

PHENOTYPIC VARIATION IN LARIX LYALLII AND
RELATIONSHIPS IN THE LARCH GENUS

by



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Submitted in Partial Fulfillment of the
Requirements for the Degree of
Masters of Science in Forestry



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ABSTRACT

Bakowsky, O. A. 1988. Phenotypic variation in Larix lyallii and relationships in the larch genus.

Key Words: cone characters, Larix Mill., Larix lyallii Parl., Larix occidentalis Nutt., needle characters, phenotypic variation

Larix lyallii Parl. (alpine larch) is a small to medium tree restricted to the timberline zone of the mountainous regions of the Pacific Northwest of the United States and the adjacent southwest of Canada. To examine the pattern of phenotypic variation expressed in alpine larch cones and needles, field collections were made in 1985 and 1986 from 11 populations covering most of the species' range. Additionally, samples were collected from 6 populations of L. occidentalis Nutt. (western larch) to compare these two closely related species.

Morphometric analyses were based on 45 needle and 11 cone characters. Alpine larch cones averaged 32.2 mm in length, 14.8 mm in diameter and possessed close to 50 cone scales. Short shoot needles were 26.0 mm long, 0.7 mm wide and 0.5 mm thick. An average of 7.8 epithelial cells surrounded each of the two resin canals in the needles.

Both principal component analysis (PCA) and discriminant analysis (DA) distinguished the two species. PCA of the alpine larch needle data indicated limited differentiation between populations. The principal components could not be correlated to latitude, longitude or elevation. DA variation expressed in the needle and cone characters was difficult to interpret; neighbouring populations were often more distinct than distant ones. Microgeographic variation in site and climate

may influence alpine larch populations to such an extent that broad geographic patterns, if present, were not detectable. Alternatively, genetic drift may be responsible for the variation displayed. Overall, phenotypic variation within L. lyallii appears to be less than that observed in L. occidentalis.

The general methodology used to examine alpine and western larch populations was applied to herbarium specimens made from the living collection of larches of the Arnold Arboretum of Harvard University, representing 7 of the 10 recognized species of Larix Mill. Based on the limited number of samples available, DA correctly classified all specimens into their correct species groups. The expressed pattern of variation was loosely associated with the geographic distribution of the species. DA, and PCA, also distinguished, and thus provided some support for, the two proposed sections of Larix, Multiseriales Patschke and Pauciseriales Patschke.

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INTRODUCTION

Of the three Larix Mill. species native to North America, Larix lyallii Parl., alpine larch, is the least studied. Work conducted to date on alpine larch has focused on examining the distribution and ecology of the species (Arno 1970) and identification of putative hybrids of L. lyallii and the closely related species L. occidentalis Nutt. in areas of range overlap (Carlson 1965; Knudsen 1966).

Carlson (1965) examined the morphological variation of a few traits of western and alpine larch but his sample was limited to six trees from a single population of each species. In recent years, work has been conducted to determine the extent and nature of genetic variation in populations of L. occidentalis, or western larch, (Rehfeldt 1980, 1982; Fins and Seeb 1986) but no studies have examined the differentiation among alpine larch populations.

Alpine larch's distribution is extremely limited, both geographically and ecologically. This distribution may be indicative of, and reflected in, low overall levels of phenotypic variability within the species. The extremely discontinuous nature of L. lyallii's distribution and large number of outlying populations would have provided ample

opportunity for a disjunct pattern of variation to have developed and be maintained between populations. Because many of the populations of alpine larch are small and isolated, genetic drift may be an important force in determining the species' variation pattern.

The objective of this study was to examine the extent and pattern of phenotypic variation among populations in needle and cone characteristics of alpine larch. The morphological variation expressed by these characters provides an indication of inter- and intrapopulation variability inherent in L. lyallii. This should help clarify the present status of the species and may provide clues to the species history. Additionally, several populations of L. occidentalis originating near the range of alpine larch were studied in order to compare the patterns of variation of the two species and examine their relationship. Finally, the methodology used in the examination of alpine and western larch cones and needles was extended to a brief survey of seven additional arboretum grown taxa of the genus Larix in an attempt to draw some inferences on the relationship of L. lyallii and L. occidentalis to the rest of the larches.

LITERATURE REVIEW

LARIX LYALLIINomenclature

Larix lyallii was not discovered until 1860 when the boundary between British Columbia and the United States was surveyed. Dr. David Lyall, surgeon and naturalist to the North American Boundary Commission initially encountered the species growing with Pinus flexilis Torr. (assumed to be P. albicaulis Engelm.) from 1980 to 2135 m in the Cascade Mountains. The species was subsequently found by Dr. Lyall in both the Galton Range and the Rocky Mountains (Lyall 1863).

A description of the species and the binomial Larix lyallii were published in 1863 by Parlatores (Arno 1970). In 1868 Parlatores transferred Larix spp. to Pinus but this treatment was not accepted. P. lyallii is the only synonym encountered.

Very early reports from the range of L. lyallii called the species Lyall larch (Leiberg 1900) and Mountain larch (Ayres 1900). These names are, however, rarely used. The common name alpine larch was used by Sudworth in 1927. The U. S. Forest Service Check List suggests the term subalpine larch be used since 'alpine' generally refers to treeless areas (Little, 1953). Arno (1970) argues that the species inhabits areas

that would otherwise be classified as alpine. The names alpine larch and subalpine larch are both commonly used. This thesis follows Hosie (1979) who reflects modern Canadian usage. No subspecific taxa have been described.

Description

Alpine larch is generally considered a small tree although large individuals are occasionally encountered. Several early reports described the species as stunted, rarely exceeding 12 m in height or diameters over 60 cm (Lieberg 1900; Sudworth 1908; Whitford and Craig 1918).

Generally heights of 12 to 20 m are attributed to the species with large individuals reaching 18 to 27.5 m (Can. Dept. Int. 1913; den Ouden and Boom 1981 and others). The tallest known individuals are slightly over 30.5 m (Arno 1970). Trunk diameters of 25 to 60 cm are common with exceptional trees reaching 1.2 m (Lieberg 1900). The largest recorded alpine larch was an individual at the forest line which was 25.6 m and had a diameter of 1.9 m (Arno 1970).

The species is long-lived and often reaches 400 - 600 years of age (Leiberg 1900; Sudworth 1908 and others). Sudworth (1908) reports trees 470 to 510 years old with diameters of 41 to 46 cm. Ostenfeld and Larsen (1930) cite an individual that was 562 years old and 50 cm in diameter.

Alpine larch typically have open, pyramidal crowns that extend up to 2/3 of the tree's height (Sudworth 1908; Whitford

and Craig 1918). The short, horizontal branches often grow irregularly, giving the crown an open, unsymmetrical appearance (Sudworth 1908; Krussmann 1985). Branches are nearly black and, in the first year, have a dense covering of grey to grey-brown pubescence (Brown 1907; den Ouden and Boom 1981; Krussmann 1985). The bark on mature trees is generally less than 2 cm thick and irregularly furrowed. The mature bark is reddish-brown or grey and exfoliates in shallow, irregular scales.

The light, bluish-green leaves are pointed, needle-like and 2.5 - 3.5 cm. The leaves are prominently keeled on the adaxial surface and often keeled on the abaxial surface giving the cross-sections a 4-angled appearance (Brown 1907; Rehder 1940 and others). Lines of stomata occur on both the abaxial and adaxial surfaces but are more abundant abaxially (Schoenike 1961). Typically, two resin ducts occur in each leaf (Sudworth 1908; Montgomery 1970).

Leaves are borne spirally on long shoots and in compact clusters of 30 to 50 on the short shoots (Sudworth 1908; Whitford and Craig 1918 and others). These short shoots are 1 to 2 cm long with grey or yellow-brown tomentum (den Ouden and Boom 1981; Krussmann 1985).

Like all larches, alpine larch bears cones singly on short shoots (Krussmann 1985). Globose male strobili are produced on leafless short shoots. Female strobili are erect, ovoid-

oblong, 3.0 to 5.0 cm long and are borne on short pedestals (Brown 1907; Ostenfeldt and Larsen 1930; Preston 1968). The young cones have dark red or yellow-green scales and dark purple bracts (Brown 1907). When mature, the scales and bracts are both typically reddish purple (Brown 1907; den Ouden and Boom 1981; Krussmann 1985). The outside surface of the scales is pubescent, especially along the outer margin which, at maturity, is recurved. The bract scales are exerted and sometimes reflexed.

Cones mature in one season, beginning expansion prior to leaf emergence with the cones ripening in August and opening soon afterwards (Arno 1970). Spent seed cones often persist for several seasons.

Little is known about seed dispersal in Larix lyallii. Good cone and seed crops are produced approximately every 10 years (Arno 1970). Seed viability can vary from 20 - 55.6% with higher rates occurring in peak production years. Seed are smaller than those of most Larix, with approximately 220,000 to 350,000 cleaned seed per kg (Shearer 1961; U.S.D.A. 1948). Embryo dormancy is suspected in alpine larch seed and germination is difficult to achieve. In several studies, no germination occurred (U.S.D.A. 1948). Shearer (1961) obtained 14% germination after soaking seed for 24 hours in a 3% hydrogen peroxide solution.

Alpine larch is rare in cultivation. It is slow growing and prefers cool climates (Schoenike 1961; den Ouden and Boom 1981; Krussmann 1985).

Distribution

Larix lyallii occupies two mountain systems, the Rockies and the Cascades, and some areas in between, in the inland portion of the Pacific Northwest of the United States and the adjacent southwest of Canada (Figure 1). At the closest point 200 km separate these two ranges. Alpine larch is distributed discontinuously from the Cascade Divide in northern Washington east to the Continental Divide in northern Montana. Its distribution extends northward to the Bow River drainage in Alberta (Arno and Habeck 1972). North to south the range extends 695 km in the Rockies and 195 km in the Cascades (Arno 1970).

Initial reports of the species' range were made at the turn of the century by Leiberg (1900) Ayres (1900) and others. Arno (1970) made an extensive aerial and ground survey in order to accurately determine the range of alpine larch.

In the Rocky Mountains of Idaho and Montana alpine larch is found in the Bitterroot Range on the Idaho-Montana Divide north of Nez Perce Pass. Its southern range limit occurs at Square Top, Montana at 45° 28' N, 114° 41' W (Shackelford 1967). Alpine larch occupies many peaks in the Anaconda-Pintlar Range northeast of Lost Trail Pass. South of Missoula,

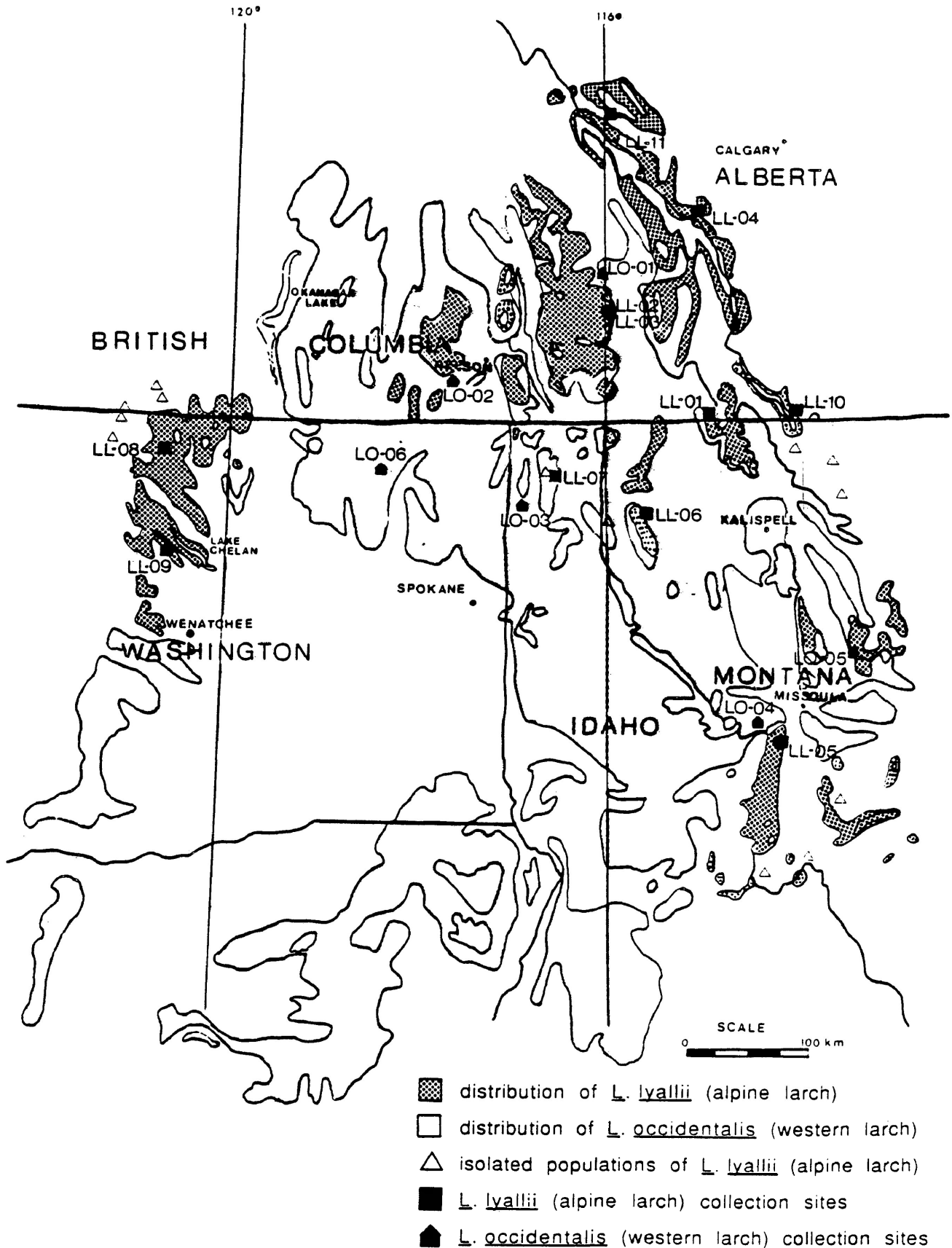


Figure 1. Distribution of *Larix lyallii* Parl. in the Pacific Northwest (from Arno 1970). Locations of *L. lyallii* and *L. occidentalis* populations sampled for this study are indicated.

Montana it is found on the Sapphire Range. In southwestern Montana the distribution extends east of the Continental Divide into the Pioneer Range (Arno 1970).

Alpine larch populations are also found in the Rockies of northern Montana and some of the high Intermountain ranges of northwestern Montana, northern Idaho and southeastern British Columbia. Here it occurs in the Mission, Swan and Cabinet Ranges as well as along the Continental Divide. In the Selkirk Mountains of Idaho L. lyallii is found only on Roman Nose. Sixty-five km containing seemingly suitable habitat separate this stand from populations further north in the Selkirks. In the Canadian Selkirks, alpine larch populations are found in the Nelson and Slocan Ranges. Extensive stands of alpine larch are found in the Purcell Mountains northwest of Kimberly, B. C.

In the southern Canadian Rockies the species occurs northward from the Flathead Range of Waterton Lakes National Park in the extreme southeast of Alberta. The range follows the Continental Divide northward to Banff National Park. It reaches its northern limit in the Bare Mountains at 51° 36' N. Distributional information for the western side of the Rockies is incomplete. The northern limit appears to be reached in British Columbia in Yoho National Park at a slightly lower latitude than that reached in Alberta. Alpine larch appears to be extensively distributed south of Yoho in the Vermilion and Hugh Ranges.

Although alpine larch's distribution in the Cascade Mountains is not as extensive as it is in the Rockies, the species achieves its greatest stature in this mountain system and often forms large, pure stands (Arno 1970).

Early reports by Sudworth (1908) of alpine larch occurring in the Cascades as far south as Oregon have been disproven (Arno 1970). The Wenatchee Mountains (47° 25' N) represent the southern limit of alpine larch in the Cascades. Its distribution extends northward through the Stuart Range and Chiwaukum Mountains. Populations are found in the Glacier Peak area and in the Chelan Range. Alpine larch reaches its western limit at Luna Peak, Washington in the Northern Cascades (48° 50' N, 121° 17' W). It is fairly abundant in Washington along much of the northern Cascade Crest. In the Canadian Cascades its distribution is generally restricted to the Okanogan Range.

Ecology

Perhaps more than any other North American conifer L. lyallii is restricted to severe sites. Its altitudinal limits are apparently 1500 to 3000 m (Arno 1970) although early reports indicated that it was 3500 m (Larsen 1930). When found fairly low in relation to the timber or forestline the species is usually found on tallus slopes and rocky clearings. It dominates the highest northern slopes throughout its range

(Arno 1970). Daubenmire (1943) assigned alpine larch stands to the ecotone of the alpine tundra and spruce-fir zones.

The species' primary tree associates are Abies lasiocarpa (Hook.) Nutt., Pinus albicaulis and Picea engelmannii Parry (Arno 1970; Arno and Habeck 1972). Alpine larch is considered intolerant of shading (Baker 1949). It is less tolerant than A. lasiocarpa and P. engelmannii (Larsen 1930) and may be less tolerant than P. albicaulis (Arno 1970).

Alpine larch does not seem to occur in distinct community types; each stand tends to be unique. Understories dominated by Vaccinium scoparium Leib., Luzula glabrata (Hoppe) Desv. and Phyllodoce empetriformis (Sw.) C. Con. are most common. Cassiope mertensiana (Bong.) G. Don, Phyllodoce glanduliflora (Hook.) Cov. and Krummholz A. lasiocarpa, all considered timberline species, are among the most common understory species (Arno 1970).

Even though it is intolerant, L. lyallii is a climax species on sites too severe for other timberline conifers to form continuous stands. It is able to continue dominating these sites where the short growing season, rocky terrain, avalanches, blizzards or extreme drought or bogginess preclude abundant survival of other tree species (Arno 1970).

Most often, alpine larch retains its erect form at the tree limit but occasionally a Krummholz form is produced (Arno 1970).

Fire, a major factor in the development and maintenance of vegetation of most mountainous areas in North America, is not an important force in established alpine larch stands. Although the species' bark is thin and easily damaged, fire damage to trees is usually moderate (Fischer and Clayton 1983). Lightning caused fires are fairly abundant but stands are generally open and have little fuel available (Herman 1976). L. lyallii usually occupies cool, damp, north slopes, reducing the potential damage caused by fires. In areas where alpine larch grows in association with A. lasiocarpa, P. engelmannii and P. albicaulis, fires allow alpine larch to retain its position as a forest component among these more tolerant tree species by establishing openings (Fischer and Clayton 1983).

Although alpine larch is generally confined to the spruce-fir and alpine tundra zone ecotones, the climate associated with alpine larch sites can, in some instances, be extremely varied. The Pacific Northwest is a complex region physiographically and this is reflected in climatic variability. In addition, microhabitat conditions are extremely varied and can have a major influence on exposure to wind, availability of sunlight and available moisture and nutrients.

Larix lyallii stands receive anywhere from 63 to 254 cm of precipitation annually. Available moisture is increased by drainage patterns of individual sites. Much of the

precipitation is in the form of snow and snowpack depths reach an average maximum of 3.0 to 3.7 m. A good portion of the ground is still covered by snow at the end of June but by mid-July most of the ground is free of snow. In these areas occasional wet snowfalls occur in July and August but substantial snow does not fall until September (Arno 1970).

Wind is an extremely important environmental factor in the mountains of western North America. Long periods of high, steady winds are common and wind gusts can be extremely strong. Arno and Habeck (1972) recorded winds steadily over 50 kph for a 72 hour period.

On most alpine larch sites soil development is extremely poor. The species is usually found on rocky, shallow, infertile soils. The severe climate promotes physical weathering of the substrate; chemical soil processes are not a major force in soil development. Soils are generally severely leached with a pH of 3.9 to 5.7. Sites with good soil development have Brown Podzolic soils (Nimlos 1963). These soils have a well developed B horizon and are strongly acidic.

Arno suggests that alpine larch may be substrate oriented. It seems to do well on and is usually found on acidic sites. In areas where limestone occurs, alpine larch is mainly associated with more acidic substrates (Baird 1968, Arno 1970; Arno and Habeck 1972).

OTHER LARIX SPECIES

The genus Larix Mill. is confined to the northern hemisphere and is generally recognized to contain ten species. Three Larix species are native to North America and the remainder are native to Eurasia (Figure 2). Species of larch are present in most of the boreal regions in the northern hemisphere but they often form only a minor vegetation component. The genus is extremely hardy; only one species (L. occidentalis) does not grow at either the arctic or alpine tree limit. Patschke (1912) divided the genus into two sections, each containing five species, based primarily on cone morphology. Section Multiseriales Patschke are montane species; they have cones over 3 cm in length, have many cone scales and possess bract scales which are exerted past the cone scales. The leaves are often keeled on both sides but are occasionally keeled only abaxially (Krussmann 1985). Section Pauciseriales Patschke cones are generally smaller, with fewer scales and have bract scales that are shorter than the cone scales. The leaves are not keeled adaxially and are often flat (Schoenike 1961; Krussmann 1985). These species are widely distributed and geographic variation is common. Extensive hybridization and introgression is recognized in this section.

Work has been done in Larix with interspecific hybrids but by far the majority of this work has been focused on section Pauciseriales. This section hybridizes naturally where



Figure 2. Worldwide distribution of Larix Mill. species (from Arno 1970)

species' ranges overlap and many hybrids have developed spontaneously in cultivation. Artificial breeding programs have indicated that most species of Pauciserales are interfertile (Schoenike 1961). Hybrids have also been produced from combinations of three species of Pauciserales.

Artificial breeding work is rarely carried out with Larix section Multiserales and little is known about intra-section fertility. Opportunities for naturally occurring hybrids to originate are extremely infrequent since range overlap rarely occurs.

A few attempts have been made to produce inter-section hybrids but the results appear to be inconclusive (Schoenike 1961).

Synonyms for Larix species are quite common. Four species of Larix are commonly referred to by at least two specific epithets and no agreement seems to be forthcoming on the proper binomial. After a brief review of the synonyms presented by Rehder (1949) and others the following nomenclature was selected:

Larix gmelinii (Rupr.) Gord. = L. dahurica Turczaninow ex
 Trautvete, L. cajanderi (Mayr)
Larix griffithiana (Lindl. & Gord.) Carr. = L. griffithii Hook.
Larix kaempferi (Lamb) Sarg. = L. leptolepis (S. & Z.) Gord.
Larix sibirica Ledebour = L. russica (Endl.) Sabine ex. Trautv.
L. sukaczewii Dylis.

The use of L. sibirica and L. kaempferi is in agreement with the new version of Native Trees of Canada (Farrar pers. comm.).

Larix Section Multiseriales contains five species of which two, L. lyallii and L. occidentalis, are North American.

L. occidentalis has a geographic range similar to L. lyallii; it is found between the Cascade and Continental Divides in northern Oregon, Washington, northern and central Idaho, western Montana and southwestern British Columbia (Arno 1970). It occurs from elevations of 600 to 2150 m, reaching its altitudinal limit in the southern portion of its range (Larsen 1930; U. S. D. A. 1965).

Western larch is a large commercially valuable tree, often reaching 50 m in height and attaining diameters over 2.0 m (U. S. D. A. 1965). It has a long, slender bole approximately half of which is free of branches. Individuals as old as 930 years have been recorded (Koch 1945) but generally 700 years represents a maximum (Arno 1970). Seed cones are ovate, 2.5 to 3.5 cm in length and have bract scales exerted past the cone scales (den Ouden and Boom 1981; Krussmann 1985). The abaxial surface of the needles are keeled. Tree species associated with L. occidentalis include Thuja plicata Donn, Pseudotsuga menziesii (Mirb.) Franco, Tsuga heterophylla (Raf.) Sarg., Picea engelmannii, Abies lasiocarpa and Abies grandis (Dougl.) Lindl.

Larix potaninii Batal., a native of the Himalayan Mountains of eastern Nepal, Sikkin and Bhutan and the Chumbi Valley of Tibet appears to be closely related to the western North American larches (den Ouden and Boom 1981). It is a montane tree found from 2,500 to 3,000 m (Schoenike 1961; Arno 1970). In favourable areas L. potaninii reaches heights of 25 to 30 m with exceptional individuals attaining 40 m (Ostenfeldt and Larsen 1930). The sessile cones are oval-oblong, 3 to 4.5 cm long and have bract scales with long awns (Krusmann 1985). The twigs are less pubescent than those of L. lyallii (den Ouden and Boom 1981). It appears as scattered individuals at lower altitudes but forms forests at higher elevations.

Larix mastersiana Rehd. & Wils. is a small tree, reaching 20 m. Its long branches are glabrous and moderately pendulous (Schoenike 1961; Krusmann 1985). Like L. potaninii and L. lyallii, its leaves are keeled on both surfaces (den Ouden and Boom 1981; Krusmann 1985). It bears erect cones 3 to 4 cm long. The bract scales are exerted and reflexed. The range of L. mastersiana is extremely local; it is native to the Niu-tou-shan Mountains in western Szechuan, China at 2,600 to 3,300 m (Krusmann 1985).

Although L. mastersiana's geographic range is completely contained within that of L. potaninii the species most closely resembles L. griffithiana and it is believed to be intermediate

between L. griffithiana and L. potaninii (Arno 1970). L. griffithiana is not a large tree, reaching only 20 m in height. The branches are pendulous and new shoots are pubescent. Its leaves are keeled abaxially only. The 5 to 11 cm long cones are borne erect and have extremely prominent bract scales which are exerted and strongly reflexed (Krussmann 1985). It grows within the Himalayan Mountains at elevations from 2,500 m to over 4,000 m in eastern Nepal, Sikkim and Bhutan and in southern Tibet (Ostenfeld and Larsen 1930; den Ouden and Boom 1981). Krussmann (1985) also reports L. griffithiana from western Szechuan, China. It is often found in pure stands or growing with Pinus griffithii McClelland (den Ouden and Boom 1981).

Larix laricina (DuRoi) K. Koch is the only North American representative of Larix Section Pauciseriales. The small tree commonly grows to 20 m and reaches diameters up to 50 cm. Maximum age of individual trees is 150 to 180 years but older individuals are encountered (U. S. D. A. 1965). The cones of L. laricina are smaller than those of any other Larix species, averaging only 1.0 to 1.5 cm in length. Like all Pauciseriales, the leaves are keeled only on the underside (den Ouden and Boom 1981; Krussmann 1985). This species usually inhabits lowland sites throughout the boreal forest region of Canada and the adjacent United States. It usually forms open stands and often grows with Picea mariana (Mill.) B. S. P.

L. sibirica occurs in northeastern Russia and western Siberia. It is a valuable tree, often attaining heights up to 40 m (Ostenfeld and Larsen 1930; den Ouden and Boom 1981). Its cones are 2.5 to 4.0 cm and the bracts, except for the lowest row of scales, are hidden.

