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A Multivariate Study Of Geographic Variation In The Cones Of Pinus Contorta In Relation To Environmental Variables

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A MULTIVARIATE STUDY OF GEOGRAPHIC VARIATION IN THE CONES OF *PINUS CONTORTA* IN RELATION TO ENVIRONMENTAL VARIABLES

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

Since *Pinus contorta* occurs under a great variety of environmental conditions within its wide natural range, it is not surprising that the literature provides many examples of the existence of geographic variation within the species. However, the most thorough previous investigation of this variation was basically qualitative and univariate. Thus, the general objectives of the present study were to provide a multivariate analysis of the pattern of geographic variation, and to relate this pattern to environmental factors. Particular objectives were to compare the variation between four previously defined subspecies to the variation within these subspecies and relate this to variation in geographic region, latitude, elevation, topographic situation, climate and soil.

In order to optimize the allocation of measurement effort, preliminary studies were undertaken to objectively select a set of characters for study, and to determine the number of cones to measure to represent each site.

Collection sites were carefully selected to meet the objectives of the study with respect to elevation, latitude, and the availability of climatic data, at a latitude where all four of the previously defined subspecies occur.

After choosing a resemblance function with desirable properties, the data structure was investigated using three-dimensional stereograms of principal components, with a demonstration that the first three principal components represented the resemblances among sites with almost no distortion. The stereograms revealed a discontinuous data structure with groups corresponding to the subspecies previously recognized, with an extension of the range of the population previously described as restricted to the neighbourhood of Mendocino, California. The Rocky Mountain group appeared divisible into two subgroups with more and less serotinous cones. The application of a wide range of clustering algorithms confirmed the robustness of this group structure.

The ranking algorithm used for character selection was applied to identify those characters having the greatest ability to distinguish between the identified groups. Then, the variation between the groups was related to various extrinsic factors, with the principal technique employed being the plotting of ranks for the extrinsic factors on stereograms of the principal components for the sites. The conclusions from this part of the study were that geographic region was clearly the most important of the extrinsic variables considered in terms of its obvious relationship to group structure, but this variable was unnable to account for the division of the populations of the coastal region into two groups or for the subdivision of the Rocky Mountain

group into two subgroups. The variable which showed the greatest potential for explaining these divisions within geographic regions was the amount of available soil phosphorus.

The variation of cone characters among the sites within the groups was examined and related to extrinsic factors. The main techniques used were principal components analysis within the groups, plotting of environmental ranks on stereograms, and application of the character ranking algorithm to compare the ability of cone characteristics to discriminate between certain pairs of sites of particular interest. The groups were shown to be essentially homogeneous except for the subdivision of the Rocky Mountain group, and the divergence of several sites which could be explained on the basis of extreme conditions associated with those sites. Trends were found within the groups associated with variation in soil phosphorus and elevation.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. R.C. Jancey, and the members of my Advisory Committee, Dr. R. Green, Dr. A. Maun, and Dr. L. Orlóci, for their helpful suggestions and advice. I would also like to thank Mr. K. Illingworth of the B.C. Forest service for providing cones for a preliminary study. Finally, I would like to thank my family, particularly my son David, for assisting me in the collection of cones and field data.

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CHAPTER 1

INTRODUCTION

The research described in this thesis consists of a study of geographic variation in the seed cones of Pinus contorta, using methods of multivariate data analysis such as ordination and clustering. This chapter indicates the motivation for this research, reviews the relevant literature, and briefly describes the objectives of the study.

1. Motivation

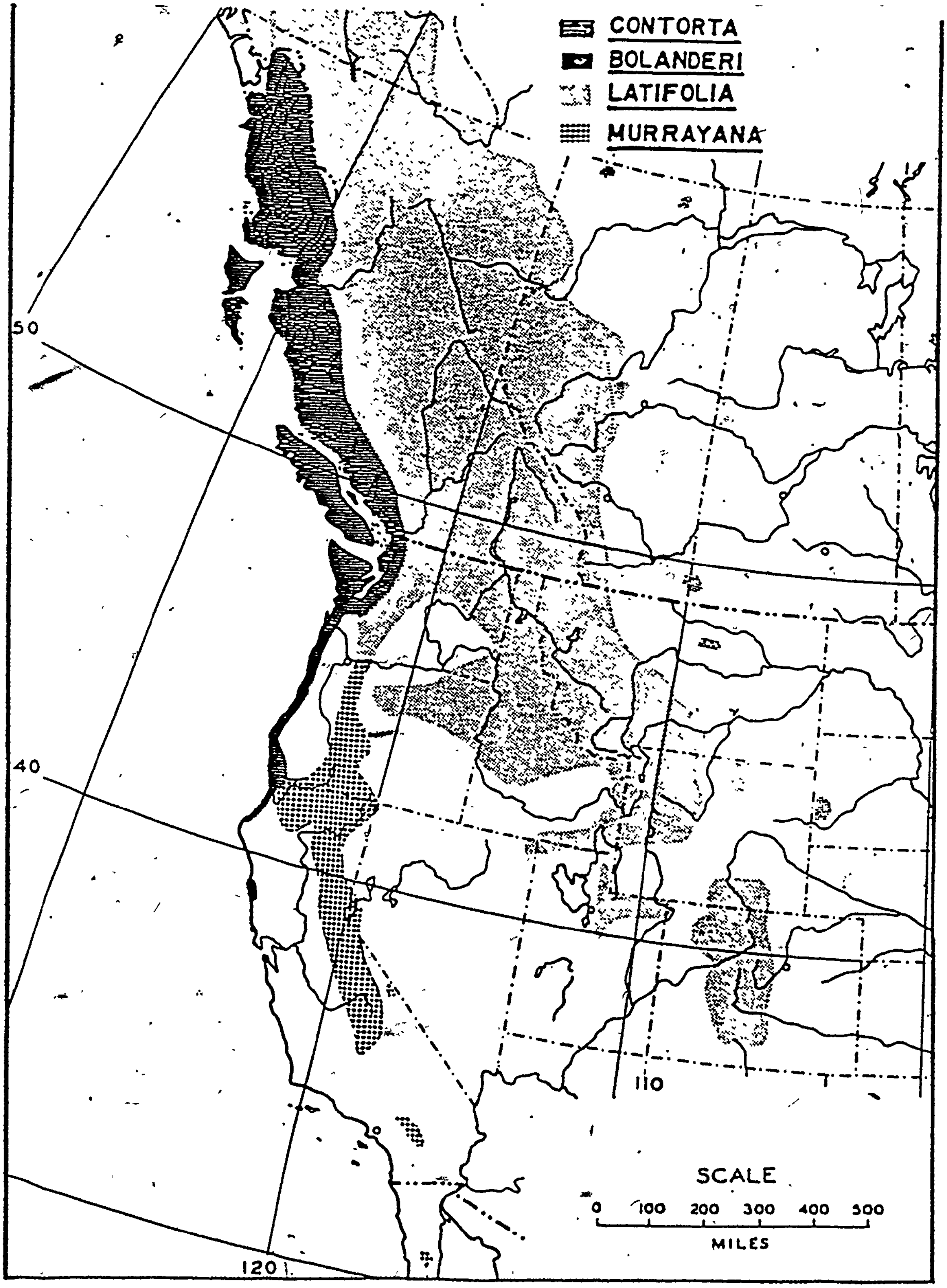
Pinus contorta is one of the most widely-distributed trees in North America, occupying the third greatest acreage of any North American tree (Roche,1962). It is native over a range from Baja California in the south to the Yukon in the north, and from the Black Hills of South Dakota on the east to the Pacific Ocean on the west (Critchfield and Little, 1966; see figure 1.1). The range of elevations at which it is found, from sea level to 3650 meters, is greater than that of any other pine (Griffin and Critchfield,1972). Within this wide range of latitude, longitude, and elevation, Pinus contorta is found growing under a wide variety of climatic and edaphic conditions; for example, it occurs in subalpine forests (Despain, 1973; Alexander, 1974; Chabot and Billings, 1972), on coastal sand dunes (Kumler, 1969; Wiedemann, 1966), and in sphagnum bogs (Illingworth and Arlidge, 1960). Fowells(1965), Edwards(1954,1955), and Rall(1979) provide additional details of the great variation in environmental conditions within the natural range of <u>Pinus contorta</u>. Such a widely-distributed species could be expected to show geographic variation whose nature would be of practical interest to foresters as well as taxonomists and ecologists.

Munger(1914) referred to <u>Pinus contorta</u> as a "practically worthless weed". This attitude towards the species persisted in North America until about 1950, after which the values of <u>Pinus contorta</u> for watershed protection and cover for wildlife, and its potential use for lumber and pulpwood began to receive increasing recognition (Trappe and Harris, 1958; Youngberg and Dyrness, 1959). By the 1970's, <u>Pinus contorta</u> was rated "very high in all the multiple use values of forests over millions of acres of the West" by a United States forester (Wellner,1975), and was also regarded as a highly-valuable tree in Canada (McDougal,1975). Wellner found that its wide ecological amplitude, great reproductive ability, and rapid juvenile growth rate made the species particularly useful in forest management, while McDougal emphasized the special values of <u>Pinus contorta</u> for watershed protection, and for scenic and recreational areas.

Pinus contorta received early recognition in Europe, where Tigerstedt(1922) reported that young trees grown from seed in Finland were growing at twice the rate of a nearby plantation of the common native pine, Pinus sylvestris. Since then, Pinus contorta has been widely-planted in Sweden (Aldhous, 1976; Hagner and Fahlroth, 1976), Norway (Dietrichson, 1976), the Netherlands (Kriek, 1976), Ireland (O'Driscoll, 1976; Savill, 1976), and New Zealand (Critchfield, 1957). In Britain Pinus contorta was found to be particularly useful on sites which were subject to severe exposure or which had soils which were too infertile for other tree species (Lines, 1976a,1976b).

The most thorough study of geographic variation in Pinus contorta was made by Critchfield (1957), but his approach, which will be discussed in more detail in a subsequent section, was basically descriptive and univariate. In fact, there have been very few applications of multivariate methods of data analysis to the study of geographic variation within a species, despite the success of these methods in the related areas of taxonomy and ecology (Orlóci,1978; Sneath and Sokal,1973). One of the best examples is a study of geographic variation in the closely-related species Pinus banksiana by Beshir(1975).

Figure 1.1 Approximate geographic range of *Pinus contorta* showing the ranges of the subspecies recognized by Critchfield(1957).



2. Previous Studies of Geographic Variation in <u>Pinus contorta</u>

Critchfield(1957) has produced the most comprehensive study of geographic variation in <u>Pinus contorta</u>. His publication incorporates a thorough review of previous studies relating to geographic variation in <u>Pinus contorta</u>, so this present review will concentrate on the subsequent period. Based on his review of the literature, examination of leaves and cones collected from natural populations throughout the range of the species, and experiments with seedling growth, he recognized four geographic subspecies (Fig. 1.1):

1. <u>Pinus contorta</u> Douglas ex Loudon ssp. <u>contorta</u>, occurring along the Pacific coast from Mendocino, California to Alaska.

2. <u>Pinus contorta</u> ssp. <u>bolanderi</u> occurring only on very acid soil near Mendocino, California.

3. <u>Pinus contorta</u> ssp. <u>latifolia</u>(Engelm. ex Wats.) stat. nov., occurring in the Rocky Mountains, as well as inland British Columbia, Washington and the Yukon.

4. <u>Pinus contorta</u> ssp. <u>murrayana</u>(Balf.) stat. nov., occurring in the Sierra Nevada Mountains of California and the Cascade Mountains in Oregon.

Although Critchfield(1957) described his study as "an application of the biometrical approach" which he considered necessary since "conspecific populations differ primarily in quantitative characteristics"; nevertheless, quantitative data were recorded for only a few of the characters he discussed. Also, for those few quantitative characters, his method of analysis was rather crude, consisting of a visual comparison of bar graphs of character values measured for the different localities.

Critchfield examined only two characteristics of the female cone in detail, namely, cone orientation, as measured by the angle formed by the axis of the cone and the branch, and specific gravity. He concluded that reflexed cones, attached to the branch at angles of 120 to 140 degrees were characteristic of the entire coastal region and much of the inland region. Pronounced departures from this orientation were found in the central and southern Sierra Nevada mountains where cones were almost perpendicular to the branch, and in the Rocky Mountains where cone angle varied widely within local populations.

Critchfield stated without any quantitative evidence that the specific gravity of cones exhibits a close association with a group of cone characteristics, including hardness, serotiny and apophysis shape. He claimed that specific gravity exhibited the greatest regularity in its variation pattern and the clearest geographical distinction of all the characters considered in his study. Based on inspection of his bar graphs, he concluded that cones from the Sierra Nevada Mountains had the lowest specific gravity, while those from the Rocky Mountains had the highest specific gravity. Cones from the highly acid soils near Mendocino, California were nearly as dense as those of the Rocky Mountains, while the other coastal populations, as well as the populations of the Cascades and Blue Mountains, had cones of intermediate specific gravity. He also suggested that specific gravity decreases with elevation; however, his sampling locations were not selected in such a way as to provide clear indication of variation of characters with elevation.

Keng and Little (1961) examined needles of trees growing in the Eddy Arboretum of the Institute of Forest Genetics at Placerville, California. Their study included a comparison of needles of _Pinus contorta_ var. _contorta_ with _Pinus contorta_ var. _murrayana_, and with hybrids of these varieties with _Pinus banksiana_. The exact location which was the source of seed for the varieties of _Pinus contorta_ studied was not given. Also, general observations were merely recorded in a comparative descriptive table, so that the value of this study in forming conclusions concerning geographic variation in _Pinus contorta_ is minimal.

Roche (1962) described geographic variation in growth habit and bark type of _Pinus contorta_ in its native habitat in coastal and inland British Columbia, and later compared these observations with trees grown on plantations in Britain (Roche, 1966). He suggested that the variation in growth habit between inland and coastal provenances was more evident in the plantations than in the native habitat since, on the coast, commercial seed has been more often collected from scrub trees because of accessibility and abundance, and thus this seed was not representative of the native population. He presented the opinion that bark thickness is not a reliable diagnostic feature for delineating intraspecific variation, while bark texture and colour are. His work included a quantitative study of only one character: the ratio of needle width to needle length, for trees grown on a plantation in Placerville, California, from seed from each of the four geographic regions defined by Critchfield. Based on an analysis of variance, he concluded that this character differs significantly among all of the groups except for the Mendocino acid-soil population, which he suggested is merely the southern extremity of the coastal population. In summarizing characteristics which distinguish the inland form of Pinus contorta from the coastal form, he stated that seeds of the inland trees have a pointed protuberance at the funicular end, and a ridge on the surface; whereas, coastal seeds lack these characters. He also stated that inland seeds are usually more than three mm. long, while coastal seeds are usually less than three mm. long, but no evidence is given of the data used to arrive at this generalization.

Black(1963) studied variation in the number, length, and position of resin canals in needles from 9 provenances growing in Scotland and representing seed from coastal, Sierra Nevada, and Rocky Mountain populations. Unfortunately, the locations of the seed sources were not specified very precisely; for example, one source was referred to only as "coastal Canada". Black concluded that coastal populations were distinguishable from the two inland populations which were both similar in terms of resin canal characteristics.

Jeffers and Black(1963) measured 19 characteristics of needles, cones and wood for the same 9 provenances as Black. Because of disparities in the manner of collecting data, only the character means for each provenance were available for analysis. Six of the variables they measured were characters of seeds and cones; namely, cone length and breadth, seed length and breadth, and seed wing length and breadth. Three methods of multivariate analysis were applied to the data.

The first method, which they referred to as "Q-technique", is a clustering method which involves the replacement of continuous measures of variables by ranks, calculation of correlation between pairs of provenances based on these ranks, and visual inspection of the correlation matrix to form clusters. No reference is given for the source or other applications of this technique and it appears to have little to recommend its use.

Their second method was a form of discriminant analysis, in which coefficients were calculated for a discriminant function based on the difference between the means of the nineteen variables for the coastal group of four provenances and the inland group of five provenances, using the pooled covariance matrix. No mention was made of the multivariate normal assumptions underlying the application of this technique. Also the application of this method when there are only four or five replicates in each group is questionable. The third method used was principal components analysis.

Their conclusions based on the first two methods supported the accepted division of the 9 provenances into two broad groups-- coastal and inland. However, since the first principal component did not correspond with this division, they claimed that a classification could be produced which would account for a greater degree of botanical variation, based on those variables having a high weighting on the first principal axis. These variables include cone breadth, seed size and seed-wing size.

In summary, although Jeffers and Black(1963) recognized the need for multivariate methods of data analysis for the study of geographic variation in Pinus contorta, the deficiencies in their data and in their choice of particular methods is such that their study merely suggests the need for further work rather than producing any firm conclusions.

Lines(1966) surveyed the performance of 22 provenances of Pinus contorta in Britain in terms of silvicultural characteristics, such as mean annual height and girth increments, and stem form. As with the previous provenance studies, the seed sources were not known very precisely, but they are all from British Columbia and the northwestern U.S. He concluded that there is probably greater natural variation due to provenance within Pinus contorta than in any other common forest tree.

Illingworth(1969,1971,1973,1975a,1975b,1976,1977) has provided interim reports on an extremely ambitious provenance study of geographic variation in Pinus contorta which is currently being undertaken in British Columbia. Seed from 144 locations throughout the range of Pinus contorta was sown in 1969 in research nurseries at Lake Cowichan (Vancouver Island) and Red Rock (central British Columbia). Measurements such as seed germination, seedling survival, and stomatal density of seedling needles have been made; however, essentially no data were recorded concerning the native populations from which the seed was collected. Univariate analyses of variance have been performed for some seedling characters, and the use of multivariate methods of data analysis is planned. Illingworth has concluded that early results from his research support the principal taxonomic subdivisions proposed for Pinus contorta by Critchfield(1957).

