66	0.68
B29	1	14.6	0.30	0.16	0.15	0.17	2.01	0.89
	2	15.0	0.26	0.16	0.18	0.14	1.66	0.89
	3	17.2	0.26	0.15	0.19	0.15	1.82	0.84
	4	13.2	0.32	0.17	0.18	0.20	1.86	1.01
	5	14.6	0.27	0.16	0.15	0.14	1.51	0.73
	6	18.7	0.36	0.11	0.23	0.18	2.21	1.06
	7	13.4	0.30	0.17	0.16	0.14	1.67	0.77
	8	14.2	0.29	0.13	0.19	0.17	1.81	0.88
	9	18.0	0.31	0.12	0.25	0.16	2.10	1.10
	10	16.1	0.29	0.17	0.18	0.16	1.66	0.85
B30	1	13.8	0.28	0.17	0.15	0.16	1.74	0.86
	2	12.5	0.33	0.21	0.21	0.15	1.72	0.95
	3	13.5	0.29	0.17	0.21	0.14	1.79	0.95
	4	15.6	0.32	0.15	0.21	0.15	2.09	0.94
	5	14.3	0.34	0.14	0.21	0.15	2.06	1.02
	6	13.6	0.35	0.21	0.22	0.16	1.82	0.93
	7	15.4	0.28	0.15	0.16	0.14	1.66	0.76
	8	13.5	0.28	0.18	0.20	0.13	1.67	0.92
	9	9.9	0.26	0.17	0.17	0.12	1.47	0.80
B31	1	12.6	0.25	0.19	0.16	0.10	1.49	0.74
	2	11.5	0.24	0.18	0.16	0.09	1.48	0.72
	3	12.6	0.37	0.17	0.19	0.15	2.11	0.97
	4	13.0	0.29	0.18	0.22	0.16	1.81	1.02
	5	10.1	0.25	0.19	0.19	0.11	1.49	0.90
	6	9.7	0.26	0.17	0.19	0.13	1.51	0.86
	7	11.7	0.30	0.21	0.22	0.12	1.75	0.94
	8	9.8	0.33	0.17	0.20	0.12	1.76	0.86
	9	10.8	0.23	0.20	0.13	0.13	1.54	0.88
B32	1	12.2	0.28	0.17	0.17	0.12	1.55	0.69
	2	7.1	0.21	0.17	0.15	0.08	1.27	0.73
	3	8.4	0.20	0.17	0.15	0.07	1.19	0.61
	4	11.7	0.25	0.19	0.16	0.11	1.55	0.82
	5	9.3	0.32	0.15	0.16	0.14	1.67	0.85
	6	10.9	0.27	0.21	0.17	0.12	1.54	0.80
	7	12.8	0.34	0.17	0.19	0.17	1.85	0.98
	8	9.1	0.23	0.16	0.14	0.10	1.32	0.65
	9	13.6	0.30	0.18	0.18	0.17	1.74	0.38
	10	11.7	0.31	0.21	0.21	0.13	1.71	0.88

APPENDIX VII

TREE MEANS FOR CONE CHARACTERS FROM 13 POPULATIONS OF *Abies lasiocarpa* AND *Abies balsamea*