The east Asian species L. gmelinii has five recognized geographic varieties and forms hybrids with L. sibirica in the zone of overlap of their ranges (see Figure 3). L. gmelinii grows to 55 m and produces cones slightly smaller than those of L. sibirica (den Ouden and Boom 1981).

L. gmelinii var. gmelinii is found from eastern Siberia through Manchuria into Kamchatka. The twigs are slightly pendulous and mainly glabrous. The cones are 2.0 to 3.5 cm long. L. gmelinii var. japonica (Regel) Pilg. has pubescent branchlets, fairly broad leaves and cones 1.5 to 2.5 cm long. This extremely hardy variety is native to the Kurile Islands. L. gmelinii var. olgensis (Henry) Ostenf. & Syrach-Larsen has densely pubescent twigs bearing cones 1.5 to 2.0 cm long. The needles are sickle-shaped. This variety grows in eastern Siberia near Olga and Vladmir Bays. L. gmelinii var. principis-rupprechtii (Mayr) Pilg. has glabrous twigs and sickle-shaped needles. Cones 3.0 to 4.0 cm in length are borne on a thick stalk up to 2 cm long. It is native to Korea, Manchuria and the extreme northeast of China. L. gmelinii var. prostrata (Regel)

Honibr. is a dwarf variety confined to extreme sites in Dahuria and east Asia (den Ouden and Boom 1981; Krussmann 1985).

A zone of introgressive hybridization exists between L. sibirica and L. gmelinii. The resulting hybrid, L. X czekonovskii Szafer, covers approximately 515,000 km² (Abaimov et al. 1980).

Authors from the U. S. S. R. generally divide the L. sibirica - L. gmelinii complex into three or more distinct species. L. sibirica is occasionally separated into L. sibirica and L. sukaczewii Dylis (Schoenike 1961), based on ecological differences with L. sukaczewii being the eastern form (Abaimov et al. 1980). L. gmelinii (Rupr.) Gord. is usually separated into L. gmelinii (Rupr.) Rupr., which occupies the eastern portion of L. gmelinii's range, and L. cajanderi on the basis of cone scale differences (Abaimov et al. 1980; Khan et al. 1983). The pattern of variability these two species exhibit has led some authors to suggest that a zone of hybridization similar to that between L. sibirica and L. gmelinii (Rupr.) Gord. exists between L. gemilinii (Rupr.) Rupr. and L. cajanderi (Abaimov et al. 1980). Occasionally L. gmelinii var. olgensis and L. gmelinii var. japonica have also been elevated to species status and referred to as L. olgensis Henry and L. kurilensis Mayr.

Larix decidua Miller is a fairly large, straight-stemmed tree reaching 25 to 35 m. The light green leaves are keeled

only abaxially. The cones are 2.5 to 4.0 cm and are borne upright on the stem (den Ouden and Boom 1981; Krussmann 1985).

Two varieties are recognized. Larix decidua var. decidua occurs throughout the Alps of Central Europe. Larix decidua var. polonica (Raciborski) Ostenf. & Syrach-Larsen, is considered an intermediate form between L. decidua var. decidua and L. sibirica (Ostenfeld and Larsen 1930, Schoenike 1961 and others). This variety is found in southern Poland, and in the Carpathian Mountains of Romania and Ukraine (den Ouden and Boom 1981; Krussmann 1985).

Larix kaempferi is a medium to large larch that reaches 30 m. The 2.5 to 3.0 cm long needles are keeled abaxially. When mature, the 2 to 3 cm long cones have recurved cone scales giving them a rosette-like appearance. Like all Pauciseriales, the bract scales do not extend past the cone scales. (Ostenfeld and Larsen 1930; den Ouden and Boom 1981). L. kaempferi occurs at elevations of 1200 to 1800 m in Japan on volcanic mountain slopes on the island of Hondo.

A common larch hybrid, L. X eurolepis A. Henry is the result of a L. kaempferi X L. decidua cross. The resulting hybrid resembles L. kaempferi in habit but can be distinguished from its maternal parent because of its stiffer, yellower twigs and shorter needles (den Ouden and Boom 1982; Krussman 1985). The cones are distinguishable from those of L. decidua by their

slightly recurved cone and bract scales (den Ouden and Boom 1982).

LARIX EVOLUTION

Larix is one of three genera in the subfamily Laricoideae of the Pinaceae (Krussmann 1985). Except for the monotypic genus Pseudolarix, Larix is the only member of the Pinaceae whose leaves are deciduous. Pseudolarix amabilis (Nelson) Rehd., a tree native to China, is morphologically similar to Larix but differs in having deciduous cone scales and bearing clusters of staminate flowers (den Ouden and Boom 1981 and Krussmann 1985). Additionally, Pseudolarix occurs in a humid temperate climate while Larix, more than any other conifer genus, is restricted to northern boreal climates (Arno 1970).

Fossil evidence of Pseudolarix from the Late Cretaceous and Paleocene has been found in eastern Siberia (Florin 1963). Picea A. Dietr. fossils of a similar age have also been discovered in a variety of locations but Larix does not appear in the fossil record until later. Arno (1970) suggests that Pseudolarix was the precursor to Larix and that Larix is one of the most modern conifer genera.

Although morphological evidence indicates that Pseudolarix is the extant genus most closely related to Larix other types of evidence lead to different conclusions.

Phylogenetic studies by Flous (1936) based on morphological and fossil evidence led him to propose that

Larix and Pseudotsuga Carr. (subfamily Abietoideae) are more closely related to each other than they are to genera of their own subfamilies. Immunological data led Prager et al. (1976) to suggest that Larix is more closely related to Pseudotsuga than to Cedrus (Laricoideae). On the basis of pollination mechanisms, Doyle (1945) grouped Larix with Pinus L., Picea and Pseudotsuga and Pseudolarix with Abies, Cedrus and Tsuga (Endl.) Carr. A study of leaf phenolics indicates a close relationship between Larix and Pseudotsuga and Tsuga (Abietoideae) (Niemann and Van Genderen 1980). Pseudolarix was not closely related to any other genus of Pinaceae studied.

The fossil record for Larix is extremely limited. Fossil records suggest that Larix, like Picea and Abies, was more widely distributed in Europe and Asia in the Oligocene, Miocene and Pliocene (Florin 1963; Stockey 1981). In Europe, the oldest Larix fossils are from the Miocene and Pliocene (Florin 1963).

In eastern North America Upper Miocene or Lower Pliocene fossils of Larix were found on Banks Island in northern Canada (Hills 1970).

The earliest record in western North America is that of Larix nevadensis in the Eocene Copper Basin Flora (Axelrod, 1966). Axelrod described L. nevadensis from fossils of one needle and two cone scales.

Beck (1945) described L. oregonensis from a single wood sample found in Oligocene deposits in western Oregon. Arno (1970) suggested the identification of this specimen as a Larix is far from certain since comparisons indicate several differences exist between the L. oregonensis sample and that of recent Larix wood. Possible Larix wood fossils were also found in Upper Miocene deposits in central Washington (Beck 1945).

Both Larix and Pseudolarix fossils are apparently found in Miocene subalpine conifer forests of Snake River Basin, Idaho (Axelrod 1968). Larix cassiana was a constituent of slope and subalpine forests. Axelrod (1964) indicates that the L. cassiana fossils (one needle and five seeds) resemble L. potaninii Batalin.

Evidence suggests that eastern Asia may be the center of origin for Larix. The majority of species and varieties are native to the region and the species often form large pure stands. In Europe and North America Larix species are not usually a dominant forest component over extensive areas.

During cool periods in the Miocene and Pliocene Larix may have extended into Europe and the Himalayas. A subsequent warming may have confined the species to mountains, creating discontinuous populations (Arno 1970). One or more of these range extensions and contractions may be responsible for the Eurasian montane larches.

Larix apparently migrated across Beringia into North America during the early- to mid-Tertiary. Hopkins (1967) suggests that an L. gmellini ancestor migrated across the Bering land bridge. The North American population spread southward and eastward as the climate cooled. Part of the population became isolated in the Rocky mountains, giving rise to L. lyallii and L. occidentalis. The main population developed into L. laricina.

A second hypothesis suggests that both a taiga and a montane species of Larix migrated into North America, with the montane species differentiating into L. lyallii and L. occidentalis (Arno 1970)

Neither of these hypotheses seem to adequately explain the Larix situation in North America. If only one species migrated into North America extensive differentiation would have had to occur over a relatively short period since the montane larches and L. laricina are so dissimilar. L. lyallii and L. occidentalis would then resemble the Eurasian montane larches (other Multiserales) and L. laricina other Pauciserales through convergence.

If, however, two separate Larix were the progenitors of North American species, a montane species must have migrated from eastern Asia. It seems somewhat doubtful that a montane species could cross Beringia since evidence indicates that this would involve migration over extensive

lowland areas. Florin (1963) indicates that an alternative migration route could have existed in the late Paleozoic to early Cenozoic. A montane species may have migrated from eastern Asia along the Kurile Islands, into Kamchatka and then along the Aleutian Islands into northwestern North America.

To determine the ancestry of the North American larches would require an extensive examination of Larix species and a more complete fossil record.

RELATIONSHIP OF THE WESTERN NORTH AMERICAN LARCHES

L. lyallii and L. occidentalis are two larch species which have similar geographic ranges and morphologies. Just how closely the two species are related has not been determined but it is likely that the two species originated from a common ancestor resembling L. potaninii.

The relationship of these two species is unique because the two are the only species in Larix Section Multiseriales that are known to overlap in range. Geographically the two species overlap considerably but elevational differences of 150 to 300 m usually separate them.

In 1964 an area of overlap was discovered near Carlton Creek in the Bitterroot Range of Montana (Carlson 1965). The overlap occurred in a snowslide path from 1800 to 2400 m in elevation. Apparently the recurring snowslides are responsible for the presence of alpine larch at elevations

lower than its normal limit. The disturbed habitat provides a suitable site for alpine larch.

In order to identify the possible natural hybrids in the vicinity of the species overlap area, Carlson developed a hybrid index based on bark texture, twig pubescence and number of epithelial cells surrounding the resin canal. L. lyallii bark is scaly and rough at the tree's top, and new shoots are densely pubescent. In western larch the uppermost bark (within 1.2 m of the top) is smooth with longitudinal fissures and the new shoots are nearly glabrous (Ostenfeld and Larsen 1930; Carlson 1965). The number of epithelial cells surrounding the resin canals is greater in alpine larch than in western larch (Carlson 1965). These characteristics are considered to reliably distinguish the two species. Based on this index twelve putative hybrids were identified in the overlap area.

Carlson (1965) was able to produce artificial hybrids between alpine and western larch. Both species were used successfully as the female and male parent. This is one of the few documented cases of hybridization in Section Multiseriales. Viability of the hybrid seed was 30%, equal to that of western larch seed and higher than that of alpine larch seed (15%). The hybrid resulting from L. lyallii X L. occidentalis was intermediate in early height growth; heterosis was not evident. The cotyledons appeared to be

more closely related to those of the maternal parent than to those of western larch.

In 1968 Knudsen examined heartwood extractives and the terpene composition of needle primordia of alpine and western larch as well in the putative hybrids in an attempt to support Carlson's findings. Heartwood was not available from the putative hybrids and only a total of five trees (two alpine larch, two western larch and one putative hybrid) were used to characterize needle terpene composition. The limited results indicate that needle terpenes may be valuable for the identification of hybridization.

Both of these studies conclude that hybrids may exist but neither provide conclusive evidence for natural hybridization.

Since 1965 two more areas of range overlap in the Montána Bitterroots have been identified (Arno 1970). In addition, aerial reconnaissance has detected range convergence in two locations in the Cabinet Range and slight overlap in a few areas of the Purcell Range.

Since alpine and western larch are apparently able to produce hybrids, the possibility of natural hybridization and subsequent backcrossing occurring in areas where the two species meet must be considered.

METHODS

FIELD COLLECTIONS

During late July and August of 1985 and 1986 eleven alpine larch and six western larch sites were sampled. The alpine larch collection sites sampled the entire range of that species, while the western larch collections were made in areas where that species range was adjacent to that of alpine larch (Figure 1).

A summary of the collection sites including location, elevation, stand description, collection information and an identification code is provided in Table 1. All four of the L. lyallii collections made in 1985 were from British Columbia. The western larch collections made in 1985 were from British Columbia and from the Selkirk range in northern Idaho. The seven alpine larch collections made in 1986 sampled the Bitterroot and Cabinet Ranges in Montana, the Selkirk Range in northern Idaho, the Cascade Mountains in north-central Washington and the Rocky Mountains in Alberta. L. occidentalis samples from the same year were from the Bitterroot and Cabinet Ranges in Montana and from northwestern Washington.

Table 1. Summary of stand and collection data for all populations sampled (1985 and 1986).

CODE	SAMPLE SIZE	LOCATION	STAND INFORMATION	COLLECTION INFORMATION
<u>LARIX LYALLII</u> POPULATIONS				
LL-01	20	Rocky Mtns. 49 5' N 115 3' W ELEV.-2018m	HT.-11.2m DBH-18.5cm AGE-73years	DATE-20/08/85 BY-WHP+BM WITH-P.engelmannii, A. lasiocarpa
LL-02	13	Doctor Creek ,B.C. Purcell Mtns. 50 0' N 116 1'W ELEV.-2176	HT.-6-8m DBH-up to 25cm	DATE-21/08/85 BY-WHP+BM WITH-P.engelmannii, A.lasiocarpa
LL-03	20	Doctor Peak ,B.C. Purcell Mtns. 50 0' N 116 1 W ELEV.-2408m	HT.-4.5-6m DBH-8-12cm	DATE-24/08/85 BY-WHP+BM WITH-few A.lasiocarpa
LL-04	18	Spray Mtns. Lawson Lake, B.C. ELEV.-2286m	DBH-14.2cm	DATE-20/08/85 BY-WHP+BM WITH-A.lasiocarpa, P.engelmannii
LL-05	20	St. Mary's, Mont. Bitterroot Mtns. 46 30'N 114 14' W ELEV.-2347m	HT.-12.8m DBH-25.5cm AGE-113.8	DATE-02/08/86 BY-MM+OB WITH-A.lasiocarpa, P.albicaulis
LL-06	16	Indian Head, Mont. Cabinet Mtns. 48 21' N 115 41' W ELEV.-1829m	HT.-11.9m DBH-13.4cm AGE-74.5	DATE-06/08/86 BY-MM+OB WITH-P.albicaulis
LL-07	13	Roman Nose, Idaho Selkirk Mtns. 48 38' N 116 35' W ELEV.-1798m	HT.-11m DBH-20 cm AGE-56	DATE-06/08/86 BY-MM+OB WITH-no other tree species
LL-08	20	Hart's Pass, Wash. Northern Cascades 48 35' N 120 40' W ELEV.-1890m	HT.-14.5m DBH-25.2cm AGE-90.6	DATE-08/08/86 BY-MM+OB WITH-A.lasiocarpa
LL-09	20	Big Hill, Wash. Chelan Range 48 01' N 120 30' W ELEV.-2073m	HT.-10.1m DBH-17.8cm AGE-50,>200	DATE-09/08/86 BY-MM+OB WITH-A.lasiocarpa, P.albicaulis, P.engelmannii

Table 1. continued.

CODE	SAMPLE SIZE	LOCATION	STAND INFORMATION	COLLECTION INFORMATION
LL-10	15	Waterton, Alta. Rocky Mtns. 49 01' N 113 51' W ELEV.-1981m	HT.-8.4m DBH-12.4cm AGE-58.6	DATE-21/08/86 BY-MM+OB WITH-A.lasiocarpa, P.engelmannii
LL-11	20	Lake Louise, Alta. Rocky Mtns. 51 19' N 116 57' W ELEV.-2225m	HT.-9.3m DBH-14.3cm AGE-66	DATE-22/08/86 BY-MM+OB WITH-P.engelmannii, few A.lasiocarpa
<u>LARIX OCCIDENTALIS</u> POPULATIONS				
LO-01	20	Purcell Mtns. 50 7' N 116 1' W ELEV.-1113m	DBH-16.6cm AGE-87.7	BY-WHP+BM WITH-P.contorta
LO-02	20	Selkirk Mtns. 49 2' N 117 5' W ELEV.-1579m	HT.-21.6m DBH-31.3cm	DATE-26/08/85 BY-WHP+BM WITH-A.lasiocarpa, P.engelmannii
LO-03	13	Priest Lake, Idaho 48 16' N 116 54' W		BY-GR
LO-04	20	Bitterroot Mtns. 46 45' N 114 25' W	HT.-17.0m DBH-20.6cm AGE-60.1	DATE-31/07/86 BY-MM+OB WITH-P.contorta
LO-05	20	Swan Range 47 19' N 113 27' W	HT.-13.6m DBH-14.5cm AGE-70.2	DATE-03/08/86 BY-MM+OB WITH-P.menzeisii, small P.contorta
LO-06	15	Kettle River Range 48 35' N 118 35' W ELEV.-1524m	HT.-21.8m DBH-29.7cm AGE-59.9	DATE-18/08/86 BY-MM+OB WITH-P.engelmannii, P. menzeisii

List of Collectors

BM - Brian Moore
GR - Gerald Rehfeldt
MM - Madelaine Maley

OB - Olenka Bakowsky
WHP - William Parker

Depending on the population size, 13 to 20 sample trees were selected from each of the collection sites. Sample trees were selected a minimum of 20 m apart to decrease the likelihood of sampling siblings. Sample trees were required to have foliage low enough to be reached with pole pruners (within approximately 7 m). This requirement had little effect on the collections of alpine larch since the populations generally had heights of 15 m and had crowns extending down over half of their boles. It did, however, affect the choice of western larch stands. Stands with fairly open or younger trees had to be sampled in order to reach the foliage.

From each sample tree two or three branch samples containing both long and short shoots were collected from the lower half of the crown. Vegetative material was pressed in the field shortly after collection. Herbarium material from all nineteen populations is stored at Lakehead University.

Cone samples were collected from a total of seven populations (five populations of L. lyallii and two populations of L. occidentalis). The majority of the cone samples were obtained in 1985. Unfortunately, 1986 was a poor cone year and only two of the ten larch populations sampled produced sufficient cones for collection. In populations producing cones, sample trees bearing cones

were selected. Whenever possible, a minimum of five cones were collected from each tree. In some cases, however, five healthy cones could not always be obtained. Because the collecting was carried out in late summer, current year's cones were already sufficiently mature for collecting. Previous years' cones often persist on alpine and western larch and were also sampled.

The average age, diameter (at breast height or 1.3 m) and height of the sampled trees were determined for populations sampled in 1986 (Table 1). This information was not determined for several of the 1985 collections.

ARNOLD ARBORETUM MATERIAL

Cone and needle samples from 27 Larix individuals were obtained from the living collection of larches from the Arnold Arboretum at Harvard University. The collection reputedly contained samples of L. decidua, L. gmelinii, L. potaninii, L. sibirica, L. kaempferi, L. X eurolepis, L. laricina and L. occidentalis (Appendix III). This collection was supplemented with L. occidentalis and L. lyallii material collected in 1985 and 1986 and L. laricina material collected in 1983 and 1984 from populations throughout the species range. In total, eight species and one hybrid were represented. The number of samples per species ranged from one to ten (Appendix III).

LAB PROCEDURES

Foliage

Five short shoot needles from each individual tree were measured in order to provide an estimate of within tree variation. In an attempt to sample parallel material, all needles selected were taken randomly from short shoots of the collected samples. Needle lengths to the nearest 0.5 mm were measured with a ruler before the needles were rehydrated and prepared for cross-sectional examination.

Preliminary examination of the foliage of L.lyallii and L.occidentalis, as well as a previously published report (Carlson 1965) were used to select characters for analysis. A total of 45 needle characteristics were measured for each needle (Table 2). All of the traits except needle length were measured on cross-sections obtained from the mid-section of each needle. Thirty variables (D1 - D30) represent radial distances from a fixed point within the needle cross-section (Figure 3 and Appendix I). These variables provide an outline of, and can detect differences in cross-sectional needle shape. The remaining variables measure needle width and thickness, vascular column size and position, resin canal size and position and the number of epithelial cells surrounding the resin canals.

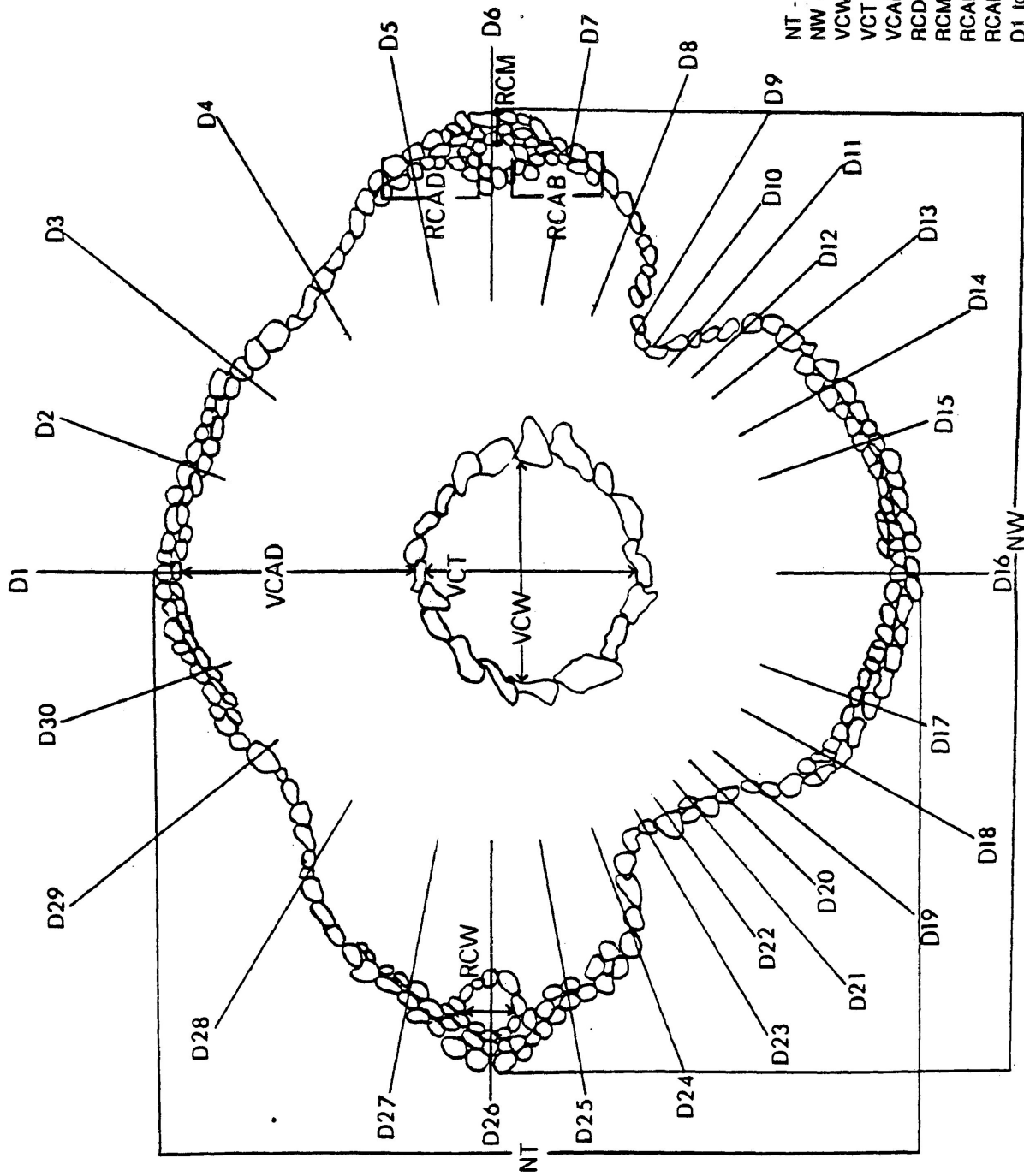
The midsections of each of the needles were rehydrated and prepared for sectioning using a Tertiary-butyl alcohol

Table 2. Codes for needle characteristics. Unless indicated, all characteristics are measured on a cross-section of the needle mid-section).

CODE	CHARACTERISTIC
RCELL	Number of epithelial cells surrounding the resin canals (average of two per section)
NL	Needle length
NW	Needle width
NT	Needle thickness
VCT	Vascular column thickness
VCAD	Distance from vascular column to adaxial surface
RCL	Left resin canal diameter
RCLAD	Distance from left resin canal to adaxial surface
RCLM	Distance from left resin canal to left margin
RCLAB	Distance from left resin canal to abaxial surface
RCR	Right resin canal diameter
RCRAD	Distance from right resin canal to adaxial surface
RCRM	Distance from right resin canal to right margin
RCRAB	Distance from right resin canal to abaxial surface
VCW	Vascular column width
D1 TO D30	Radial distances (see Figure 3 and Appendix I)

Table 3. Codes for cone characteristics examined (scale and bract measurements are for middle cone scale).

CODE	CHARACTERISTIC
CL	Cone length
CD	Cone diameter
PL	Pedestal length
PD	Pedestal diameter
SN	Number of scales
SL	Scale length
SW	Scale width
BL	Bract length
AWL	Awn length
BW	Bract width
ADM	Cone axil diameter (at mid-point)



NT - needle thickness
 NW - needle width
 VCW - vascular column width
 VCT - vascular column thickness
 VCAD - distance from vascular column to the adaxial surface
 RCD - resin canal diameter
 RCM - distance from the resin canal to margin (right or left)
 RCAD - distance from the resin canal to the adaxial surface
 RCAB - distance from the resin canal to the abaxial surface
 D1 to D30 - radial distances

Figure 3. Larch needle cross-sectional characters measured.

dehydration series and two paraffin and polymer waxes (TissuePrep 2*) (Appendix II). The midsections were then embedded in paraffin blocks. Using a rotary microtome, 7 μm sections were made from the paraffin blocks. The sections were stained using Johansen's Safranin and a 0.5% solution of Fast Green FCF in 95% ethanol (Gray, 1958).

All needle traits except needle length and number of epithelial cells surrounding the resin canals were measured with a light microscope and a Houston Hipad Digitizer**. A program written by Dr. W. H. Parker of Lakehead University for the Apple IIe *** recorded the measurements made on the Digitizer.