Several authors have mentioned geographic variation in terpenes in Pinus contorta as part of studies of hybridization between Pinus contorta and Pinus banksiana (Mirov,1956; Zavarin, Critchfield, and Snajberk,1969; Lotan and Joye,1970). These two species are quite similar in their morphology and their ranges overlap in Alberta where they form a natural hybrid swarm. The main morphological differences between the two species noted by these authors are in cone orientation, and presence or absence of spines. They noted that the terpenes in trees of the Sierra Nevada contained a considerable percentage of sesquiterpenes while trees of the coast and Rocky Mountains contained almost none of these compounds. They also noted the presence of terpenes characteristic of Pinus banksians in Pinus contorta trees as far away from the region of overlap as Colorado, suggesting widespread introgression of Pinus banksiana genes into Pinus contorta in the Rocky Mountains. Forrest(1977) was able to subdivide the natural range of Pinus contorta into fifteen major geographic regions based on the relative proportions of different monoterpenes in the resin. He stated that these proportions are under direct genetic control, and that environmental factors have little or no effect on the proportions. He noted that several of the regions could be further subdivided using the monoterpene data, although in the central parts of the range it was impossible to allocate chemical boundaries with any degree of precision.

Lamb(1970) studied variation in needle characteristics within provenances of Pinus contorta in Scotland. Based on univariate analyses of variance, he concluded that variation between trees was of much greater magnitude than variation within trees.

Lopushinsky(1975) reported that differences in rate of photosynthesis have been observed for coastal and inland provenances of Pinus contorta. Cannell(1976a) also reported differences in photosynthetic rate between provenances, but found that the effect of these differences in producing the differing growth rates of the provenances was much less than the effect of differences between provenances in the production of needles and internodes. Cannell(1974) had previously investigated differences in the amount of needle tissue and stem wood produced by differing Pinus contorta provenances planted in Scotland. The seed sources of these provenances were inland and coastal British Columbia and coastal Alaska, Washington and Oregon. He found differences not only between coastal and inland provenances, but also between northern and southern provenances along the coast. In subsequent papers (Cannell and Willett,1975; Cannell,1976b) he provided evidence that the growth differences between provenances were largely due to the number of needle primordia predetermined in the winter buds the year before the shoots extended, and noted variation between provenances in apical dome size, apical dome relative growth rate, and time of activity. Roberts and Wareing(1975) supported the conclusions of Cannell based on observation of two coastal and two inland provenances planted in Wales, and Thompson(1976) also supported these conclusions based on his study of two provenances planted at Teindland Forest, Morayshire, Scotland.

McMillan(1956) investigated the possible existence of edaphic races in Pinus contorta by comparing the growth of seedlings from five different native populations on four different soils: a "control" soil whose base status was said to resemble many agriculture soils, a serpentine soil, a soil of pH 4.5 from the area where seeds of Pinus contorta ssp. bolanderi had been collected in the Mendocino "pygmy forest", and an even more acid soil (pH3.8) from another nearby "pygmy forest" location. Growth of all seedlings was uniformly poor except for two combinations; namely, the "pygmy" race of Pinus contorta grew very well on its "native" soil (but not on the more acid soil from the other pygmy forest site), and seedlings from the Oregon coast showed good growth on the control soil. McMillan followed-up this study with a long-term investigation of survival of the same five strains of Pinus contorta transplanted to a location in the Mendocino pygmy forest and, after thirteen years, reported much higher survival rates for the seedlings whose seed originated at that location, thus indicating an inherited adaptation to the unusual soil conditions (McMillan,1964).

Several authors have commented on geographic variation in cone serotiny. Crossley(1956) studied natural populations of three different ages in a subalpine forest in Alberta and observed that in the stand of 17 year old trees most of the cones were open; whereas, most cones were closed in the stands of 55 year old and older trees. He also reported that he found no difference in the cone serotiny of trees on north- and south-facing aspects. Perry and Lotan(1977), in a study of the temperatures at which serotinous cones opened, came to the similar conclusion that there was no apparent correlation between the various opening temperatures and the aspect of the trees from which the cones were collected. Mowat(1960) found no serotinous cones in trees of any age in natural populations of central Oregon. Jenny, Arkley, and Schultz(1969) noted that the heritability of the serotinous cones of <u>Pinus contorta</u> ssp. <u>bolanderi</u> had been confirmed by plantings at Placerville, California. Wirsing and Alexander(1975) observed that in southeastern Wyoming serotinous cones were more prevalent in sites below 2774 meters in elevation, and discussed the implications of serotinous cones for timber management. Lotan(1975) studied natural populations in the northern Rocky Mountains of the United States. He supported Crossley's observation that young trees have open cones; whereas, older trees have cones which are usually closed, and noted that he observed the closed-cone habit beginning at about 20 to 30 years of age in Pinus contorta in Montana. He found significant variation in the percent of trees with serotinous cones between locations in the northern Rocky Mountains, and obtained conflicting evidence on the question of whether cone serotiny varied with elevation.

Perry, Lotan, Hinz, and Hamilton(1978) compared the variation in resistance to osmotic stress (induced by polyethylene glycol 6000) among families to the variation in this characteristic between populations from six different locations. They concluded that families varied significantly, although there was no significant variation among populations in this stress resistance.

Birot(1978) studied variation in the weight of seeds collected from 140 locations throughout the range of Pinus contorta. He found that seeds from the Sierra Nevada and the Oregon Cascades were significantly heavier than those from elsewhere in the species range, and noted the existence of clines of decreasing seed weight with increasing latitude and with increasing distance from the Pacific Ocean, and a cline of increasing seed weight with increasing altitude. An exception to the decrease in seed weight with latitude was noted for the Mendocino population, whose seeds were much lighter than those from other populations at the same latitude.

Rall(1979) collected cone-bearing branches from natural populations at ten locations: eight sites were in small disjunct mountain areas east of the Rocky Mountains in Alberta, Saskatchewan, Montana and Wyoming; one site was near Lake Tahoe, California, and one site was on the highly acid soil near Mendocino, California. She also collected samples of pollen, resin and male cones from some of the sites. After studying various characters associated with pollen, resin, male and female cones, seeds and needles, she decided to confine her analysis to characters of the female cones and seeds. Her decision was based on measurement effort, comparative variation among and between locations, preliminary ordination and clustering analyses, and the assumption that reproductive structures would be less subject to phenotypic plasticity than vegetative structures, and thus more representative of the underlying genotype. She determined that the assumptions necessary to apply rigorous statistical multivariate techniques involving tests of significance were not satisfied by the data, so her multivariate analysis made use of the deterministic application of principal components analysis and agglomerative clustering. She concluded that the stands could be divided into two groups: one group consisting of trees from Mendocino, Lake Tahoe, and the Big Horn Mountains of Wyoming; the other group consisting of the remaining stands from Montana , Alberta and Saskatchewan. She was unable to explain the grouping of the Big Horn trees with those from California, but speculated that it might be due to the high elevation of the Big Horn stand; however, her choice of sampling locations did not allow any firm conclusions regarding the variation of Pinus contorta with elevation. She also speculated on a latitudinal gradient for several characters, but again her choice of sampling locations was not adequate to support definite conclusions. She further noted the need for more environmental information for the sampled localities to provide a basis for interpretation of her results.

3. Review of Studies of Geographic Variation in Cones of other Species

Schoenike(1962,1976) studied geographic variation in silvical, needle, and cone characters in natural population of Pinus banksiana. His first study was strictly univariate, relying on univariate analysis of variance. In his later study, he reanalyzed the same data using a multivariate approach: generalized distances were computed between all pairs of stands and used for plotting contour maps of similarity, and in cluster analysis. Each character measured was also correlated with four environmental variables: latitude, elevation, mean annual temperature, and mean annual precipitation. The largest correlations computed for cone characters were of magnitude of about .4, and showed negative correlation with temperature and positive correlation with latitude for cone serotiny, weight and volume, and apophysis length and width.

Beshir(1975) also studied geographic variation among natural populations of <u>Pinus banksiana</u>. He applied a sum of squares ranking technique developed by Orloci(1973) to the data published by Schoenike(1962) and concluded that silvical characters were least useful for distinguishing among stands; so his measurements and analysis were confined to characters of cones and needles. Although Beshir used one univariate technique, namely, trend surface analysis, he also employed a wider variey of multivariate techniques than any other study of geographic variation encountered in the literature. Techniques employed included: a Monte Carlo test for homogeneity (Orloci and Beshir,1976), principal components analysis, agglomerative sum-of-squares clustering (Orloci,1967), discontinuity analysis (Jancey,1974), non-metric multidimensional scaling (Kruskal,1964), non-hierarchical clustering (Carlson,1972), and two additional methods of hierarchical clustering, namely, complete linkage and single linkage clustering (Johnson,1967).

<u>Pinus sylvestris</u> in Eurasia is considered the geographic and ecological equivalent of the pair of species, <u>Pinus contorta</u> and <u>Pinus banksiana</u> in North America

(Dansereau,1957). Wright (1976) reviewed the extensive literature on geographic variation in *Pinus sylvestris* beginning with the oldest well-documented study by De Vilmorin in France, in 1821; however, the only characters of cones or seeds mentioned were early cone abundance, and seed size. The latter was found to increase almost threefold from northern to southern Europe.

Squillace(1962) included several cone and seed characters in his study of geographic variation in *Pinus elliotti*; namely, cone weight and length, seed weight, and the number of seeds per cone. His method of analysis was the same as Schoenike: univariate analysis of variance, plus computation of generalized distances between stands for use in contour mapping and cluster analysis.

Barnes(1967) studied variation of *Pinus monticola* with elevation in a single stream drainage, measuring several cone and seed characters as well as silvical characters. His analysis was completely univariate. None of the cone and seed characters were considered to show a strong predictable change with elevation.

Steinhoff and Andresen(1971) compared the geographic variation within each of two closely related species, *Pinus flexilis* and *Pinus strobiformis*, to variation between these species. Eight of the eleven characters they measured for parental trees were characters of seeds and cones. Their method of analysis consisted only of univariate analysis of variance.

Myers and Bormann(1963) studied variation in the ratio of the lengths of cone scales to bracts in response to elevational and geographic gradients in Abies balsamea using univariate analysis of variance and concluded that an elevational cline existed.

Daubenmire(1968) concluded that a north-south gradient of decreasing cone size, narrower scales, and more irregular phyllotaxy occurred in Picea sitchensis. He used a graphical univariate method, similar to the method used by Critchfield(1957), to analyze his data. He continued his work with this genus using similar methods to compare geographic variation within Picea glauca and Picea engelmanii to variation between these two species (Daubenmire,1974). In this latter study, he concluded that there were no recognizable north-south trends in cone characters.

4. Objectives

As the review of the literature has demonstrated, an adequate multivariate analysis of geographic variation in Pinus contorta has not yet been performed, although Rall(1979) has made a beginning. Such a multivariate analysis could reveal patterns which are not evident from univariate analysis. Thus, a general objective of this research is to apply multivariate methods of data analysis to seek clines, clusters or other patterns of variation which would be of predictive value for taxonomy, ecology and forestry, and to relate these patterns to geographic location and the environment. In particular, the sample locations have been chosen so that variation between the subspecies recognized by Critchfield(1957) may be compared to variation within these subspecies, and so that evidence may be obtained concerning variation with elevation and latitude.

CHAPTER 2

ALLOCATION OF MEASUREMENT EFFORT

1. Introduction

In a project of this scope, the allocation of measurement effort is critical. The total effort required is roughly proportional to the effort required to measure the characters of one cone, times the number of cones studied per location, times the number of locations for which cones are studied. Thus, an increase in the number of cones examined at each location, or an increase in the number of characters measured for each cone, must result in a decrease in the number of locations which can be included in the study for a given amount of available time. The following sections describe two pilot studies which address this problem. The first study was used to determine the number of cones which should be measured for each location, and the second study was used to decide which characters to measure.

2. Choice of Sample Size

Examination of the literature revealed that the sample sizes which had been used in studies of geographic variation were usually arbitrary or based on assumptions and/or objectives which were not consistent with the procedures and objectives of this research; for example, methods have been used for selecting sample sizes for the purpose of estimating values of single characters to a specified degree of accuracy, assuming random sampling from a univariate normal distribution (Berglund, Leaf, and Leonard, 1976). In this study of geographic variation of pine cones, the main objective is not a univariate determination of precise estimates of each of the characters of a pine cone, but rather the computation and analysis of relative similarity between cones from different geographic locations; hence, the procedure for choosing a sample size for each location is based on this objective.

Rall(1979) recorded data on 75 cones for each location (5 cones for each of 15 trees); this number was chosen arbitrarily. Her data for four widely-separated locations (namely: Mendocino and Lake Tahoe, California, Cypress Hills, Alberta, and the Big Horn Mountains, Wyoming) were used in the present study for a pilot study to provide an objective basis for a decision on the number of cones needed to represent a location. This study involved making random selections of cones from each of the locations and correlating resemblance matrices for the locations using a reduced number of cones with a resemblance matrix based on 75 cones per location. The resemblance function used was the same one used by Rall; namely, standardized Euclidean distance.

As a first step, one cone was randomly selected from each of the 5 cones measured for each tree, the resemblance matrix between stands was computed and correlated with the matrix based on 75 cones per location. This procedure was repeated 10 times with independent random selections each time. The resulting correlations averaged .96, and ranged from .86 to .99. Then, the number of trees sampled per location was reduced from 15 to 10, and the same procedure was carried out of random selection of cones, computation of a resemblance matrix, and correlation with the resemblance matrix based on 75 cones. In this case the average correlation based on 10 repetitions was .95, with a range from .88 to .99. The procedure was repeated for samples of 9 cones per location, resulting in an average correlation of .93, with a range from .72 to .99. On the basis of this study it was concluded that 10 cones would be an adequate sample for each location.

3. Selection of Characters

a. The Character Ranking Procedure and its Philosophy

In selecting characters for a multivariate analysis of geographic variation in a species, there are two constraints which must be considered. The first constraint has already been referred to; that is, an increase in the number of characters measured must result in a decrease in the number of individuals which can be included in the study for a given amount of time available. Also, many characters may actually contribute so much "noise" to the data as to obscure the underlying patterns. Therefore, a study was carried out to objectively determine those characteristics of the cones of Pinus contorta which would be most useful in a study of geographic variation. The material used for this pilot study consisted of forty cones of Pinus contorta; that is, ten cones randomly selected from each of four locations, with each location chosen from a different one of the four geographic regions for which Critchfield defined subspecies. Three of these locations were selected from the stands studied by Rall (i.e. Mendocino and Lake Tahoe, California, and the Cypress Hills, Alberta); the fourth location was represented by a collection of cones provided by Illingworth (from Hauser Dunes on the Oregon coast).

The procedure used was one developed by Jancey(1979) which evaluates characters based on the ratio of their variance among locations to their variance within locations. One advantage of this ranking procedure as compared to other ranking procedures is that this procedure utilizes the information obtained by the replication of sampling within each location. The philosophy behind the use of the procedure is that the criterion for selecting a useful character for studying variation among locations is not the variation of that character in a pooled data set which ignores the source of the variation, but rather a consideration of whether the variation of the character among locations is large compared to its variation within locations..

The details of the basic method are as follows:

1. Standardize the data by computing $x_{ij} = (x'_{ij} - \bar{x}'_j)/S_j$

where x'_{ij} is the value of character j for cone i,

$\bar{x}'_j$ is the mean value of character j averaged over all cones,

S_j is the standard deviation of character j.

2. Compute the total sum of squares for character j,

$$T_j = \sum_{i=1}^{N} x_{ij}^2 = N - 1$$

where N is the total number of cones.

3. Compute the pooled within group sum of squares,

$$W_j = \sum_{k=1}^{E} \sum_{i \in k}^{N_k} (x_{ij} - \bar{x}_{kj})^2$$

where E is the number of groups (in this case, groups correspond to locations), and N_k is the number of cones in group k.

4. Obtain the between groups sum of squares by subtraction,

$$B_j = T_j - W_j .$$

5. Calculate the between groups variance,

$$V_{B_j} = B_j / (E-1)$$

and the within groups variance,

$$V_{W_j} = W_j / (N-E)$$

6. Use the ratio,

$$F_j = V_{B_j} / V_{W_j}$$

as a measure for ranking character j relative to the other characters.

Jancey(1979) suggests that as a variation on this basic method, all pairwise comparisons between groups could be considered. This latter procedure was used for this study, since it was reasoned that a character which had a high ability to distinguish between some particular pair of locations should be included in the study regardless of its ability at distinguishing among the remaining locations. Thus, characters were ranked on the basis of their highest "F-value" for all pairwise comparisons between groups.

b. Description of Characters

The characters being considered are given in the following list. For some characters, an abbreviation is provided which will be used to identify that character in the tabular summary of results.

1. Cone weight: measured after the cones had been oven-dried at 63° C for 24 hours.
2. Cone volume: measured using the volume-equivalent method: a beaker containing water was weighed first; then the cone, placed on the end of a needle, was just immersed in the water, and the increase in weight was recorded. This increase is the weight of the water displaced, and is equal to the volume of the cone. This is the method which was judged most accurate by Critchfield(1957), after his experimental evaluation of various methods of determining the volume of pine cones.
3. Cone length: the greatest linear dimension of the cone; see figure 2.1. for a comparison of this to the next character.
4. Cone length from tip to point of attachment of the peduncle.
5. Cone width: cones were soaked in warm water before measurement, so that they were closed.

6. Cone serotiny: measured on a scale of 1 to 3, using the method of Rall in which 1 represents fully open cones, 3 represents fully closed cones, and 2 represents cones which were partially open.

7. Cone scale length: This character and the following three characters were measured for a cone scale approximately one-quarter of the distance from the tip, on the abaxial side of the cone, as was done by Rall. Figure 2.1 illustrates the measurement of these characters, as well as the other apophysis measurements.

8. Apophysis width

9. Apophysis height

10. Apophysis tip angle

11. Apophysis width: This and all of the following apophysis measurements were made on a cone scale approximately one-quarter of the distance from the base, on the abaxial side of the cone. The reason for choosing this location was that, based on visual examination, it appeared that the differences in apophyses between cones from different locations was more pronounced in this region of the cone than closer to the tip.

12. Apophysis length

13. Apophysis height

14. Apophysis longest lateral slope: referred to by the abbreviation "slope1".

15. Apophysis shortest lateral slope: referred to by the abbreviation "slope2".

In addition to these basic variables, various combinations of them were also evaluated. The reason for evaluating these combinations is that while the variation within a location for "size" characters, such as, cone length or cone width, may be too great compared to their variation between locations for them to be of much diagnostic value; nevertheless, some combination of these characters such as cone width divided by cone length, which is a "shape" character, may be relatively constant for any particular location while varying between locations.