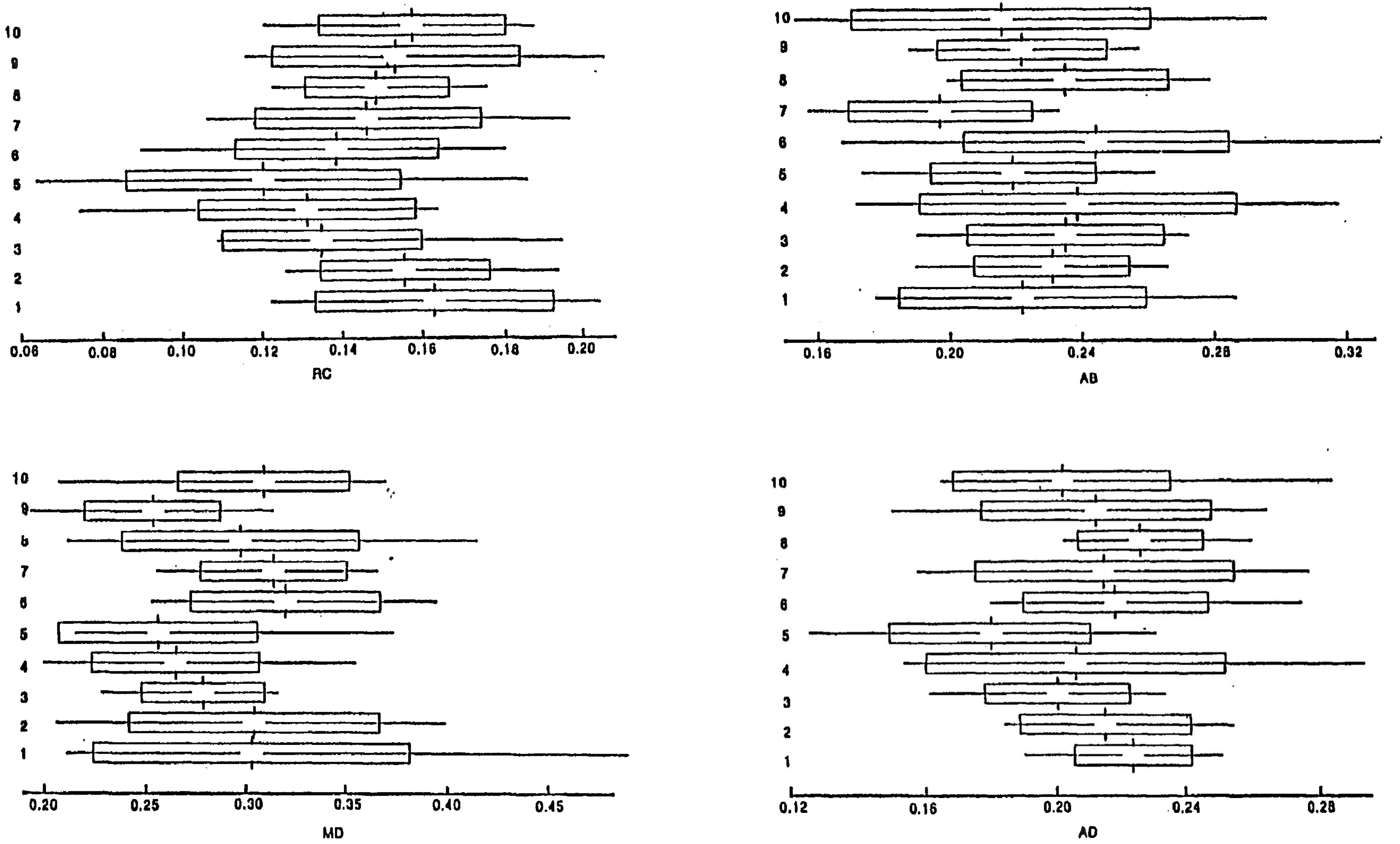
		Cone Character									
Pop.	Tree	ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
W11	1	3.9	3.7	64.0	3.1	4.7	4.9	2.7	5.2	27.1	17.6
	2	3.0	3.0	68.0	3.4	4.3	4.4	2.8	6.8	24.1	14.7
	3	3.6	3.2	75.0	3.8	4.9	4.3	2.6	6.8	22.6	13.3
	4	3.3	3.1	90.0	3.4	5.1	4.3	3.8	6.6	22.6	17.0
	5	2.8	2.8	63.0	2.2	4.1	3.9	1.9	4.3	21.7	13.7
	6	3.8	3.5	92.0	3.0	5.3	4.9	3.2	5.9	23.4	16.1
	7	3.2	3.7	49.0	2.9	5.2	5.7	3.1	6.8	19.8	11.9
	8	3.6	3.5	76.0	3.5	7.1	4.6	3.5	8.0	21.9	15.2
	9	3.7	3.4	89.0	2.8	5.1	4.0	4.2	4.5	22.2	16.3
W12	1	2.9	2.7	62.0	3.2	4.3	4.6	2.3	5.4	17.7	12.4
	2	3.8	3.6	89.0	4.2	3.8	4.7	2.3	5.8	19.9	13.8
	3	3.6	3.2	85.0	3.3	4.6	4.6	3.1	5.7	25.1	15.9
	4	3.6	3.4	75.0	2.9	4.2	4.4	2.4	6.3	19.4	14.2
	5	2.6	2.6	53.0	2.9	4.4	4.3	2.4	5.5	18.7	12.6
	6	3.1	3.3	73.0	3.3	4.4	5.0	2.9	5.8	22.3	15.4
	7	2.7	2.4	59.0	2.9	4.9	5.1	3.2	6.2	19.0	11.8
	8	3.2	3.1	66.0	2.6	6.4	4.4	5.4	4.5	19.7	14.3
	9	3.6	3.4	76.0	3.3	5.0	4.4	3.1	8.0	18.8	12.3
	10	3.3	3.1	77.0	3.4	4.6	5.1	2.2	6.5	23.0	16.8
	11	3.1	2.8	73.0	2.7	3.5	4.0	1.7	7.4	19.1	11.2
	12	3.1	2.7	60.0	3.2	4.7	4.4	2.7	6.2	19.8	13.3
	13	2.6	2.7	62.0	3.2	3.6	4.8	2.5	4.4	19.8	12.9
	14	2.9	2.8	62.0	3.1	4.6	4.6	2.6	6.7	16.8	9.9