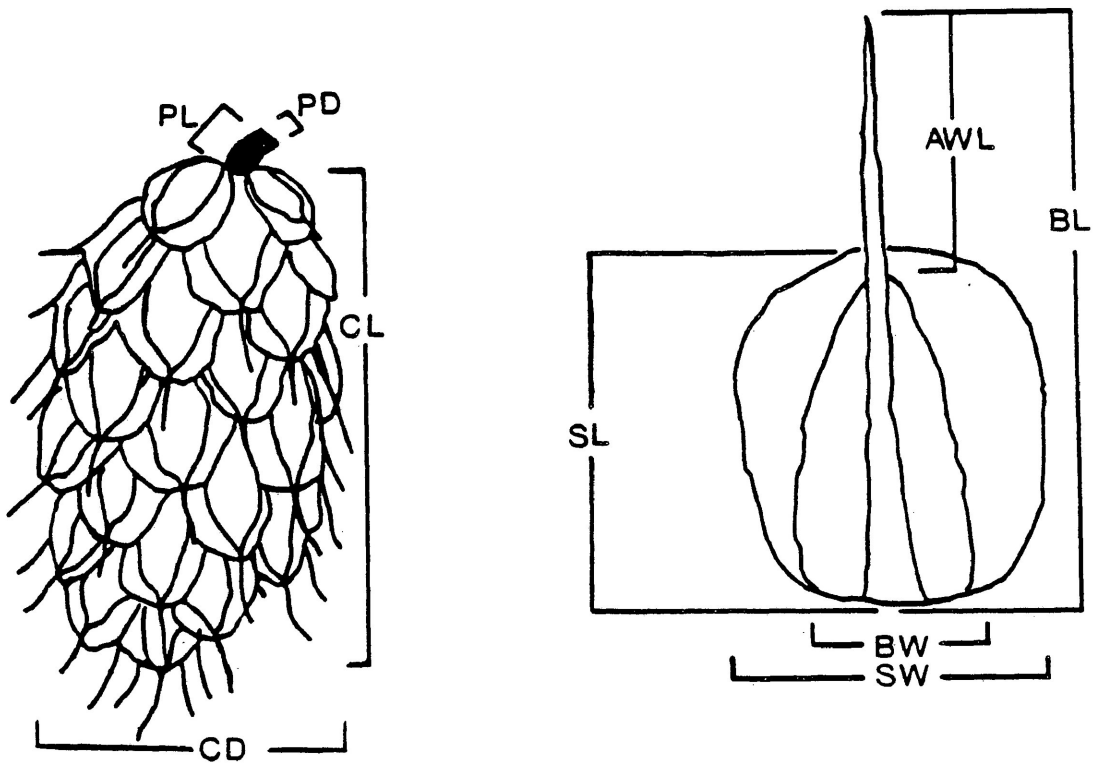
Cones

Eleven macroscopic cone traits were selected for measurement. Cones were soaked for a minimum of 24 hours in a 0.1% detergent solution to open and soften the cones. Cone length and diameter, pedestal length and diameter, and axil diameter were measured for each cone using calipers. (Figure 4). The middle scale of each cone was determined by counting the total number of scales, and this scale was used to determine length and width, bract length (including awn) and width, and bract length. Whenever the middle scale was damaged or deformed, one of the two neighbouring scales was

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*** Registered trademark of Apple Computer Inc.



CL - cone length
 CD - cone diameter
 PL - pedestal length
 PD - pedestal diameter
 SL - scale length
 SW - scale width
 BL - bract length
 AWL - awn length
 BW - bract width

Figure 4. Larch cone characters measured (scale and bract measurements are for middle cone scale).

selected for measurements. Table 3 lists the abbreviations used for the cone characters.

Arnold Arboretum Material

The procedures used for preparing and measuring alpine and western larch foliage were also used for samples obtained from the Arboretum and the supplementary specimens.

Measurements conducted on cones were modified in order to preserve cone material for future reference. Cones were soaked for a minimum of 24 hours in a 0.1% detergent solution and then cone and pedestal length and width were recorded. The number of scales per cone were counted without damaging the cone. Five scales and bracts from the mid-section of each cone were removed and scale length and width, bract length and width and awn length measured. Cone axis diameter could not be determined.

DATA ANALYSIS

Results from the five samples from each individual were averaged for use in subsequent analyses. All statistical analyses were done on a Vax* 11/780 computer using the Statistical Package for the Social Sciences (SPSS 1986) at the Computer Centre of Lakehead University.

Univariate statistics were used to examine interpopulation or species character differentiation. A

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graphics algorithm written by Dr. W. H. Parker for the MacIntosh* computer was used to display the mean, standard deviation and range of selected characters (Hubbs and Hubbs 1953).

Principal component and discriminant analyses were utilized to examine the patterns of variation expressed in the overall data set.

Principal components analysis (PCA) examines the relationship among a set of variables, making no assumptions about the underlying structure of the data (Chatfield and Collins 1980). PCA transforms a set of original, correlated variables into a set of uncorrelated principal components. These components are linear combinations of the original variables and are ordered by magnitude. For this study, the number of components contributing substantially to the variance expressed in the data set was determined by graphing the eigenvalues associated with the components. Those components whose eigenvalues formed the sloped portion of the curve were considered significant. Once the slope of the eigenvalues approached zero, the components were not considered significant. PCA was derived from the correlation matrix and was used primarily to reduce the dimensionality of the data.

Discriminant analysis (DA) also utilizes linear combinations of variables but uses data predefined into

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groups. DA identifies combinations of variables that are able to best discriminate the predetermined groups (Chatfield and Collins 1980). Stepwise analysis minimizing Wilks lambda was the DA method selected for this study. Although DA assumes a multivariate normal distribution and equal variance-covariance matrices within each group, these assumptions were not always met by the data. However, Klecka (1975) contends that the SPSS discriminant analysis procedure is very robust and these assumptions are not critical.

Ordinations of populations or species on the PCA and DA axes were produced on the MacIntosh computer using an algorithm developed by Dr. W. H. Parker.

RESULTS

Population averages for the needle and cone characteristics measured are given in Table 4 and Appendix IV. Hubb's diagrams for selected characters are presented in Figures 5 and 6. The first and sixth radial distance measurements of L. lyallii and L. occidentalis needle cross sections (D1 and D6) were excluded from any analysis to avoid inclusion of ipsative variables since, in some needle sections, the needle thickness and width corresponded to the sum of two radial distances (ie. D1 + D16 and D6 + D26).

NEEDLE AND CONE CHARACTERS

Based on all five L. lyallii populations, average cone length and diameter were 3.2 and 1.5 cm respectively. The cones possessed an average of 49 cone scales. These cone scales averaged 8.4 mm long and 7.1 mm wide. Bracts were, on average, 14.2 mm in length including a 3.8 mm awn.

Examination of the data reveals that cones from the Big Hill, Washington population (LL-09) were the largest of the five alpine larch populations. Cones from Big Hill averaged 3.6 cm in length and 1.7 cm in diameter. Cones from population LL-09 were also unique because of their very long bracts and awns. Respectively, the average bract and awn length for this

Table 4. Mean and standard deviations of selected cone and needle variables by larch species and population. Unless indicated, values are expressed as mm x 10E-2. Variables not included are presented in Appendix II.

LARIX LYALLII POPULATIONS																		
CODE	CL* (mm)		CD (mm)		PL (mm)		PD (mm)		SN		SL (mm)		SW (mm)		BL (mm)		AWL (mm)	
	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s
LL-01	34.2	4.0	16.5	2.0	6.1	1.2	3.1	0.4	48	0.7	9.3	1.5	7.7	0.9	14.3	1.4	3.7	1.1
LL-02	30.9	5.0	13.4	2.2	5.5	1.4	3.0	0.4	48	0.8	6.8	2.1	6.1	1.6	13.5	0.5	4.1	1.0
LL-03	30.7	4.4	13.4	1.8	5.8	1.4	3.1	0.4	50	0.8	7.7	1.8	6.5	1.4	13.7	1.3	3.9	1.0
LL-04																		
LL-05	28.4	4.8	13.8	1.9	4.3	1.1	3.0	0.4	45	1.0	8.6	0.8	7.1	0.4	12.1	1.2	2.8	0.9
LL-06																		
LL-07																		
LL-08																		
LL-09	36.3	6.4	16.7	2.8	5.3	1.6	3.3	0.6	55	1.0	9.4	1.9	7.9	1.7	17.2	2.5	4.6	1.4
LL-10																		
LL-11																		
L. lyallii	32.1	4.9	14.8	2.1	5.4	1.3	3.1	0.4	49.1	0.9	8.4	1.6	7.1	1.2	14.2	1.4	3.8	1.1
LARIX OCCIDENTALIS POPULATIONS																		
LO-01	20.1	3.9	13.7	1.6	2.8	0.8	3.9	0.6	5.1	0.8	6.0	1.2	5.8	1.0	9.3	1.3	2.8	1.1
LO-02	25.3	4.9	15.3	1.7	4.3	1.4	4.1	0.9	4.7	1.0	7.4	1.2	7.1	0.9	11.1	1.9	3.4	1.3
LO-03																		
LO-04																		
LO-05																		
LO-06																		
L. occidentalis	22.7	4.4	14.5	1.7	3.6	1.1	4.0	0.8	4.9	0.9	6.7	1.2	6.5	1.0	10.2	1.6	3.1	1.2

* CL = CONE LENGTH, CD = CONE DIAMETER, PL = PEDESTAL LENGTH, PD = PEDESTAL DIAMETER, SN = SCALE NUMBER, SL = SCALE LENGTH, SW = SCALE WIDTH, BL = BRACT LENGTH, AWL = AWN LENGTH

Table 4. continued

LARIX LYALLII POPULATIONS

BW*(mm)		ADM(mm)		RCELL		NL(cm)		NW		NT		VCT		VCAD		RCL		RCLAD	
\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s
5.4	0.7	5.0	0.9	7.7	1.1	2.5	0.4	66.4	6.8	52.6	5.1	12.8	1.9	19.4	2.5	2.5	1.0	6.3	2.0
4.9	0.9	4.8	0.9	8.1	1.3	2.4	0.5	59.8	5.6	45.6	5.4	13.4	1.5	15.9	2.5	2.4	0.7	6.7	2.6
5.2	0.6	4.5	0.9	8.4	1.2	2.7	0.5	65.7	4.1	53.5	4.6	13.9	1.4	19.2	2.6	2.9	1.2	6.6	2.2
4.9	0.8	6.7	0.8	7.6	1.4	2.5	0.6	69.3	7.7	52.3	5.9	13.9	1.5	18.7	2.7	2.7	1.1	6.0	2.1
				8.0	1.2	2.3	0.4	70.8	7.5	58.0	5.6	14.3	1.5	20.8	2.6	3.2	0.9	6.7	2.3
				8.0	1.1	2.3	0.4	63.5	5.3	47.7	4.5	12.4	1.0	17.1	2.2	3.0	0.9	5.1	1.9
				7.6	0.9	2.8	0.5	69.2	6.8	48.8	5.2	12.9	1.2	17.6	2.4	3.5	1.0	4.6	1.6
				7.1	1.3	3.0	0.6	71.3	6.9	54.1	6.0	14.2	1.5	19.6	2.4	2.3	1.5	7.0	2.5
5.0	0.6	4.4	1.1	8.4	1.2	3.1	0.7	73.7	6.7	56.8	7.0	14.8	1.4	20.4	2.7	2.5	1.3	7.2	2.7
				7.0	1.1	2.4	0.5	65.9	6.0	48.4	4.5	13.2	1.2	16.8	2.1	2.4	0.6	5.2	1.5
				8.1	1.2	2.5	0.4	67.5	6.8	53.2	6.2	14.1	1.5	18.6	3.1	3.0	0.9	5.6	1.9
5.1	0.7	5.1	0.9	7.8	1.2	2.6	0.5	67.6	6.4	51.9	5.5	13.6	1.4	18.6	2.5	2.8	1.0	6.1	2.1

LARIX OCCIDENTALIS POPULATIONS

4.0	0.5	3.6	1.0	6.1	1.1	2.2	0.3	71.8	7.6	51.1	6.9	13.0	1.5	18.4	3.1	2.7	2.2	3.6	1.6
4.8	0.6	4.6	1.2	5.8	1.1	3.6	0.8	76.4	8.4	48.0	4.0	13.6	1.2	17.4	2.0	3.3	3.1	3.5	1.2
				5.4	0.9	3.2	0.6	71.0	7.5	53.0	5.5	14.8	1.8	18.9	2.4	3.6	3.1	4.5	2.0
				5.8	0.7	2.7	0.5	76.6	7.1	47.7	4.7	13.1	1.3	17.1	2.2	2.6	2.4	2.9	1.0
				5.8	0.9	2.5	0.6	76.5	6.2	46.2	4.3	12.2	1.1	17.2	2.0	2.8	2.4	2.6	0.6
				5.3	0.8	2.9	0.6	71.9	6.1	44.1	5.9	12.3	1.5	15.8	2.4	2.8	2.7	2.5	0.8
4.4	0.6	4.1	1.1	5.7	0.9	2.9	0.6	74.0	7.2	48.4	5.2	13.2	1.4	17.5	2.4	3.0	2.7	3.3	1.2

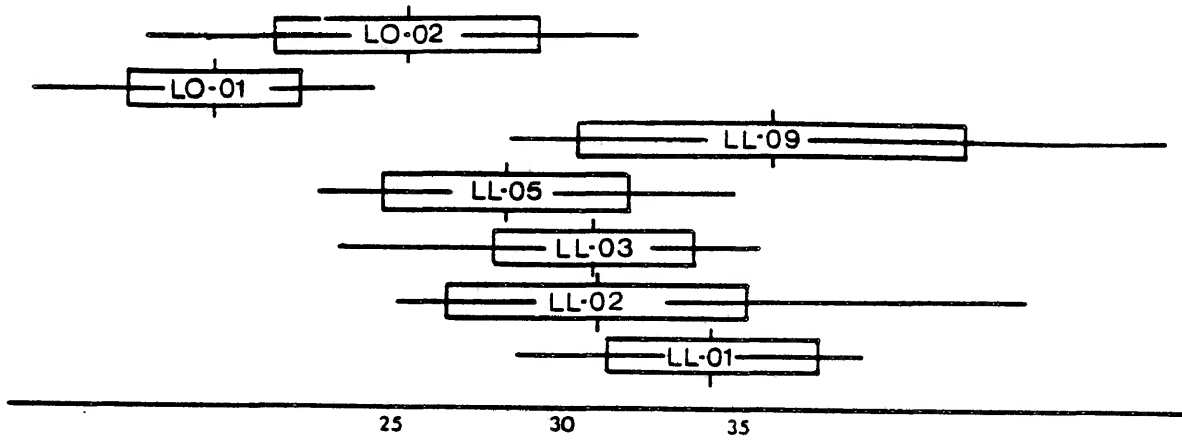
* BW = BRACT WIDTH, ADM = CONE AXIL DIAMETER, RCELL = NUMBER OF EPITHELIAL CELLS, NL = NEEDLE LENGTH, NW = NEEDLE WIDTH, NT = NEEDLE THICKNESS, VCT = VASCULAR COLUMN THICKNESS, VCAD = VASCULAR COLUMN ADAXIAL DISTANCE, RCL = LEFT RESIN CANAL DIAMETER, RCLAD = DISTANCE FROM LEFT RESIN CANAL TO ADAXIAL SURFACE

Table 4. continued.

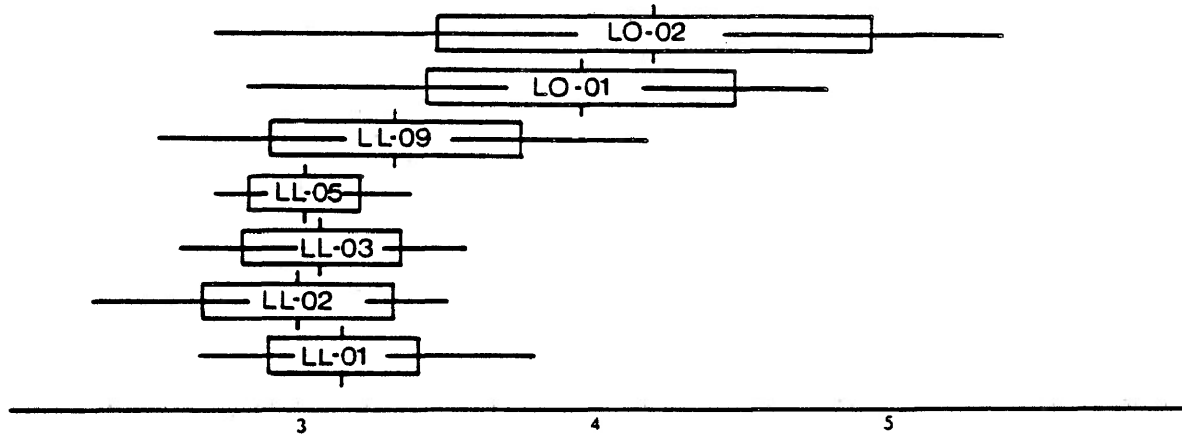
LARIX LYALLII POPULATIONS													
RCLM		RCLAB		RCR		RCRAD		RCRM		RCRAB		VCW	
\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s
2.8	0.4	6.8	2.1	2.3	0.7	6.2	1.7	2.8	0.5	7.4	2.5	13.7	1.6
2.7	0.5	5.3	2.0	2.2	0.7	6.9	2.2	2.8	0.4	5.1	1.9	14.1	1.4
2.7	0.4	7.1	2.2	2.7	0.7	6.7	2.1	2.8	0.4	7.6	2.4	14.3	1.5
2.8	0.5	7.8	2.4	2.6	1.0	6.1	2.0	2.9	0.5	7.9	2.8	14.4	1.8
2.7	0.4	8.1	2.7	3.2	0.9	7.6	2.4	2.9	0.5	8.3	2.1	15.0	1.6
2.3	0.4	7.8	2.2	3.1	0.9	5.8	1.6	2.6	0.4	7.6	2.1	12.7	1.0
2.3	0.3	6.7	2.1	3.4	0.7	6.1	1.6	2.5	0.4	6.4	1.8	13.4	1.2
2.8	0.5	6.8	2.2	2.4	1.5	7.8	2.4	2.9	0.6	6.9	2.0	14.8	1.6
2.8	0.4	7.0	2.2	2.4	0.9	8.5	2.9	3.0	0.6	7.4	2.4	15.3	1.6
2.5	0.4	7.3	2.4	2.6	1.2	5.4	1.7	2.7	0.3	8.0	2.1	13.6	1.6
2.7	0.5	7.8	2.6	2.8	0.8	6.1	1.8	2.9	0.5	7.8	2.4	14.9	1.6
2.6	0.4	7.1	2.3	2.7	0.9	6.7	2.0	2.8	0.5	7.3	2.2	14.2	1.5

LARIX OCCIDENTALIS POPULATIONS													
RCLM		RCLAB		RCR		RCRAD		RCRM		RCRAB		VCW	
\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s
2.2	0.4	8.6	3.4	2.5	2.0	3.6	1.3	2.3	0.4	8.8	2.9	15.0	1.9
2.5	0.5	11.0	4.2	3.8	3.3	4.0	1.6	2.7	0.5	10.7	3.8	14.7	1.2
2.4	0.6	8.7	3.8	2.9	2.7	4.5	1.3	2.5	0.6	8.7	2.7	16.7	1.9
2.1	0.4	8.0	3.6	2.4	1.9	3.2	1.1	2.4	0.4	8.2	3.4	15.1	1.7
2.1	0.4	9.1	3.8	2.7	2.4	3.2	0.9	2.4	0.4	9.1	3.2	14.0	1.6
2.0	0.4	9.3	3.2	3.3	3.2	3.0	0.8	2.2	0.4	9.5	3.1	13.6	1.4
2.2	0.5	9.1	3.7	2.9	2.6	3.6	1.2	2.4	0.5	9.2	3.2	14.9	1.6

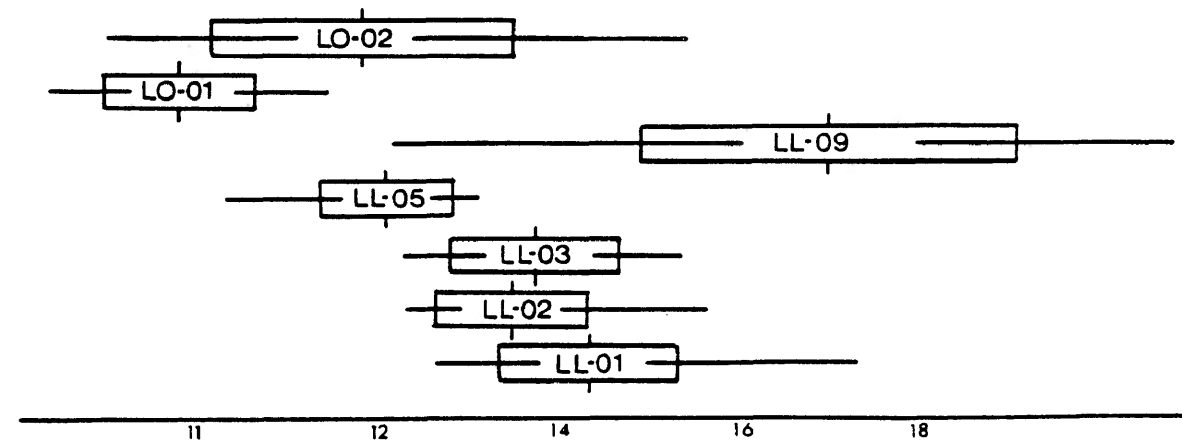
RCLM = DISTANCE FROM LEFT RESIN CANAL TO LEFT MARGIN, RCLAB = DISTANCE FROM LEFT RESIN CANAL TO ABAXIAL SURFACE, RCR = RIGHT RESIN CANAL DIAMETER, RCRAD = DISTANCE FROM RIGHT RESIN CANAL TO ADAXIAL SURFACE, RCRM = DISTANCE FROM RIGHT RESIN CANAL TO RIGHT MARGIN, RCRAB = DISTANCE FOR RIGHT RESIN CANAL TO ABAXIAL SURFACE, VCW = VASCULAR COLUMN WIDTH



a) cone length (mm)

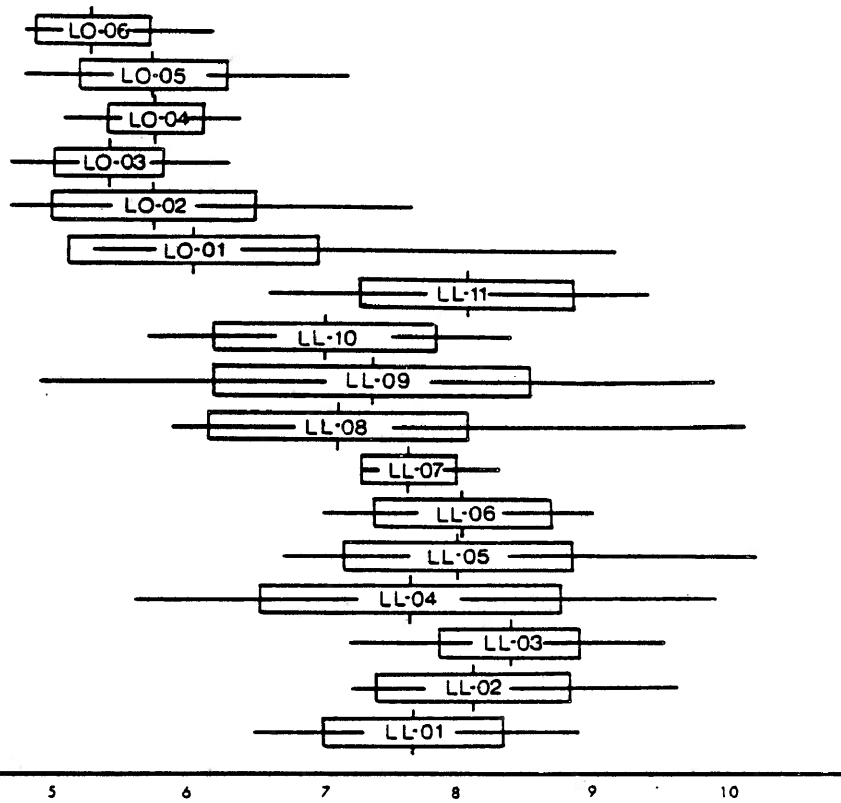


b) pedestal diameter (mm)

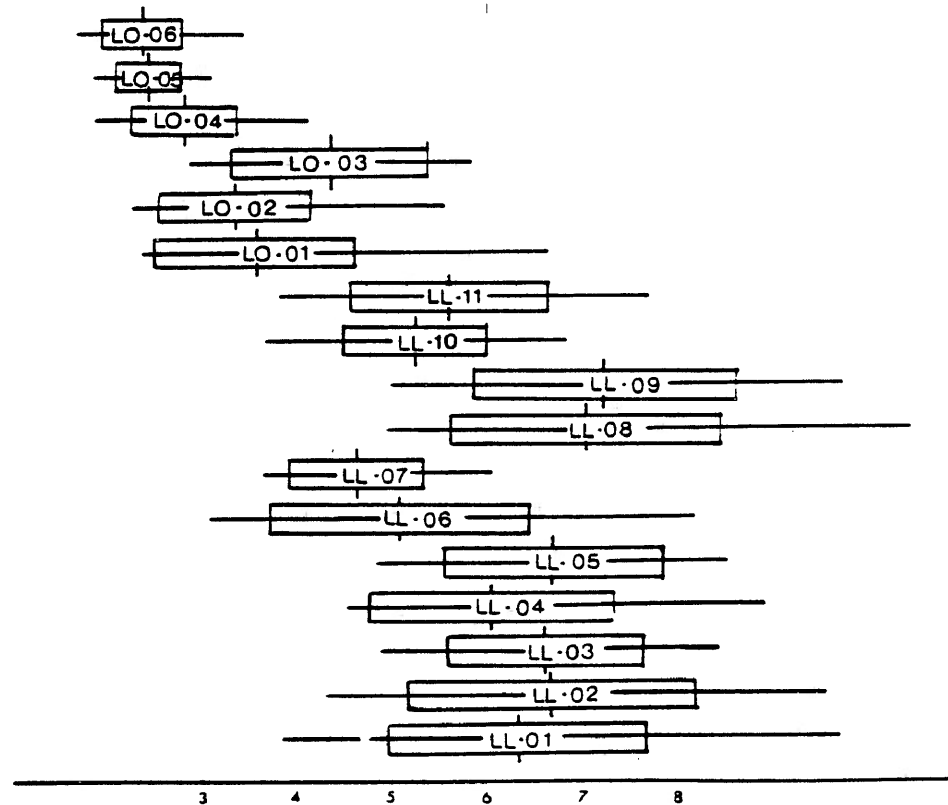


c) bract length (mm)

Figure 5. Hubb's diagrams for a) cone length (mm), b) pedestal diameter (mm) and c) bract length (mm). Population means are indicated by vertical lines, standard deviations identified by rectangles and ranges expressed by horizontal lines



a) number of epithelial cells surrounding the resin canals



b) distance from left resin canal to margin ($\text{mm} \times 10^{-2}$)

Figure 6. Hubb's diagrams for a) number of epithelial cells surrounding the resin canals and b) distance from left resin canal to margin ($\text{mm} \times 10^{-2}$). Population means are indicated by vertical lines, standard deviations identified by rectangles and ranges expressed by horizontal lines.

population were 2.9 and 0.5 mm longer than that from any other population. The smallest cones belonged to population LL-05 from St. Mary's, Montana. These cones averaged only 28.4 cm in length. The average number of cone scales per cone ranged from a low of 45 for population LL-05 to a high of 55 for population LL-09.