There has been considerable controversy concerning the use of ratio characters (Atchley, Gaskins, and Anderson,1976; Corruccini,1977; Hills,1978; Dodson,1978; Albrecht,1978; Atchley and Anderson,1978; Atchley,1978). The main argument against the use of this type of character is that if the original characters are linearly related, then non-linearity is introduced into the data by the use of ratios of these characters. However, this problem is easily avoided if logarithms are used, since

$\log(x/y)=\log(x)-\log(y)$, which is a linear relationship. Furthermore, it may be argued that the use of logarithms provides a more reasonable expression of the resemblances among the cones than do the untransformed measurements. For example, if cone B is twice as long as cone A, and cone C is twice as long as cone B, it is reasonable to consider that, in terms of the character "cone length", cone B resembles cone A to the same extent as cone C resembles cone B; this is the resemblance implied in the use of the logarithm of cone length; whereas, the untransformed length implies that cone C differs form cone B by twice the amount by which cone B differs from cone A. Therefore, in this study, ratio characters were allowed and the logarithmic transformation was used.

Examples of combined characters are:

1. Specific gravity
2. Cone width/cone length
3. Cone length from the tip to the point of attachment of the peduncle, divided by the maximum length of the cone. This character may be regarded as a measure of cone symmetry, since it has a maximum value of 1 for symmetric cones, and lesser values for cones that are asymmetrically curved to one side. Thus, it is referred to by the abbreviation: "symmetry".

4. Cone length multiplied by the square of cone width multiplied by pi/4. This is the volume of a cylinder with length equal to the length of the cone, and diameter equal to the width of the cone. This character is referred to by the abbreviation: "cylindrical volume" or "cylvol".

5. Cone volume divided by the preceding character: This is a measure of cone shape which is larger for cones with little taper, which approximate the shape of a cylinder, and smaller for cones which taper more. It is referred to by the abbreviation: "vol./cylvol".

6. Apophysis length divided by apophysis width

7. Apophysis height divided by apophysis width

8. Apophysis height divided by apophysis length

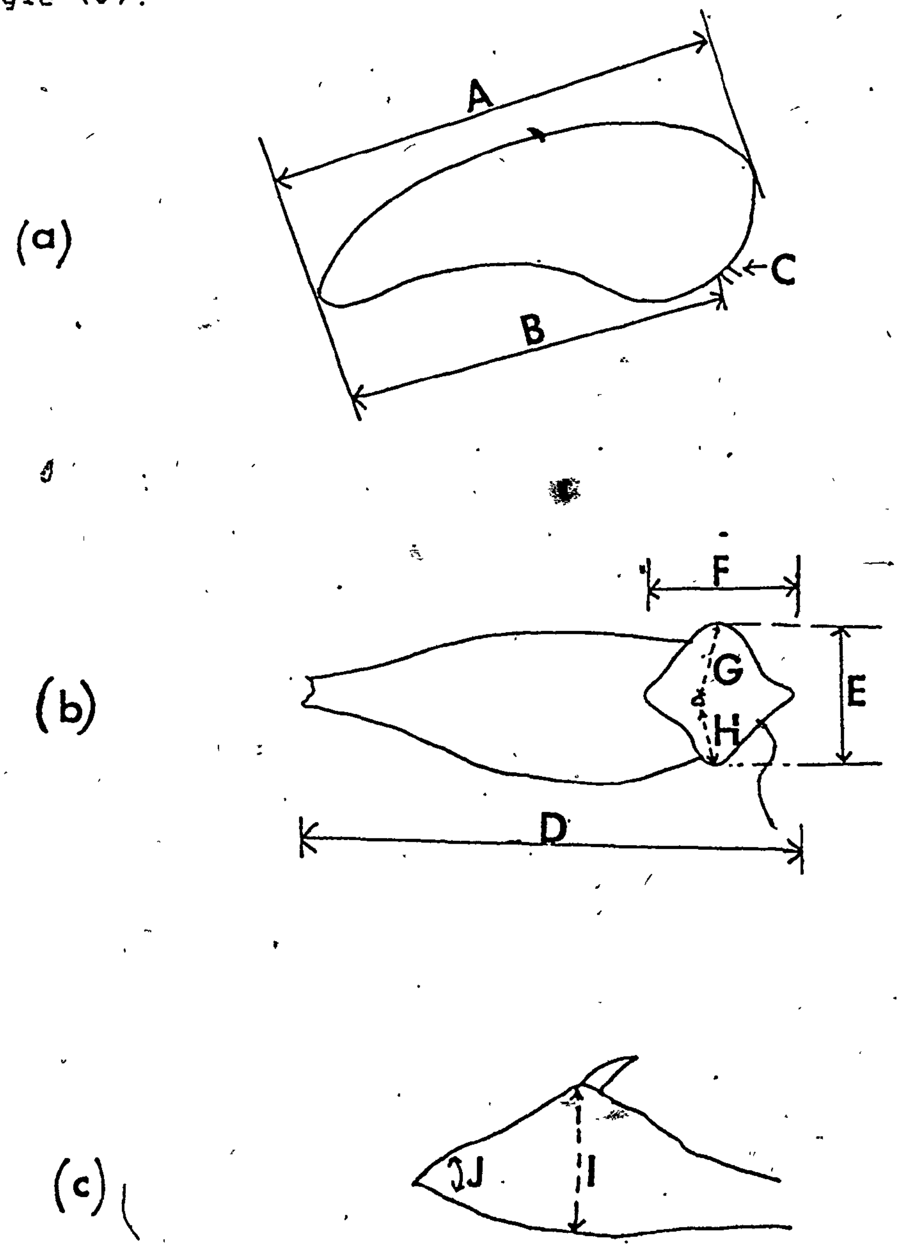
9. Sum of apophysis lateral slopes; that is, slope1 plus slope2.

Figure 2.1 Illustration of some cone characters.

(a) Two measures of cone length: greatest linear dimension (A); length (B) from tip to point of attachment of the peduncle (C).

(b) Abaxial view of cone scale illustrating: cone scale length (D); apophysis width (E); apophysis length (F); apophysis longest lateral slope (G); apophysis shortest lateral slope (H).

(c) Longitudinal section through apophysis of cone scale illustrating: apophysis height (I); apophysis tip angle (J).



c. Choosing from the Ranked Characters

Table 2.1 summarizes the results of the ranking procedure by listing the characters described in the previous section in order of their highest ratio of variances based on comparisons between all pairs of locations, and also names the corresponding pair of locations. In addition to the characters listed in the table, the ranking procedure was also applied to various monotonic functions of these characters; for example, logarithms, the cube roots of volume and weight, and inverses of the ratio characters. The variance ratios corresponding to these monotonic transformations were approximately equal to those corresponding to the original characters, suggesting that the numerical values of the ratios are not very sensitive to the form of the underlying statistical distribution of the character values. Thus, a reasonable method for determining a "cut-off" point for selecting characters, could be based on a comparison of the magnitudes of the variance ratios to the F-statistic (with 1 and 18 degrees of freedom, since comparison is between 2 groups with 10 cones each). To be conservative in accepting the hypothesis that a character showed significant variation between a pair of locations, a "cut-off" of F=8.29, corresponding to a significance level of 1%, could be used.

Table 2.1 Highest ranking for each character, with the corresponding pair of locations.

CHARACTER	F VALUE	LOCATIONS
cone width	54.9	Tahoe,Cypress Hills
cone serotiny	52.4	Tahoe,Cypress Hills
cone volume	42.7	Tahoe,Cypress Hills
cone weight	41.9	Tahoe,Cypress Hills
cylindrical volume	36.6	Tahoe,Cypress Hills
cone width/length	29.7	Mendocino,Cypress Hills
apophysis height	24.9	Tahoe,Cypress Hills
apoph. ht./length	16.9	Cypress Hills,Hauser
cone length	16.3	Tahoe,Hauser
apoph. ht./width	15.0	Mendocino,Tahoe
symmetry	14.3	Mendocino,Tahoe
length to peduncle	12.9	Tahoe,Hauser
apoph. length	10.6	Tahoe,Hauser
vol./cylvol	9.1	Mendocino,Tahoe
specific gravity	9.0	Mendocino,Hauser
apoph. width/len.	6.8	Mendocino,Tahoe
apoph. width(Rall)	6.2	Tahoe,Cypress Hills
scale length	5.5	Tahoe,Cypress Hills
apoph. slope1	5.0	Tahoe,Cypress Hills
apoph. width	4.1	Tahoe,Hauser
apoph. sum slopes	3.6	Tahoe,Cypress Hills
apoph. tip angle	2.9	Tahoe,Cypress Hills
apoph. slope2	2.5	Tahoe,Hauser
apoph. height(Rall)	2.5	Mendocino,Tahoe

Four of the top five ranked characters (namely, cone width, cone volume, cone weight, and cone cylindrical volume), are all basically expressing information about cone size. Of these four characters, cone volume was selected as providing the best single measure of overall cone size; the other size measurements were then considered as ratios to express various aspects of cone "shape". In particular, the following three characters were selected to represent cone "shape": cone width divided by cone length, cone weight divided by cone volume (specific gravity), and cone volume divided by the volume of a cylinder of equal length and diameter. It is of interest to note that these three "shape" characters along with the character cone volume, each have their greatest diagnostic ability for a different location pair (i.e., cone volume receives its highest ranking based on the comparison between Tahoe and Cypress Hills, specific gravity receives its highest ranking based on the comparison between Mendocino and Hauser, etc.); whereas, the four original size variables all had their greatest diagnostic ability for the same location pair.

Cone serotiny was selected as a character, but it was decided that an improved method of measurement would be used. Recall, that serotiny had been measured on a scale of 1 to 3, where 1 indicated a "fully-open" cone, 3 indicated a fully-closed cone, and 2 indicated an intermediate cone.

Fully-closed cones are quite obvious; however, the distinction between a "fully-open" cone and an intermediate cone is rather vague, since some of the scales next to the peduncle are closed even in the most open cones. The new method of measuring cone serotiny is based on the observation that the cones open from the tip, and that a varying proportion of the length of the cone remains closed at the end adjacent to the peduncle. Thus, the proportion of the total length of the cone which is closed is used as a measure of cone serotiny; this measurement is made on the abaxial side of the cone. The new method of measuring cone serotiny not only converts the measure to a continuous scale rather than an interval scale, so that it is more compatible with the measurements of the other characters, but also is more informative of the degree of serotiny expressed by a cone. This new idea for measuring cone serotiny did not occur until after the cones in the pilot study had been treated in ways which made this measurement impossible for those cones; however, the high rank for the serotiny character based on the earlier method of measurement indicates the diagnostic ability of the characteristic.

The highest-ranked character, based on measurements of apophyses, was apophysis height. Thus, this character was selected to describe the apophyses along with the "shape" characters apophysis height divided by apophysis length, and apophysis height divided by apophysis width. Notice, that like the four characters already selected to describe cone size and shape, these apophysis characters each have their greatest diagnostic ability for a different pair of locations.

Finally, the ratio of the length from the point of attachment of the peduncle to the tip of the cone, compared to the total length of the cone was included in the character-set as a measure of cone symmetry.

In summary, the characters selected to describe the cones are:

1. cone volume

2. cone width divided by cone length

3. cone specific gravity

4. cone taper as measured by the volume of the cone divided by the volume of a cylinder of equal length and diameter

5. cone serotiny, using the new method of measurement described in this section

6. cone symmetry, measured as described in the previous paragraph

7. apophysis height, measured on an apophysis one-quarter of the distance from the base on the abaxial side of the cone.

8. apophysis height divided by apophysis width

9. apophysis height divided by apophysis length.

CHAPTER 3

COLLECTION OF CONES AND SITE DATA

1. Sampling of Cones at a Site

As Beshir(1975) and Rall(1979) point out, completely random selection of cones at a site is not possible; however, it is possible and desirable to sample using a consistent set of rules in which cones are selected using a similar procedure at each site so that the sites may reasonably be compared. Rall(1979) also mentions the practical consideration that shaded, crowded trees in the interior of a stand do not produce accessible cone-bearing branches.

The sampling criteria used for this project were as follows:

1. For each site consider only trees within a visually homogeneous area of the same elevation and topography.
2. Select 10 apparently healthy, mature trees (at least 20 years old) which have accessible cones.
3. For each tree, collect 5 mature cone-bearing branches from as close as possible to middle-height on the tree.

4. Later, randomly select one cone for each tree, rejecting any cones which are found to be damaged.

2. Other Data Collected for Each Site

In addition to the collecting of cones and branches, other information was also collected for possible use in the interpretation of results. The latitude, longitude and elevation of each site were recorded, and the exact location of each site was indicated on a topographic map or other detailed map of the area. Also, photographs were taken of each tree from which cones were collected. These exact locations and photographs may be useful to future investigators who wish to study other characteristics of the same trees.

For each tree from which cones were collected, the age, diameter and proportion of serotinous cones on the tree were recorded. The determination of the ages of the trees was particularly important to assure that the trees were mature since, especially with the "pygmy" trees of the Mendocino populations, the size of a tree is not a reliable indication of its maturity.

Soil samples were collected from five locations at each site (corresponding to every second tree which was sampled), by inserting a tube to a depth of 15 cm. These five samples were mixed for each site, and then sent to the University of Guelph for the determination of pH and the amounts of exchangeable phosphorus, magnesium, and potasssium. Phosphorus was determined as the portion that was extracted through the use of 0.5 molar sodium bicarbonate solution (Olsen and Dean, 1965). Magnesium and potassium were extracted with neutral normal ammonium acetate (Gagnon, 1979).

The topography of each site was categorized as either a valley bottom, a ridge top, or a slope. For slopes, the aspect and percent of slope were recorded. The general habitat-type of the site was noted, for example, whether it was a bog, meadow, subalpine forest, sand dune, etc. Other tree species which were present on the site were listed. In many cases, _Pinus contorta_ grows in pure stands without other tree species; in those cases, other tree species present on nearby sites of similar elevation, habitat-type and topography were noted where possible.

Since each site was only visited once, it was not possible to collect climatic data in the field. To compensate for this, an attempt was made to choose sampling locations where climatic data were available from weather stations or from previous studies. The result of this attempt was to reveal that there was an almost complete lack of climatic data for mountainous areas of the western United States; nevertheless, two useful studies were identified, (Marr,1961; Chabot and Billings,1972), and these influenced the choice of sampling locations as explained in the subsequent section. Even in the rare cases where good standard meterological data is available for a location, the usefulness of such data for depicting the climate which affects the vegetation is questionable, particularly in a mountainous region (Satterlund,1975; Geiger,1965; Bates,1924; Baker,1944). For example, the amount of moisture actually received by a plant in a mountainous area may be greatly affected by the patterns of blowing and melting snow (Geiger,1965).

3. Locations Sampled

This section provides information concerning the locations from which samples were collected, including the motivation for the choice of these particular sites, as well as comments on meteorological and other environmental data. Tables 3.1 to 3.6 summarize the data collected for each location, and also provide site numbers and code names which will be used to identify the sites in later results.

The major geographic pattern for sampling consisted of an east-west transect across the range of Pinus contorta at a latitude of about 39 degrees North, with an intersecting north-south transect in the Sierra Nevada. The locations of the sampled sites are shown on figure 3.1, where the sites are identified by the numbers which will be given later in this section.

The approximate latitude of 39 degrees N. was chosen for the east-west transect so that all four of the subspecies recognized by Critchfield(1957) would be intluded; the north-south transect was chosen in the Sierra Nevada, rather than in the Rocky Mountains or along the coast, since the Sierra Nevada provide a single continuous north-south mountain range; whereas, the Rocky Mountains are much more discontinuous, and the distribution of Pinus contorta along the coast is not continuous at this latitude.

a. Sierra Nevada Locations

These sites were chosen to provide information on variation in the cones of Pinus contorta with elevation and latitude, and to compare the populations on the eastern and western sides of the mountain range. Three different elevations (approximately 1750 meters, 2400 meters, and 3050 meters) were sampled at four different latitudes, spanning the range of _Pinus contorta_ in the Sierra Nevada from approximately 36 degrees 30 minutes North latitude to 39 degrees 20 minutes North latitude. All of the sites chosen in the Sierra Nevada had essentially zero slope, so that the effects of aspect and slope would not complicate the comparison of different elevations and latitudes. (The effect of varying aspect and slope was included in the Rocky Mountain sampling and will be discussed later.) A transect of five sites was sampled at 37 degrees 15 minutes N. latitude to compare the populations on the eastern and western sides of the Sierra Nevada; all other sites were chosen on the eastern side of the mountain range since the more rapid change in elevation on that side of the mountain range enabled a comparison of the effect of changes in elevation between populations which were relatively nearby geographically. One additional collection, which while not strictly in the Sierra Nevada was closer to that region than to the other regions, was made at Big Bear Lake in the isolated San Bernardino Mountains about two degrees of latitude south of the Sierra Nevada. This latter site is of particular interest, not only because it represents an isolated occurrence of _Pinus contorta_ near the extreme southern portion of its geographic range, but also because the largest _Pinus contorta_ in the world grows there.

Pinus contorta was not present at all three elevations at all four latitudes; for example, it was present at only the highest elevation in the southern part of the Sierra

Nevada, and present only at the low and intermediate elevations in the northern Sierra Nevada. This variation in elevational distribution of Pinus contorta with latitude appears to be correlated with a striking variation in climate on the eastern side of the Sierra Nevada over a relatively small difference of 3 degrees of latitude. For example, the elevation of the lower limit of timberline with the desert in the southern Sierra Nevada is approximately the same elevation as the upper, alpine limit of timberline in the northern Sierra Nevada.

The latitude of 37 degrees 15 minutes was selected for the transect from east to west across the Sierra Nevada, not only because Pinus contorta was known to occur throughout a wide range of elevations at this intermediate latitude in the mountain range (Critchfield,1957), but also because of the availability of meteorological data, recorded for two summer months in 1967 and 1968 by Chabot and Billings(1972) for a transect from the desert to alpine tundra on the east side of the mountain range. Also, there is a U.S. Weather Bureau station at this latitude on the west side of the mountain range at Huntingdon Lake (elevation 2100 meters).