W13	1	2.8	2.9	67.0	3.0	4.0	5.0	2.3	6.4	19.3	11.8
	2	2.8	2.7	54.0	3.0	3.1	3.8	2.0	5.4	18.3	11.5
	3	3.0	2.5	58.0	2.1	3.6	3.7	1.6	7.3	19.2	12.6
	4	3.2	3.0	67.0	2.8	4.2	4.6	2.5	5.1	22.4	16.1
	5	2.7	2.7	52.0	2.4	4.8	4.6	2.5	4.7	18.4	12.9
	6	2.9	2.7	60.0	2.5	5.5	5.0	3.1	4.8	21.6	14.8
	7	2.6	2.3	63.0	3.1	3.7	4.1	2.1	5.8	20.6	13.3
	8	2.8	2.8	56.0	2.2	5.4	5.1	2.8	5.4	17.8	10.2
	9	3.1	2.9	74.0	2.4	5.4	5.6	2.8	5.9	22.6	15.2
	10	2.7	2.8	55.0	2.1	3.7	4.4	1.8	7.1	18.4	11.8
	11	3.4	3.2	68.0	2.4	5.3	3.9	3.9	6.3	19.5	12.5
	12	3.0	2.8	67.0	2.2	4.4	4.5	2.5	5.3	17.8	11.2
	13	3.7	3.7	79.0	3.5	5.1	5.4	2.7	5.5	22.8	13.4
	14	2.8	2.7	62.0	3.1	4.2	4.1	2.5	6.5	19.8	12.5
	15	2.7	2.6	54.0	2.8	4.0	4.5	2.6	5.9	17.5	10.8
W14	1	3.8	3.4	79.0	3.8	5.2	4.2	2.4	5.8	23.8	16.8
	2	3.7	3.4	86.0	2.5	6.9	5.0	4.7	5.8	24.8	18.2
	3	3.1	2.7	86.0	3.5	4.0	4.1	2.2	6.7	20.5	13.3
	4	2.8	2.8	78.0	3.7	4.4	5.1	2.4	6.7	23.5	13.8
	5	3.4	2.9	88.0	5.5	6.6	4.8	5.6	6.1	25.7	16.3
	6	3.9	3.5	78.0	2.5	6.0	5.0	4.3	6.3	20.0	13.3
	7	3.3	2.7	51.0	2.3	3.5	4.4	2.1	5.2	18.8	12.3
	8	2.9	2.8	64.0	2.1	4.5	4.9	2.5	6.1	18.9	13.1
	9	3.5	3.2	71.0	2.9	4.1	4.8	2.4	6.2	20.9	13.9
	10	2.9	3.0	62.0	2.9	4.4	5.5	2.3	5.8	22.2	12.8