The average number of epithelial cells surrounding the resin canals was quite consistent within the alpine larch needles, ranging from 7.1 to 8.4. The needles averaged 2.6 cm in length, 0.7 mm in width and 0.5 mm in thickness. Needles from the two Washington populations (LL-08 and LL-09) were the longest and widest of the eleven populations sampled.

Alpine larch cones were consistently longer than western larch cones. Western larch cones, however, generally had more cone scales. Alpine larch cone and bract scales were considerably longer than those of western larch. The pedestals of alpine larch were longer and thinner than those of western larch.

Needles from L. occidentalis and L. lyallii could not be distinguished on the basis of needle length or thickness. Western larch needles were generally wider than those of alpine larch. In all populations of alpine and western larch, the average width of the vascular cylinder exceeded the average vascular column thickness, indicating the vascular columns are somewhat flattened.

L. LYALLII POPULATIONS

Analysis of Combined Cone and Needle Data (5 Populations)

Sufficient cones for analysis were collected from only five populations of alpine larch. As Figure 1 indicates, at least one cone collection was obtained from each of the three major areas of distribution of alpine larch.

As expected, the majority of needle cross-sectional variables were strongly and positively correlated (Appendix V). Neighbouring radial distances had correlations ranging from 0.71 to 0.97 and averaging 0.93. Correlations ranging from 0.35 to 0.65 were obtained between the relative positions of the two resin canals in the needle sections. The size of the two resin canals within a cross-section were closely related, displaying a correlation of 0.75.

The highest correlation between cone and needle traits was 0.62 for bract length and needle length (Appendix V). The remaining correlations between needle and cone characteristics were below 0.50.

Cone length was most strongly correlated with cone diameter, scale number and bract length (0.73, 0.73 and 0.63 respectively). The correlations between cone diameter and scale length and width were both 0.77 while that between bract and awn length was 0.73. The remaining correlations among cone characteristics were below 0.60.

Principal component analysis (PCA) based on the correlation matrix of the combined cone and needle traits indicated that the variables could be examined as a single group since no distinct groups of variables appeared to be present.

Examination of the pattern of eigenvalues revealed that the first 7 vectors contributed substantially to the variation present and accounted for 78.3% of the variation present in the data set. The first three vectors accounted for 48.9%, 10.8% and 6.2 % of the variation respectively. Coefficients for the first two principal component functions are presented in Appendix VI.

An ordination of the individual component scores for the first two principal components is provided in Figure 7. The plot of the first two components shows three distinct groupings. The two U. S. populations (LL-05 and LL-09) form one group, as do populations LL-01 and LL-03 from the Purcell and Rocky Mountains. Population LL-02 is separate and displays more variability along the first PC than any other population.

Needle sections from population LL-02 appeared very different than those from all other populations (Figure 8). The needles were strongly keeled on both the abaxial and adaxial surfaces. Initially, it was suspected that the needles had not been rehydrated properly but subsequent attempts at preparing

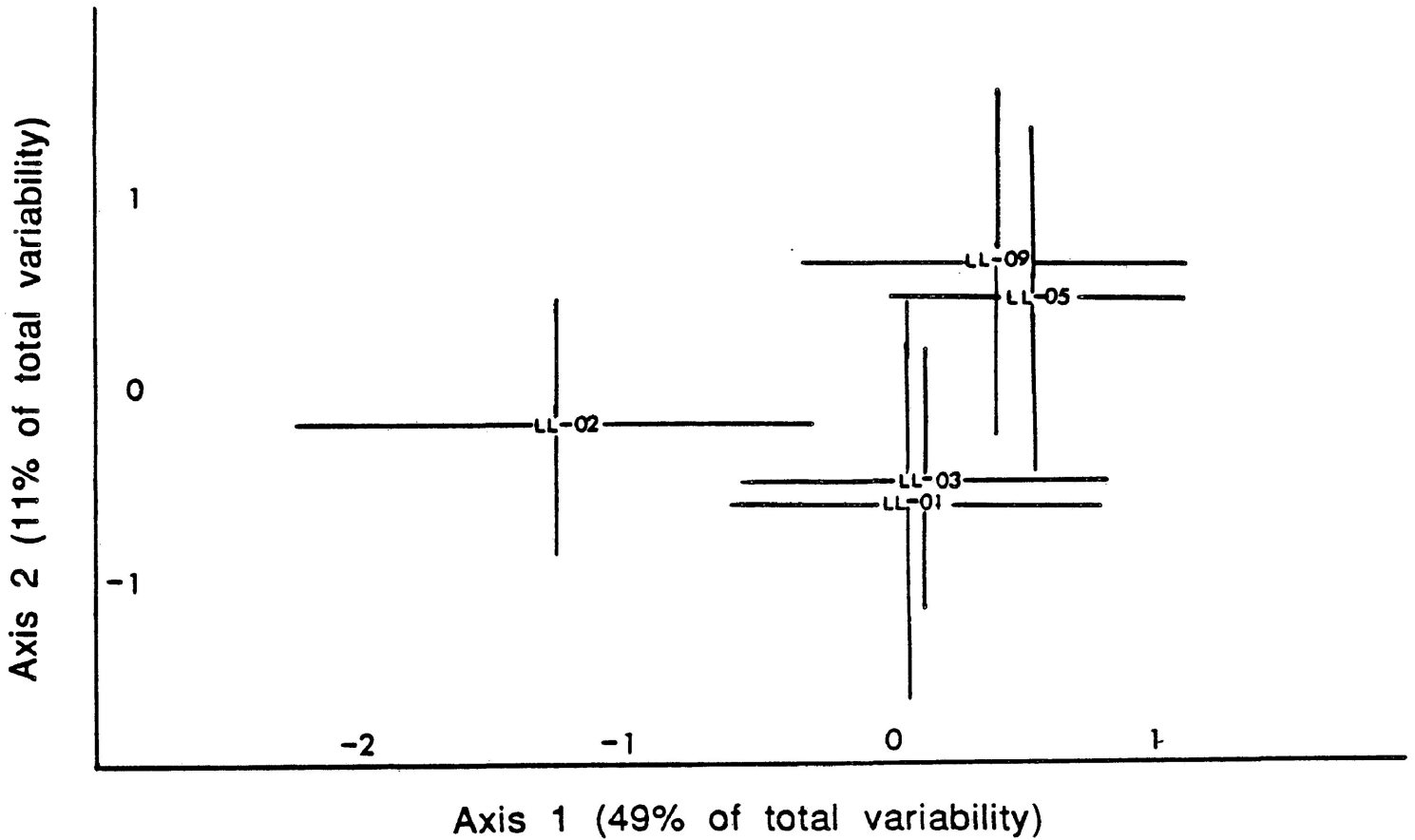


Figure 7. Principal component analysis ordination of cone and needle characters of five *L. lyallii* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

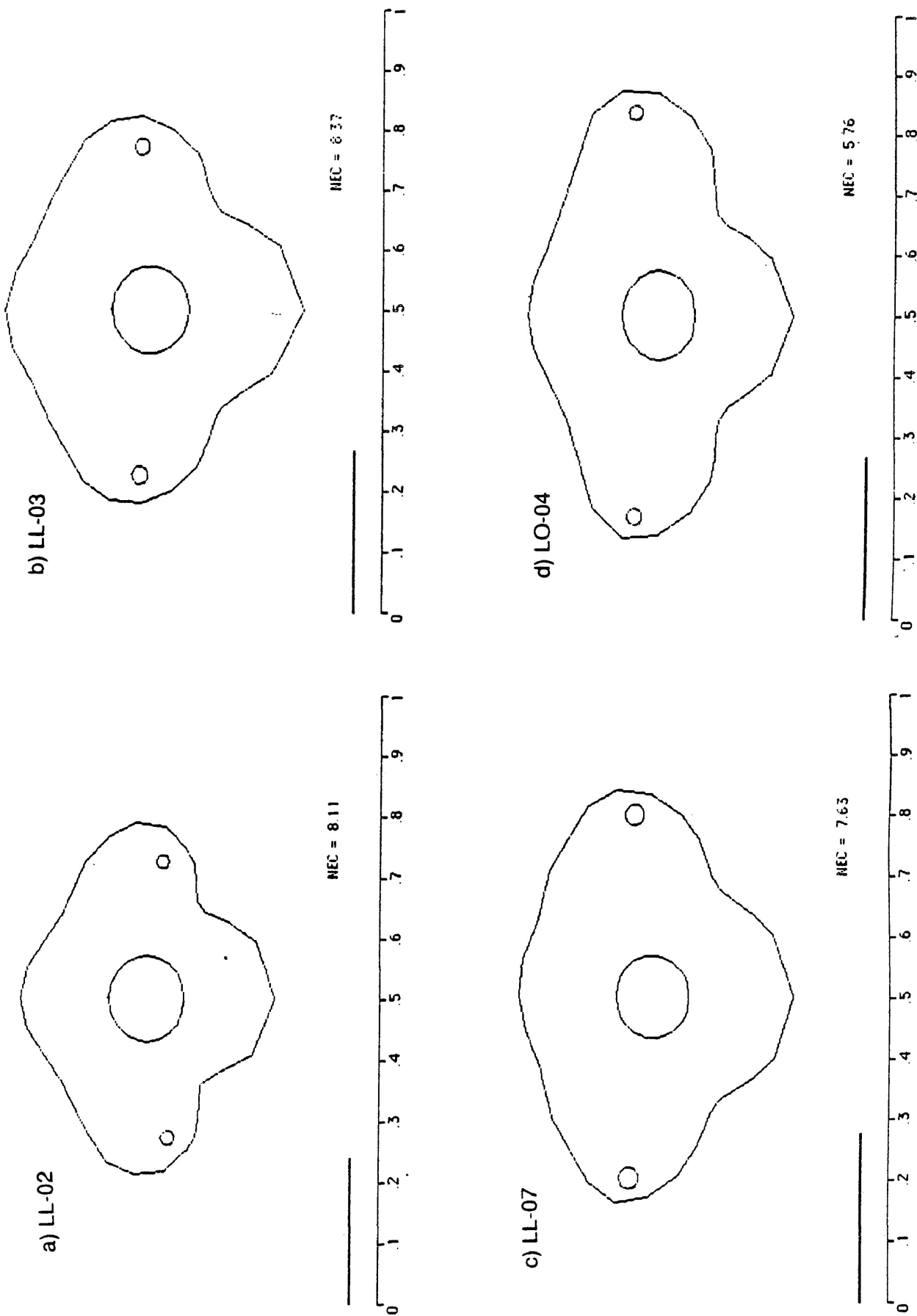


Figure 8. Computer drawn outlines of the average cross-section of *L. lyallii* populations a) LL-02, b) LL-03 and c) LL-07 and *L. occidentalis* population d) LO-04. Bottom scale indicates needle cross-sectional size (mm) and needle length (horizontal bar) (dm). Average number of epithelial cells per resin canal (NEC) is also included.

the specimens yielded the same results. A review of field collection notes did not provide an explanation for the unusual needle shape. The results from the PCA reflect this difference in needle cross section.

Analysis of variance was conducted on the scores of the first two PC axes to determine the significance of variation between collection sites. The first principal component accounted for 55% of the variation expressed in the data set. Sixty-two percent of the variation attributable to this component is expressed between sites (Appendix VII). In the second PC, which accounts for 9% of the variability, 29% of the variation is expressed between populations (Appendix VII). Evidently much of the main component of variation is expressed between collection sites.

Discriminant analysis was performed using all individuals from the five populations. In the population analysis, the stepwise process minimizing Wilk's lambda selected 27 variables for inclusion based on the criteria of a minimum F value for entrance of 1.0. Four discriminant functions were computed. The first, second and third functions accounted for 42.4%, 33.8% and 14.4%, respectively, of the variation present. Appendix VIII contains the coefficients for the first two discriminant functions.

The first discriminant function was primarily correlated with a large number of radial distances, needle width and

vascular column width and thickness. No cone variables were strongly correlated with this function. Needle length, the number of epithelial cells surrounding the resin canals and several cone variables dominate the second function while the third is influenced by a variety of needle and cone variables.

Using the discriminant functions obtained from this analysis 97.8% of the individuals were correctly reclassified into their original populations.

The ordination of the individual discriminant scores of the first two discriminant functions (Figure 9) clearly separates each of the populations from the United States (LL-09 and LL-05) from the Canadian Purcell and Rocky Mountain populations. It should be noted that populations LL-02 and LL-03 are not widely separated by the discriminant analysis which emphasizes variables which distinguish population groups.

Analysis of Needle Data (11 Populations)

Short shoot needles from the complete set of eleven alpine larch populations were available for measurement and analysis. As in the combined data set, many of the traits examined were highly correlated (Appendix IX). Needle length and number of epithelial cells surrounding the resin canals were not strongly correlated to any other needle variables, exhibiting no correlations greater than 0.35. Needle width and thickness were both strongly correlated with vascular column measurements and radial distances. Resin canal

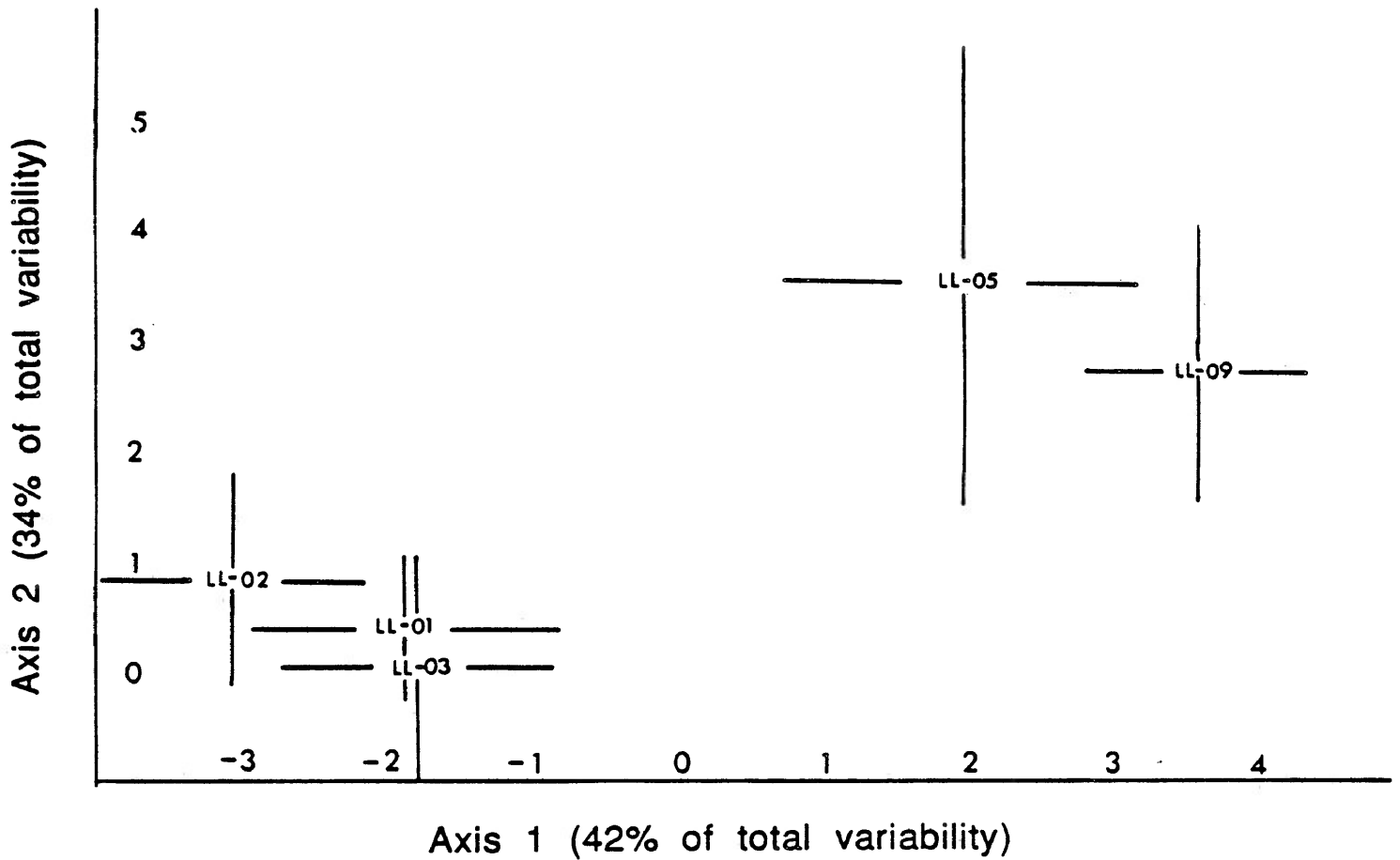


Figure 9. Discriminant analysis ordination of cone and needle characters of five *L. lyallii* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

position and size variables displayed correlations between 0.50 and 0.66. Proximal radial distances possessed average correlations of 0.93 and ranged from 0.85 to 0.96. Vascular column width and thickness had a correlation value of 0.84, indicating a close relationship between the two.

The PCA of the needle data grouped all variables together with the number of epithelial cells somewhat separated from the main group of variables. Respectively, the first three principal components accounted for 55.4%, 9.0% and 5.8% of the variation present in the data. The first seven components account for a total of 84.8% of the variation, with subsequent components each accounting for less than 1.0% and not contributing sizably to the variation present. Coefficients for the first two principal component functions appear in Appendix VI.

The individual principal component scores of the first and second axes clearly distinguish population LL-02 from the remaining populations (Figure 10). Within the main group of populations a continuum of principal component scores is evident. Considerable overlap between populations is evident in the ordination.

In an attempt to correlate the principal components to environmental factors, a correlation was attempted with the first three PC's on latitude, longitude and elevation. None of

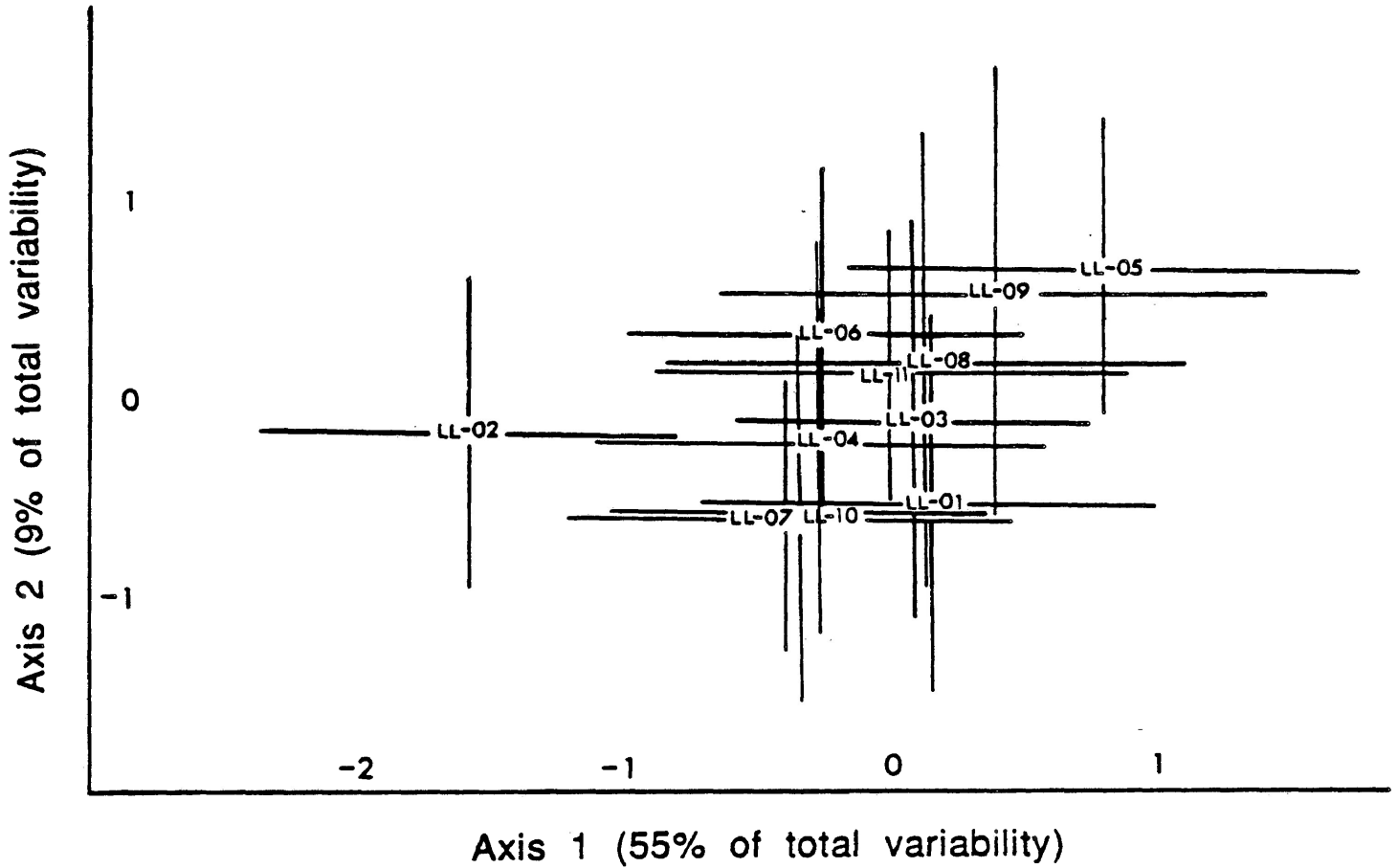


Figure 10. Principal component analysis ordination of needle characters of eleven *L. lyallii* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

these factors were at all related to the principal component scores.

Stepwise discriminant analysis of the eleven L. lyallii populations included 27 variables. Six discriminant functions accounted for 90.0% of the variation present. The first three functions accounted for 30.2%, 26.9% and 11.1% of the variation respectively. Coefficients for the first two functions are presented in Appendix VIII.

The first discriminant function was strongly influenced by the radial distances while the second was primarily related to resin canal size and position. A mixture of resin canal variables and radial distances indicative of needle thickness were the dominant variables in the third function.

Based on the discriminant function derived from all the alpine larch individuals, 78.0 % of the individuals were correctly reclassified into their original eleven populations. Of the individuals misclassified, 88.9% were within the B. C. - Alberta group. Only one of the Roman Nose individuals was misidentified; it was grouped with the western Montana population (LL-06). Seventy percent of the Washington individuals misclassified were still placed into a Washington population.

Scores of the first two discriminant functions clearly separate population LL-02 from all other populations (Figure 11). This indicates that characters with strong

interpopulation discriminatory power separate LL-02 from other L. lyallii populations. The remaining B. C. - Alberta populations form a central cluster. The two Washington populations (LL-08 and LL-09) and the Roman Nose population form are located at one end of the ordination.

L. LYALLII AND L. OCCIDENTALIS POPULATIONS

Analysis of Combined Cone and Needle Data (7 Populations)

Cones for analysis were available from only two L. occidentalis populations. The populations were located in the Purcell and Selkirk Mountains of British Columbia.

Principal component analysis of the combined cone and needle characters indicated the variables form a single group and could be examined together. The first seven principal components contributed substantially to the variation present. The first three vectors accounted for 64.6% of the variation present, slightly less than that accounted for in the alpine larch populations alone by the same components. The first three components accounted for 39.2%, 15.4% and 10.0% of the variation, respectively. Appendix VI presents the first two principal component functions.

Inclusion of the western larch populations changes the relationship expressed by the alpine larch populations alone (Figure 7). The plots of the individual component scores for the first two components are presented in Figure 12.