Table 3.4 provides approximate values for the average annual temperature and precipitation for the locations from which cones were collected in the Sierra Nevada (sites 6 to 16). The values of these climatic variables for the Sierra Nevada sites were compiled from a variety of sources

(Dale, 1966; Schaffer, 1978; Chabot and Billings, 1972; Baker, 1944) covering various periods of time and, in some cases, rough estimates have been employed for the effect of elevation on climate; therefore, this data should be used with caution. In general, proceeding from west to east, precipitation in the Sierra Nevada increases with elevation up to about 1600m. and then decreases slowly to the crest and more rapidly on the eastern side. There is also a pronounced north-south decrease in precipitation, with maximum values for average annual precipitation of about 170 cm. in the northern Sierra Nevada compared with maximum values of about 115 cm. in the southern part of the region. Throughout the mountain range the summer season is very dry, with only about 2% of the yearly precipitation occurring in the three months from June through August; thus, most of the moisture available at the elevations where _Pinus contorta_ grows in the Sierra Nevada is derived from melting snow. Although the temperature at the foot of the mountains does not vary much from south to north, the rate of temperature decrease with elevation is more rapid in the north than in the south so that, at higher elevations, the northern part of the range is cooler than the southern part.

b. Rocky Mountain Locations

The purposes for sampling these locations were: to make possible a comparison of the Rocky Mountain populations with those from the other geographic regions, to study variation with elevation and topography within the Rocky Mountain populations, and to compare the populations on the eastern and western slopes of the Front Range in the Rocky Mountains. All of the sites studied were at a latitude of about 40 degrees north, and all except one site were located in the Front Range of the Rocky Mountains in Colorado; the other site was located on the west slope of the Uintah Mountains in Utah.

The Front Range is a belt of mountains about 65km. wide extending from the Colorado-Wyoming border in the north to the Arkansas River drainage in the south. This range forms the eastern edge of the Rocky Mountains at these latitudes, rising rather abruptly from the Great Plains to elevations of up to 4620m. The reason for choosing the Front Range of the Rocky Mountains as a location for the study of the variation of the cones of Pinus contorta with topography and elevation was that the east side of this range had been the location of a thorough study by Marr(1961) of the effect of topography and elevation on mountain climates, and also, there is a weather station on the west side of the range at about the same latitude at

Fraser (elevation 2635m.). The sites sampled on the east slope were the same as those for which Marr collected meteorological data where possible, and otherwise were of the same elevation, slope and aspect. These Colorado sites were all within a relatively small area near the eastern limit of the range of Pinus contorta at this latitude in the Rocky Mountains; the Utah site was chosen near the western limit of the range of Pinus contorta at this latitude in the Rocky Mountains. The distance of this site from the Colorado sites is approximately 500 km., while it is approximately 770 km. from the Utah site t[illegible]e sites at the same latitude in the Sierra Nevada. Thus, the Utah site is of interest in providing an indication of the range of variation within the Rocky Mountain populations at this latitude, and as a possible intermediate between the Sierra Nevada populations and the Colorado populations. Table 3.1 gives the slope, aspect, and elevation of the five sites on the east side of the Front Range. The other three sites in this region, along with all of the sites from the other regions, were located in areas with essentially zero slope, so that aspect was not a meaningful variable.

Table 3.1 Slope, aspect, and elevation for the sites on the east side of the Front Range.

Site Number	Elevation (meters)	Slope (%)	Aspect
17	3050	0	ridge
18	3100	15	SSE
19	3100	0	valley
20	2540	0	valley
21	3050	15	NNE

Table 3.4 provides meteorological data for these Rocky Mountain locations (sites 17 to 24) based on data from Marr(1961), Baker(1944), Browne(1960), and Berry(1968). Average annual air temperatures on the east side of the Front Range are about equal to those for the Sierra Nevada at the same latitude and elevation, while the average temperatures on the west side of the Front Range are cooler. Baker(1944) speculates that the cooler temperatures on the west side are the result of greater stores of snow and the absence of chinook winds. Valley locations are cooler than other locations at the same elevation, probably due to poor air drainage resulting in temperature inversions. There is little difference in average air temperature between north and south-facing slopes (at an elevation of 3050m.), and

there is also little difference between these slopes in the pattern of variation of air temperature throughout the day or the year; rather, the significant difference between the north and south-facing slopes is in soil temperature (measured at a depth of 2 to 3 cm.) which has an average annual value of 5.5 degrees C. on south-facing slopes, as compared to an average annual value of 3.3 degrees C. on north-facing slopes at an elevation of 3050m. This difference in soil temperature is most pronounced in spring and fall. Average soil temperatures for the valley sites are about equal to the soil temperatures of the north-facing slopes at the same elevation; while the ridge sites have an average soil temperature which is intermediate between that of the north and south-facing slopes (Marr,1961).

Unlike the Sierra Nevadas, the precipitation in the Front Range of the Rocky Mountains does not follow a pattern of increasing to a maximum at an intermediate elevation and then decreasing; instead, there is a general increase in precipitation with increasing elevation on both sides of the Front Range, with wide variation in the amount of precipitation at the same elevation (Baker,1944). Also, the proportion of the yearly precipitation which falls in the three summer months of June, July, and August is much greater in the Front Range than in the Sierra Nevada: being about 30% in the Front Range and only 2% in the Sierra Nevada (Marr,1961)..

c. Pacific Coast Locations

As mentionned previously, Critchfield(1957) recognized two coastal subspecies of Pinus contorta: subspecies contorta, an open-coned subspecies occurring along the Pacific Coast from Mendocino, California, to Alaska; and subspecies bolanderi, a closed-coned subspecies occuring only on very acid soil near Mendocino, California. The growth of this latter subspecies is so stunted that the area in which it occurs has been preserved within a California state park as a "pygmy forest", containing mature specimens of Pinus contorta only a few feet tall. One of the purposes of the coastal sampling locations was to quantitatively compare the differences between populations representing these two coastal subspecies with the differences among all of the subspecies recognized by Critchfield. For this purpose, three locations were sampled at a latitude of about 39 degrees north near Mendocino, California: one location provided a sample of a normal-sized population, with all of its cones open, growing on a low bluff adjacent to the Pacific Ocean (site number 3); one location sampled an extreme "pygmy" population with almost all of its cones closed (site number 1); the third location sampled a population of intermediate sized trees for which many of the cones were open (site number 2). This latter population was of interest as a possible intermediate between the two coastal subspecies.

Although the distribution of Pinus contorta along the Pacific Coast is essentially continuous from northern California to Alaska, there is a gap of about two and a half degrees of latitude between the Mendocino populations and the more northern populations. Critchfield concluded that the open-coned coastal population near Mendocino was much more similar to the open-coned coastal populations further north than it was to the adjacent closed-cone population. To investigate this conclusion, samples were collected from an open-coned coastal population near Crescent City, California, at a latitude of about 42 degrees north. The Crescent City sampling location is also of interest for comparison with a closed-cone population in the low mountains about 20km. inland from Crescent City. Although Critchfield did not collect material from this inland locality, he reported that he had examined two herbarium specimens with a total of three cones from this location and that these cones were serotinous. My visit to this latter site revealed that the Pinus contorta trees growing there closely resembled the extreme pygmy trees near Mendocino although both the associated tree species and the soil parent material were completely different for each of the two locations. The "pygmy forests" near Mendocino contained Cupressus pygmaea and Pinus muricata and were growing on soil derived from sandstone; whereas, the "pygmy forest" near Crescent City contained Pinus attenuata and Pinus monticola and was growing on soil derived from serpentine.

It was hoped that a collection of cones and environmental data from this northern "pygmy" population would not only clarify the relation of this population to the subspecies defined by Critchfield, but would also provide some insight into the relation between variation in Pinus contorta and environmental variables.

The striking contrast between the Mendocino pygmy forests and the surrounding forests of giant redwoods has inspired a number of studies of the vegetation of this region, with special attention being given to the unusual soil (McMillan, 1956, 1964; Gardner and Bradshaw, 1954; Jenny, Arkley and Schultz, 1969; Westman, 1975). Table 3.2 combines information from Westman(1975) with the results of soil tests for sampling locations 1 and 2 to provide a comparison of these soil test results with average values for the pygmy forests and the nearby redwood forests. This table indicates that the soil test results for locations 1 and 2 are similar to the average values for the A1 horizon for pygmy forest soils. In comparison with soils of the redwood forests, the A horizons of the soils of the pygmy forests are seen to contain particularly low amounts of exchangeable calcium, magnesium, potassium, and certain micronutrients (zinc, copper, manganese), and to have a much higher concentration of aluminum ions. Although levels of both calcium and magnesium are low for pygmy forest soils, Westman(1975) notes that the ratio of calcium to magnesium is much lower in the pygmy forests than in the redwood forests and he remarks that this low ratio suggests a similarity to serpentine soils. McMillan(1956) had previously commented on the low calcium saturation as a possible common denominator of serpentine and highly-acid soils.

Table 3.2 Comparison of some soils near Mendocino, Cal. (Exchangeable ions in parts per million of soil air dry weight)

Ion	Redwood forest	Pygmy forest		Site Number	
	A horizon	A	A1	1	2
Calcium	3740	18.4	52.7		
Magnesium	796	17.3	66.6	42	52
Sodium	34	15.5	26.5		
Potassium	225	20.6	42.0	44	52
Aluminum	3.7	75.8	49.1		
Phosphate	0.816	0.371	2.830	2	2
Zinc	0.194	0.035	0.049		
Copper	0.132	0.038	0.021		
Iron	0.17	0.53	0.22		
Manganese	42.0	0.078	0.068		
pH	5.5	4.1		3.8	4.5

Whittaker(1960) compared the vegetation in the Siskiyou Mountains of southwestern Oregon and northwestern California growing on soils derived from serpentine parent material with the vegetation growing on soils derived from quartz diorite and soils derived from olivine gabbro parent material. His serpentine study-sites were at an elevation of 610m to 915m and at a distance of about 30km from the Pacific Ocean; that is, they were at a similar elevation to sampling location 5, but approximately 10km further inland. Although he mentioned the frequent occurrence of congeneric pairs of trees and shrubs in serpentine and non-serpentine flora, with the serpentine species being of smaller stature in all cases, he did not mention any occurrences of a pygmy race of Pinus contorta with serotinous cones. However, his species list for the serpentine sites did show the presence of a few individuals identified as Pinus contorta ssp. murrayana; their assignment without any special comment to that subspecies would suggest that they probably had non-serotinous cones and were "normal-sized" rather than being pygmy trees with serotinous cones. Unfortunately, this reference was not seen before the field work for this project had been completed, since it would have been very interesting to locate Whittaker's sites and compare the Pinus contorta growing there to the stunted trees with serotinous cones growing on serpentine soil near Gasquet, as well as comparing them to the "normal-sized" coastal trees with non-serotinous cones and the trees of the Sierra Nevada.

One feature of the pygmy forest soil which presents a challenge to the vegetation is a concrete-like hardpan at a depth of about 45cm. This hardpan not only interferes with root development, but also interacts with the wide seasonal variation in precipitation to create a perched water-table which floods the soil surface in winter and early spring and then evaporates later in the year resulting in extremely xeric conditions above the hardpan. The high water-table for part of the year could be a cause of the stunted growth in the Mendocino pygmy forests. Illingworth(1976) speculated that the high water-table cut back the roots of Pinus contorta growing at Tofino on the west coast of Vancouver Island to produce a "Japanese Bonsai effect". Aldhous(1976) noted that when soil was disturbed (for example, by road or airfield construction) adjacent to muskegs near the coasts of Alaska or British Columbia where stunted Pinus contorta was growing, then the disturbed soil was invaded by vigorous well-formed trees which he presumed were the progeny of the stunted trees. In both cases, the trees had the non-serotinous cones which are normal for coastal populations. In the same report, Illingworth(1976) specifically noted the existence of unusual coastal stands in which about 10% of the trees had serotinous cones; however these sites were on dry rocky bluffs rather than in areas with a high water-table and the trees were quite large rather than stunted.

Climatic data for the coastal sites were obtained from Whittaker(1960), Gardner and Bradshaw(1954), and Dale(1966), and is summarized in table 3.4. As expected these low elevation sites have an average annual air temperature which is significantly warmer than the mountain sites; also the influence of the Pacific Ocean moderates the variation in temperature throughout the year so that, for example, at Fort Bragg (near Mendocino) less than 6% of the days of the year on the average have maximum temperatures of 21 degrees C. or higher, and less than 3% have minimum temperatures of 0 degrees C. or lower. The average annual precipitation differs greatly between the three more southerly coastal sites and the two northern sites: The three more southerly sites have an average annual precipitation only slightly greater than that of some of the inland mountain sites; whereas, the two northern sites have about twice as much precipitation. The distribution of precipitation throughout the year on the coast is similar to that in the Sierra Nevada in that only about 2% of the yearly precipitation occurs in the three summer months of June, July and August. In the Sierra Nevadas this summer moisture deficit is ameliorated by melting snow; whereas, on the coast there is frequent summer fog.

Figure 3.1 Location of collection sites:

A. sites 1,2,3

B. sites 4,5

C. sites 6,7,13,14,15

D. site 8

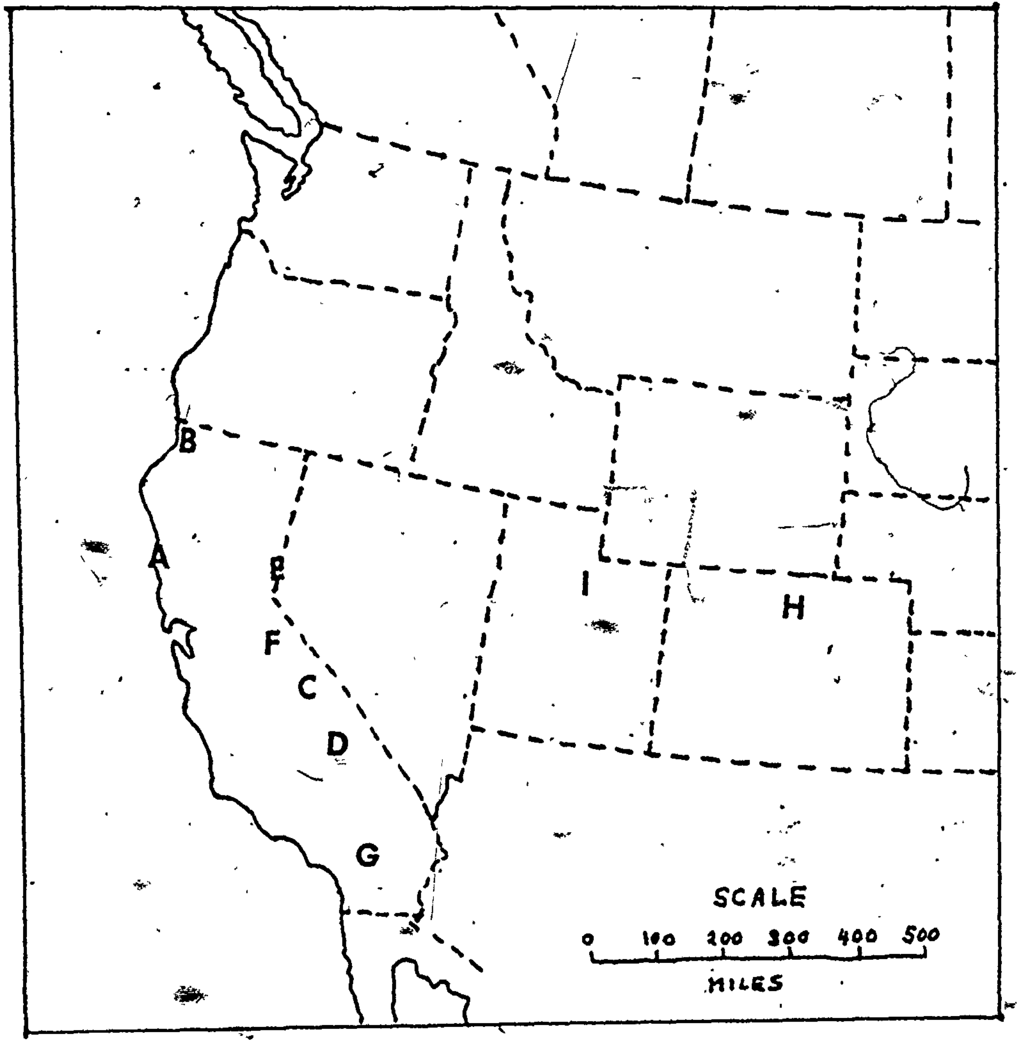
E. sites 9,10

F. sites 11,12

G. site 16

H. sites 17 to 23

I. site 24



d. Summary of Data for Locations

This section contains tables summarizing the data collected for each of the sites. Table 3.3 identifies the sites by number, code-name, latitude, longitude and elevation; table 3.4 provides climatic data; table 3.5 presents the results of the soil tests; and, table 3.6 identifies the other tree species which were present on each site or on nearby sites of approximately the same elevation and topographic situation. Some of the information in these tables has been referred to in the previous sections, and these tables will also be used later in discussing the results of the analysis of the data.