		Cone Character									
Pop.	Tree	ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
W16	1	3.6	2.9	73.4	3.2	5.6	5.1	4.4	6.3	20.9	14.2
	2	3.9	2.9	82.0	3.1	5.0	5.2	3.8	5.9	23.0	18.3
	3	3.2	2.5	66.8	3.4	5.9	5.0	4.6	6.3	21.6	13.8
	4	4.0	3.6	84.8	2.5	5.6	5.6	4.0	6.0	22.6	17.5
	5	3.0	2.5	71.9	3.2	4.5	4.7	3.7	5.3	20.2	15.1
	6	3.0	2.3	70.2	2.7	5.5	5.0	4.4	6.4	21.3	13.2
	7	3.5	2.6	80.3	3.0	5.0	5.5	4.1	6.3	22.3	13.9
	8	3.1	2.5	71.8	3.6	5.1	5.3	3.4	7.4	21.9	13.0
	9	2.9	2.6	61.6	2.8	4.5	5.4	3.7	6.1	19.4	11.6
	10	3.5	2.7	74.2	3.8	5.9	5.8	3.9	9.0	25.3	17.5
E21	1	3.0	2.2	65.0	3.5	4.6	4.6	2.7	6.2	17.5	13.9
	2	3.2	3.3	79.0	3.9	4.7	4.4	3.2	7.4	20.7	16.4
	3	3.2	2.4	66.0	3.9	3.4	4.9	2.4	5.7	22.8	17.1
	4	2.7	2.4	55.0	3.4	3.5	4.4	2.4	6.8	17.2	13.9
	5	2.9	2.8	52.0	3.4	2.9	4.4	2.2	5.0	17.4	13.9
	6	3.2	2.8	71.0	3.4	5.7	5.4	3.5	6.1	21.9	15.4
	7	2.4	2.6	79.0	3.9	4.4	3.5	3.7	6.2	19.0	14.0
	8	3.4	2.7	75.0	3.7	3.9	4.7	2.2	6.9	21.0	17.3
E22	1	2.6	2.4	42.0	3.5	4.2	4.2	2.5	6.7	18.9	12.1
	2	2.6	2.5	43.0	3.5	2.9	3.7	1.7	6.4	15.3	10.6
	3	2.6	2.8	64.0	3.0	4.1	4.1	2.4	8.2	18.5	12.5
	4	2.7	2.6	45.0	3.9	3.0	4.1	1.9	6.0	15.8	11.2
	5	2.7	2.5	49.0	2.7	3.4	3.7	2.4	6.6	18.7	12.9
	6	3.0	2.7	58.0	2.5	3.2	3.5	2.2	6.6	15.4	10.2
	7	2.6	2.3	60.0	3.2	3.7	4.2	2.5	5.6	19.0	12.9
	8	2.4	2.4	42.0	2.5	2.5	3.5	2.0	5.7	13.5	9.1
	9	2.7	2.3	57.0	3.7	3.4	3.7	2.0	7.2	19.6	12.8
	10	2.7	2.3	48.0	2.9	2.9	3.9	2.0	6.4	15.1	9.4
E23	1	3.3	3.0	87.0	5.1	4.7	5.6	3.5	6.1	24.7	19.6
	2	2.7	2.7	65.0	2.5	3.4	4.6	1.7	7.2	21.6	18.0
	3	2.9	2.7	75.0	4.2	3.9	4.9	2.7	6.1	21.5	16.3
	4	2.2	2.4	46.0	2.7	3.5	4.9	2.2	7.0	9.4	6.7
	5	4.1	3.6	97.0	5.1	7.1	4.6	5.1	7.8	23.0	19.7
B28	1	2.2	2.2	56.0	2.1	2.2	4.3	2.4	5.7	13.7	13.9
	2	2.1	2.0	56.0	2.8	2.1	3.6	2.1	6.9	15.5	15.9
	3	1.9	1.8	53.0	2.2	2.5	4.6	2.6	6.7	14.8	14.4
	4	2.4	2.2	55.0	2.0	2.2	4.0	2.5	5.1	14.3	15.6
	5	2.0	2.1	50.0	2.0	2.0	3.9	2.2	5.8	13.6	12.5
	6	2.2	1.9	48.0	2.0	2.3	4.1	2.4	6.2	12.6	12.4
	7	2.6	2.2	64.0	2.3	2.3	4.5	2.4	5.8	15.6	17.0
	8	2.4	2.3	52.0	2.5	2.2	4.0	2.3	6.6	14.7	13.8
	9	3.0	2.5	73.0	2.2	2.7	4.8	3.1	5.2	16.4	18.8
	10	2.8	2.6	71.0	2.6	2.9	4.9	3.1	5.5	17.4	16.3
B29	1	2.8	2.6	66.0	2.8	3.0	5.1	3.3	5.5	15.2	15.2
	2	2.1	1.8	48.0	2.9	2.2	4.4	2.4	5.6	12.6	12.8
	3	3.0	2.6	69.0	2.4	2.5	4.4	2.6	6.0	16.1	16.0
	4	2.6	2.5	60.0	2.4	2.4	4.4	2.6	5.4	14.5	16.6
	5	2.4	2.5	58.0	3.9	2.7	4.9	3.0	5.1	13.7	15.0
	6	3.2	2.8	72.0	2.8	2.9	5.0	3.1	6.7	15.0	16.5
	7	2.2	2.5	51.0	3.0	2.2	4.7	2.4	5.0	15.6	14.3
	8	2.5	2.1	57.0	2.9	2.7	4.8	2.7	6.1	13.8	14.4
	9	2.7	2.8	63.0	3.0	2.8	5.1	2.9	6.3	16.2	15.7
	10	2.7	2.3	60.0	2.9	2.3	4.5	2.5	5.9	14.7	15.6