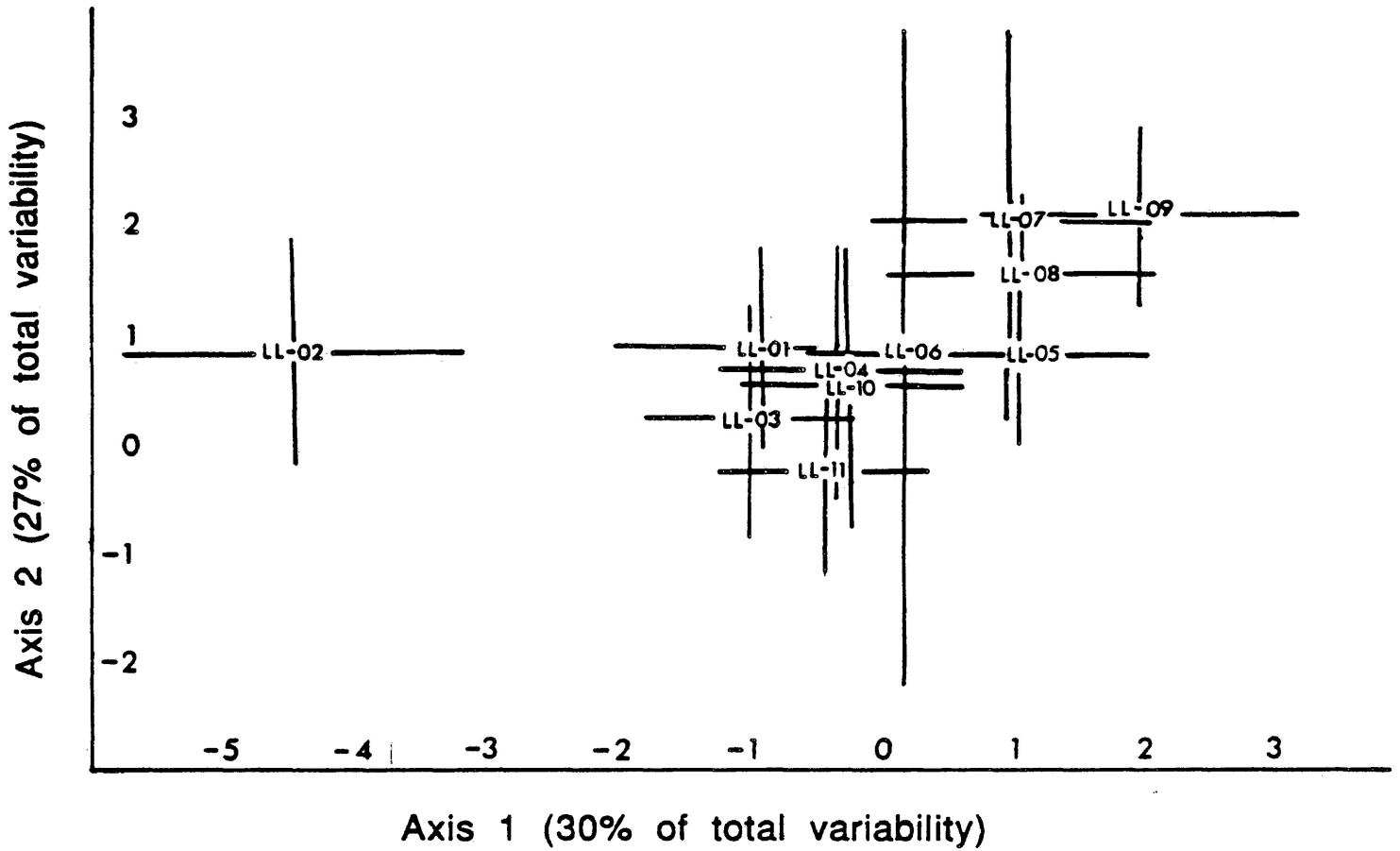


Figure 11. Discriminant analysis ordination of needle characters of eleven *L. lyallii* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

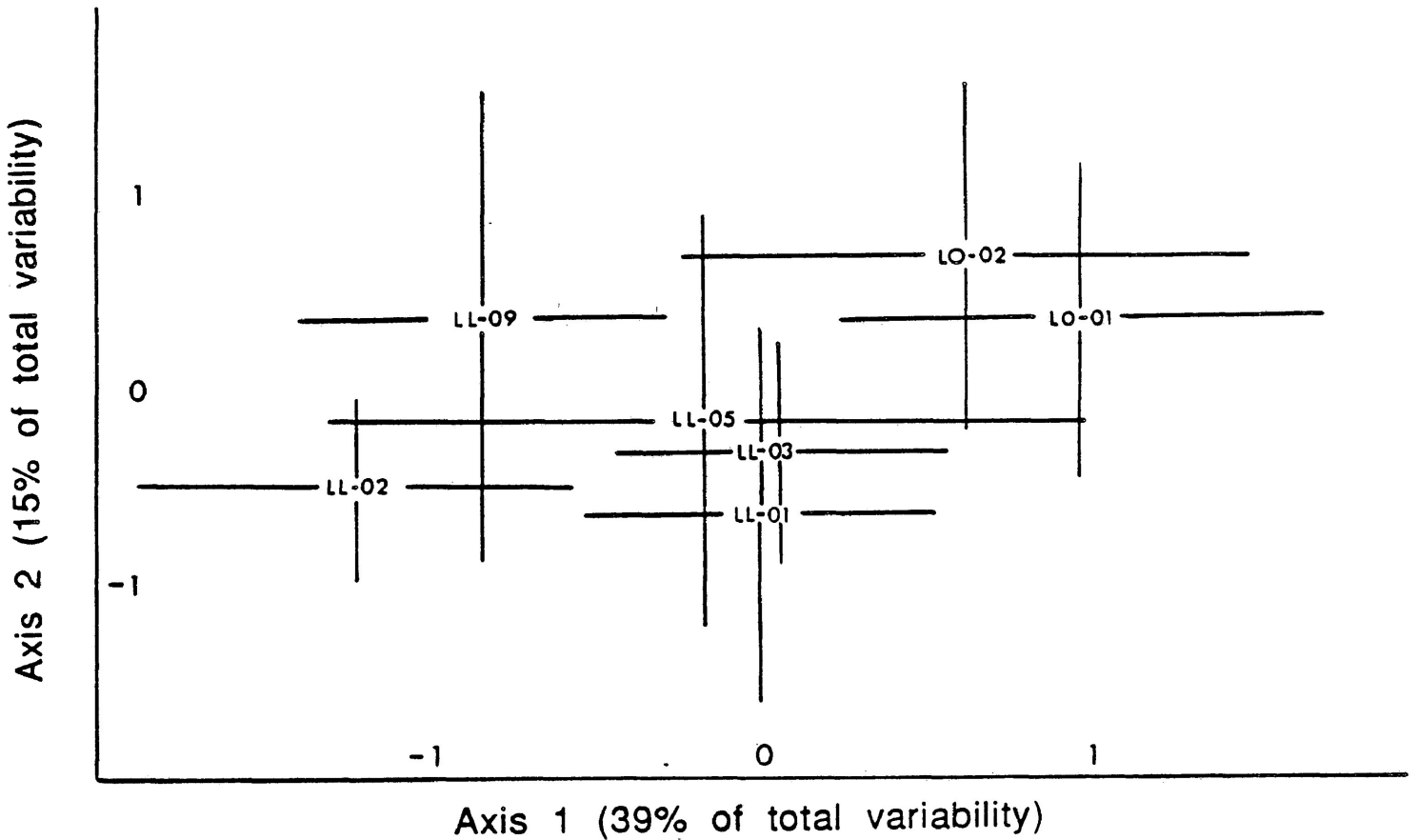


Figure 12. Principal component analysis ordination of cone and needle characters of five *L. lyallii* and two *L. occidentalis* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

Examination of these two principal components shows that alpine larch populations LL-01, LL-03 and LL-05 form a central cluster. Purcell Mountain population LL-02 is separated from the main alpine larch cluster. The Washington alpine larch population (LL-09) is distinguishable from the main group and is grouped with the two western larch populations by the second principal component. The two western larch populations (LO-01 and LO-02) are quite distinct.

Discriminant analysis was used to distinguish alpine from western larch as well as separate the seventeen individual populations

Stepwise discriminant analysis performed on the combined needle and cone data of the population groups selected 28 variables for inclusion in the discriminant function. The first three functions respectively accounted for 53.0%, 18.9% and 13.0% of variation. The first two discriminant functions are presented in Appendix VIII.

Bract length, cone length, pedestal diameter and several resin canal position variables were primarily correlated with the first function. Axil diameter, pedestal length, bract width, vascular column adaxial distance and radial distances 15 and 16 were principally expressed in the second discriminant function. The third discriminant function was

strongly correlated with needle length and width and the remaining radial distances.

The discriminant functions obtained from the analysis correctly reclassified 97.7% of the 132 individuals.

The first two discriminant functions easily separate the western larch populations from those of alpine larch (Figure 13). The Purcell and Rocky Mountain alpine larch populations form a main cluster from which the Montana (LL-05) and Washington population (LL-09) are distinguishable. Population LL-02 is, in this ordination, grouped with its neighbouring population, LL-03, and Purcell Mountain population LL-01. Since the first two discriminant functions were strongly correlated with cone variables, it is apparent that population LL-02 is not distinguishable from its neighbouring populations on the basis of cone characters.

A single discriminant function strongly correlated with pedestal diameter and length, cone length, bract length, adaxial position of the resin canals and the number of epithelial cells surrounding the resin canals was able to correctly reclassify 98.5% of the individuals included in the analysis. All individuals misclassified were western larch. Twenty-one discriminating variables were included in the analysis by the stepwise procedure.

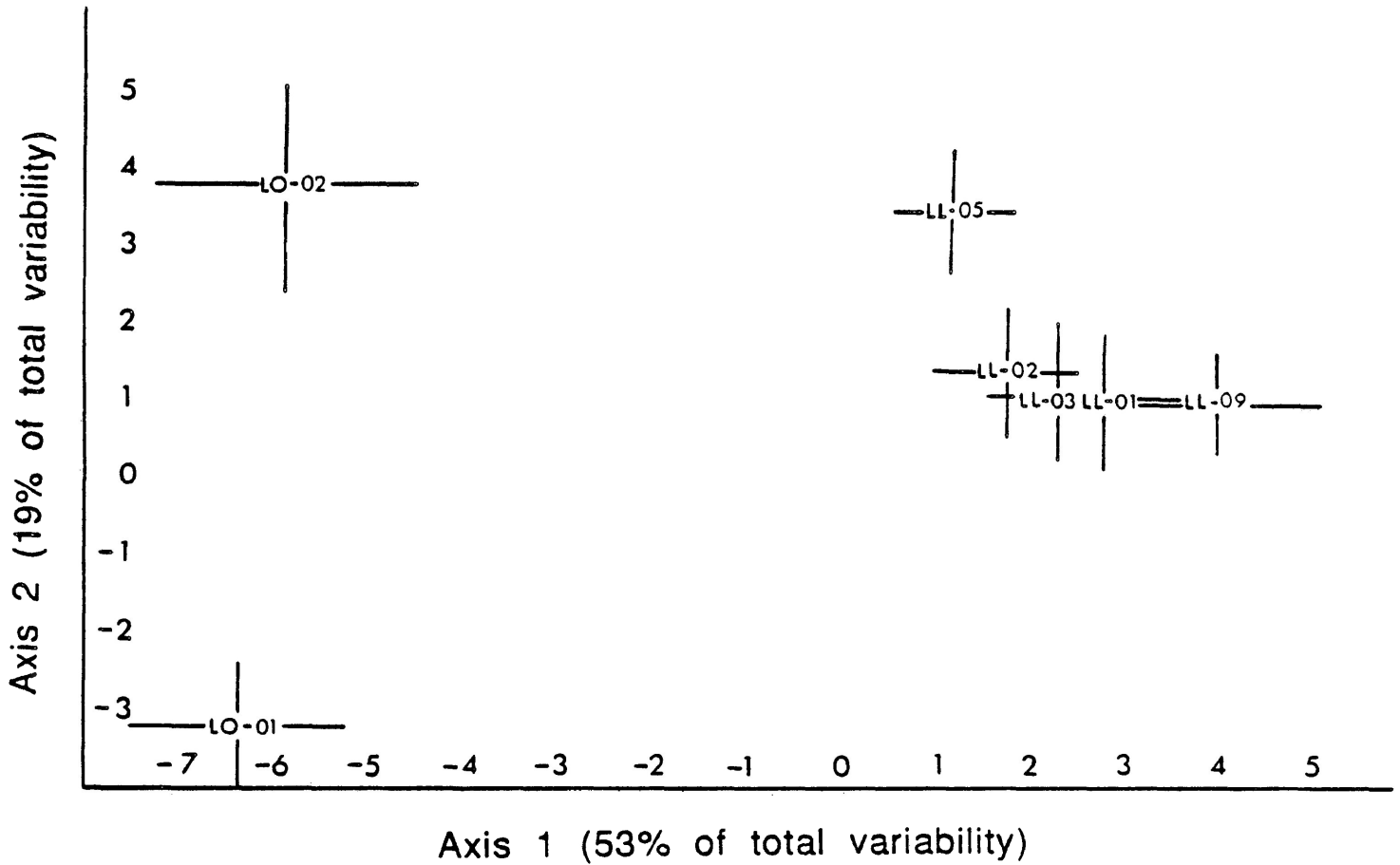


Figure 13. Discriminant analysis ordination of cone and needle characters of five *L. lyallii* and two *L. occidentalis* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

Analysis of Needle Data (17 Populations)

Needles for analysis were available from 17 populations of L. lyallii and L. occidentalis (11 and 6 populations respectively).

Once again, principal component analysis indicated all variables formed one group and could be analyzed together. Five components that contributed substantially to the variation present were extracted. The eigenvalues of all five of these components was greater than 1.0. The first principal component accounted for 46.7% of the variation present and the second accounted for an additional 17.0%. The first five components combined to explain 79.3% of the variation in the data. Coefficients for the first two principal components are found in Appendix VI.

Individual scores of the first two components clearly separated population LL-02 from all other populations (Figure 14). Four of the six western larch populations form a cluster distinct from the remaining alpine and western larch populations. These four geographically dispersed populations, LO-02, LO-04, LO-05 and LO-06, were collected from the Selkirk and Bitterroot Mountains and the Swan and Kettle River Ranges. Western larch populations LO-01 and LO-03 group with the main British Columbia - Alberta cluster of alpine larch. These populations were collected from Idaho and from the Purcell and Rocky Mountains. All the British

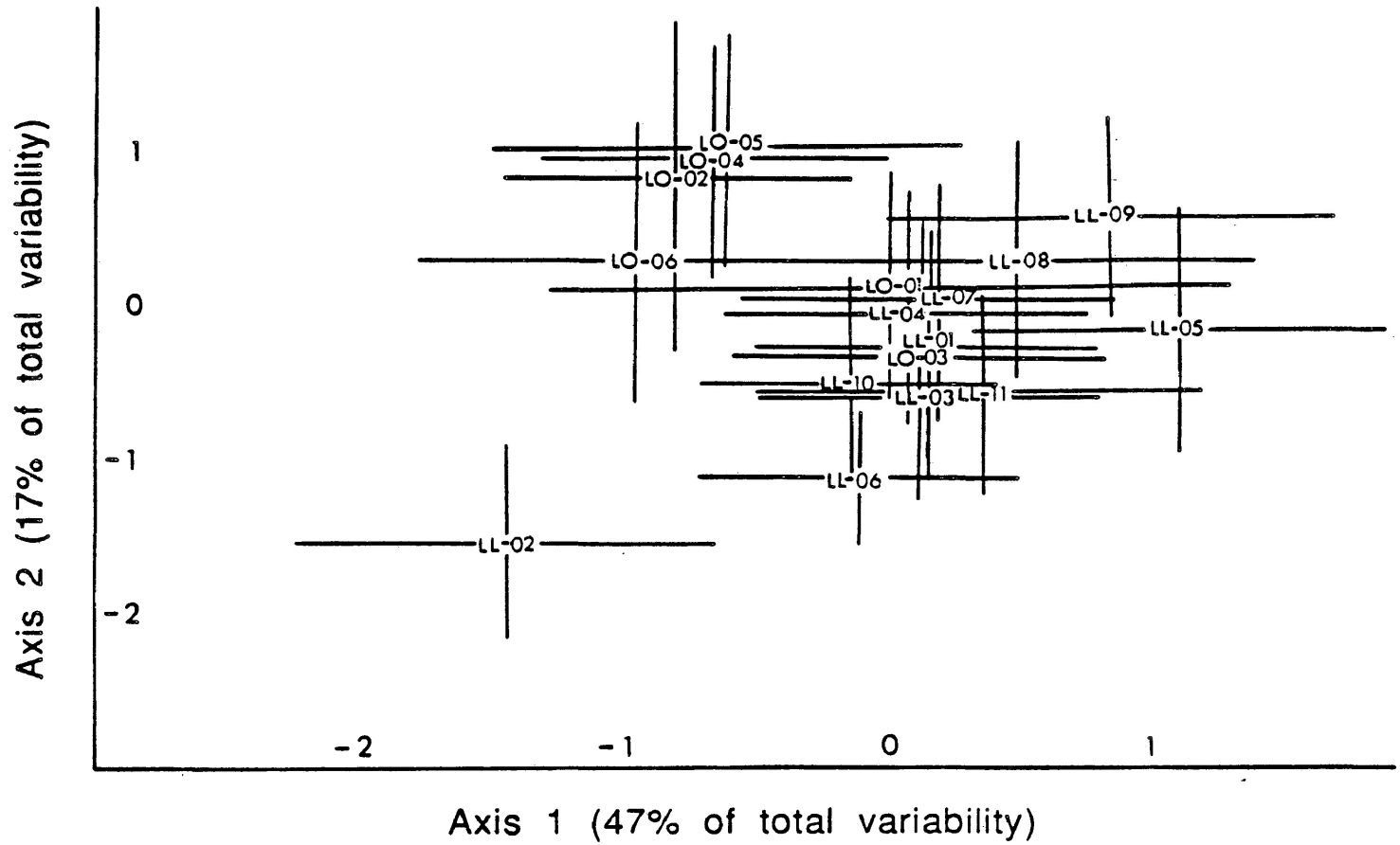


Figure 14. Principal component analysis ordination of needle characters of eleven *L. lyallii* and six *L. occidentalis* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

Columbia - Alberta populations of alpine larch other than LL-02 are part of this main cluster. In addition, the two western larch populations and the Roman Nose alpine larch population (LL-07) are included in this cluster. The two Montana populations are weakly separated from the main L. lyallii group and are completely separated from each other. The two Washington populations, especially LO-05, are also weakly separated from the main cluster.

Stepwise discriminant analysis of population groups selected 33 variables for inclusion in the discriminant functions. The first three discriminant functions accounted for 50.6%, 12.7% and 9.5% of the variation respectively. The first two discriminant functions are presented in Appendix VIII.

The resin canal adaxial distances are most strongly correlated with the first discriminant function. Radial distances 4, 5, 27 and 28, all indicators of adaxial keeling, are expressed chiefly by the second function. Needle length and vascular column width and thickness are primarily correlated with the third discriminant function.

The discriminant functions determined by the needle variables correctly reclassified 82.4% of the L. occidentalis individuals and 76.3% of those of L. lyallii into their correct populations. Combined, 78.5% of the individuals were correctly reclassified into their original populations. Two

western larch trees (i.e. 0.7%), one each from populations LO-01 and LO-02, were incorrectly grouped into alpine larch populations.

The first discriminant function alone discriminates between the two species of larch (Figure 15). The western larch populations from the United States (LO-03, LO-04 and LO-05) are closely grouped by the first two discriminant functions. The Selkirk and Purcell Mountain populations (LO-02 and LO-01) are distinguishable from the main western larch cluster. Population LL-02 is separated from the remaining alpine larch populations which form a tight cluster. The distinction occurs along the second discriminant axis which is strongly correlated with adaxial keeling.

A separate discriminant analysis of the two species groups correctly reidentified 99.0% of the 302 individuals (results not shown) included in the analysis. Stepwise discriminant analysis selected 22 variables for inclusion in the discriminant function. Resin canal adaxial and marginal position and the number of epithelial cells surrounding the resin canals were all dominant variables in the discriminant function.

ARNOLD ARBORETUM MATERIAL

Average values for the cone and needle characteristics of the eight taxa received from the Arnold Arboretum are presented in Table 5. The collection was augmented with

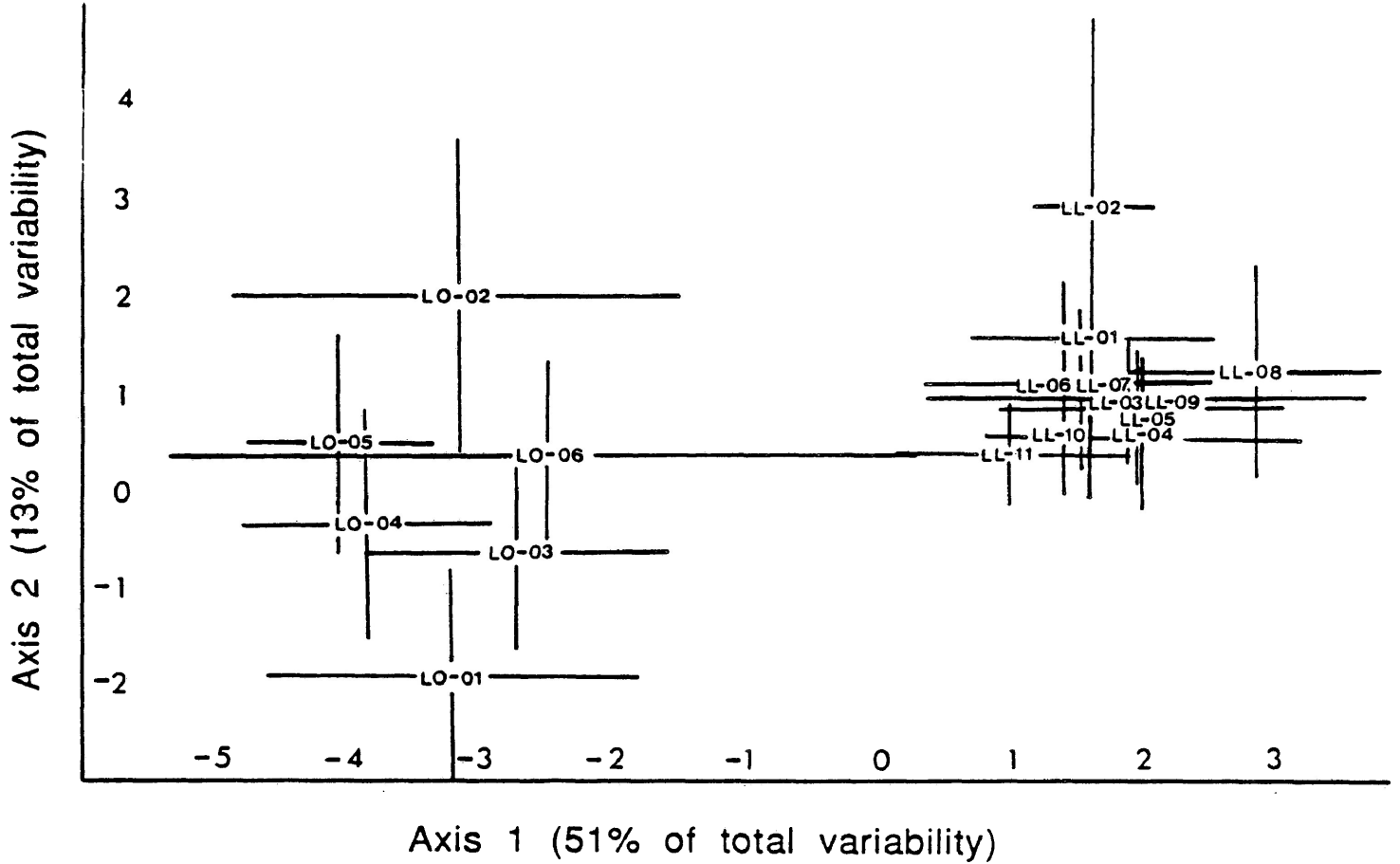


Figure 15. Discriminant analysis ordination of needle characters of eleven *L. lyallii* and six *L. occidentalis* populations, axis 1 versus axis 2. Population codes identify the population centroids while the population standard deviation is indicated by horizontal and vertical bars.

additional samples of the three North American species from various locations.

The largest cones were those of L. X eurolepis and L. sibirica. Cones from L. lyallii and L. kaempferi were also quite long, both averaging over 2.9 cm in length. The widest cones and the most cone scales were found in L. kaempferi and its hybrid, L. X eurolepis. Cones of L. laricina were smallest and contained the fewest cone scales. L. gmelinii cones were larger than those of L. laricina but were still smaller than those of the remaining taxa.

All five species of Section Pauciseriales are represented in the collection. In all cases, the average scale length exceeds the bract length, an important identifying feature of this section. Three of the five species in Section Multiseriales are represented. On the basis of cone characteristics, the specimen identified by the Arnold Arboretum as L. potaninii was misidentified since it did not possess exserted bracts.

Needles of western larch were close to 1.0 cm longer than those of any other species examined. Alpine larch and L. sibirica needles averaged 26.9 and 25.5 mm in length respectively. The shortest needles belonged to L. laricina. On average, needles from the specimen identified as L. potaninii were wider than those of any other species (Figure 16). The thickest needles were found in alpine and western larch.

Table 5. Means of selected cone and needle characters for larch specimens received from the Arnold Arboretum. Unless indicated, values are expressed as mm x 10E-2.