Table 3.3 Latitude, Longitude, Elevation, Identification Codes and Numbers for the Sites

Location Number	Code	Latitude (° N.)	Longitude (° W.)	Elevation (meters)
1	MENDO1	39 16'	123 45'	180
2	MENDO2	39 17'	123 46'	150
3	MENDSHOR	39 14'	123 47'	50
4	CRESCENT	41 47'	124 13'	20
5	GASQUET	41 50'	123 54'	790
6	BP2400	37 15'	118 35'	2400
7	BP3050	37 14'	118 39'	3050
8	COTNWOOD	36 27'	118 10'	3050
9	MT.ROSE	39 20'	119 52'	2380
10	TRUCKEE	39 21'	120 10'	1780
11	SADDLBAG	37 58'	119 16'	3050
12	UP.HORSE	37 56'	119 08'	2380
13	KAISER	37 17'	119 05'	3020
14	DINKEY	37 03'	119 10'	1710
15	HUNTING.	37 16'	119 08'	2430
16	BIG.BEAR	34 13'	117 12'	2320
17	RIDG3050	40 02'	105 33'	3050
18	SOU3100	40 02'	105 33'	3100
19	VALL3100	40 05'	105 32'	3100
20	VALL2540	39 59'	105 31'	2540
21	NOR3050	40 02'	105 33'	3050
22	FRASER	39 57'	105 50'	2635
23	MEAD.CR.	40 03'	105 44'	3050
24	UTAH	40 19'	111 16'	2390

Table 3.4 Mean Annual Temperature and Precipitation

Location Number	Code	Mean Annual Temperature (C.)	Mean Annual Precipitation (cm.)
1	MEND01	12	95
2	MEND02	12	95
3	MENDSHOR	12	95
4	CRESCENT	11	193
5	GASQUET	11	190
6	BP2400	8	126
7	BP3050	4	52
8	COTNWOOD	6	<52
9	MT.ROSE	3	>79
10	TRUCKEE	6	79
11	SADDLBAG	2	76
12	UP.HORSE	6	62
13	KAISER	1	<83
14	DINKEY	10	81
15	HUNTING.	5	83
16	BIG.BEAR	5	90
17	RIDG3050	1	65
18	SOU3100	2	79
19	VALL3100	0	66
20	VALL2540	3	44
21	NOR3050	2	76
22	FRASER	1	44
23	MEAD.CR.	-2	>44
24	UTAH	3	41

Table 3.5 Results of Soil Tests (Exchangeable ions in parts per million of soil air dry weight)

Location	Phosphate	Potassium	Magnesium	pH
1 MENDO1	2	44	42	3.8
2 MENDO2	2	52	52	4.5
3 MENDSHOR	4	212	>200	5.8
4 CRESCENT	2	96	>200	5.2
5 GASQUET	2	40	>200	6.5
6 BP2400	29	304	>200	6.2
7 BP3050	11	136	85	5.7
8 COTNWOOD	27	112	55	4.7
9 MT.ROSE	14	116	119	5.7
10 TRUCKEE	19	192	>200	5.6
11 SADDLBAG	5	148	44	5.5
12 UP.HORSE	19	220	87	5.8
13 KAISER	56	56	17	4.7
14 DINKEY	51	120	22	5.4
15 HUNTING.	34	120	29	5.5
16 BIG.BEAR	12	84	91	5.3
17 RIDG3050	5	168	150	5.3
18 SOU3100	6	164	>200	5.3
19 VALL3100	10	112	105	5.0
20 VALL2540	6	268	>200	5.9
21 NOR3050	6	120	144	4.8
22 FRASER	15	256	>200	5.6
23 MEAD.CR.	11	168	115	4.8
24 UTAH	9	300	>200	6.2

Table 3.6 Other tree species present on sites (or on nearby sites of approximately the same elevation and topography).

Location	Tree species
1 MENDO1	*Cupressus pygmaea*, *Pinus muricata*
2 MENDO2	*Cupressus pygmaea*, *Pinus muricata*
3 MENDOSHOR	*Pinus muricata* (at slightly higher elevations, further from shore)
4 CRESCENT	*Picea sitchensis*
5 GASQUET	*Pinus attenuata*, *Pinus monticola*
6 BP2400	*Pinus jeffreyi*, *Populus tremuloides*
7 BP3050	*Pinus balfouriana*, *Pinus albicaulis*, *Populus tremuloides*
8 COTNWOOD	*Pinus balfouriana*
9 MT.ROSE	*Pinus monticola*, *Pinus jeffreyi*, *Abies concolor*
10 TRUCKEE	*Pinus jeffreyi* (nearby)
11 SADDLBAG	*Pinus albicaulis*
12 UP.HORSE	*Pinus jeffreyi*, *Populus tremuloides*
13 KAISER	*Pinus monticola*, *Abies magnifica*
14 DINKEY	*Pinus jeffreyi*, *Abies concolor*
15 HUNTING	*Abies magnifica*, *Populus tremuloides*
16 BIG.BEAR	*Pinus jeffreyi*, *Abies concolor*

Table 3.6 (continued)

17	RIDG3050	*Picea engelmannii*, *Populus tremuloides*
18	SOU3100	*Picea engelmannii*, *Pinus flexilis*
19	VALL3100	*Picea engelmannii*, *Pinus flexilis*, *Abies lasiocarpa*
20	VALL2540	*Populus tremuloides* (along the lake shore with P. contorta); *Pinus ponderosa*, *Pinus flexilis*, (at slightly higher drier elevations)
21	NOR3050	*Pinus flexilis*, *Picea engelmanii*, *Abies lasiocarpa*, *Populus tremuloides*
22	FRASER	none
23	MEAD.CR.	*Picea engelmanii* (nearby)
24	UTAH	*Abies lasiocarpa*, *Populus tremuloides*

CHAPTER 4

PRELIMINARY DATA ANALYSIS

1. Introduction

The general plan for data analysis for this study consisted of an iterative sequential approach, where the results of one method suggest application of another method, or suggest application of a method to a subset of the data. As a first step in this procedure for data analysis, it was necessary to determine the basic type of data structure which was to be analyzed, where the term "data structure" refers to the way the sample points (corresponding to cones or locations) are arranged in a sample space defined in terms of cone characters. The basic types of data structure may be categorized as continuous or discontinuous, and linear or non-linear. Orloci(1978) provides a fuller discussion of these concepts.

The raw data is given in Appendix A for the measured cone characters, and also for the derived cone characters. Each row in the data table gives the values for the ten cones used to represent a particular location, with the names of the characters and the locations identified by the abbreviations given in previous sections. However, the data structure cannot be determined directly from this raw data, since the structure of the sample space is determined not only by the raw data, but also by the resemblance function which is applied to this data. Thus, the selection of a resemblance function is of critical importance to any investigation of data structure.

For ease of interpretation of the data structure in terms of a spatial analogy, a Euclidean resemblance function is desirable. However, the standardization or weighting of variables must be carefully considered to avoid misrepresentation or distortion of the resemblance structure.

In its simplest form, the Euclidean distance between a pair of individuals, j and k, each described by the same p variables, is defined by

$$E(j,k)= \left[\sum_{h=1}^{p} (X_{hj} - X_{hk})^{2}\right]^{1/2}$$

where X_{hj} and X_{hk} are the values of the hth variable for individuals j and k, respectively. However, this simple form has serious problems in that it requires commensurable variables, and even then, is dominated by those variables with the largest variation. Hence, standardization is usually carried out by dividing the variables by their standard deviation, so that a difference between a pair of individuals with respect to any variable is expressed in units of standard deviations of that variable. The problem with such standardization is that it can have the effect of obscuring trends, by forcing a spherical shape on the data strucure.

In the present study, advantage was taken of the fact that there was replicated sampling of cones at each location, and thus for each variable a standard deviation could be computed based on the portion of variation which is within locations. When this set of standard deviations is used to standardize the Euclidean distance, a spherical shape is not forced on the data, but rather there is greater dispersion in the distribution of sample points in sample space in the direction of those variables for which the variation between locations is largest in relation to their variation within locations.

Thus, the resemblance function used for investigation of the data structure is given by

$$e(j,k) = \left[\sum_{h=1}^{p} (X_{hj} - X_{hk})^2 / Q_h^2 \right]^{1/2}$$

where $Q_h = \left[\sum_{m=1}^{a} \sum_{h=1}^{p} \frac{(X_{hlm} - \overline{X}_m)^2}{a(n-1)} \right]^{1/2}$

is the standard deviation of variable h within locations,

a is the number of locations,

n is the number of replicates per location,

X_{hlm} is the value of variable h for replicate l at location m,

$\overline{X}_{hm}$ [illegible] the average value of variable h at location m.

A computer program was written to perform this data standardization and at the same time compute and print the means, standard deviations, minima, and maxima for each variable at each location prior to standardization, as well as an ordered list of the standardized values of the stand means; these results are presented in Appendix B.

2. Three-Dimensional Views of the Data Structure

A very useful tool for the investigation of data structure has been provided by Fewster and Orlóci (1978), who have developed a program which plots data points in the form of a stereogram to enable a three-dimensional view of the data structure. Since the data for this study were defined in terms of nine dimensions (corresponding to the nine selected cone characters), a procedure was required to reduce the data to three dimensions in order to allow such a three-dimensional view. The most efficient method for summarizing linear variation in fewer dimensions is principal component analysis (Orlóci, 1978). Although the presence of non-linear variation, and the reduction of dimensionality may both cause distortion in the representation of the data structure; nevertheless, widespread applications of this technique have shown that it is quite robust and useful in providing insight into data structure. (Several dozen references to successful applications of principal component analysis are given on page 117 of Orloci(1978).) Thus, it was decided to apply this linear technique, in order to obtain whatever insights it could provide, and then follow-up with an investigation of the extent of distortion of the data structure.

Principal component analysis produces an ordered set of orthogonal axes (referred to as components), which have the property that the first axis is chosen in the direction of maximum variance of the sample points in sample space, and successive axes are chosen so that each maximizes along itself the variance remaining from the preceding axes, in a direction perpendicular to those axes. The score of individual j on component i (referred to as a component score) is computed by the linear transformation

$$Y_{ij} = A_j' b_i$$

where b_i is the ith eigenvector of the cross-product matrix $S=A_jA_j'$, normalized so that $b_i'b_i=1$,

A_j is the vector representing individual j in terms of the original data set, after centering the data with respect to each character; that is,

$$A_{hj} = (x_{hj} - \bar{x}_h)/Q_h$$

where Q_h in this case was chosen to be the standard deviation within locations for character h, so that the representation of distances between sample points would be consistent with the standardized Euclidean distance discussed previously.

The elements of the eigenvectors (referred to as component coefficients) are direction cosines expressing the direction of component i in terms of the original characters. Associated with each eigenvector is an eigenvalue or characteristic root, λ_i , whose relative magnitude gives the proportion of the variance in the direction of component i. The algorithm used for principal component analysis was the R-algorithm described in Orloci(1978), with minor modifications to the computer program which is given in that book. These modifications included the explicit computation and printing of the percent of variance associated with each component, and the linear correlation of the components with the original variables. The correlation coefficient of the ith component with the hth character is defined by (Orloci,1978)

$$r_{hi} = b_{hi} (\lambda_i / S_{hh})^{1/2}$$

As a first step, principal components analysis was applied to the set of 240 cones (24 locations with 10 cones per location), and a stereogram of the first three principal components was plotted (Fig. 4.1). The computer print-out of the results is presented in Appendix C, and the main features of these results are discussed below. In this case, the first three principal components account for a total of 82% of the variance. Except for cone volume, which has a correlation of only -.05, all of the cone characters have correlations with the first principal component of magnitudes greater than .6; these large correlations are not unexpected since this first component accounts for 59% of the variance. The general conclusion that can be drawn is that the main variation among the cones (relative to variation within locations) is a variation in the serotiny and shape of the cones rather than their size. The largest magnitudes of correlations with the first principal component are for the following characters: apophysis height/width (.89), serotiny (.86), and apophysis height/length (.84). Thus, the main trend in the data expressed in the direction of the first principal component is an increase in cone serotiny and "knobbiness" of the apophyses. Associated with this trend is an increase in specific gravity, an increase in the ratio of cone width to cone length, a decrease in the symmetry of the cones, and a decrease in the ratio of cone volume to the volume of a cylinder of the same length and width (i.e. an increase in the extent to which the cones depart from a cylindrical shape). The second principal component has a moderately large negative correlation with specific gravity (-.57), and a moderately large positive correlation with cone volume (.51), and so appears to correspond to a trend along which cones become larger in volume although their weight remains approximately constant so that their specific gravity decreases. The third principal component has a moderately large negative correlation with volume (-.64), although the correlation with specific gravity is relatively small (-.11); hence, this component appears to correspond to a trend along which cone volume decreases while specific gravity remains approximately constant.

Examination of the stereogram of the 240 cones plotted on their first three principal components (Fig. 4.1), reveals what is apparently a single cloud of points with no evident group structure. However, when this same data is replotted with each cone represented by a symbol corresponding to its geographic region (with separate symbols being used for the populations with and without serotinous cones in the coastal region), this single cloud is seen to consist of four overlapping groups (Figure 4.2).

Figure 4.1 Stereogram of the 240 cones plotted on their first three principal components.

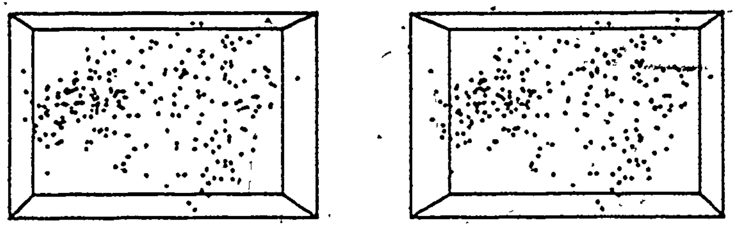


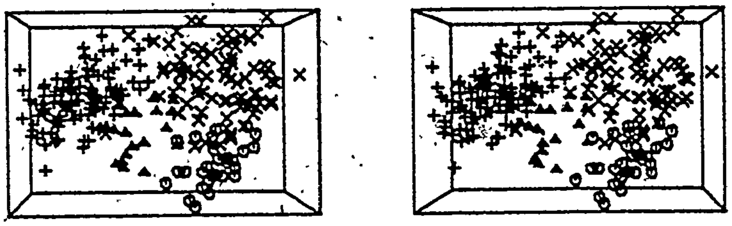
Figure 4.2 Stereogram of the 240 cones plotted on their first three principal components.

Circles identify the populations with serotinous cones of the coastal region.

Triangles identify the populations with non-serotinous cones of the coastal region.

Plus signs identify the populations of the Sierra Nevada region.

X's identify the populations of the Rocky Mountain region.



The geographic regions identified by these symbols are as follows:

circles identify the populations with serotinous cones of the coastal region;

triangles identify the populations with non-serotinous cones of the coastal region;

a plus sign identifies the Sierra Nevada region;

an X identifies the Rocky Mountain region.

A much clearer picture of group structure is obtained when advantage is again taken of the replication of cones at each location. Recall that the number of replicates was chosen so as to most efficiently represent a location, since the main objective of this research is the investigation of the variation among locations rather than among individual cones. Figure 4.3 shows that when the "noise" associated with variation within locations is reduced by averaging the character values for each location, then a very clear group structure is revealed. Figure 4.3 is a stereogram of the first three principal components resulting from the application of principal components analysis to the mean values of the cone characters for each location (standardized as previously described). The same notation is used in Figure 4.3 as was used in Figure 4.2 to represent geographic regions.

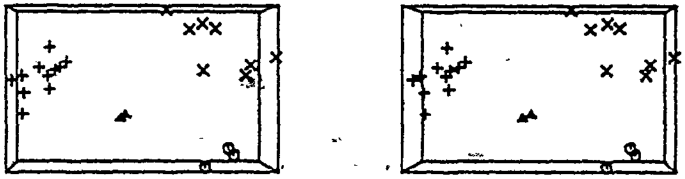
Figure 4.3 Stereogram of the 24 locations plotted on their first three principal components.

Circles identify the populations with serotinous cones of the coastal region.

Triangles identify the populations with non-serotinous cones of the coastal region.

Plus signs identify the populations of the Sierra Nevada region.

X's identify the populations of the Rocky Mountain region.



The detailed results of the principal components analysis of the 24 locations are presented in Appendix D. 94% of the total variance is accounted for by the first three principal components. The first principal component, which accounts for 75% ~~of the variance~~, has essentially the same interpretation as for the first principal component in the analysis of the individual cones, but with even higher correlation with those characters expressing cone shape and serotiny; for example, the largest correlations are a correlation of .96 with apophysis height/width, and a correlation of .94 with cone serotiny. The second principal component has a moderately large negative correlation with specific gravity (-.52), and a moderately large positive correlation with cone volume (.51), a result which is similar to that for the second principal component for the individual cone data; however, there is a difference between the two cases in that the second principal component for the location means also has a moderately large positive correlation with the ratio of cone width to cone length (.51). This suggests that this character is of more importance for distinguishing variation among locations than it was for distinguishing variation among individual cones. In terms of geographic regions, this second component separates the Rocky Mountain locations from the closed-cone coastal populations. The third principal component for the location data has a moderately large positive correlation with cone volume (.64) and relatively small correlation with specific gravity, (.03); thus, it has essentially the same interpretation as for the principal components analysis of the individual cones, only the sign of the axis is reversed with respect to cone volume.

The fact that the first three principal components account for 94% of the variance suggests that there is probably not much distortion in representation of the data structure for the locations by a three dimensional stereogram; however, it was considered desirable to investigate the extent of distortion due to reduction of dimensionality and possible non-linearity by an independent approach. The technique used, and the motivation for that technique, were the same as for the pilot-study used to determine the number of replicates for each location; namely, a correlation of matrices of resemblances between locations. Appendix E presents the results of the computation of Euclidean distances between the locations (standardized as previously described), based on the full set of cone characters; Appendix F presents the corresponding matrix of Euclidean distances based only on the three first principal components. The correlation between the two sets of distances given by these two matrices was computed to be .993, indicating that the three dimensional stereogram provides a very accurate overall representation of the resemblances among locations.

The conclusion at this stage of the investigation was that there appeared to be a strong group structure in the data, conforming to the geographic regions recognized by Critchfield(1957), with the addition that the closed-cone population from the coastal mountains of northwestern California was grouped with the closed-cone population from Mendocino. The next steps of the data analysis, motivated by this three dimensional investigation of data structure, were the application of clustering techniques as additional checks on the group structure, followed by an investigation of the differences among groups, and then the application of ordination techniques to study variation within the identified groups. These analyses are discussed in the sections which follow.

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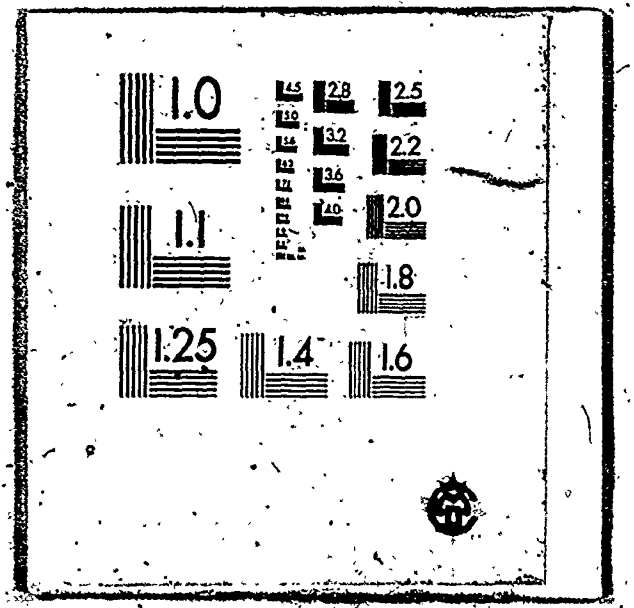


CHAPTER 5

DISCOVERY AND COMPARISON OF GROUPS

1. Clustering

This section describes the application of various clustering algorithms in an attempt to identify natural groups in the data, where the term "natural groups" is used to indicate that the distribution of sample points in sample space is discontinuous, consisting of high density clusters separated from each other by regions of low density. Since a division of the stands into four natural groups has already been suggested by the three-dimensional stereogram of the first three principal components, the first clustering method applied consisted of an algorithm designed to provide a deterministic test of the hypothesis that a specified number of natural groups exist in the data. This method, which is referred to as clustering by neighbourhoods, was developed by Orloci(1976) through modifications of a method originally described by Jancey(1974). The method is based on a definition of discontinuity according to which one group of data points is discontinuous with another group if none of its point neighbourhoods, with given radius r, overlap with any of the neighbourhoods with the same radius in the other group. The algorithm was implemented using program TRGRPS which is given in Orloci(1978). Details of the method are presented in the following paragraph.