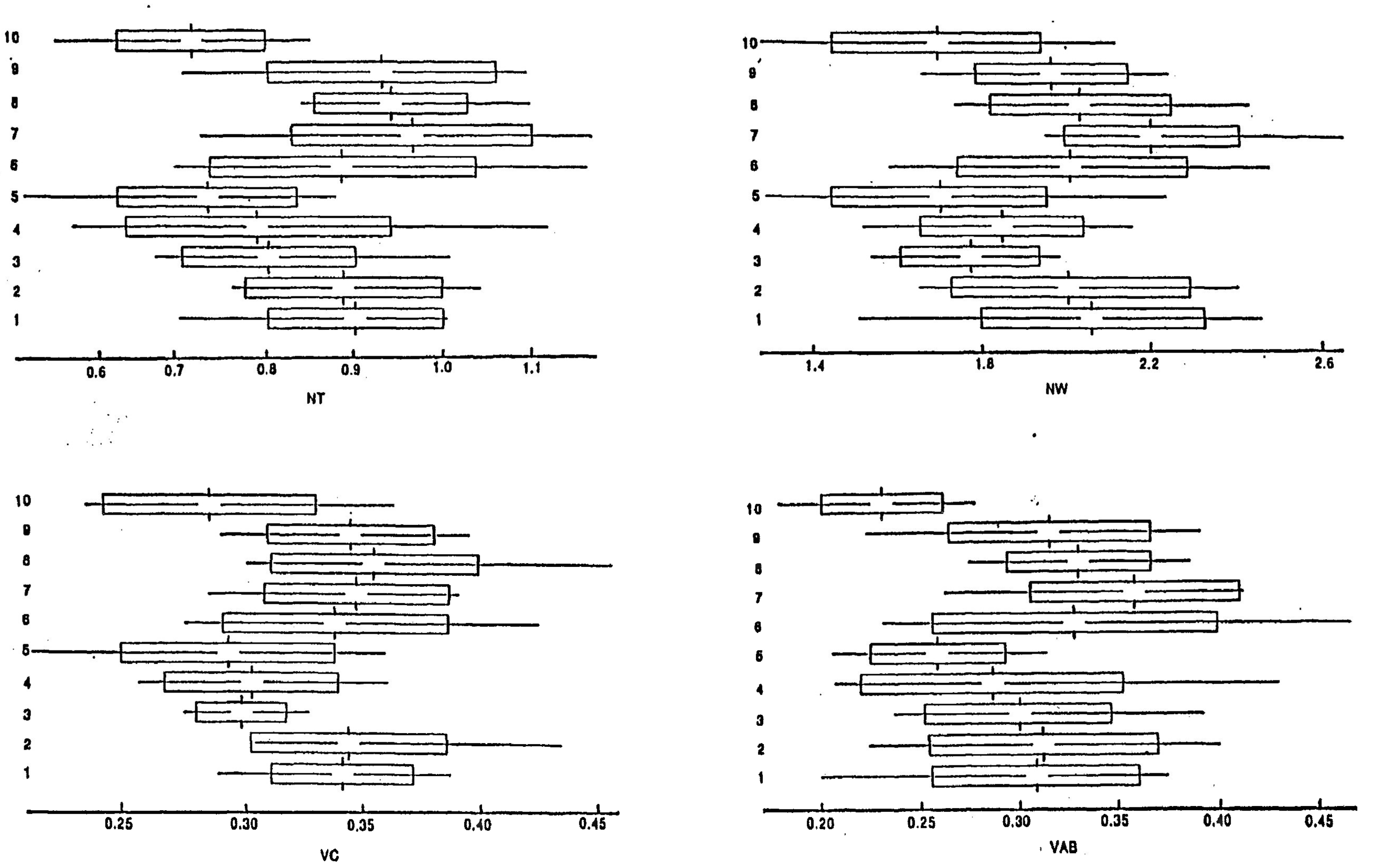
		Cone Character									
Pop.	Tree	ADB (mm)	ADM (mm)	CL (mm)	AL (mm)	BL (mm)	BW (mm)	D (mm)	An	SW (mm)	SL (mm)
B30	1	2.4	2.4	55.0	2.9	2.4	4.6	2.8	4.9	11.9	12.3
	2	2.3	2.0	42.0	2.7	2.5	4.5	2.9	5.2	11.0	8.8
	3	2.6	2.4	40.0	2.5	2.5	4.3	2.7	5.5	11.6	10.2
	4	2.8	2.5	46.0	3.3	2.8	5.0	2.9	6.2	11.4	10.6
	5	2.4	2.4	45.0	3.9	2.6	5.1	2.9	5.3	12.9	10.2
	6	2.7	2.4	49.0	2.9	2.4	4.4	2.7	5.5	12.9	11.4
	7	2.4	2.2	49.0	2.8	2.4	4.8	2.9	4.6	12.6	11.7
	8	2.8	2.3	54.0	3.2	2.5	4.3	2.6	6.2	12.3	11.7
	9	2.2	2.7	43.0	3.0	2.6	4.6	2.8	5.7	12.4	12.1
	10	2.3	2.2	37.0	2.7	2.9	4.2	2.8	7.5	12.6	12.2
B31	1	2.6	2.4	59.0	3.3	3.2	5.2	3.1	7.5	15.2	13.0
	2	2.1	2.1	49.0	2.8	2.7	4.5	2.7	6.7	14.4	12.9
	3	2.4	2.2	58.0	3.1	2.8	5.0	2.9	6.1	13.5	11.4
	4	2.1	2.1	49.0	3.6	2.6	4.9	2.7	6.7	14.7	12.3
	5	2.2	2.1	57.0	3.6	2.0	4.7	2.4	5.0	14.4	11.3
	6	2.3	2.0	47.0	2.5	2.5	4.5	2.6	6.2	15.0	11.9
	7	2.7	2.1	58.0	2.8	2.8	4.7	2.7	7.9	15.8	14.8
	8	2.2	2.0	49.0	3.0	2.4	4.5	2.6	5.9	13.5	11.1
	9	2.3	1.9	43.0	2.5	2.6	4.5	2.5	7.6	13.5	12.5
	10	2.4	2.4	51.0	3.2	2.6	4.4	2.7	7.0	14.3	12.3
B32	1	1.9	2.9	34.0	2.3	2.2	4.2	2.5	4.8	12.2	10.5
	2	2.2	2.5	45.0	1.5	2.3	4.3	2.5	5.0	12.3	12.4
	3	2.6	3.0	44.0	2.9	2.5	4.2	2.5	6.7	13.6	12.9
	4	2.4	2.2	40.0	2.3	2.5	4.6	2.5	6.7	12.0	11.1
	5	2.1	2.3	49.0	2.6	2.4	4.2	2.3	6.6	12.8	12.9
	6	2.8	2.6	53.0	2.4	2.0	4.1	2.2	5.2	13.5	12.1
	7	2.3	2.7	37.0	3.0	2.4	4.0	2.5	6.3	12.3	10.7
	8	2.4	2.6	64.0	3.1	2.5	4.9	2.8	5.3	14.8	14.4
	9	2.7	2.4	57.0	3.3	2.4	4.4	2.5	6.1	14.8	13.0
	10	2.4	2.3	49.0	1.8	2.5	3.8	2.5	7.4	13.6	13.7