Species	CL*	OD	PL	PD	SN	SL	SW	BL	AWL	BW	RCELL	NL	NW
<i>L. decidua</i>	25.3	14.3	5.6	3.5	43.5	9.2	9.2	7.4	1.3	3.9	4.2	2.3	82.1
<i>L. gmelinii</i>	18.4	13.7	4.2	2.8	28.5	8.4	8.1	6.5	1.1	3.2	4.7	1.7	76.5
<i>L. potaninii</i>	25.9	14.9	3.2	3.0	33.5	10.6	10.5	8.2	1.6	4.4	3.9	2.3	85.9
<i>L. sibirica</i>	31.7	17.0	3.4	2.9	45.0	11.6	10.1	8.0	0.7	4.5	5.2	2.6	62.2
<i>L. kaempferi</i>	29.3	19.4	4.8	4.2	63.6	10.8	10.5	8.2	0.8	4.3	4.1	2.3	80.8
<i>L. X eurolepis</i>	33.3	20.4	4.5	4.7	61.4	12.3	11.2	9.3	0.8	4.7	4.5	2.2	74.1
<i>L. laricina</i>	12.8	7.2	3.4	2.1	18.5	7.5	6.3	4.4	0.6	3.3	5.5	1.5	64.9
<i>L. occidentalis</i>	27.7	16.5	4.6	4.0	50.9	8.6	8.5	12.4	3.8	5.4	5.9	3.6	71.3
<i>L. lyallii</i>	29.9	14.5	5.1	3.3	43.8	9.5	7.8	14.3	4.2	6.0	8.3	2.7	68.1

Species	NT	VCT	VCAD	RCL	RCLAD	RCLM	RCLAB	FOR	RCRAD	RCRM	RCRAB	VCW
<i>L. decidua</i>	36.7	12.6	12.6	4.5	3.1	1.9	4.4	5.2	3.4	2.3	5.0	14.9
<i>L. gmelinii</i>	35.8	12.4	12.4	4.0	3.9	2.1	4.1	4.5	4.9	2.3	4.3	14.0
<i>L. potaninii</i>	34.4	12.6	11.9	5.9	3.2	2.2	3.8	4.4	3.4	1.9	4.7	14.1
<i>L. sibirica</i>	38.5	12.5	13.3	3.1	3.7	2.1	6.2	2.9	4.8	2.3	7.3	13.8
<i>L. kaempferi</i>	37.1	12.8	13.5	3.9	3.4	2.2	4.4	5.1	3.9	2.5	4.5	15.1
<i>L. X eurolepis</i>	36.9	12.7	12.6	5.3	2.9	2.4	5.0	5.2	3.5	2.5	5.9	14.8
<i>L. laricina</i>	41.1	11.5	15.5	2.8	3.2	2.0	5.7	2.7	3.6	2.3	6.3	12.8
<i>L. occidentalis</i>	52.6	14.6	18.6	2.0	4.0	2.1	10.1	4.7	4.3	2.5	9.8	15.9
<i>L. lyallii</i>	53.7	14.1	18.6	2.7	5.9	2.9	7.6	2.9	8.1	2.8	7.6	15.1

* CL = CONE LENGTH, CD = CONE DIAMETER, PL = PEDESTAL LENGTH, PD = PEDESTAL DIAMETER, SN = SCALE NUMBER, SL = SCALE LENGTH, SW = SCALE WIDTH, BL = BRACT LENGTH, AWL = AWN LENGTH, BW = BRACT WIDTH, RCELL = NUMBER OF EPITHELIAL CELLS SURROUNDING RESIN CANALS, NL = NEEDLE LENGTH, NW = NEEDLE WIDTH, NT = NEEDLE THICKNESS, VCT = VASCULAR COLUMN THICKNESS, VCAD = DISTANCE FROM VASCULAR COLUMN TO ADAXIAL SURFACE, RCL = LEFT RESIN CANAL DIAMETER, RCLAD = DISTANCE FROM LEFT RESIN CANAL TO ADAXIAL SURFACE, RCLM = DISTANCE FROM LEFT RESIN CANAL TO LEFT MARGIN, RCLAB = DISTANCE FROM LEFT RESIN CANAL TO ABAXIAL SURFACE, RCR = RIGHT RESIN CANAL DIAMETER, RCRAD = DISTANCE FROM RIGHT RESIN CANAL TO ADAXIAL SURFACE, RCRM = DISTANCE FROM RIGHT RESIN CANAL TO RIGHT MARGIN, RCRAB = DISTANCE FROM RIGHT RESIN CANAL TO ABAXIAL SURFACE, VCW = VASCULAR COLUMN WIDTH

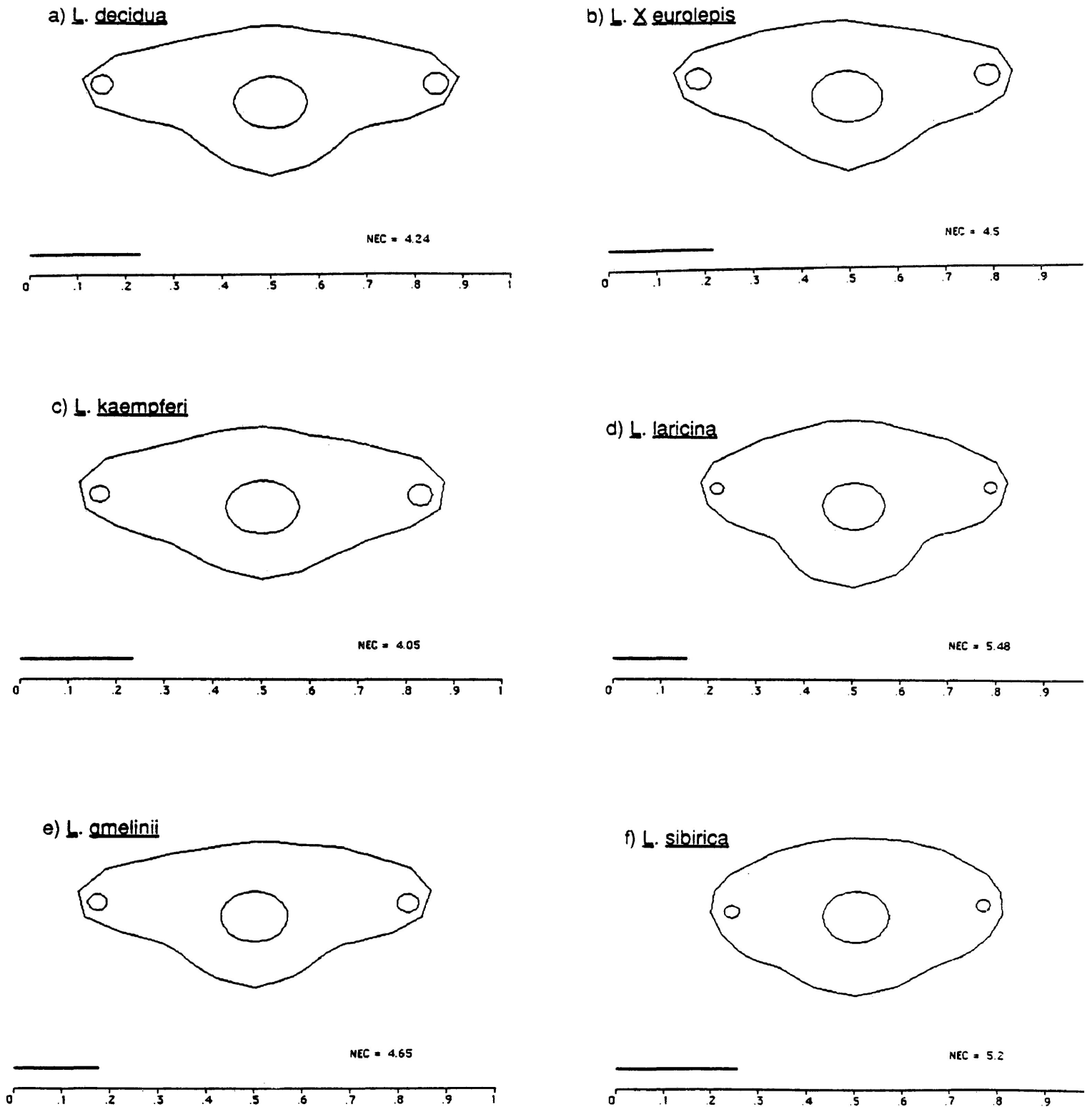


Figure 16. Computer drawn outline of the average cross-section of a) L. decidua, b) L. X eurolepis, c) L. kaempferi, d) L. laricina, e) L. gmelinii and f) L. sibirica. Bottom scale indicates needle cross-sectional size (mm) and needle length (horizontal bar) (dm). Average number of epithelial cells per resin canal (NEC) is also included.

Principal component analysis tended to divide the variables into two clusters. Bract length and width and awn length grouped closer to the needle variables than to the remaining cone variables. The right and left resin canal size tended to be grouped with the majority of cone traits. Because these clusters were not distinct, the variables were examined as a single group.

The eigenvalues determined for the principal component factors indicated that four factors explained a substantial portion of the variation present. The first principal component alone accounted for close to one half (45.4%) of the variation present in the data. The second and third components accounted for 15.9% and 10.8% respectively. The ordination of the first two components placed L. lyallii and L. occidentalis at one end of the cluster of species (Figure 17). L. lyallii is further removed from the main cluster of species than is L. occidentalis. L. X eurolepis is very distinct from both its parent species. The European larches L. sibirica, L. gmelinii and L. decidua displayed a continuum of component scores on both the first and second axes. L. laricina is most closely associated with L. sibirica.

Discriminant analysis was performed to differentiate the 39 individuals into nine taxa. The stepwise process selected 23 variables for inclusion in the analysis. The first discriminant function alone accounted for 93.6% of the

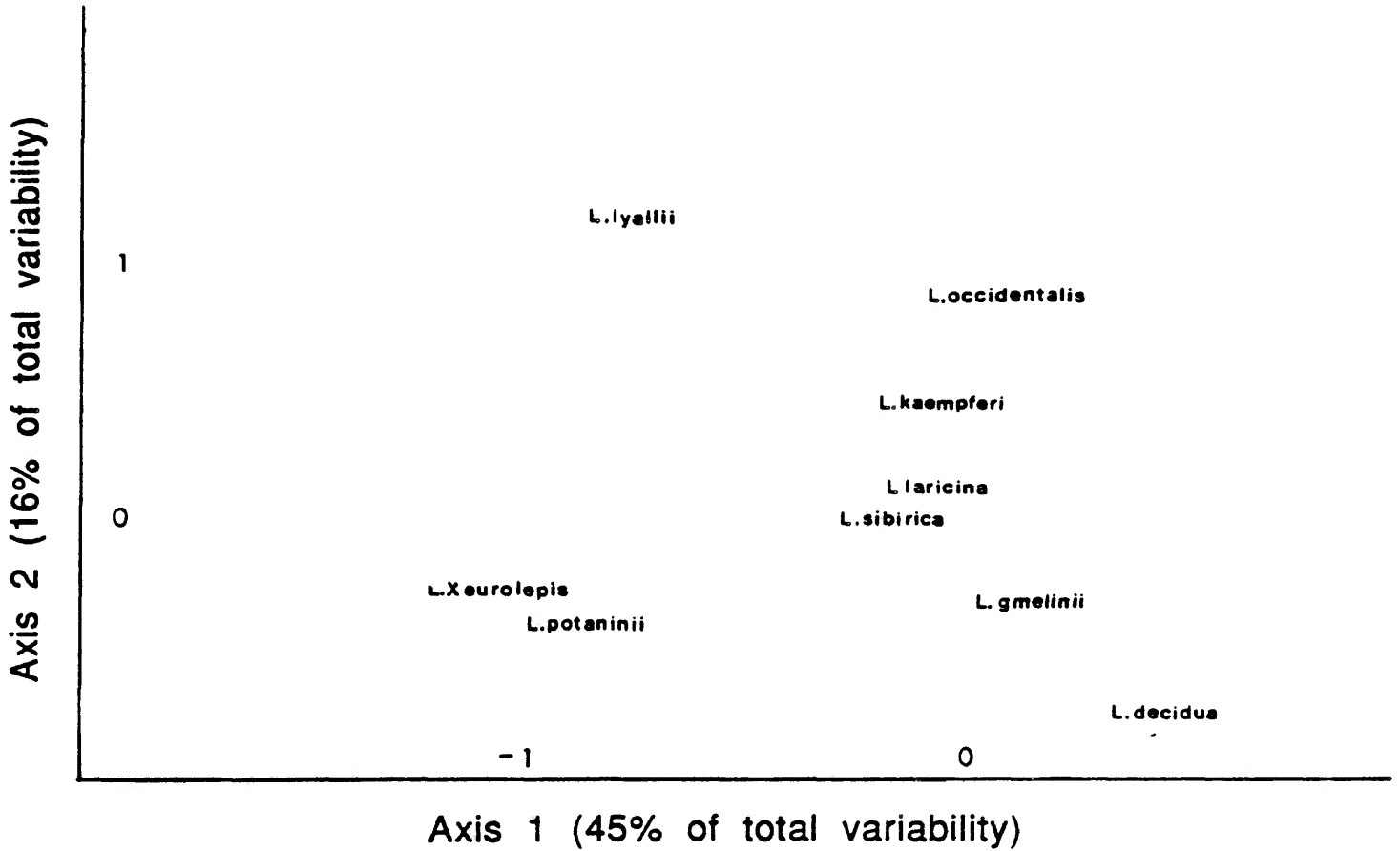


Figure 17. Principal component analysis ordination of needle and cone characters of samples of nine taxa of *Larix* Mill., axis 1 versus axis 2. Taxa names identify the population centroids.

variation present, and the second function accounting for an additional 3.4%. The first function was most strongly correlated with needle length and D27 which is an indicator of adaxial keeling. Scale width, D8 and the distance from the right resin canal to its proximal margin figured prominently in the second discriminant function. The discriminant function obtained determined by the analysis reclassified all individuals correctly.

The plot of the first and second discriminant functions, clearly separates L. sibirica, L. occidentalis and L. lyallii from the remaining taxa (Figure 18). The close association of L. sibirica with L. occidentalis is interesting because the two species belong to two different Sections. It should be taken into consideration, however, that only one L. sibirica specimen with a single cone was available for measurement. The specimen identified as L. potaninii is closely associated with L. gmelinii. This supports the hypothesis that the specimen is actually a misidentified L. gmelinii and not representative of Section Multiserialis. L. laricina and L. gmelinii are very closely associated.

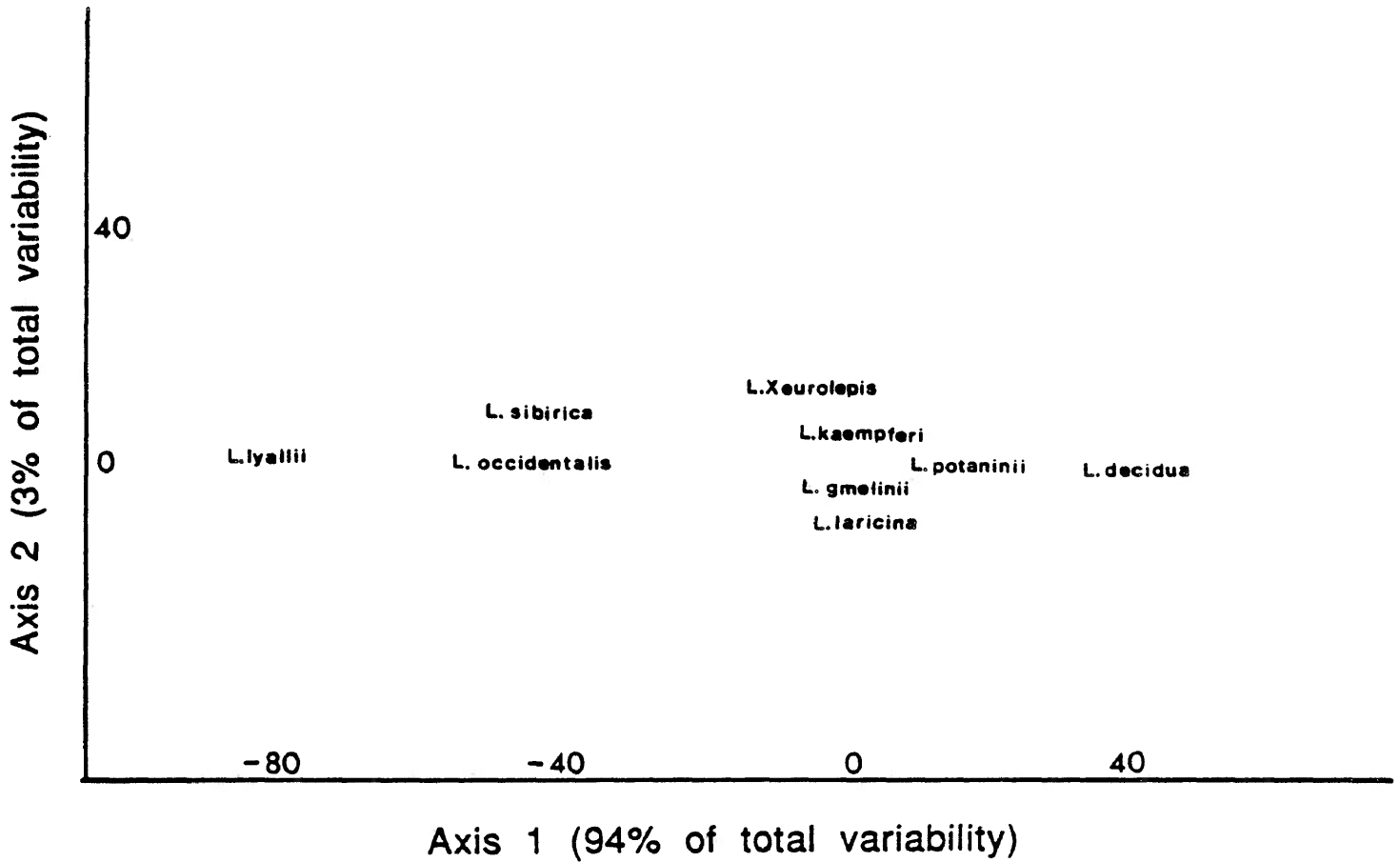


Figure 18. Discriminant analysis ordination of needle and cone characters of samples of nine taxa of *Larix* Mill., axis 1 versus axis 2. Taxa names identify the population centroids.

DISCUSSION

Since no previous work has examined variation in L. lyallii in depth, it is impossible at this point to determine if the results obtained in this study are consistent with the pattern of geographic variation expressed by other characters. Although the possibility exists that the needle and cone characters examined are not indicative of overall geographic variation, previous work by Langlet (1962) indicated needle and cone characters can be strongly related to the growth and phenological characters of a species. Work conducted by Rehfeldt (1985) indicated a high rate of heritability in needle characteristics of some conifers. Until further work proves otherwise, one can only assume that variation in the cone and needle characters are generally consistent with those of other genotypic and phenotypic characters.

The pattern of phenotypic variation expressed by alpine larch populations is difficult to interpret and does not appear to reflect the disjunct nature of the species' range. No relationship was discerned between physiographic variables such as elevation and latitude and the pattern of variation displayed.

Several basic hypotheses can be advanced to explain the pattern of variation displayed in cones and needles of alpine larch. Firstly, the variation may be clinal and reflect environmental variables not considered in this study. Alternately, the environmental differentiation between alpine larch sites may not be dramatic enough to produce a detectable pattern of clinal variation. Finally, the variation displayed by alpine larch populations may be the result of genetic drift.

On the basis of our results it would be premature to draw a definite conclusion regarding the origin of the differentiation expressed. Further work would be required to determine if the pattern of variation can be related to environmental factors.

Despite the often limited population size, alpine larch appears to possess a substantial amount of intrapopulation variation. Variation between populations is also significant. The variance expressed by individual characters and the principal component analysis indicate that, overall, the amount of variation expressed in alpine larch appears similar to that displayed by western larch populations originating from a similar geographic range.

L. LYALLII POPULATIONS

The pattern of genotypic and phenotypic variation exhibited by a species is, to a large extent, influenced by environmental

variation. Environmental variation helps determine a species' distribution pattern and directs selection pressure.

Gradual changes in the environment are generally reflected in gradual shifts in selection pressures. Consequently, the pattern of variation exhibited by species in such environments is often continuous. Gene flow usually exists between populations and is instrumental in maintaining a clinal pattern of variation (Stebbins 1950).

Species with limited ecological amplitude occurring in regions where the environment changes dramatically over relatively short distances are often characterized by disjunct populations. The discontinuous spatial distribution results in isolated populations which adapt to local conditions. Limited or non-existent interpopulation gene flow creates reproductively isolated populations which maintains and reinforces genetic differentiation between populations.

L. lyallii is an example of a species with a discontinuous geographic distribution (Figure 1). In the United States portion of the species range over 200 km separate the two mountain ranges occupied by the species. The species distribution is characterized by numerous outlying populations separated from the nearest populations by distances of up to 65 km. There is little doubt that gene flow between many of the populations is severely limited because of the distances involved.

Given the distribution pattern of alpine larch, a disjunct or ecotypic variation pattern would be expected in the needle and cone characters examined. It might be expected that major range discontinuities, such as that occurring between the Cascade and Rocky Mountains in the United States, would be reflected in L. lyallii's pattern of variation. This does not appear to be the case, however.

Since the needle and cone characters of alpine larch examined in this study display a continuum of principal component and discriminant function scores, one might conclude that a clinal pattern of variation exists in the species. Clinal or continuous patterns of variation typically develop in species with a continuous distribution and usually reflect environmental gradients. General environmental clines are usually correlated to latitude and longitude. In mountainous habitats, elevation represents a major environmental gradient. Small changes in elevation have a marked influence on climate.

Phenotypic, not genotypic, characters were examined in this study. Differentiation expressed by these characters is composed of an environmental as well as a genetic component. Therefore, these characters would be expected to reflect environmental variation quite strongly.

If the needle and cone characters of alpine larch display a clinal pattern of variation, it would be expected that

environmental factors such as elevation, latitude and longitude would correlate with the variation pattern exhibited. In alpine larch, however, this correlation did not occur. The pattern of variation, represented by principal component scores, did not correlate with elevation, latitude or longitude; no relationship with these environmental factors was discernable.

The variation pattern expressed may in fact be clinal but might reflect environmental factors not considered. In this study only latitude, longitude and altitude were considered when attempting to make geographic interpretations. These factors are usually broadly correlated to climate.

No consideration was given to the substrate and microclimate of the sites sampled. In mountainous regions, the substrate can vary dramatically between areas; the soil matrix in widely separated areas may be more similar than in two populations separated by a few miles.

Climate in the range of alpine larch is even less consistent than substrate. Broad climatic changes are present in the region, but site to site differences can be important. Differences in the climate between north and south slopes can be much more significant than large differences in latitude or elevation. Because of the strong influence of microgeography, climatic data can not be interpolated from nearby weather

stations. Thus, no estimates for precipitation, degree days, etc. are available for the sample sites.

It is possible that microgeographic variation in site and climate override large scale geographic pattern. The pattern of variation expressed may be related to environment but may reflect factors not considered in this study.

It can also be hypothesized that the pattern of variation expressed simply reflects limited environmental differentiation between alpine larch sites. Although substantial differences are apparent between L. lyallii sites, the overall range of environments occupied by the species may be fairly uniform. Alpine larch sites are characterized by short growing seasons, poorly developed soils and adequate precipitation. Under fairly consistent environmental conditions, one would not expect to detect a clinal pattern of variation.

Only a detailed examination of climate at each collection site would be able to determine if an environmental basis exists for the pattern of variation expressed in the characters being considered.

The possibility can not be ruled out that the differentiation expressed in the needles and cones of L. lyallii is random and not related to environmental factors. Interpopulation differentiation may primarily result from genetic drift.

Whenever reproductive isolation exists, genetic drift may influence populations. The likelihood of genetic drift affecting a population increases in small populations (Ayala and Kiger 1984).

Alpine larch's distribution is extremely disjunct and interpopulation gene flow is often restricted or non-existent. Many of the populations are quite small. Under these conditions, the possibility of random drift occurring is high. Much of the differentiation expressed between alpine larch populations may be the result of random drift. This would account for the failure to detect an environmentally interpretable pattern of variation.

If genetic drift were influencing L. lyallii populations, one might expect to see populations that were quite distinct from each other, especially if the populations have been isolated for some time. Alpine larch populations, however, show considerable overlap in individual characters and in PC and DA scores. It is possible that many of the alpine larch populations included in this study have been separated only since the last glaciation. This relatively short period would then account for the overlap exhibited by the alpine larch populations.

It is also possible that the variation expressed between populations does not have a genetic basis and instead, is the result of phenotypic plasticity. Work conducted with some

conifers suggests that species with a restricted ecological amplitude tend to be generalists that exhibit substantial phenotypic plasticity (Rehfeldt 1984). Western larch is considered to be a generalist (Rehfeldt 1984). Since alpine larch has a narrower ecological and geographical range than western larch, the importance of phenotypic plasticity in alpine larch populations should not be overlooked. If the variation were due primarily to phenotypic plasticity, however, the pattern of variation would be expected to be correlated with environmental variables (Heslop-Harrison 1964). In this study, no physiographic relationships were detected.

One of the most interesting results noted in this study was the difference between alpine larch population LL-02 and all other alpine larch populations including its neighbouring population (LL-03). Population LL-03 was collected close to LL-02 but at an elevation approximately 230 m higher. The needles of the two populations are very different but cone characters appear to be quite similar.

The reason for the differences in needles characters of population LL-02 can only be speculated upon. It is possible that the distinct needle shape and resin canal position (Figure 8) were the result of some type of physiological stress but no indication of stress was noticed at the time of field collection. It is also possible that the difference in shape

resulted from hybridization at some time with L. occidentalis. If either of these explanations were valid, however, it might be expected that the cones would also be differentiated from those of other alpine larch populations. This was not the case.

The results from this study do little to clarify the glacial history of L. lyallii. It is assumed that many alpine larch populations survived the most recent glacial periods at lower elevations than at present, having been forced to migrate by the growing alpine glaciers (Arno 1970). It is not known where populations within areas affected by continental glaciation survived. Our results are inconclusive and do not eliminate the hypothesis of many glacial refugia or the existence of common refugia.

RELATIONSHIP OF L. LYALLII AND OTHER NORTH AMERICAN LARCHES

Work conducted by Rehfeldt (1984) emphasizing growth potential and phenological characters indicates substantial variability exists within L. occidentalis populations.

Previous work by the same author (1970) on the genealogy of L. laricina indicated populations at the southern limit of the species' range in Wisconsin were also highly variable genetically. Continuity of genetically controlled characters existed between these populations even though the populations were disjunct.

Phenotypic work conducted by Parker and Dickinson (in preparation) on L. laricina detected far less between-population- variability in cone and needle traits within this species than was detected in the two western larch species. Nested analysis of variance of a limited number of L. laricina populations indicated only 4.8 and 13.2 % of the variation present in the first two principal components respectively was expressed between sites (Dickinson et al. 1987).

The present results indicate that alpine larch, like L. laricina and L. occidentalis, possesses considerable variability within populations. Analysis of variance of the principal component scores and ordinations of the principal component scores confirmed that substantial within population variation was apparent.

These analyses also confirmed that significant interpopulation differentiation exists. Based on the principal component analysis, it appears that the relative variability expressed by L. lyallii and L. occidentalis populations is comparable. Examination of the standard deviations of the univariate characters measured and the ordinations of PC analyses all indicate the two closely related species express similar patterns of variation. The discriminant analyses, however, attribute greater variation to the L. occidentalis populations. It should be emphasized however, that this

analysis is heavily weighted with selected characters and may not be an accurate indicator of overall variation levels.

ARNOLD ARBORETUM MATERIAL

Principal component and discriminant analyses both tended to separate the Section Multiseriales species L. lyallii and L. occidentalis from the Section Pauciseriales taxa. The specimen identified as L. potaninii was clearly misidentified and was obviously from Pauciseriales. Visual assessment of the material as well as PCA and discriminant analyses associated the specimen with L. gmelinii or L. decidua. Analysis of the cones of the specimen indicate they are most similar to L. gmelinii. Characteristics not measured, such as cone colour and scale margin strongly support the hypothesis that the specimen is actually L. gmelinii. Discriminant analysis of the needle variables alone associated the misidentified specimen with L. decidua. When the variables are analyzed together, the specimen is once again most closely allied with L. gmelinii.

The influence of specimen source on the results obtained in the various analyses should not be overlooked. The three North American taxa were represented primarily by samples collected from populations within the species' natural range. Growth conditions varied drastically between these sample locations. The European and Asiatic specimens were all grown in a similar environment at the Arnold Arboretum.

It is unfortunate that sample material was obtained only for the two North American representatives of Section Multiseriales. Because material from all three Asiatic Multiseriales was not available, the relationship of the North American Section members to their Asiatic counterparts can not be determined.

Sample material from Section Pauciseriales is more complete; five species and one well-known hybrid are represented. The North American member, L. laricina, is consistently most closely associated with L. gmelinii in the discriminant analysis. In the PCA, L. laricina is more closely allied to L. sibirica. It should be remembered, however, that L. sibirica is represented in the collection by only one specimen. Cone morphology easily distinguishes the two species but differences in needle characteristics appear to be less dramatic.

Geographically, L. gmelinii appears to be a logical L. laricina progenitor. This species occurs in eastern Asia with L. gmelinii var. japonica extending onto the Kurile Islands on Asia's eastern coast. Compared to the other Larix spp. cones, cones of L. gmelinii var. japonica and L. gmelinii var. olgensis are most similar in size to L. laricina cones.

L. decidua and L. gmelinii appear to be morphologically quite similar even though the two species are widely separated geographically. It is interesting to note that these

two species are the only Larix spp. with recognized sub-specific taxa.

L. sibirica, located geographically between L. gmelinii and L. decidua, might be expected to be intermediate between the two species morphologically. Instead, the single sample available for analysis (foliage and a single cone) seemed to be intermediate between Section Pauciserales individuals and the two Section Multiserales representatives. The significance of this association can not be determined without more representatives of L. sibirica and samples from the remaining Section Multiserales species.