The neighbourhood of an individual data point, for a given radius r, is defined as the set of data points which are within distance r of that individual data point. In this particular application, the distances used were the Euclidean distances, standardized as described in a previous section. Neighbourhoods are said to be overlapping if they have one or more data points in common. Input to the algorithm consists of a hypothesis specifying the number of groups, G, an initial value of neighbourhood radius, r=c, and an increment D for this radius. Neighbourhoods of radius r are formed around the data points and the points are assigned to the same group if their neighbourhoods overlap with those of any other point in that group. If the resulting number of groups, g, equals G, then the hypothesis regarding the number of groups is accepted. If g is greater than G, then the neighbourhood radius is incremented by D, and the clustering and counting of groups is repeated. If g is less than G, then the original hypothesis is rejected (in terms of radii greater than or equal to r), and the program proceeds to test the hypothesis of G-1 groups.

Clustering by neighbourhoods was performed for the data representing 24 locations, each described by 9 cone characters, specifying as a hypothesis that there existed four groups. The result was that the hypothesis was accepted, and the members of the four groups were identical to those of the four groups previously recognized by inspection of the stereogram of the first three principal components. This result provides further evidence of lack of significant distortion in the three-dimensional view of sample space.

To investigate the possible existence and composition of other numbers of groups, clustering by neighbourhoods could have been applied with other numbers of groups specified as hypotheses; however, an equivalent procedure was used instead. Clustering by neighbourhoods is a particular form of a more general clustering method known as single-linkage clustering. Clustering by neighbourhoods is an efficient procedure if one particular hypothesis concerning the number of groups is of interest; otherwise, a more general single-linkage algorithm may be more efficiently used to generate all possible groups consistent with the definition of discontinuity used in clustering by neighbourhoods.

Single-linkage clustering is a sequential agglomerative method; that is, starting with the individual data points, groups are formed by a sequential fusion of data points with other points or with existing groups. At each step, fusion occurs between the pair of data points (which aren't yet in the same group) which are most similar, or equivalently, which are separated by the smallest distance in sample space. If one or both of the points which are fused have previously been fused with other points to form a group, then the groups of which they are members are fused. Thus, this technique implies that the distance between any two groups is equal to the minimum distance between any pair of data points such that one member of the pair is a member of each group. Additional details of the method are given in Sneath and Sokal(1973), and in Jardine and Sibson(1971). The computer program used to implement the method is part of the CLUSTAN package developed by Wishart(1978).

Figure 5.1 provides a dendrogram of the results of single-linkage clustering of the 24 locations. The locations are identified by their code-names, and the vertical scale of the dendrogram gives the square of the distance between data points, or groups, at which fusions take place. The four groups previously defined by clustering by neighbourhoods are clearly evident. It is also evident that there is a significant range of values of dissimilarity (or from the point of view of clustering by neighbourhoods, neighbourhood radius) corresponding to which the data divides into those four groups. Thus, this grouping may be regarded as stable in the sense that perturbations in values of cone characters resulting in relatively small perturbations in the dissimilarity between pairs of locations will be unlikely to modify the content of these four groups. In contrast, relatively small perturbations in dissimilarity could significantly alter the pattern of fusions at lower levels in the dendrogram, indicating that these groupings are more arbitrary.

The dendrogram shows that the four groups are combined by single-linkage clustering to form two larger groups, one of which consists of the combination of the closed-cone coastal populations with the Rocky Mountain populations, and the other consists of the combination of the open-cone coastal populations with the Sierra Nevada populations. The Rocky Mountain group could be further subdivided into two groups: a group of three sites which have mainly serotinous cones and a group of five sites for which the cones are mainly non-serotinous. The dendrogram shows that these two Rocky Mountain groups were more similar to each other than either was to the closed-cone coastal group. It is also of interest to note that although both the overall division of the locations into two groups, as well as the interpretation of the first principal component, emphasized cone serotiny as one of the most important diagnostic characters; nevertheless, the open-cone and closed-cone populations of the Rocky Mountains fused to form a single group; that is, differences in cone serotiny did not over-ride similarity based on other characteristics of these cones from the Rocky Mountain region.

Within the Sierra Nevada group, two of the eleven locations display a noticeable difference from the other nine; namely, Big Bear Lake and the lower elevation site near Bishop Creek. However, this difference between these two sites and the other Sierra Nevada sites is not large when compared to the difference between Sierra Nevada sites and locations from other geographic regions. An investigation of these differences among the Sierra Nevada sites will be discussed in a subsequent section.

Single linkage clustering is often called nearest neighbour clustering, because the distance between two groups (where a group may consist of a single point) is defined to be the distance between the two nearest neighbours in each of the groups. The direct opposite of this technique is complete linkage clustering (Sorensen,1948), which is also called farthest neighbour clustering, because the distance between two groups is defined to be the distance between the two points which are farthest neighbours in each of the groups. Both single linkage clustering and complete linkage clustering are described by Lance and Williams(1967) as "space distorting", in the sense that the space in the vicinity of a cluster appears to become distorted as a cluster grows through the addition of new points. Single linkage clustering and complete linkage clustering each distort space in an opposite manner: single linkage clustering is "space contracting", which means that as a group grows larger its computed distance from other groups decreases as though the space around the group were contracting; complete linkage clustering is "space dilating", which means that as a group grows larger its computed distance from other groups increases as though it were receeding from them in space. As a result of these opposite types of space distortion, single linkage clustering usually produces long chains as clusters; whereas, complete linkage clustering tends to produce compact, hyperspherical groups.

To avoid the extremes of space distortion resulting from either single linkage clustering or complete linkage clustering, Sokal and Michener(1958) developed a family of techniques known as average linkage clustering, which are space conserving in the sense that group size does not affect the computed distance between groups. These techniques all involve the computation of an average distance between two groups, but differ in the way that they define this average distance. The particular average linkage clustering technique used for this study is the one referred to as unweighted centroid sorting. In this technique, the distance between a pair of groups is defined to be the distance between the centroids of the two groups. This technique is described in Orloci(1978) in terms of similarity; however, for ease of comparison with the results of single linkage clustering and complete linkage clustering, implementation of the technique was carried out in terms of distances using a computer program from the CLUSTAN package (Wishart,1978). (This package was also used for complete linkage clustering, as well as for single linkage clustering.)

Dendrograms of the results of complete linkage clustering and average linkage clustering are given in

Figures 5.2 and 5.3, respectively. The notation used for these dendrograms corresponds to that used for Figure 5.1, with the vertical scale providing the square of the distance between groups at which fusion takes place. As expected from the definitions of distances between groups for each algorithm, these fusion distances are generally greater for average linkage clustering than for single linkage clustering, and are greatest for complete linkage clustering; however, it is a comparison of the pattern of fusion which is of interest rather than the numerical values at which fusion takes place.

For all three clustering techniques, the same sites are combined to form the same four groups, thus providing strong confirmation of the existence of these four natural groups which correspond to the four subspecies recognized by Critchfield(1957) (with the extension of his Mendocino subspecies to include the closed cone population from Gasquet, 15 miles from the northern California coast). This strong discontinuity in the data could be the result of discontinuous sampling, but this is the only possible sampling at this latitude since (except for the coastal groups) the groups are geographically separated. It would be interesting to perform this same analysis for samples from sites further north, where the geographic separation between the subspecies defined by Critchfield is less. (See Figure 1.1.)

The three clustering results have other similarities which are worth noting. The four groups fuse to form the same two groups for all methods; namely, a combination of the closed-cone coastal populations with the Rocky Mountain populations, and a combination of the Sierra Nevada populations with the open-coned coastal populations. For all three methods, the Rocky Mountain group is subdivided into two groups corresponding to open-cone and closed-cone populations. Within the Sierra Nevada group, the same two sites fuse last with the rest of the group according to all three methods; namely, Big Bear Lake and the site at an elevation of 2400 meters near Bishop Creek.

The only difference in the pattern of fusion for the different methods occurs within the Sierra Nevada group. With all three techniques it is evident from the dendrograms that the pattern of fusion within the Sierra Nevada group would be sensitive to small perturbations in similarity between sites. Thus, comparison of the three dendrograms implies the existence of an essentially continous data structure within the Sierra Nevada group. Notice that the dendrogram for average linkage clustering displays "reversals" within the fusion pattern; for example, the Kaiser and Huntingdon Lake populations fuse at an average distance which is greater than the average distance at which their centroid subsequently fuses with the population from 3050 meters elevation near Bishop Creek. Jardine and Sibson(1971) reject average linkage clustering on theoretical grounds because of this lack of monotonicity in the fusion pattern; however, in the present application it can be seen that the reversals in the fusion pattern do not seriously affect the interpretation of the clustering results.

The acceptance of the existence of the four natural groups suggests the need for investigation of the differences between the groups in terms of their cone characteristics, and also their environments, as well as more detailed study of the variation within each group. For example, in what ways are the closed-cone coastal populations more similar to the geographically distant Rocky Mountain populations than they are to the geographically adjacent open-cone coastal populations? (There is obviously more involved than cone serotiny, since the Rocky Mountain group is composed of both serotinous and non-serotinous populations, and the Rocky Mountain and closed-cone coastal populations combine not only for single linkage clustering but also for complete linkage clustering.) A parallel question could be asked concerning similarities in the environments of the closed-cone coastal sites and the Rocky Mountain sites, as compared to differences between the adjacent open-cone and closed-cone coastal sites. Also, although the clustering results imply that variation among the four groups is much greater than variation within any group; nevertheless, a search for secondary patterns of variation within the groups with respect to variables such as elevation and latitude is still of interest. Investigations of topics such as these are discussed in subsequent sections.

Figure 5.1 Dendrogram based on single-linkage clustering.

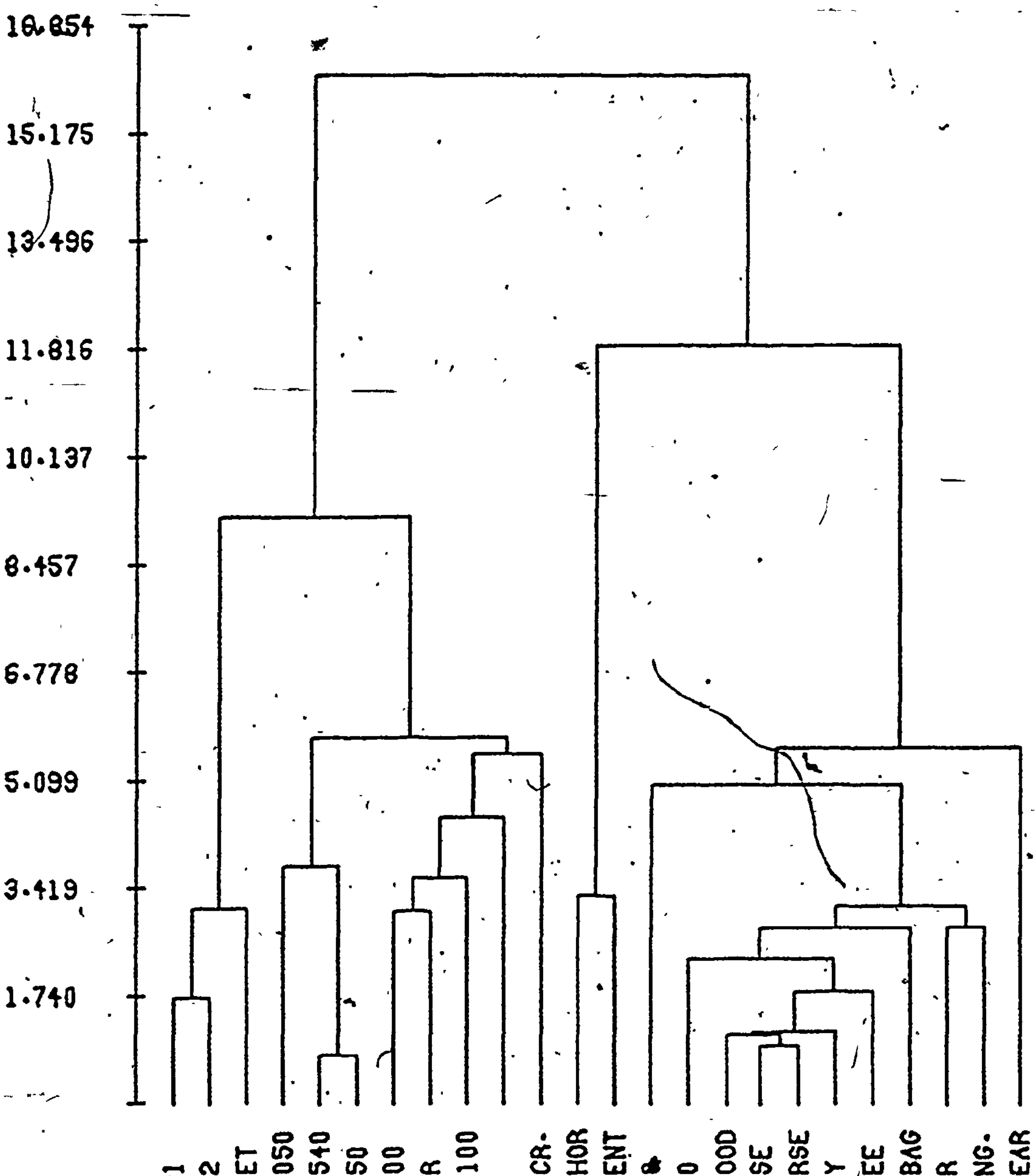


Figure 5.2 Dendrogram based on complete-linkage clustering.

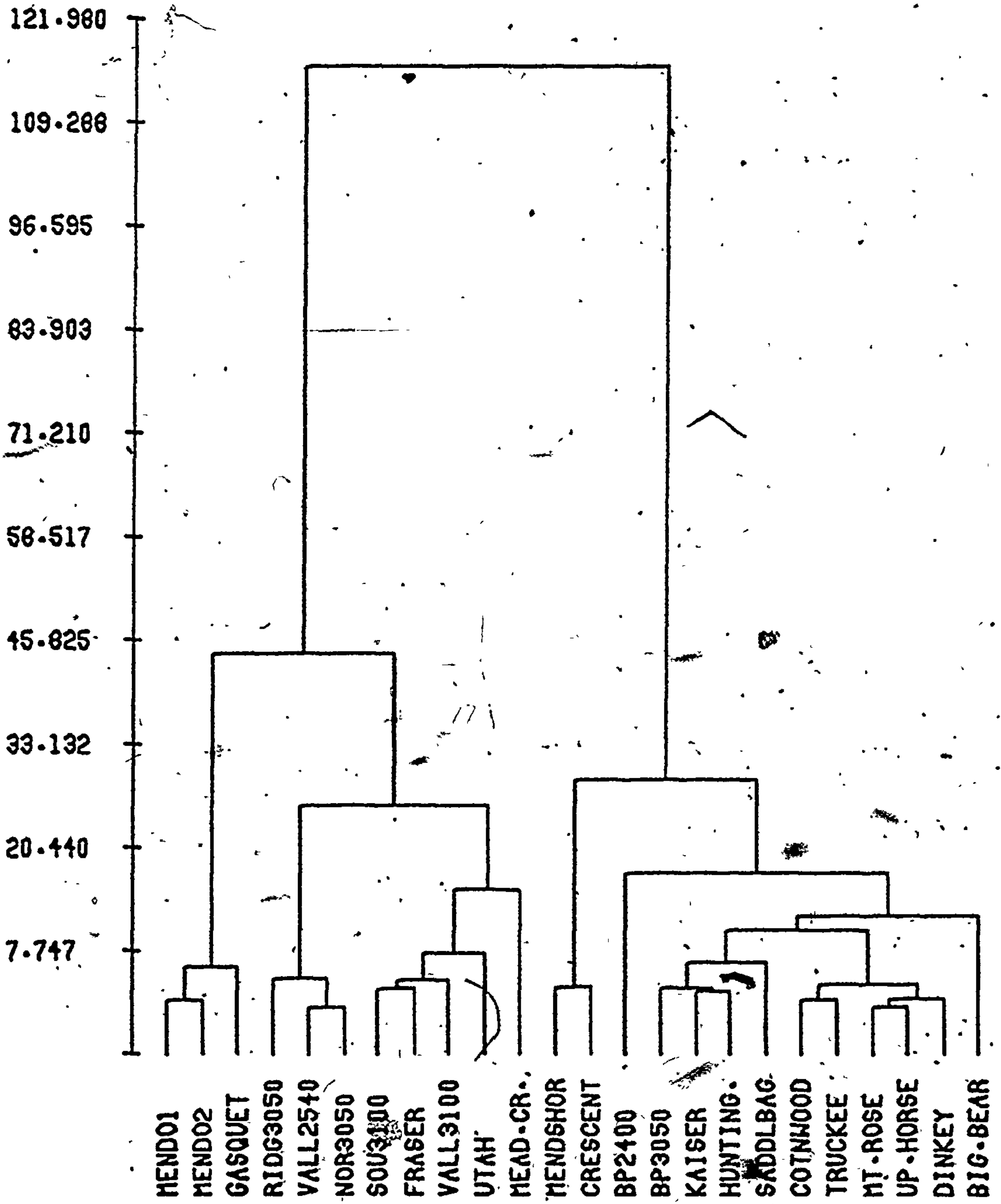
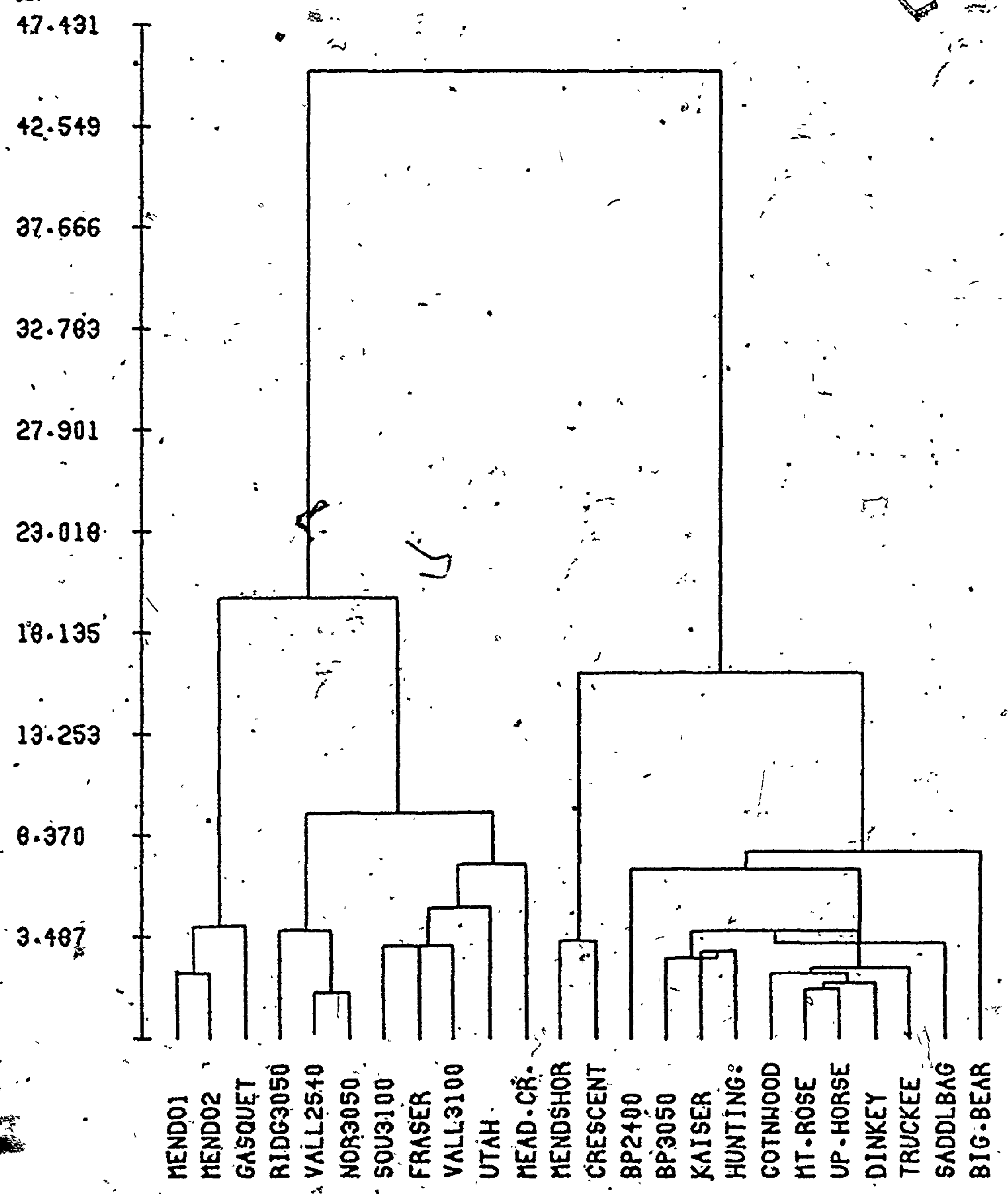