APPENDIX VIII

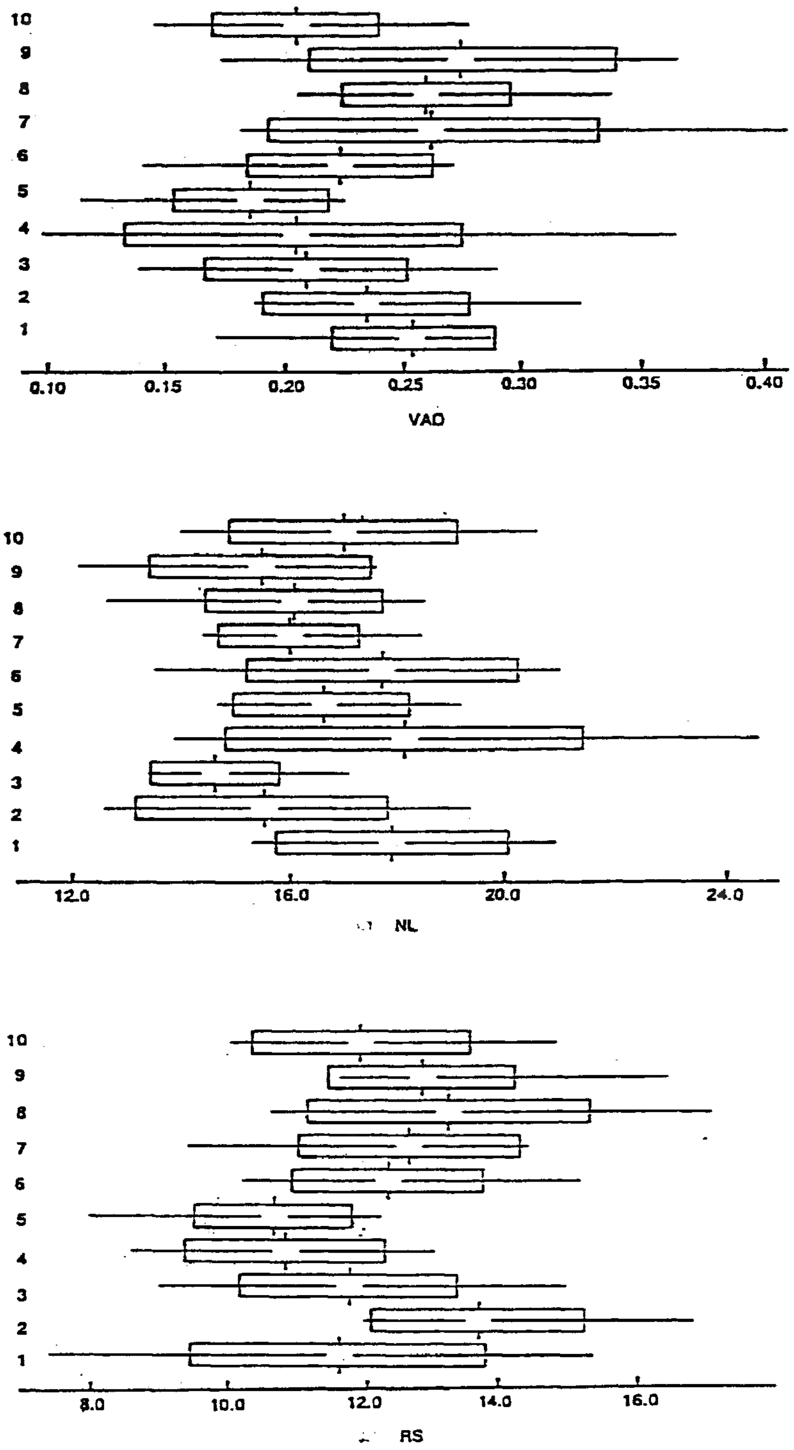
HUBBS DIAGRAMS FOR 11 NEEDLE CHARACTERS FROM 10 NORTHERN POPULATIONS OF *Abies lasiocarpa*



Appendix VIII a. Means, ranges and standard deviations of four quantitative needle characters for ten northern populations of *Abies lasiocarpa*. Vertical lines indicate mean values; horizontal lines indicate the range of observed values; broad bars represent one standard deviation on each side of the mean. RC. Resin canal diameter. AB. Distance from the resin canal to the abaxial needle surface. MD. Distance from the resin canal to the needle margin. AD. Distance from the resin canal to the adaxial needle surface. All scales are in millimetres.