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APPENDICES

APPENDIX I

ANGLES ASSOCIATED WITH THE THIRTY RADIAL DISTANCES
MEASURED

D1 - 0°	D16 - 180°
D2 - 20°	D17 - 200°
D3 - 40°	D18 - 210°
D4 - 60°	D19 - 220°
D5 - 80°	D20 - 225°
D6 - 90°	D21 - 230°
D7 - 100°	D22 - 235°
D8 - 110°	D23 - 240°
D9 - 120°	D24 - 250°
D10 - 125°	D25 - 260°
D11 - 130°	D26 - 270°
D12 - 135°	D27 - 280°
D13 - 140°	D28 - 300°
D14 - 150°	D29 - 320°
D15 - 160°	D30 - 340°

APPENDIX II

NEEDLE REHYDRATION AND EMBEDDING SERIES

- 1) Boiling in water - 20 minutes
- 2) JOH 1 - 95% Ethyl alcohol:Tertiary-butyl alcohol:distilled water at 5:4:1
- 2 hours
- 3) JOH 2 - 95% Ethyl alcohol:Tertiary-butyl alcohol:distilled water at 5:2:3
- overnight
- 4) JOH 3 - 95% Ethyl alcohol:Tertiary-butyl alcohol:distilled water at
5:3.5:1.5
- 8 hours
- 5) JOH 4 - 95% Ethyl alcohol:Tertiary-butyl alcohol at 1:1
- overnight
- 6) JOH 5 - 95% Ethyl alcohol:Tertiary-butyl alcohol at 1:3
- 4 hours
- 7) JOH 6 - Tertiary-butyl alcohol
- 24 hours
- 8) JOH 7 - Tertiary-butyl alcohol:paraffin wax at 1:1
- 2 hours
- 9) Paraffin wax - 24 hours
- 10) Paraffin wax - 24 hours

APPENDIX III

ANNOTATIONS OF ARNOLD ARBORETUM SPECIMENS OF LARIX

<u>Arnold Arboretum Identification</u>	<u>Accession No.</u>	<u>Annotation</u>
<u>Larix laricina</u> (Du Roi) K. Koch	510-49-D	!
<u>Larix occidentalis</u> Nuttall	1559-A	
<u>Larix decidua</u> Miller	1171-67-A	
<u>Larix decidua</u> Miller	2775-F	
<u>Larix decidua</u> Miller	14937	
<u>Larix decidua</u> Miller	23208-A	
<u>Larix decidua</u> Miller 'Pendula'	804-33-A	<u>Larix decidua</u> Miller
<u>Larix decidua</u> Miller 'Pendula'	804-33-D	<u>Larix decidua</u> Miller
<u>Larix decidua</u> Miller 'Pendula'	23208-A	<u>Larix decidua</u> Miller
<u>Larix decidua</u> Miller var. <u>polonica</u> (Raciborski ex Szafer) Ostenfeld & Syrach-Larson	1188-63-B	
<u>Larix decidua</u> Miller var. <u>polonica</u> (Raciborski ex Szafer) Ostenfeld & Syrach-Larson	19708	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva	14936-B	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva	18503-G	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva	21784-B	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva var. <u>japonica</u> (Regel) Pilger	90-69-A	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva var. <u>japonica</u> (Regel) Pilger	1098-A	
<u>Larix gmelinii</u> (Ruprecht) Kuzeneva var. <u>principis-rupprechtii</u> (Mayr) Pilger	247-75-B	See note below

<u>Arnold Arboretum Identification</u>	<u>Accession No.</u>	<u>Annotation</u>
<u>Larix potaninii</u> Batalin	640-67	<u>Larix gmelinii</u>
<u>Larix sibirica</u> Ledebour	14948-A	!
<u>Larix kaempferi</u> (Lamb) Sargent	1097-C	
<u>Larix kaempferi</u> (Lamb) Sargent	14939-B	
<u>Larix kaempferi</u> (Lamb) Sargent	852-33	
<u>Larix kaempferi</u> (Lamb) Sargent	10496-Mass	
<u>Larix kaempferi</u> (Lamb) Sargent	11276-Mass	
<u>Larix X eurolepis</u> A. Henry	6103-G	
<u>Larix X eurolepis</u> A. Henry	11278-A	
<u>Larix X eurolepis</u> A. Henry	129-32-A	!

Notes: 1. The specimen identified as L. potaninii (640-67) was a typical specimen of L. gmelinii.

2. The specimen identified as L. gmelinii var. principis-rupprechtii (247-75-B) could not be positively identified due to its very stunted vegetative growth and the deteriorated condition of the seed cones that accompanied it.

3. The designation L. decidua 'Pendula' represents an anamoly in crown form that cannot be discerned in herbarium specimens. Therefore, the specimens so identified could only be confirmed to be representatives of L. decidua on the basis of material provided.

APPENDIX IV

MEANS AND STANDARD DEVIATIONS OF NEEDLE
CROSS-SECTIONAL RADIAL DISTANCES (EXPRESSED AS $\text{MM} \times 10^{-2}$)
(DEFINITION OF DISTANCES PROVIDED IN FIGURE 3)

LARIK LYALLII POPULATIONS

CODE	D1		D2		D3		D4		D5		D6		D7		D8	
	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s
LL-01	19.1	2.5	18.3	2.5	18.1	2.8	21.6	4.3	29.2	3.5	31.8	3.4	32.8	3.7	31.9	3.8
LL-02	15.6	2.4	15.2	2.6	14.7	3.1	16.1	4.0	22.7	4.7	26.4	4.3	29.4	3.5	29.9	3.2
LL-03	19.0	2.9	18.4	3.1	18.2	3.2	21.7	3.5	28.5	3.3	31.3	2.8	32.8	2.5	32.0	2.5
LL-04	18.6	2.6	18.5	2.7	18.9	2.7	23.1	3.7	30.7	3.5	33.5	3.6	34.4	3.9	33.3	3.8
LL-05	20.7	2.6	20.7	2.5	21.1	2.7	25.5	3.7	32.8	3.7	35.2	3.8	35.8	3.9	34.8	3.7
LL-06	17.2	2.2	17.2	2.2	18.2	2.1	22.6	2.7	29.1	2.7	31.4	2.7	31.9	3.1	30.8	3.0
LL-07	17.7	2.5	17.9	2.3	18.6	2.4	23.9	3.2	31.6	3.4	34.1	3.6	33.9	3.8	32.1	3.7
LL-08	19.7	2.4	19.7	2.7	20.2	2.9	24.2	3.6	31.5	3.4	34.2	3.4	35.6	3.8	34.5	4.0
LL-09	20.5	2.8	20.5	2.7	21.1	2.9	25.2	3.5	32.6	3.4	35.3	3.5	36.5	3.8	35.7	4.1
LL-10	16.9	2.1	16.8	2.1	17.7	2.2	22.4	3.3	29.6	3.5	31.9	3.4	32.2	3.3	31.0	3.3
LL-11	18.7	3.1	18.8	3.1	19.3	3.2	23.0	3.9	29.8	3.9	32.4	4.0	33.3	4.0	32.4	3.7
L. Lyallii	18.5	2.6	18.4	2.6	18.7	2.7	22.7	3.6	29.8	3.5	32.5	3.5	33.5	3.6	32.6	3.5

LARIK OCCIDENTALIS POPULATIONS

LO-01	18.3	3.1	18.4	3.1	18.6	3.3	22.4	4.7	32.0	4.3	35.0	3.8	35.1	3.9	33.6	3.9
LO-02	17.5	1.9	17.5	2.0	17.6	2.2	23.3	4.5	34.8	5.0	37.4	4.3	37.2	4.5	35.5	4.3
LO-03	18.9	2.3	18.7	2.4	18.9	2.7	21.9	4.0	30.5	3.8	33.9	3.3	34.9	3.9	34.0	4.1
LO-04	17.1	2.2	17.1	2.1	17.7	2.2	21.6	3.7	33.8	4.1	37.3	3.8	37.4	3.6	35.3	3.6
LO-05	21.6	4.0	17.3	2.2	17.9	2.4	23.7	4.5	35.7	4.6	38.1	3.6	37.3	3.1	35.1	3.0
LO-06	15.7	2.4	15.7	2.1	16.4	2.2	21.5	3.8	33.2	3.2	35.7	3.0	35.0	3.4	33.0	3.5
L. occidentalis	18.2	2.7	17.5	2.3	17.9	2.5	22.4	4.2	33.3	4.2	36.2	3.6	36.2	3.7	34.4	3.7

LARIK LYALLI POPULATIONS

	D9	D10	D11	D12	D13	D14	D15	D16	D17
	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}	\bar{x}
	s	s	s	s	s	s	s	s	s
	29.9	28.2	26.6	25.4	25.2	28.3	31.1	33.3	30.2
	4.0	4.3	4.2	3.8	3.4	3.3	3.3	3.8	3.1
	28.2	33.3	24.5	30.2	22.5	26.9	28.3	24.1	27.3
	4.2	3.8	4.5	4.6	4.1	3.8	3.7	3.8	3.2
	30.5	28.8	26.8	25.9	25.7	28.4	31.9	34.5	30.7
	2.6	3.2	3.5	3.0	2.8	3.0	3.1	3.2	3.3
	30.9	28.8	26.8	25.4	25.6	28.0	30.7	33.6	31.6
	3.9	4.2	3.9	3.4	3.4	3.5	3.7	3.9	3.8
	32.5	31.1	29.7	28.8	29.1	31.6	34.7	37.4	35.1
	3.2	3.1	3.0	2.9	3.0	3.4	3.5	3.7	4.0
	29.3	28.2	27.4	26.8	26.7	27.8	29.2	30.8	29.4
	2.9	2.9	2.6	2.2	2.2	2.3	2.5	2.9	2.9
	29.5	27.7	26.2	25.6	25.9	27.6	29.5	31.3	29.8
	3.7	3.5	3.1	2.8	2.9	3.0	3.0	3.3	3.3
	32.1	30.2	28.3	26.9	26.6	29.2	31.9	34.6	32.7
	4.2	4.6	4.5	3.8	3.5	4.0	3.9	4.3	3.6
	33.4	31.5	29.7	28.3	28.2	30.6	33.3	36.4	34.5
	4.1	4.6	4.6	4.3	3.9	4.1	4.6	5.1	4.2
	28.6	26.9	25.5	24.7	24.8	26.5	29.0	31.6	29.4
	3.4	3.6	3.2	2.7	2.7	3.0	2.9	3.0	2.9
	30.4	29.0	27.5	26.5	26.9	29.9	32.5	34.6	32.7
	3.8	3.7	3.5	3.4	3.5	4.1	3.9	3.8	4.0
	30.5	29.4	27.2	26.8	26.1	28.6	31.1	32.9	31.2
	3.6	3.8	3.7	3.4	3.2	3.4	3.5	3.7	3.5

LARIK OCCIDENTALIS POPULATIONS

30.8	4.2	28.7	4.1	26.5	4.3	24.7	4.4	24.4	4.0	27.0	4.6	30.2	4.7	32.8	4.4	29.4	4.2
32.4	4.4	29.7	4.5	27.5	4.0	25.6	3.1	25.0	2.4	26.5	2.4	28.5	2.4	30.6	2.8	28.8	2.7
31.8	4.0	30.0	4.6	28.3	4.4	26.9	4.0	26.6	3.5	28.7	3.7	31.1	3.6	34.1	3.7	31.8	4.2
31.6	3.6	28.5	4.2	25.8	4.0	24.0	3.2	23.8	2.8	26.0	2.8	28.3	3.0	30.5	3.3	28.3	2.5
31.6	3.5	29.1	3.7	26.5	3.6	24.2	3.3	23.7	3.1	25.7	3.1	27.5	2.9	29.1	2.7	27.2	2.7
29.2	4.9	26.7	4.8	24.4	4.4	22.9	3.4	22.6	2.5	24.6	2.5	26.5	3.2	28.6	4.1	27.0	3.9
31.2	4.1	28.8	4.3	26.5	4.1	24.7	3.6	24.4	3.1	26.4	3.2	28.7	3.3	31.0	3.5	28.8	3.4

LARIX LYALLII POPULATIONS

	D18	D19	D20	D21	D22	D23	D24	D25	D26								
\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s								
26.9	2.8	24.2	3.1	24.6	3.6	26.0	4.1	27.8	4.2	29.6	3.9	31.7	3.7	33.0	3.7	32.2	3.3
24.6	3.6	21.8	4.3	26.0	4.6	25.5	4.2	27.7	3.9	28.8	3.4	30.0	2.8	29.2	3.4	26.6	4.2
27.2	3.5	25.4	3.1	26.1	3.2	27.6	3.4	29.0	3.2	30.4	2.8	31.9	2.3	32.6	2.3	31.6	2.9
28.9	3.7	25.9	3.4	26.1	3.6	27.5	4.1	29.2	4.4	31.2	4.2	33.1	4.0	34.2	3.9	33.6	3.4
31.8	4.1	29.3	4.0	29.1	3.6	29.7	3.5	30.8	3.5	32.0	3.5	33.8	3.6	34.6	3.7	33.8	3.6
27.6	2.7	26.3	2.7	26.5	2.8	27.1	2.9	28.0	3.0	28.9	3.0	30.1	2.9	31.0	3.0	30.5	2.6
27.7	3.1	25.6	2.8	25.2	2.7	25.7	3.1	27.0	3.5	28.8	3.6	31.7	3.5	33.5	3.6	34.0	3.2
29.8	3.4	26.9	3.3	27.0	3.6	28.2	4.2	30.0	4.5	31.7	4.5	34.2	4.2	35.1	3.7	34.1	3.5
31.7	3.4	28.8	3.6	28.4	3.6	29.6	4.2	31.3	4.6	33.4	4.4	35.8	3.9	36.8	3.6	35.6	3.7
27.0	3.1	24.9	3.1	24.7	3.3	25.5	3.6	27.0	3.6	28.6	3.6	30.9	3.3	32.5	3.2	32.4	2.8
30.2	4.1	27.6	3.5	27.5	3.2	28.3	3.4	29.6	3.5	30.9	3.5	32.7	3.4	33.5	3.6	32.7	3.6
28.5	3.4	26.1	3.4	26.5	3.4	27.3	3.7	28.9	3.8	30.4	3.7	32.4	3.4	33.3	3.4	32.5	3.3

LARIX OCCIDENTALIS POPULATIONS

25.9	4.1	23.8	4.4	24.2	4.8	26.1	4.9	28.3	4.7	30.3	4.5	33.1	4.0	34.6	4.1	34.7	4.0
26.5	2.5	24.7	2.1	25.4	3.1	27.4	3.9	29.9	4.3	32.0	4.1	35.2	4.1	37.0	4.4	36.8	4.6
29.2	4.1	27.1	4.1	27.3	4.3	28.5	4.6	30.5	4.6	32.1	4.2	34.2	4.3	35.4	4.2	34.3	3.5
26.0	2.3	24.2	2.8	24.4	3.6	26.0	4.7	28.7	4.8	31.5	4.3	35.0	3.9	37.0	3.8	36.8	3.5
25.0	2.8	23.5	2.9	24.3	3.4	26.4	3.9	28.9	3.7	31.0	3.4	34.0	3.2	36.2	3.3	36.9	3.7
24.7	3.2	22.6	3.1	22.8	3.6	24.5	4.3	27.0	4.3	29.3	4.0	32.5	3.5	34.5	3.4	35.0	3.2
26.2	3.2	24.3	3.2	24.7	3.8	26.5	4.4	28.9	4.4	31.0	4.1	34.0	3.8	35.8	3.9	35.8	3.8

LARIX LYALLII POPULATIONS

\bar{x}	s	D28		D29		D30	
		\bar{x}	s	\bar{x}	s	\bar{x}	s
29.0	3.6	21.9	4.1	18.9	3.1	19.2	2.7
21.7	4.9	15.8	3.2	14.7	2.9	15.2	2.7
28.6	3.1	21.8	3.3	18.6	2.8	18.8	2.8
29.9	3.1	22.7	3.5	18.7	2.9	18.4	2.6
30.9	3.6	24.2	3.5	20.5	2.9	20.4	2.7
27.8	2.9	22.0	3.2	18.3	2.3	17.2	2.1
31.0	3.1	23.3	3.0	18.0	2.7	17.5	2.5
30.7	3.8	23.6	4.0	19.8	3.0	19.5	2.7
31.9	4.0	24.4	4.3	20.8	3.4	20.5	3.4
29.7	3.2	22.7	3.4	18.0	2.4	17.1	2.2
29.4	3.6	22.3	3.9	19	3.3	18.6	3.1
29.1	3.5	22.2	3.6	18.7	2.9	18.4	2.7

LARIX OCCIDENTALIS POPULATIONS

31.2	4.4	21.4	4.6	18.2	3.3	18.2	3.1
33.2	5.7	22.1	4.5	17.4	2.3	17.3	1.8
30.1	3.8	20.8	4.1	18.3	2.9	18.4	2.7
32.2	4.3	20.2	3.1	17.2	2.3	17.1	2.4
33.8	5.2	22.4	4.9	17.7	3.0	17.2	2.2
31.8	3.8	20.9	3.6	16.2	2.2	15.6	2.5
32.1	4.5	21.3	4.1	17.5	2.7	17.3	2.5

APPENDIX V

CORRELATION MATRIX OF CONE AND NEEDLE CHARACTERS
OF FIVE L. LYALLII POPULATIONS
(ABBREVIATIONS EXPLAINED IN TABLES 2 AND 3)

	CL	CD	PL	PD	SN	SL	SW	BL	AWL	BW	ADM	RCELL
CL	1.00											
CD	0.73	1.00										
PL	0.35	0.23	1.00									
PD	0.31	0.41	0.27	1.00								
SN	0.73	0.39	0.11	0.31	1.00							
SL	0.56	0.77	0.07	0.26	0.17	1.00						
SW	0.60	0.77	0.20	0.41	0.29	0.77	1.00					
BL	0.63	0.58	0.32	0.41	0.43	0.42	0.42	1.00				
AWL	0.48	0.28	0.30	0.26	0.41	0.41	0.12	0.73	1.00			
BW	0.37	0.38	0.31	0.20	0.22	0.22	0.44	0.20	0.09	1.00		
ADM	0.42	0.36	0.33	0.24	0.36	0.36	0.23	0.26	0.28	0.42	1.00	
RCELL	-0.35	-0.40	-0.04	-0.24	-0.14	-0.14	-0.30	-0.41	-0.37	0.05	0.05	1.00
NL	0.38	0.42	0.18	0.31	0.32	0.32	0.29	0.62	0.32	0.05	0.11	-0.17
NW	0.07	0.24	-0.18	0.17	0.13	0.13	0.30	0.24	-0.08	-0.01	-0.26	-0.09
NT	-0.23	-0.14	-0.30	-0.16	-0.18	-0.18	-0.03	-0.19	-0.39	-0.07	-0.23	0.29
VCT	-0.28	-0.25	-0.30	-0.24	-0.15	-0.15	-0.17	-0.11	-0.16	-0.22	-0.26	0.29
VCAD	-0.14	0.01	-0.23	-0.04	-0.13	-0.13	0.09	-0.10	-0.34	0.01	-0.25	0.18
RCL	-0.37	-0.27	-0.16	-0.27	-0.21	-0.21	-0.16	-0.41	-0.43	0.03	-0.27	0.32
RCLAD	0.00	-0.04	-0.11	0.02	-0.02	-0.02	-0.01	0.11	-0.01	0.01	-0.05	0.22
RCLM	0.08	0.13	0.05	0.11	0.09	0.09	0.30	0.09	-0.09	0.17	0.08	0.19
RCLAB	-0.08	0.07	-0.17	0.08	-0.02	-0.02	0.20	-0.19	-0.32	-0.01	-0.33	0.03
RCR	-0.29	-0.23	-0.21	-0.32	-0.14	-0.14	-0.12	-0.36	-0.46	-0.03	-0.31	0.09
RCRAD	0.08	0.02	-0.22	0.13	0.24	0.24	0.10	0.24	0.03	0.02	-0.13	0.08
RCAM	-0.09	-0.02	-0.18	0.08	0.00	0.00	0.13	0.11	-0.07	-0.06	-0.03	0.16
RCRAB	-0.16	0.07	-0.30	-0.01	-0.13	-0.13	0.16	-0.16	-0.38	-0.09	-0.25	0.14
VCW	-0.22	-0.27	-0.27	-0.18	-0.10	-0.10	-0.18	-0.12	-0.17	-0.17	-0.23	0.32
D2	-0.08	0.02	-0.25	0.01	-0.04	-0.04	0.11	0.00	-0.26	-0.01	-0.30	0.13
D3	-0.05	0.07	-0.26	0.09	0.02	0.02	0.17	0.05	-0.24	-0.01	-0.30	0.07
D4	-0.15	0.01	-0.29	0.02	-0.07	-0.07	0.13	-0.02	-0.35	-0.07	-0.29	0.11
D5	-0.17	-0.03	-0.27	-0.05	-0.11	-0.11	0.06	-0.05	-0.35	-0.10	-0.27	0.12
D7	-0.19	-0.12	-0.24	-0.09	-0.11	-0.11	-0.03	-0.06	-0.29	-0.11	-0.25	0.19
D8	0.01	0.14	-0.22	0.13	0.10	0.10	0.22	0.19	-0.10	-0.02	-0.31	-0.01
D9	0.02	0.09	-0.17	0.12	0.10	0.10	0.20	0.16	-0.08	0.04	-0.30	0.04
D10	-0.01	0.04	-0.17	0.12	0.09	0.09	0.15	0.08	-0.14	0.02	-0.32	0.10
D11	-0.04	0.07	-0.21	0.14	0.07	0.07	0.17	0.05	-0.20	0.05	-0.32	0.11
D12	-0.03	0.09	-0.22	0.14	0.08	0.08	0.21	0.04	-0.24	0.04	-0.34	0.09
D13	-0.08	0.07	-0.33	0.08	0.05	0.04	0.21	-0.02	-0.28	-0.01	-0.35	0.02
D14	-0.09	0.09	-0.37	-0.02	0.01	0.01	0.22	-0.06	-0.29	0.00	-0.32	0.03
D15	-0.10	0.06	-0.35	-0.02	0.00	0.00	0.21	-0.08	-0.31	0.02	-0.32	0.11
D16	-0.08	0.10	-0.37	0.01	0.01	0.01	0.22	-0.04	-0.28	-0.03	-0.33	0.08
D17	-0.04	0.14	-0.39	0.06	0.07	0.07	0.25	0.02	-0.26	-0.07	-0.33	0.04
D18	-0.03	0.14	-0.35	0.13	0.08	0.08	0.28	0.07	-0.20	-0.06	-0.35	-0.05
D19	-0.04	0.08	-0.25	0.12	0.06	0.06	0.25	0.05	-0.21	-0.03	-0.40	-0.03
D20	-0.05	0.02	-0.20	0.08	0.04	0.19	0.21	0.03	-0.17	-0.01	-0.37	0.00
D21	-0.01	0.00	-0.17	0.03	0.07	0.17	0.17	0.06	-0.12	0.01	-0.34	0.07
D22	0.02	0.02	-0.15	0.04	0.09	0.16	0.18	0.11	-0.08	0.02	-0.29	0.09
D23	0.08	0.10	-0.13	0.08	0.14	0.21	0.22	0.21	-0.03	0.02	-0.24	0.05
D24	0.13	0.21	-0.15	0.15	0.20	0.27	0.29	0.27	0.01	0.02	-0.20	-0.03
D25	0.13	0.29	-0.17	0.20	0.18	0.34	0.34	0.27	-0.04	0.00	-0.19	-0.08
D26	0.10	0.32	-0.18	0.22	0.16	0.38	0.35	0.22	-0.10	-0.03	-0.20	-0.09
D27	0.04	0.27	-0.21	0.21	0.10	0.36	0.31	0.16	-0.19	-0.04	-0.27	-0.06
D28	-0.02	0.18	-0.22	0.20	0.00	0.30	0.27	0.08	-0.30	-0.03	-0.29	0.01
D29	-0.02	0.16	-0.17	0.23	0.02	0.26	0.26	0.09	-0.25	0.00	-0.25	0.04
D30	-0.02	0.16	-0.20	0.14	0.00	0.27	0.23	0.06	-0.23	0.05	-0.24	0.05

	NL	NW	NT	VCT	VCAD	RCL	RCLAD	RCLM	RCLAB	RCR	RCRAD	RCAM
NL	1.00											
NW	0.33	1.00										
NT	0.23	0.50	1.00									
VCT	0.29	0.36	0.76	1.00								
VCAD	0.23	0.60	0.90	0.53	1.00							
RCL	-0.19	0.22	0.32	0.29	0.29	1.00						
RCLAD	0.15	0.11	0.30	0.22	0.29	-0.03	1.00					
RCLM	0.07	0.35	0.18	0.09	0.24	0.03	0.08	1.00				
RCLAB	0.10	0.34	0.44	0.25	0.50	0.33	-0.23	0.18	1.00			
RCR	-0.09	0.32	0.42	0.35	0.38	0.75	0.00	0.10	0.39	1.00		
RCRAD	0.30	0.29	0.30	0.32	0.27	0.04	0.35	0.10	0.17	0.22	1.00	
RCAM	0.20	0.44	0.33	0.33	0.31	0.08	0.08	0.53	0.24	0.22	0.43	1.00
RCRAB	0.07	0.42	0.53	0.29	0.59	0.40	0.00	0.21	0.65	0.40	0.01	0.24
VCW	0.23	0.46	0.76	0.88	0.58	0.24	0.21	0.16	0.22	0.35	0.30	0.36
D2	0.26	0.66	0.87	0.56	0.93	0.31	0.22	0.23	0.56	0.42	0.42	0.37
D3	0.29	0.70	0.82	0.54	0.86	0.30	0.19	0.19	0.59	0.42	0.46	0.35
D4	0.29	0.68	0.84	0.59	0.83	0.34	0.13	0.16	0.58	0.47	0.37	0.31
D5	0.25	0.69	0.87	0.64	0.81	0.32	0.08	0.19	0.47	0.44	0.31	0.32
D7	0.24	0.70	0.86	0.71	0.74	0.31	0.16	0.24	0.30	0.40	0.29	0.37
D8	0.27	0.94	0.49	0.41	0.05	0.27	0.20	0.33	0.33	0.35	0.39	0.47
D9	0.27	0.84	0.51	0.46	0.53	0.30	0.29	0.32	0.37	0.35	0.44	0.44
D10	0.23	0.79	0.55	0.48	0.55	0.32	0.30	0.28	0.41	0.38	0.44	0.41
D11	0.23	0.76	0.58	0.45	0.61	0.32	0.31	0.27	0.47	0.38	0.42	0.42
D12	0.20	0.75	0.62	0.44	0.66	0.30	0.28	0.26	0.55	0.40	0.38	0.38
D13	0.16	0.74	0.66	0.46	0.71	0.29	0.23	0.26	0.56	0.40	0.32	0.34
D14	0.16	0.69	0.70	0.52	0.74	0.29	0.21	0.26	0.53	0.35	0.28	0.34
D15	0.21	0.67	0.74	0.55	0.75	0.35	0.27	0.23	0.54	0.42	0.34	0.38
D16	0.26	0.67	0.71	0.54	0.71	0.32	0.27	0.20	0.58	0.44	0.37	0.40
D17	0.26	0.74	0.62	0.49	0.65	0.29	0.19	0.25	0.63	0.45	0.46	0.49
D18	0.24	0.74	0.55	0.42	0.61	0.24	0.10	0.26	0.66	0.37	0.44	0.46
D19	0.24	0.73	0.54	0.41	0.61	0.28	0.18	0.22	0.66	0.37	0.43	0.40
D20	0.21	0.66	0.50	0.40	0.53	0.28	0.24	0.18	0.60	0.35	0.42	0.41
D21	0.24	0.68	0.50	0.43	0.52	0.29	0.30	0.22	0.52	0.36	0.46	0.44
D22	0.28	0.73	0.53	0.47	0.55	0.28	0.30	0.27	0.46	0.37	0.50	0.48
D23	0.35	0.84	0.53	0.47	0.56	0.22	0.27	0.33	0.38	0.33	0.48	0.51
D24	0.37	0.94	0.51	0.42	0.58	0.17	0.23	0.37	0.30	0.28	0.40	0.49
D25	0.36	0.97	0.50	0.33	0.62	0.18	0.14	0.37	0.31	0.28	0.25	0.40
D26	0.33	0.93	0.51	0.29	0.66	0.19	0.10	0.31	0.41	0.29	0.17	0.32
D27	0.30	0.84	0.54	0.26	0.70	0.22	0.14	0.23	0.49	0.31	0.15	0.24
D28	0.28	0.68	0.65	0.33	0.78	0.24	0.27	0.17	0.58	0.34	0.25	0.20
D29	0.33	0.66	0.66	0.32	0.81	0.18	0.34	0.18	0.51	0.29	0.26	0.24
D30	0.31	0.66	0.70	0.33	0.88	0.20	0.36	0.23	0.50	0.30	0.27	0.28