Figure 5.3 Dendrogram based on average-linkage clustering.



2. Differences among the Groups with respect to Cone Characteristics

The previous section provided strong evidence for the existence of four natural groups based on characteristics of the cones of Pinus contorta. The goals of this section are to provide a summary of the characteristics of the cones for each of the identified groups, and to determine which cone characteristics best distinguish between each pair of groups.

Table 5.1 provides a summary of the mean values, standard deviations, minima and maxima for each cone character for each of the four identified groups. In this table, the notation "Mendocino" is used to refer to the group containing not only the populations with serotinous cones from near Mendocino, but also the population from near Gasquet; the notation "coastal" is used to refer to the coastal populations with non-serotinous cones.

Table 5.1 Summary of Cone Characteristics for the identified Groups.

VARIABLE: serotiny

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.89	0.24	0.31	1
COASTAL	0.28	0.047	0.21	0.37
SIERRAS	0.17	0.046	0.1	0.29
ROCKIES	0.58	0.32	0.13	1

VARIABLE: volume

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	6.09	1.66	4.1	11.2
COASTAL	5.93	1.85	3.9	9.3
SIERRAS	8.35	2.82	3.7	19
ROCKIES	8.08	2.28	3.8	14.7

VARIABLE: apoph.ht.

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	2.92	0.56	1.9	4
COASTAL	2.58	0.51	2	3.7
SIERRAS	2.45	0.50	1.5	4
ROCKIES	3.88	0.87	1.7	6.2

Table 5.1 (continued)

VARIABLE: sp.gr.

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.78	0.048	0.7	0.92
COASTAL	0.65	0.076	0.53	0.80
SIERRAS	0.53	0.049	0.41	0.67
ROCKIES	0.64	0.0721	0.45	0.80

VARIABLE: cone.wid/l.

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.52	0.041	0.43	0.62
COASTAL	0.48	0.042	0.41	0.57
SIERRAS	0.47	0.056	0.35	0.66
ROCKIES	0.64	0.061	0.49	0.80

VARIABLE: vol/cylvol

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.37	0.039	0.27	0.46
COASTAL	0.34	0.027	0.30	0.39
SIERRAS	0.38	0.035	0.31	0.46
ROCKIES	0.32	0.034	0.24	0.42

Table 5.i (continued)

VARIABLE: symmetry

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.85	0.042	0.79	0.94
COASTAL	0.88	0.046	0.79	0.95
SIERRAS	0.95	0.029	0.87	1.01
ROCKIES	0.85	0.049	0.76	0.97

VARIABLE: apoph.h/l.

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.45	0.074	0.31	0.61
COASTAL	0.36	0.064	0.28	0.54
SIERRAS	0.34	0.065	0.22	0.56
ROCKIES	0.52	0.110	0.32	0.85

VARIABLE: apoph.h/w.

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	0.44	0.078	0.30	0.60
COASTAL	0.36	0.053	0.31	0.52
SIERRAS	0.30	0.053	0.17	0.43
ROCKIES	0.48	0.094	0.28	0.8

In order to determine which cone characteristics best distinguish between each pair of groups, the same algorithm was employed as had been used earlier for ranking characters in order to choose the set of characters for study (Jancey,1979). Although the lack of random sampling within each group prevents a strict statistical interpretation of the resulting "F-values"; nevertheless, these values are useful in a deterministic sense in emphasizing those characters whose variation between a pair of groups is greatest relative to their variation within the groups. The following discussion presents tables comparing each pair of groups, where the groups are identified by numbers:

1 refers to the coastal group with serotinous cones,
2 refers to the coastal group with non-serotinous cones,
3 refers to the Sierra Nevada group,
4 refers to the Rocky Mountain group.

The ranking of the characters based on their discrimination between the serotinous and non-serotinous coastal groups shows a rather clear distinction between a set of four characters which have quite large differences between these groups compared to their variation within the groups, and the remaining five characters which have much smaller differences between the groups compared to their variation within the groups. The four characters with the "greatest diagnostic ability" for distinguishing between this pair of groups are measures of cone serotiny, specific gravity and apophysis shape; whereas, four of the other five characters are measures of cone size and cone shape. In other words, the two coastal groups have cones which are not distinguishable based on their size and shape, but which can be distinguished not only on the basis of cone serotiny, but also on the basis of cone specific gravity and apophysis shape. From table 5.1, it can be seen that the coastal group with serotinous cones has cones which have higher specific gravity than the coastal group with non-serotinous cones, as well as having apophyses whose height is greater compared to their length and width.

Table 5:2 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 1 AND 2

RANK	CHARACTER	NUMBER	F VALUE
1	apoph.h/l.	8	96.7038
2	serotiny	1	87.5106
3	sp.gr.	4	59.1173
4	apoph.h/w.	9	18.58
5	cone.wid/l.	5	3.86918
6	apoph.ht.	3	3.4759
7	symmetry	7	1.62802
8	vol/cylvol	6	1.19356
9	volume	2	0.10325
		SUM=	272.182

At this point, it might be interesting to look at a comparison of the two subgroups within the Rocky Mountain group, since that division was also related to cone serotiny and yet the clustering techniques did not make as sharp a distinction between the Rocky Mountain populations with serotinous and non-serotinous cones as was made between the coastal populations with serotinous and non-serotinous cones.

Table 5.3 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN THE TWO ROCKY MOUNTAIN SUBGROUPS

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	115.57
2	apoph.ht.	3	9.1157
3	sp.gr.	4	6.60619
4	apoph.h/w.	9	1.72544
5	vol/cylvol	6	1.56601
6	apoph.h/l.	8	1.0829
7	symmetry	7	0.33942
8	volume	2	0.20450
9	cone.wid/l.	5	0.04728
		SUM=	136.257

From table 5.3 it is evident that cone serotiny is much more important than any other character at distinguishing between the two Rocky Mountain subgroups and that, by comparison, other characters such as specific gravity and apophysis shape show relatively little differentiation between the populations with serotinous cones and the populations with non-serotinous cones. Thus, although the coastal subdivision supports a generalization by Critchfield(1957) that variation in cone serotiny is accompanied by variation in a group of cone characteristics, including specific gravity and apophysis shape; nevertheless, the comparison of the two Rocky Mountain subgroups demonstrates that this generalization is limited in its applicability. Furthermore, the similarity of the two Rocky Mountain subgroups in all other cone characteristics except cone serotiny supports the conclusion that the Rocky Mountain populations represent a single natural group with similar cones except that some of them are open while others remain closed (possibly for purely environmental reasons, without any inherited difference). Recall that the serotinous condition of the coastal cones has been shown to be inherited (Jenny, Arkley, and Schultz,1969).

Consider next the comparison of the coastal group with serotinous cones and the Rocky Mountain group. From table 5.4 it can be seen, that the most important distinction between these groups is in the ratio of cone width to cone length, and that there is also a definite difference in the ratio of cone volume to the volume of a cylinder of equal length and diameter; that is, there are distinctive differences in shape between the coastal group with serotinous cones and the Rocky Mountain group. There are also significant differences in cone volume and in apophysis height and a lesser difference in specific gravity; however, the cones of the two groups are not distinguished on the basis of cone serotiny, apophysis shape, or cone symmetry. From table 5.1, it is seen that the coastal group with serotinous cones has cones of a narrower, more cylindrical shape than the Rocky Mountain group. Also, although the Rocky Mountain group has apophyses with greater height (which accounts for some of the difference in cone shape); nevertheless, the apophyses of the two groups are essentially the same shape.

Table 5.4 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 1 AND 4

RANK	CHARACTER	NUMBER	F VALUE
1	cone.wid/l.	5	41.7309
2	apoph.ht.	3	26.2844
3	volume	2	15.1092
4	vol/cylvol	6	14.3656
5	sp.gr.	4	12.8166
6	apoph.h/l.	8	5.69391
7	serotiny	1	4.14867
8	apoph.h/w.	9	2.76009
9	symmetry	7	0.233432
		SUM=	123.143

The final comparison for the coastal group with serotinous cones is with the Sierra Nevada group, as shown in table 5.5. Cone serotiny is, by far, the most important character distinguishing between these two groups and, as for the comparison of the two coastal groups, there are also important differences in specific gravity and apophysis shape. Notice that the ratio of apophysis height to apophysis width shows much greater difference between the coastal group with serotinous cones and the Sierra Nevada group than the ratio of apophysis height to apophysis length; whereas, for the comparison of the two coastal groups the reverse was true. Another difference between these two comparisons is that cone symmetry differs greatly between the coastal group with serotinous cones and the

Sierra Nevada group; whereas, cone symmetry for the two coastal groups was similar. A similarity in both comparisons, is that cone size and cone shape do not show significant differences. From table 5.1, it can be seen that, compared to the coastal group with serotinous cones, the cones from the Sierra Nevada group have lower specific gravity, greater symmetry, and less "knobby" apophyses, as well as being non-serotinous.

Table 5.5 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 1 AND 3

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	308.368
2	sp.gr.	4	134.517
3	symmetry	7	107.794
4	apoph.h/w.	9	56.6592
5	apoph.h/l.	8	21.4067
6	volume	2	5.81334
7	apoph.ht.	3	5.60781
8	cone.wid/l.	5	4.94893
9	vol/cylvol	6	2.46769
		SUM=	647.582

Now consider the comparison of the remaining two "California" groups, that is, the coastal group with non-serotinous cones and the Sierra Nevada group, which is shown in table 5.6. The most significant difference between these two groups is in cone symmetry (with the Sierra Nevada group having more symmetric cones). The second most significant difference between the two groups is in cone serotiny. This may be a surprise, since both groups are described as having non-serotinous cones; however, this difference has been detected as a result of using the more precise continuous measure of cone serotiny. This measure reveals that Sierra Nevada cones are consistently open "more completely" than the non-serotinous cones of the coastal species. There is also an important difference between these two groups in specific gravity; thus, the three most important differences between the cones of the Sierra Nevada group and the cones of the coastal group with non-serotinous cones occur in the same characters as were most important in distinguishing the coastal group with serotinous cones from the Sierra Nevada group, thus demonstrating the affinity between the two coastal groups. As was the case for the other comparisons among the "California" groups, differences in cone size and cone shape are relatively less important, although the Sierra Nevada cones do have a more cylindrical shape. Differences between the coastal group with non-serotinous cones and the Sierra Nevada group are also relatively small in apophysis height and shape except that the Sierra Nevada cones tend to have relatively wider apophyses.

Table 5.6 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 2 AND 3

RANK	CHARACTER	NUMBER	F VALUE
1	symmetry	7	39.0575
2	serotiny	1	27.6107
3	sp.gr.	4	22.3056
4	vol/cylvol.	6	11.8829
5	apoph.h/w.	9	9.36737
6	volume	2	4.38132
7	apoph.ht.	3	0.41671
8	apoph.h/l.	8	0.38147
9	cone.wid/l.	5	0.27955
		SUM=	115.683

Table 5.7 compares the coastal group with non-serotinous cones to the Rocky Mountain group. The two most significant differences are in the ratio of cone width to cone length, and in apophysis height; recall that these were also the most significant differences between the Rocky Mountain group and the coastal group with serotinous cones. There are also important differences in apophysis shape, but notice that these shape differences are less important than the difference in apophysis size. Except that the Rocky Mountain cones are somewhat larger, there are no other distinctive differences in the cones of the two groups. In particular, there is not a significant difference in cone

serotiny between these two groups since not only is there wide variation in this character within the Rocky Mountain populations, but also the cones of the coastal group with non-serotinous cones show some tendency toward serotiny when measured on a continuous scale.

Table 5.7 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 2 AND 4

RANK	CHARACTER	NUMBER	F VALUE
1	cone.wid/l.	5	58.7062
2	apoph.ht.	3	45.2298
3	apoph.h/l.	8	24.6878
4	apoph.h/w.	9	22.1052
5	volume	2	8.31267
6	vol/cylvol	6	4.97938
7	serotiny	1	3.11545
8	symmetry	7	0.98608
9	sp.gr.	4	0.04714
		SUM=	168.163

The final comparison, which is between cones of the Sierra Nevada group and the Rocky Mountain group, is provided by table 5.8. This table reveals that there are important differences between these two groups in all of the measured cone characters except for cone volume. Notice that although there is a significant difference between these two groups in specific gravity (the cone character that Critchfield regarded as most useful for diagnostic purposes); nevertheless, specific gravity is ranked eighth of the eight characters which show significant differences between the two groups. The most important difference between the two groups is in the ratio of apophysis height to apophysis width, with the Sierra Nevada group having relatively wider apophyses compared to their height. The next most important characteristic for distinguishing between the cones of these two groups is the ratio of cone width to cone length, with the Sierra Nevada cones being narrower relative to their length. Recall that this character was the most important one for distinguishing between the Rocky Mountain populations and the other "California" populations. Of almost equal importance as this character in distinguishing between the Sierra Nevada group and the Rocky Mountain group is cone symmetry, with the Sierra Nevada cones being more symmetric.

Table 5.8 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN GROUPS 3 AND 4

RANK	CHARACTER	NUMBER	F VALUE
1	apoph.h/w.	9	153.67
2	cone.wid/l.	5	111.138
3	symmetry	7	110.497
4	apoph.ht.	3	86.1132
5	apoph.h/l.	8	81.9959
6	vol/cylvol	6	81.8493
7	serotiny	1	64.1009
8	sp.gr.	4	26.7879
9	volume	2	0.06492
		SUM=	716.216

The main conclusions based on the preceeding analysis are listed in the following paragraphs:

The difference between the two Rocky Mountain subgroups with respect to cone serotiny is much greater than their differences with respect to any other cone character; whereas, for the two coastal groups, the difference between them in cone serotiny is accompanied by differences of comparable magnitude in specific gravity and apophysis shape, with the more serotinous cones having higher specific gravity and "knobbier" apophyses.

The cones of the two coastal groups do not show significant differences in their size, overall shape, symmetry, or the height of their apophyses.

The most useful of the characters for distinguishing between cones from the California groups and cones from the Rocky Mountain group is the ratio of cone width to cone length, with the California cones being narrower relative to their length than the Rocky Mountain cones. All of the California groups also have significantly shorter apophyses than the Rocky Mountain group. The shape of the apophyses of the coastal group with non-serotinous cones and of the Sierra Nevada group differs significantly from the shape of the apophyses of the Rocky Mountain group; whereas, the shape of the apophyses of the coastal group with serotinous cones does not differ significantly from those of the Rocky Mountain group.

A unique distinction between the cones of the Sierra Nevada group and the cones of any other group is that the Sierra Nevada cones are much more symmetric.