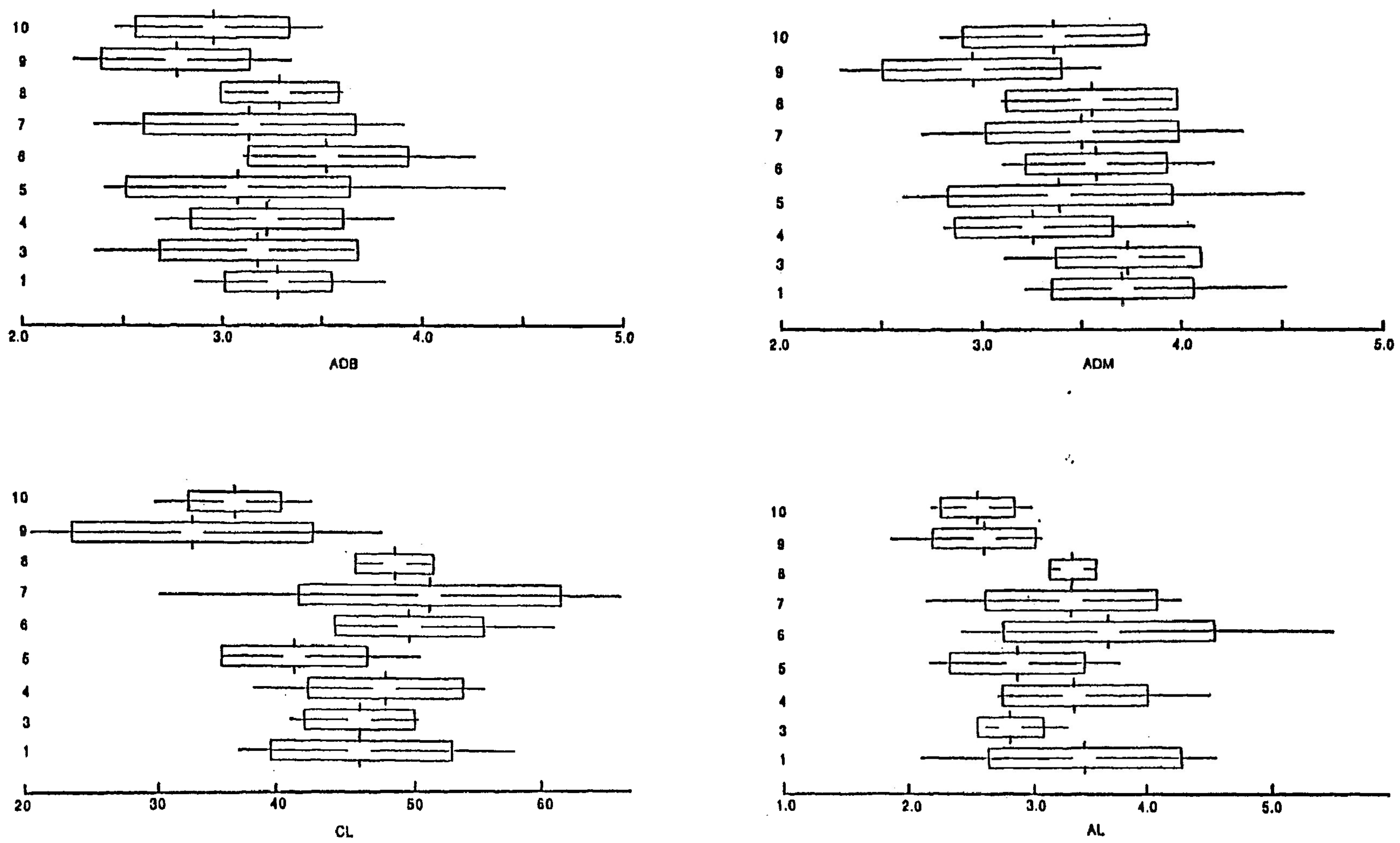
Appendix VIII b. Means, ranges and standard deviations of four quantitative needle characters for ten northern populations of *Abies lasiocarpa*. Vertical lines indicate mean values; horizontal lines indicate the range of observed values; broad bars represent one standard deviation on each side of the mean.. NT. Needle thickness. NW. Needle width. VC. Diameter of the vascular cylinder. VAB. Distance from the vascular cylinder to the abaxial needle surface. All scales are in millimetres.



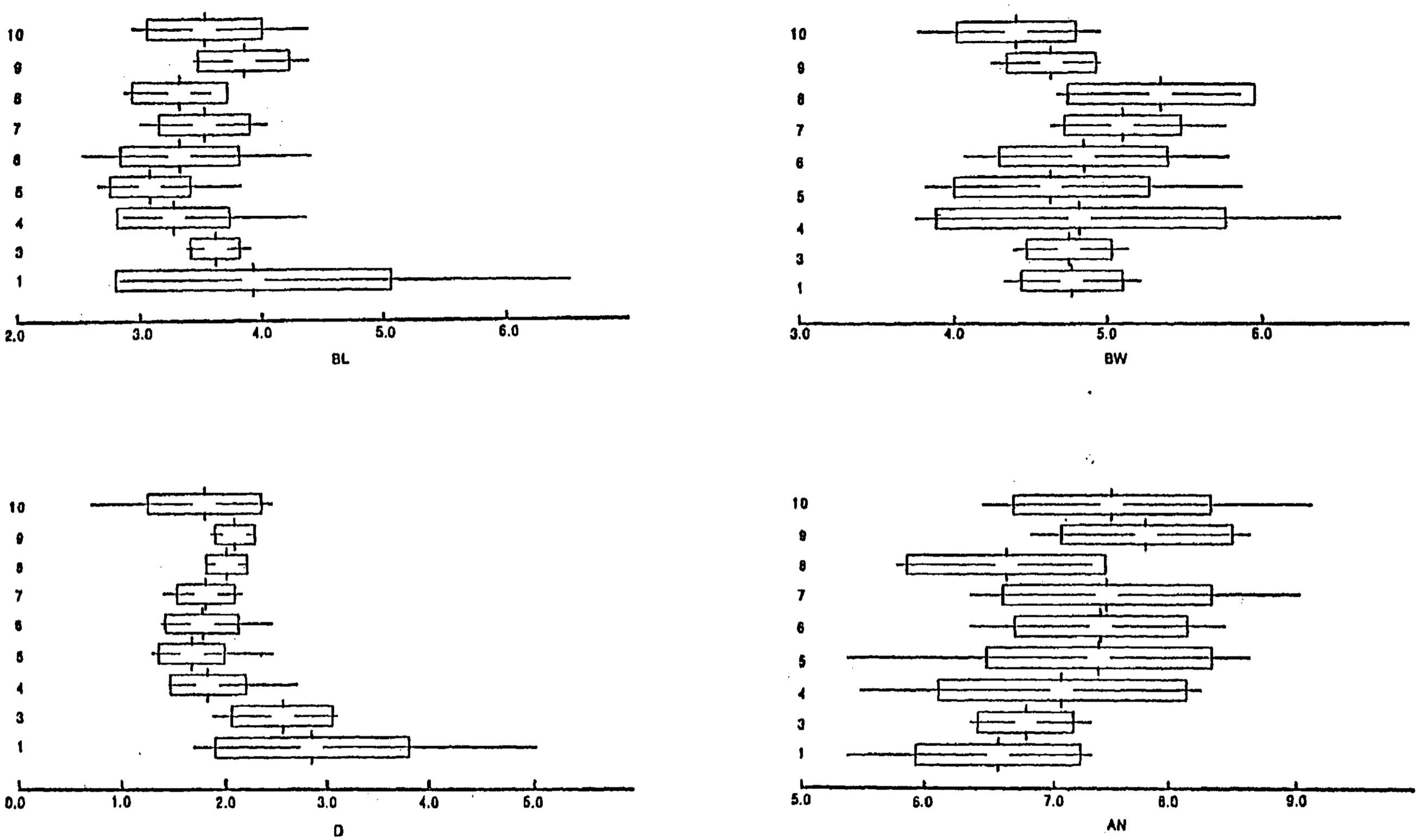
Appendix VIII c. Means, ranges and standard deviations of three quantitative needle characters for ten northern populations of *Abies lasiocarpa*. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean. VAD. Distance from the vascular cylinder to the adaxial needle surface. NL. Needle length. RS. Number of rows of stomata on the adaxial needle surface. Scales for VAD and NL are in millimetres.