	RCRAB	VCW	D2	D3	D4	D5	D7	D8	D9	D10	D11	D12
RCRAB	1.00											
VCW	0.24	1.00										
D2	0.52	0.63	1.00									
D3	0.54	0.62	0.96	1.00								
D4	0.64	0.63	0.88	0.93	1.00							
D5	0.56	0.70	0.84	0.85	0.94	1.00						
D7	0.40	0.81	0.77	0.78	0.83	0.93	1.00					
D8	0.38	0.51	0.62	0.67	0.61	0.84	0.71	1.00				
D9	0.41	0.54	0.61	0.66	0.60	0.60	0.69	0.95	1.00			

	RCRAB	VCW	D2	D3	D4	D5	D7	D8	D9	D10	D11	D12
D10	0.43	0.56	0.62	0.67	0.60	0.58	0.67	0.90	0.97	1.00		
D11	0.51	0.52	0.65	0.69	0.65	0.59	0.63	0.83	0.89	0.95	1.00	
D12	0.58	0.51	0.70	0.74	0.71	0.64	0.62	0.76	0.79	0.86	0.94	1.00
D13	0.61	0.52	0.73	0.76	0.76	0.68	0.63	0.71	0.71	0.76	0.85	0.94
D14	0.61	0.52	0.74	0.73	0.72	0.65	0.58	0.64	0.62	0.66	0.74	0.83
D15	0.62	0.52	0.75	0.72	0.69	0.63	0.58	0.66	0.66	0.70	0.75	0.82
D16	0.59	0.46	0.73	0.71	0.67	0.61	0.54	0.67	0.65	0.67	0.70	0.77
D17	0.52	0.47	0.73	0.75	0.71	0.64	0.55	0.73	0.68	0.70	0.74	0.80
D18	0.50	0.44	0.72	0.77	0.72	0.63	0.53	0.71	0.67	0.67	0.72	0.79
D19	0.50	0.45	0.70	0.75	0.70	0.59	0.52	0.72	0.71	0.74	0.81	0.85
D20	0.42	0.44	0.63	0.68	0.60	0.49	0.48	0.69	0.72	0.76	0.82	0.83
D21	0.37	0.49	0.62	0.66	0.56	0.48	0.53	0.75	0.81	0.85	0.86	0.82
D22	0.33	0.52	0.64	0.68	0.58	0.52	0.60	0.81	0.86	0.89	0.86	0.80
D23	0.30	0.55	0.66	0.70	0.61	0.57	0.66	0.88	0.89	0.89	0.85	0.78
D24	0.33	0.52	0.66	0.69	0.62	0.61	0.68	0.93	0.88	0.85	0.81	0.76
D25	0.45	0.43	0.66	0.69	0.67	0.67	0.67	0.88	0.78	0.74	0.73	0.73
D26	0.57	0.37	0.68	0.72	0.73	0.70	0.62	0.80	0.70	0.66	0.68	0.72
D27	0.65	0.32	0.70	0.75	0.77	0.70	0.58	0.71	0.62	0.59	0.64	0.72
D28	0.67	0.35	0.78	0.82	0.84	0.72	0.57	0.59	0.57	0.59	0.67	0.73
D29	0.59	0.34	0.78	0.79	0.78	0.65	0.54	0.58	0.55	0.58	0.66	0.73
D30	0.61	0.34	0.82	0.78	0.74	0.65	0.53	0.59	0.56	0.58	0.67	0.73

	D13	D14	D15	D16	D17	D18	D19	D20	D21	D22	D23	D24
D13	1.00											
D14	0.92	1.00										
D15	0.66	0.95	1.00									
D16	0.79	0.85	0.94	1.00								
D17	0.81	0.81	0.84	0.91	1.00							
D18	0.81	0.78	0.74	0.79	0.95	1.00						
D19	0.84	0.77	0.76	0.77	0.89	0.93	1.00					
D20	0.78	0.71	0.72	0.72	0.81	0.84	0.95	1.00				
D21	0.73	0.64	0.68	0.68	0.74	0.74	0.87	0.95	1.00			
D22	0.72	0.64	0.68	0.67	0.73	0.72	0.81	0.89	0.97	1.00		
D23	0.72	0.64	0.66	0.65	0.73	0.72	0.78	0.82	0.90	0.96	1.00	
D24	0.73	0.67	0.66	0.65	0.72	0.73	0.74	0.72	0.78	0.85	0.94	1.00
D25	0.74	0.68	0.64	0.64	0.70	0.72	0.70	0.62	0.63	0.68	0.80	0.94
D26	0.76	0.71	0.67	0.68	0.72	0.73	0.70	0.59	0.56	0.58	0.69	0.84
D27	0.77	0.73	0.69	0.71	0.72	0.73	0.70	0.57	0.51	0.52	0.59	0.73
D28	0.77	0.74	0.70	0.71	0.72	0.74	0.74	0.62	0.55	0.55	0.57	0.62
D29	0.77	0.76	0.73	0.71	0.72	0.71	0.71	0.61	0.55	0.56	0.58	0.63
D30	0.77	0.79	0.79	0.77	0.72	0.67	0.67	0.59	0.56	0.57	0.59	0.60

	D25	D26	D27	D28	D29	D30
D25	1.00					
D26	0.96	1.00				
D27	0.88	0.96	1.00			
D28	0.72	0.78	0.88	1.00		
D29	0.70	0.77	0.84	0.93	1.00	
D30	0.69	0.76	0.82	0.87	0.95	1.00

APPENDIX VI
 PRINCIPAL COMPONENT FUNCTION COEFFICIENTS
 (ABBREVIATIONS EXPLAINED IN TABLES 2 AND 3)

	<u>L. lyallii</u> populations				Combined populations			
	Five		Eleven		Seven		Seventeen	
	F1	F2	F1	F2	F1	F2	F1	F2
CL	.016	-.009			.016	-.009		
CD	.025	-.025			.025	-.025		
PL	-.044	.002			-.044	.019		
PD	-.004	.023			-.004	.023		
SN	.052	.009			.052	.009		
SL	.016	-.018			.016	-.018		
SW	.006	-.008			.006	-.008		
BL	.008	-.021			.008	-.021		
AWL	.003	-.027			.004	-.027		
BW	-.016	-.010			-.016	-.010		
ADM	-.020	-.024			-.020	-.024		
RCELL	-.007	.009	-.053	-.124	-.007	.009	-.029	.062
NL	-.035	-.035	.021	-.038	-.035	-.035	-.007	.005
NW	-.051	.087	-.074	-.025	-.051	.087	-.029	.175
NT	.075	-.062	.114	-.074	.075	-.062	.097	-.022
VCT	.011	-.012	-.022	-.038	.011	-.012	.015	-.036
VCAD	.091	-.069	.137	-.077	.091	-.069	.113	.007
RCL	.005	-.012	-.005	-.018	.005	-.012	.014	.003
RCLAD	.017	.012	.137	.053	.017	.012	.015	.030
RCLM	-.044	.014	-.044	-.079	-.044	.014	-.081	.065
RCLAB	.018	-.040	-.008	.017	.018	-.040	-.044	-.100
RCR	-.009	-.043	-.004	.014	-.009	-.043	-.027	-.004
RCRAD	.021	.014	.028	.009	.021	.014	.003	.032
RGRAM	-.047	.037	-.061	-.038	-.046	.037	-.089	.053
RCRAB	.011	-.050	.120	.015	.011	-.050	-.025	-.064
VCW	.011	.013	-.040	-.030	.011	.013	.022	-.008
D2	.093	-.061	.090	-.072	.093	-.061	.110	.010
D3	.091	-.050	.072	-.041	.091	-.050	.111	.016
D4	.080	-.077	.058	-.068	.080	-.077	.100	.048
D5	.008	-.029	-.009	-.091	.008	-.029	.018	.139

	<u>L. lyallii</u> populations				Combined populations			
	Five		Eleven		Seven		Seventeen	
	F1	F2	F1	F2	F1	F2	F1	F2
D7	-.047	.046	-.079	-.010	-.047	.046	-.035	.164
D8	-.066	.126	-.075	.053	-.066	.126	-.052	.134
D9	-.061	.134	-.050	.126	-.061	.134	-.050	.055
D10	-.046	.138	-.029	.179	-.046	.138	-.045	-.006
D11	-.020	.116	.009	.202	-.020	.116	-.025	-.051
D12	.018	.072	.055	.169	.018	.072	.021	-.061
D13	.048	.028	.080	.108	.048	.028	.054	-.043
D14	.081	-.019	.102	.033	.081	-.019	.079	-.031
D15	.086	-.018	.104	-.006	.086	-.018	.079	-.036
D16	.093	-.023	.087	-.062	.093	-.023	.079	-.041
D17	.083	-.005	.023	-.053	.083	-.005	.062	-.032
D18	.074	.000	-.012	-.020	.074	-.000	.054	-.028
D19	.058	.033	-.021	.089	.058	.033	.032	-.070
D20	.036	.070	-.043	.161	.036	.070	-.004	-.093
D21	.001	.110	-.054	.185	.001	.110	-.034	-.072
D22	-.019	.119	-.064	.163	-.019	.119	-.047	-.031
D23	-.034	.117	-.076	.123	-.034	.117	-.050	.032
D24	-.053	.113	-.079	.156	-.053	.113	-.047	.119
D25	-.045	.080	-.055	-.108	-.045	.080	-.026	.166
D26	-.015	.038	-.019	-.072	-.015	.038	.004	.166
D27	.029	-.019	.046	-.096	.029	-.019	.045	.147
D28	.094	-.073	.141	-.034	.094	-.073	.115	.041
D29	.096	-.052	.176	-.014	.096	-.052	.120	.008
D30	.098	-.053	.172	-.047	.098	-.053	.120	.008

APPENDIX VII
ANALYSIS OF VARIANCE OF THE FIRST TWO PRINCIPAL
COMPONENT SCORES DETERMINED FROM NEEDLE CHARACTERS
OF ELEVEN L. LYALLII POPULATIONS

Analysis of variance expressed in the first principal component (cone and needle characters of 5 populations of L. lyallii included in the analysis).

Source of Variation	df	MS	Proportion of variance
Between Populations	4	12.46	62.2%
Within Populations	60	0.56	37.8%
Total	64	1.30	

Analysis of variance expressed in the second principal component (cone and needle characters of 5 populations of L. lyallii included in the analysis).

Source of Variation	df	MS	Proportion of variance
Between Populations	4	5.29	29.2%
Within Populations	60	0.83	70.8%
Total	64	1.11	

APPENDIX VIII

DISCRIMINANT FUNCTION COEFFICIENTS
(ABBREVIATIONS EXPLAINED IN TABLES 2 AND 3)

<u>L. lyallii</u> populations					
	Five			Eleven	
CL	0.06	0.19	RCELL	0.04	0.03
OD	0.21	0.44	NL	0.28	0.16
PL	-0.73	0.27	NW	-0.91	-0.04
PD	0.19	-0.27	NT	-0.49	1.49
SN	0.36	0.18	VCT	0.13	-0.17
SL	-0.05	-0.62	VCAD	-0.14	-0.36
SW	0.52	-0.38	RCL	0.03	-0.21
BL	0.47	0.72	RCLAD	-0.04	0.12
BW	-0.59	-0.05	RCLM	-0.14	0.20
ADM	-0.65	0.27	RCLAB	-0.18	-0.10
NL	0.04	0.35	RCR	-0.11	-0.52
RCL	0.56	0.35	RCRAD	0.34	0.44
RCLAB	-0.57	-0.14	RCRAB	0.21	0.32
RCR	-0.21	-0.66	VCW	-0.55	0.44
RCRM	0.12	0.36	D3	0.34	0.01
RCRAB	-0.13	0.29	D7	0.97	-0.32
VCW	-0.25	0.23	D11	0.60	0.21
D5	0.61	-0.81	D13	-0.37	-0.95
D11	0.49	-0.08	D14	0.76	0.73
D15	-0.58	-0.78	D15	-1.15	-1.17
D16	0.35	0.58	D16	0.71	-0.12
D19	1.20	0.90	D17	0.15	0.03
D20	-0.42	-1.28	D19	0.44	-0.29
D23	-0.27	0.63	D23	-0.67	0.07
D27	-0.62	0.41	D25	0.18	0.80
D29	0.46	-0.01	D26	0.41	0.016
			D27	0.44	-0.30

Combined populations					
	Seven			Seventeen	
CL	1.08	0.51	RCELL	0.21	0.03
CD	-0.5	0.22	NL	-0.08	0.46
PL	0.24	0.29	NW	-1.98	-1.16
PD	-0.39	-0.00	NT	-0.36	0.97
SN	-0.56	-0.27	VCT	0.35	0.31
SL	-0.13	-0.28	VCAD	0.10	-0.44
SW	-0.33	-0.52	RCL	-0.05	0.08
BL	0.55	-0.09	RCLAD	0.37	0.01
BW	-0.07	0.20	RCLM	0.22	-0.13
ADM	-0.10	0.73	RCLAB	-0.22	-0.09
RCELL	0.39	0.12	RCR	-0.13	0.22
NL	-0.10	0.52	RCRAD	0.34	0.15
NW	-1.43	0.87	RCRM	0.21	0.20
NT	-0.60	0.82	RCRAB	-0.28	0.25
VCT	0.27	0.48	VCW	-0.65	-0.72
RCLAB	-0.20	0.18	D3	0.00	-0.19
RCR	-0.30	0.13	D4	0.15	0.48
RCAM	0.32	0.26	D7	0.65	0.97
RCRAB	-0.32	0.37	D11	0.16	0.04
VCW	-0.60	0.01	D12	-0.30	0.38
D3	0.10	-0.68	D13	0.24	-0.37
D7	0.81	-1.01	D14	0.06	0.92
D11	1.07	-0.98	D15	0.29	-1.51
D12	-0.99	0.81	D17	-0.17	-0.96
D15	0.38	-0.92	D18	0.51	1.11
D16	0.40	0.80	D19	-0.02	-0.33
D17	-0.46	-2.23	D21	1.16	0.50
D18	0.60	1.54	D22	-2.08	0.28
D19	0.40	-1.40	D23	0.85	-0.74
D20	-0.30	0.91	D25	0.29	0.46
D24	-0.56	0.85	D26	0.72	0.49
D26	1.35	-1.38	D28	-0.01	0.24
D27	-0.09	0.94	D30	-0.12	-0.23

APPENDIX IX

CORRELATION MATRIX OF NEEDLE CHARACTERS
OF ELEVEN L. LYALLII POPULATIONS
(ABBREVIATIONS EXPLAINED IN TABLES 2 AND 3)

	RCELL	NL	NW	NT	VCT	VCAD	RCL	RCLAD	RCLM	RCLAB	RCR	RCRAD
RCELL	1.00											
NL	-0.10	1.00										
NW	0.04	0.20	1.00									
NT	0.11	0.18	-0.64	1.00								
VCT	0.12	0.27	-0.54	0.68	1.00							
VCAD	0.07	0.15	-0.62	0.92	0.50	1.00						
RCL	0.19	-0.19	0.14	0.13	0.07	0.12	1.00					
RCLAD	0.08	0.22	0.25	0.47	0.39	0.45	-0.10	1.00				
RCLM	0.19	0.08	0.39	0.47	0.40	0.42	-0.08	0.42	1.00			
RCLAB	0.01	-0.09	0.12	0.37	0.18	0.61	0.14	-0.24	0.14	1.00		
RCR	0.18	-0.15	0.17	0.16	0.09	0.13	0.65	-0.13	-0.10	0.23	1.00	
RCRAD	0.05	0.32	0.31	0.44	0.44	0.40	-0.03	0.50	0.34	0.00	0.06	1.00
RCRM	0.15	0.10	-0.45	0.53	0.51	0.45	-0.02	0.35	0.66	0.22	0.03	0.45
RCRAB	-0.05	-0.15	0.13	0.40	0.16	0.34	0.15	0.00	0.10	0.50	0.17	-0.16
VCW	0.13	0.21	-0.65	0.68	0.84	56.00	0.03	0.41	0.50	0.14	0.06	0.41
D2	0.05	0.17	-0.66	0.88	0.52	-0.92	0.15	0.32	0.37	0.41	0.20	0.48
D3	0.00	0.18	-0.66	0.78	0.44	0.80	0.13	0.22	0.26	0.46	0.24	0.15
D4	0.03	0.13	-0.65	0.65	0.32	0.65	0.18	0.02	0.10	0.50	0.31	0.30
D5	0.03	0.13	-0.82	0.63	0.36	0.63	0.19	0.01	0.17	0.39	0.28	0.28
D7	0.04	0.18	-0.97	0.65	0.55	0.62	0.16	0.26	0.38	0.16	0.20	0.38
D8	0.07	0.20	-0.92	0.64	0.61	0.60	0.13	0.39	0.44	0.09	0.16	0.45
D9	0.07	0.19	-0.81	0.64	0.62	0.58	0.14	0.47	0.45	0.13	0.19	0.50
D10	0.07	0.15	-0.73	0.63	0.60	0.57	0.14	0.46	0.41	0.19	0.23	0.48
D11	0.08	0.14	-0.68	0.65	0.54	0.60	0.17	0.41	0.36	0.29	0.27	0.43
D12	0.06	0.12	-0.64	0.70	0.49	0.64	0.17	0.34	0.28	0.36	0.28	0.38
D13	0.03	0.08	-0.64	0.73	0.49	0.68	0.17	0.28	0.28	0.40	0.26	0.31
D14	0.04	0.11	-0.61	0.86	0.59	0.74	0.16	0.34	0.38	0.35	0.17	0.33
D15	0.10	0.14	-0.60	0.93	0.69	0.79	0.17	0.44	0.46	0.36	0.17	0.41
D16	0.13	0.18	-0.60	0.96	0.74	0.79	0.13	0.44	0.46	0.39	0.16	0.43
D17	0.14	0.19	-0.68	0.89	0.71	0.75	0.15	0.32	0.44	0.45	0.22	0.46
D18	0.09	0.15	-0.69	0.76	0.60	0.68	0.15	0.18	0.37	0.52	0.22	0.41
D19	0.07	0.10	-0.65	0.68	0.51	0.60	0.18	0.17	0.29	0.55	0.25	0.36
D20	0.11	0.10	-0.61	0.64	0.54	0.55	0.16	0.27	0.32	0.48	0.23	0.39
D21	0.10	0.14	-0.64	0.63	0.59	0.55	0.14	0.39	0.40	0.36	0.19	0.46
D22	0.09	0.17	-0.69	0.63	0.62	0.56	0.12	0.44	0.46	0.27	0.17	0.51
D23	0.07	0.22	-0.80	0.63	0.63	0.59	0.08	0.44	0.49	0.18	0.13	0.50
D24	0.05	0.25	-0.92	0.64	0.61	0.60	0.06	0.41	0.49	0.10	0.09	0.44
D25	0.04	0.22	-0.97	0.64	0.52	0.63	0.10	0.31	0.41	0.10	0.13	0.29
D26	0.01	0.19	-0.92	0.63	0.43	0.62	0.14	0.17	0.28	0.20	0.17	0.15
D27	0.00	0.15	-0.80	0.64	0.34	0.65	0.17	0.14	0.17	0.31	0.21	0.11
D28	-0.10	0.12	-0.58	0.65	0.28	0.68	0.17	0.21	0.11	0.43	0.26	0.18
D29	-0.02	0.15	-0.56	0.78	0.38	0.81	0.08	0.40	0.24	0.36	0.19	0.30
D30	0.04	0.17	-0.60	0.89	0.47	0.94	0.10	0.48	0.36	0.28	0.14	0.36

	RCM	RCRAB	VCW	D2	D3	D4	D5	D7	D8	D9	D10	D11
RCRM	1.00											
RCRAB	0.18	1.00										
VCW	0.58	0.11	1.00									
D2	0.45	0.30	0.58	1.00								
D3	0.35	0.35	0.51	0.93	1.00							
D4	0.21	0.43	0.34	0.77	0.89	1.00						
D5	0.28	0.35	0.41	0.72	0.79	0.89	1.00					
D7	0.45	0.12	0.65	0.67	0.67	0.64	0.82	1.00				
D8	0.50	0.10	0.70	0.63	0.61	0.52	0.68	0.96	1.00			
D9	0.50	0.14	0.69	0.60	0.59	0.45	0.55	0.86	0.94	1.00		
D10	0.49	0.17	0.66	0.59	0.57	0.42	0.48	0.77	0.87	0.96	1.00	
D11	0.47	0.28	0.60	0.61	0.61	0.50	0.51	0.69	0.78	0.87	0.94	1.00
D12	0.41	0.39	0.57	0.66	0.68	0.61	0.59	0.65	0.69	0.74	0.81	0.92
D13	0.39	0.45	0.57	0.69	0.71	0.66	0.64	0.64	0.64	0.65	0.70	0.81
D14	0.43	0.43	0.64	0.73	0.69	0.59	0.58	0.60	0.61	0.61	0.64	0.71
D15	0.51	0.43	0.70	0.77	0.68	0.56	0.54	0.60	0.63	0.65	0.66	0.70
D16	0.53	0.41	0.70	0.77	0.70	0.59	0.58	0.61	0.62	0.63	0.62	0.64
D17	0.57	0.33	0.72	0.80	0.76	0.68	0.68	0.69	0.68	0.65	0.66	0.69
D18	0.51	0.32	0.65	0.77	0.79	0.74	0.72	0.69	0.65	0.62	0.63	0.67
D19	0.45	0.33	0.56	0.71	0.75	0.71	0.66	0.65	0.63	0.63	0.68	0.75
D20	0.50	0.24	0.58	0.63	0.65	0.55	0.52	0.62	0.66	0.70	0.75	0.80
D21	0.53	0.15	0.63	0.62	0.61	0.45	0.45	0.66	0.74	0.80	0.84	0.84
D22	0.57	0.10	0.67	0.62	0.59	0.42	0.46	0.72	0.81	0.86	0.87	0.84
D23	0.58	0.07	0.71	0.63	0.60	0.43	0.52	0.81	0.88	0.90	0.88	0.82
D24	0.53	0.60	0.72	0.63	0.61	0.49	0.63	0.90	0.94	0.90	0.84	0.77
D25	0.42	0.17	0.64	0.65	0.65	0.61	0.75	0.92	0.89	0.80	0.72	0.67
D26	0.29	0.31	0.52	0.65	0.68	0.74	0.85	0.85	0.76	0.64	0.57	0.56
D27	0.20	0.42	0.41	0.67	0.73	0.83	0.87	0.74	0.62	0.50	0.45	0.49
D28	0.15	0.52	0.30	0.70	0.77	0.85	0.75	0.52	0.44	0.41	0.41	0.51
D29	0.31	0.47	0.42	0.77	0.78	0.75	0.64	0.53	0.50	0.49	0.51	0.59
D30	0.40	0.41	0.52	0.85	0.77	0.67	0.63	0.59	0.57	0.56	0.57	0.62

	D12	D13	D14	D15	D16	D17	D18	D19	D20	D21	D22	D23
D12	1.00											
D13	0.93	1.00										
D14	0.81	0.91	1.00									
D15	0.75	0.81	0.94	1.00								
D16	0.68	0.71	0.83	0.94	1.00							
D17	0.72	0.74	0.78	0.84	0.91	1.00						
D18	0.72	0.76	0.74	0.72	0.76	0.94	1.00					
D19	0.78	0.77	0.71	0.67	0.68	0.82	0.91	1.00				
D20	0.78	0.72	0.66	0.66	0.64	0.74	0.80	0.94	1.00			
D21	0.77	0.67	0.63	0.66	0.63	0.69	0.69	0.81	0.93	1.00		
D22	0.73	0.63	0.60	0.65	0.62	0.68	0.66	0.73	0.85	0.96	1.00	
D23	0.71	0.63	0.60	0.64	0.61	0.68	0.66	0.68	0.78	0.90	0.96	1.00
D24	0.68	0.64	0.61	0.62	0.61	0.67	0.66	0.65	0.69	0.78	0.85	0.94
D25	0.63	0.63	0.61	0.60	0.59	0.65	0.67	0.63	0.59	0.62	0.69	0.81

	D12	D13	D14	D15	D16	D17	D18	D19	D20	D21	D22	D23
D26	0.60	0.63	0.59	0.56	0.57	0.64	0.67	0.61	0.51	0.48	0.51	0.62
D27	0.58	0.64	0.60	0.56	0.57	0.62	0.65	0.60	0.46	0.38	0.38	0.46
D28	0.61	0.67	0.61	0.57	0.58	0.61	0.65	0.63	0.48	0.38	0.35	0.37
D29	0.67	0.73	0.72	0.71	0.69	0.68	0.67	0.64	0.54	0.49	0.48	0.49
D30	0.68	0.72	0.76	0.79	0.77	0.73	0.66	0.60	0.54	0.53	0.53	0.55

	D24	D25	D26	D27	D28	D29	D30
D24	1.00						
D25	0.94	1.00					
D26	0.79	0.94	1.00				
D27	0.62	0.81	0.94	1.00			
D28	0.45	0.59	0.73	0.85	1.00		
D29	0.52	0.59	0.65	0.73	0.88	1.00	
D30	0.58	0.63	0.64	0.69	0.77	0.93	1.00