APPENDIX IX

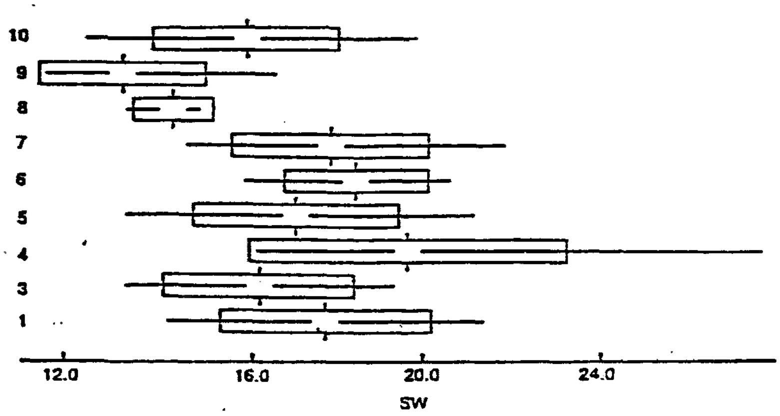
HUBBS DIAGRAMS FOR 10 CONE CHARACTERS FROM 9 NORTHERN POPULATIONS OF *Abies lasiocarpa*

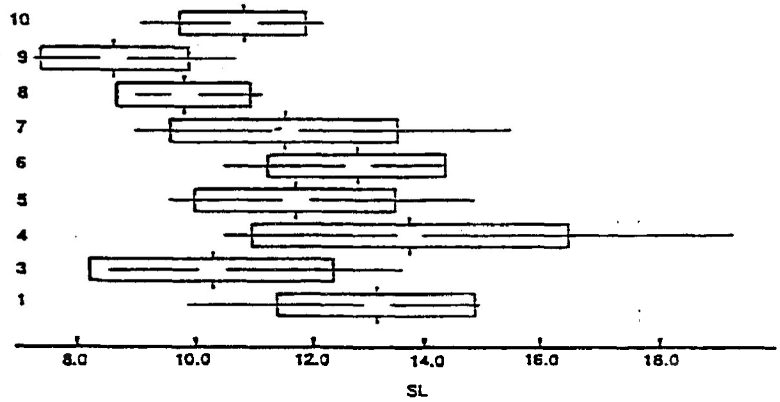


Appendix IX a. Means, ranges and standard deviations of four quantitative cone characters for nine northern populations of *Abies lasiocarpa*. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean. ADB. Diameter of the seed cone axis at the base. ADM. Diameter of the seed cone axis at the midpoint. CL. Cone length. AL. Bract awn length. All scales are in millimetres.



Appendix IX b. Means, ranges and standard deviations of four quantitative cone characters for nine northern populations of *Abies lasiocarpa*. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean. BL.Cone-scale bract length. BW. Cone-scale bract width. D. Distance from the widest point of the bract to the fusion point. AN. Angle of the apex of the cone-scale bract excluding the awn. All scales are in millimetres except that of AN which is in degrees.





Appendix IX c. Means, ranges and standard deviations of two quantitative cone characters for nine northern populations of *Abies lasiocarpa*. The vertical lines indicate mean values; the horizontal lines indicate the range of observed values; the broad bars represent one standard deviation on each side of the mean. SW. Cone-scale width. SL. Cone-scale length. Scales are in millimetres.