The use of a continuous measure of cone serotiny reveals significant differences between the degree of serotiny of the Sierra Nevada cones and the "non-serotinous" cones of the coast, with the Sierra Nevada cones being more open.

Critchfield(1957) regarded cone specific gravity as being the most useful character for distinguishing between the cones of the four groups. The results of the present study show that although there are significant differences in specific gravity between some of the groups; nevertheless, other characters are generally more highly-ranked based on their ability to distinguish between the groups.

3. Relationship of Group Structure to Extrinsic Variables

The goals of this section are to summarize the values of various extrinsic variables for each of the four groups identified in the previous sections, as well as for the two Rocky Mountain subgroups, and to look particularly for those extrinsic variables which might expain the grouping. The term "extrinsic variable" is used to refer to variables other than the cone characteristics which were used to cluster the populations from the different sites.

Two main techniques were generally applied for all of the extrinsic variables; then additional methods were used to look more closely at certain variables, as suggested by the results of the first two techniques. The first technique consisted of a simple summarization of mean values, standard deviations, maxima and minima for soil and climatic variables for each of the groups. However, this summary was complicated by the fact that, for some sites, the environmental values are known only in terms of inequalities; for these cases the values used in the summary tables were computed based on the limiting values, and the effect of using these values on the comparisons between groups is discussed below whenever it is considered important. As before, the label "coastal" as used in these summary tables refers only to those coastal populations with non-serotinous cones while the label "Mendocino" refers to the coastal populations with serotinous cones. In addition, these tables display separate statistics for each of the two Rocky Mountain subgroups, with the label "serot.Rock." referring to the Rocky Mountain subgroup with the more serotinous cones, while the label "non-serot.Rock." refers to the Rocky Mountain subgroup with less serotinous cones.

The second technique consisted of plotting ranks of environmental variables on stereograms of the first three principal components of the ordination of sites based on their cone characters. Ranks from 1 to 9 were used so that each site could be depicted on the plot by a single digit, and also the use of ranks rather than continuous values allowed for a more flexible procedure for the handling of inequalities; for example, sites with greater than 200 parts per million of exchangeable magnesium were all given a rank of 9 and, in other cases, reasonable judgment could be used to assign a rank to a variable represented by an inequality where a continuous estimate would not have been meaningful. Tables 5.9 and 5.10 give the ranges of each variable corresponding to their ranks. The ranks for the exchangeable soil ions are based on equal divisions of a logarithmic scale in order to be consistent with the logarithmic nature of the expression of pH.

Table 5.9 Ranks for Elevation, Temperature and Precipitation

Rank	Corresponding Range of Values for each Variable		
	Elevation (meters)	Mean Annual Temperature (degrees C.)	Mean Annual Precipitation (cm.)
1	20 to 180	-2	26
2	790	0	41 to 50
3	1710 to 1780	1 to 2	51 to 60
4	2320 to 2635	3 to 4	61 to 70
5	3020 to 3100	5 to 6	71 to 80
6		7 to 8	81 to 90
7		9 to 10	91 to 100
8		11 to 12	190 to 193

Table 5.10 Ranks for Soil Variables

Rank	Corresponding Range of Values for each Variable (Exchangeable ions in parts per million of soil air dry weight)			
	Phosphate	Potassium	Magnesium	pH
1	2	40 to 44	17	3.8
2		52 to 56	22	
3	4 to 5		29	4.5 to 4.7
4	6	84 to 96	42 to 44	4.8 to 5.0
5	9 to 12	112 to 120	52 to 55	5.1 to 5.3
6	14 to 19	136 to 148	85 to 91	5.4 to 5.6
7	27 to 29	164 to 192	105 to 119	5.7 to 5.9
8	34	212 to 256	144 to 150	6.0 to 6.2
9	51 to 56	268 to 304	>200	6.3 to 6.5

This second technique appeared particularly useful for this study since not only do the first three principal components account for 94% of the variance, but also it has been shown, in a previous section, that there is very little distortion of the resemblance relationships between the sites when they are plotted in terms of the first three principal components, and also the group structure is clearly displayed on these stereograms. Thus, examination of the stereograms should reveal not only the extent to which extrinsic variables have different values in different groups, but should also portray trends in these variables, and provide additional insight by depicting whether those sites in two different groups which are most similar in terms of cone characteristics are also most similar in terms of particular extrinsic variables.

The extrinsic variable which is most obviously related to group structure is not included in the above tables of ranks. This variable is "geographic region", and the effect of plotting ranks corresponding to this variable on a stereogram can be observed by re-examination of figure 4.3, where the symbols "circle" and "triangle" can both be taken as referring to the coastal region, while "plus" refers to the Sierra Nevada region, and "X" refers to the Rocky Mountain region. This stereogram demonstrates that geographic location is sufficient to account for the correct allocation of every site to one of three groups: a coastal group, a Sierra Nevada group, and a Rocky Mountain group. The only deficiency in this variable is that it is not able to account for the division of the populations of the coastal region into two groups nor does it account for the subdivision of the Rocky Mountain group into two subgroups. Consequently, emphasis will be placed in the subsequent discussion on the role of other extrinsic variables in providing possible explanations for these latter divisions.

Since both average annual temperature and average annual precipitation are essentially the same in both coastal groups, it is obvious that these climatic variables can not account for the separation of the coastal populations into two groups. From tables 5.11 and 5.12 it appears that both of these variables decrease as one moves inland from the coast to the Sierra Nevadas, and from there to the Rocky Mountains; however, considering the inequality signs in the data for the mountain locations, the average annual precipitation for the Rocky Mountain sites is probably closer to that of the Sierra Nevada sites than the computed mean values would indicate, and thus there is no basis for asserting that the Rocky Mountain sites have less precipitation than the Sierra Nevada sites. Nevertheless, as was mentionned earlier, the distribution of precipitation throughout the year is much different for the Sierra Nevada sites than for the Rocky Mountain sites. Hence, as might be expected, each of the three geographic regions has a different climate, but the existence of this difference does not contribute any new insight into the factors underlying the group structure, except to allow for the possibility that cones within a region may differ from those of other regions due to some possible adaptation to the climate of the region. However, the great variation in precipitation between the northern and southern coastal sites accompanied by relatively little variation in cone characters makes it unlikely that precipitation bears much relationship to the cone characters; similarly, the wide variation in temperature within the single Sierra Nevada group makes it unlikely that temperature is an important factor underlying group structure. Tables 5.11 and 5.12 also summarize the climatic variables for the two Rocky Mountain subgroups, with no significant difference evident in the climate of these two subgroups.

Figure 5.4 reveals no clear trends for the variation of precipitation, but figure 5.5 reveals a tendency for the mountain sites with cooler temperatures to be further away from the coastal sites (on the stereogram), and this trend corresponds to a decrease in temperature along the direction of the second principal compnent. It was previously shown that this second principal component had a moderately large positive correlation (+.51) with cone volume, and a moderately large negative correlation (-.52) with cone specific gravity. This suggests that as temperature decreases cones become larger in volume while retaining the same weight. The effect of climatic variables on the variation of cone characters will be discussed further in a subsequent section dealing with the variation within groups.

Figure 5.4 Stereogram showing ranks for precipitation.

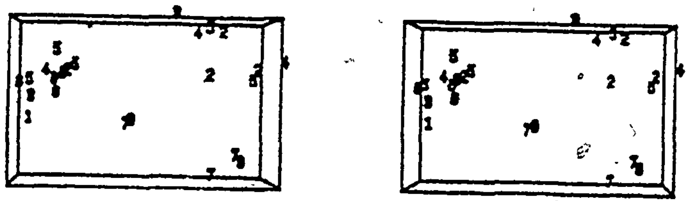


Figure 5.5 Stereogram showing ranks for temperature.

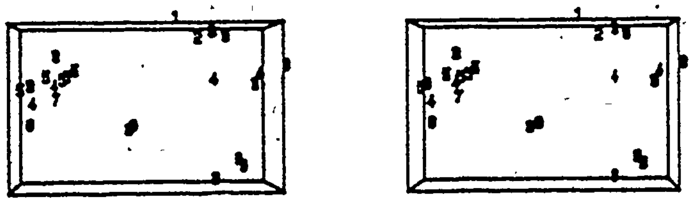


Figure 5.6 Stereogram showing ranks for elevation.

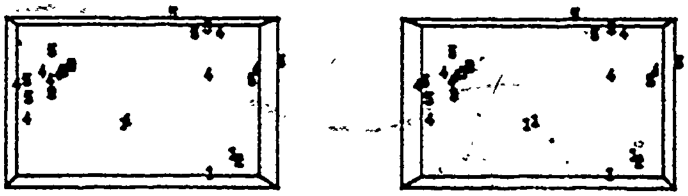


Table 5.11 Summary Statistics for Temperature Within Groups (degrees C.)

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	11.6667	0.57735	11	12
COASTAL	11.5	0.70710	11	12
SIERRAS	5.0909	2.58668	1	10
ROCKIES	1.25	1.66905	-2	3
SEROT.ROCK.	2.0	1.0	1	3
NON-SER.ROCK.	0.8	1.92354	-2	3

Table 5.12 Summary Statistics for Precipitation within Groups (cm.)

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	126.667	54.8483	95	190
COASTAL	144.	69.2965	95	193
SIERRAS	69.363	19.2368	26	90
ROCKIES	57.375	15.8199	41	79
SEROT.ROCK.	61.666	16.2583	44	76
NON-SER.ROCK.	54.8	16.8434	41	79

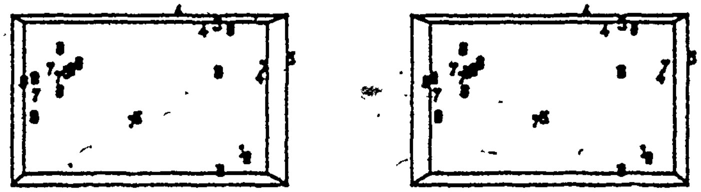
No tabular summary is provided of the elevations sampled within each group, since the sampling within the mountain regions was obviously non-random with respect to this variable and the coastal sites were clearly at lower elevations than the mountain sites. However, from examination of figure 5.6, it is interesting to note that the two lowest elevation Sierra Nevada sites are located on the stereogram among those Sierra Nevada sites which are most similar to the coastal sites. This suggests the possibility that increases in elevation are related to the divergence of the Sierra Nevada cones from the coastal cones. A more detailed examination of the relationship between cone characteristics and elevation will be discussed in a subsequent section, as part of the study of variation within the mountain groups.

The unusual soil near Mendocino, California, on which the pygmy Pinus contorta trees with serotinous cones are growing has led to the conclusion that these trees represent an edaphic race (Critchfield,1957). Also, the extremely low pH of these unusual soils has led to the implication that pH is the most important factor related to the formation of this edaphic race, as well as to the other striking differences in vegetation between these highly-acid soils and the other soils of the same region (Westman,1975; McMillan,1956, Jenny, Arkley, and Schultz,1969). However, the close similarity of the cones of the population growing on serpentine soil of pH 6.5 to the cones of the populations growing on the highly-acid soils (with pH as low as 3.8), makes this implication unlikely. Table 5.13 also casts doubt on any direct relationship between pH and cone serotiny since both of the Rocky Mountain subgroups, which differ in cone serotiny, have essentially the same average pH. In addition, figure 5.7 does not detect any definite trends in pH related to cone characteristics.

Table 5.13 Summary Statistics for pH within Groups

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	4.93333	1.40119	3.8	6.5
COASTAL	5.5	0.424263	5.2	5.8
SIERRAS	5.46364	0.445584	4.7	6.2
ROCKIES	5.3625	0.509728	4.8	6.2
SEROT.ROCK.	5.33333	0.550757	4.8	5.9
NON-SER.ROCK.	5.38	0.549545	4.8	6.2

Figure 5.7 Stereogram showing ranks for soil pH.

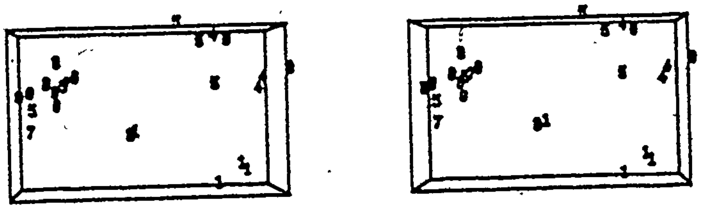


Examination of table 5.14 and figure 5.8 reveals that levels of exchangeable phosphorus in the soil are much lower in both coastal groups than in either mountain group, and that phosphorus levels are highest in the Sierra Nevadas. Also, the level of exchangeable soil phosphorus is significantly less in the soils of the Rocky Mountain sites with serotinous cones than in the soils of the Rocky Mountain sites with non-serotinous cones. Except for the anomaly of low phosphorus levels in the "normal" coastal sites, there thus appears to be a definite trend of increasing cone serotiny associated with decreasing soil phosphorus..

Table 5.14 Summary Statistics for Soil Phosphorus
(parts per million of soil air dry weight)

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	2	0	2	2
COASTAL	3	1.41421	2	4
SIERRAS	25.1818	16.4184	5	56
ROCKIES	8.5	3.42261	5	15
SEROT.ROCK.	5.6667	0.57735	5	6
NON-SER.ROCK.	10.2	3.27109	6	15

Figure 5.8 Stereogram showing ranks for phosphorus.



Westman(1975) noted that although levels of exchangeable phosphorus in the pygmy forest soils are low; nevertheless, the surface soil values are comparable to those of the surrounding forest soils of the region. However, he pointed out that exchangeable phosphorus is not always a good indicator of available phosphorus, and that foliar analysis has revealed occasional deficient levels in pygmy forest species. He speculated that a combination of low pH and high levels of aluminum in the pygmy forest soils might inhibit the uptake of phosphorus and cited a number of studies which investigated this relationship between pH, aluminum and phosphorus, and which offer possible explanations for the mechanism of their interaction (Clarkson, 1969; Russell, 1961; Wright and Donahue, 1953). McMillan(1956) found that additions of phosphorus alone did not stimulate growth of _Pinus contorta_ of _Cupressus pygmaea_ on pygmy forest soils, but that a combination of nitrogen and phosphorus did improve growth. Westman(1975) suggested that the addition of nitrogen might have improved phosphorus uptake by stimulating protein synthesis and rapid root growth, or by an effect on mycorrhizae. This suggests an additional possible cause for greater phosphorus uptake from the "normal" coastal soils as compared to the pygmy forest soils; namely, the probable existence of greater root development on the more easily penetrated sandy coastal soil as compared to the necessarily limited root development associated with the pygmy forest "hardpan" and seasonal high

Water-table.

Both McMillan(1956) and Westman(1975) noted that a feature which both serpentine soils and the highly-acid pygmy forest soils have in common is a low level of calcium. Buckman and Brady(1969) state that inorganic phosphorus compounds in the soil fall into one of two groups: (1) those containing calcium, and (2) those containing iron and aluminum. The iron and aluminum compounds are extremely insoluble and hence unavailable for plant growth; whereas, the calcium compounds which are present at moderate pH are readily available for plant growth. Thus, even though the pH is almost neutral in the serpentine soils near Gasquet; nevertheless, the low levels of calcium and the relatively impenetrable soil could result in low levels of available phosphorus. In summary, although levels of exchangeable phosphorus are very low in all three of the coastal soil-types included in this study, the availability of phosphorus to the vegetation is almost certainly more restricted on the highly-acid soils and the serpentine soils than on the "normal" sandy coastal soils.

Table 5.15 Summary statistics for Soil Potassium
(parts per million of soil air dry weight)

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	45.333	6.1101	40	52
COASTAL	154	82.0244	96	212
SIERRAS	146.182	69.2904	56	304
ROCKIES	194.5	70.7167	112	300
SEROT.ROCK.	185.333	75.5072	120	268
NON-SER.ROCK.	200	76.1577	112	300

Table 5.15 and figure 5.9 reveal that levels of potassium in the soils of the coastal group with serotinous cones are much lower than in the other groups, but that otherwise there are no significant differences between the groups or between the two Rocky Mountain subgroups compared to the large variation within the groups. Also, there are no detectable trends related to cone characteristics. Thus, the main relationship between this variable and the groups based on cone characteristics is that low levels of soil potassium in the soil provide another similarity between the serpentine soils and the highly-acid Mendocino soils. This common low level of potassium could also contribute to the reduced availability of phosphorus from the soils of the coastal group with serotinous cones as compared to the coastal group with non-serotinous cones since potassium is known to encourage strong root growth which could increase nutrient uptake (Buckman and Brady,1969).

Table 5.16 Summary Statistics for Soil Magnesium (parts per million of soil air dry weight)

LOCATION	MEAN	ST.DEV.	MIN.	MAX.
MENDOCINO	98	88.476	42	200
COASTAL	200	0.0	200	200
SIERRAS	86.2727	64.7597	17	200
ROCKIES	164.25	40.8158	105	200
SEROT.ROCK.	164.667	30.7463	144	200
NON-SER.ROCK.	164	49.4217	105	200

Table 5.16 and figure 5.10 show that magnesium levels are high at both of the coastal sites with non-serotinous cones, and also high at some sites within each of the other regions. Average levels of magnesium appear to be higher for the Rocky Mountain sites than for the Sierra Nevada sites, but the many data points for which magnesium levels are known only as having a value exceeding a very high level, as well as the great variability within the groups, preclude any implication that magnesium is related to group structure. Also, no trends are evident from figure 5.10 which would relate the variation in levels of soil magnesium to cone characters. In general, compared to the low values for phosphorus, potassium, and pH which occur in the soils of some of the sites, magnesium levels would appear to be more than adequate for all sites.

Although some interactions between soil variables have been discussed in the preceeding paragraphs, the technique of examination of stereograms which has been used has been essentially univariate in terms of soil variables even though it has been multivariate in terms of the consideration of principal components based on cone characteristics. To examine interactions among the four soil variables which were measured, another method was employed. Each of the sites was described in terms of pH and the logarithms of the levels of exchangeable soil ions; logarithms were used so that all of the soil variables were described in scale free units consistent with the description of pH. Then a principal components analysis was performed for the sites in terms of their soil variables, and the sites were plotted on a stereogram based on the first three principal axes. The sites were labelled on the stereogram using the same numbers which were used previously to identify the groups, except that the number 4 was used to refer only to the Rocky Mountain subgroup with more serotinous cones, and the number 5 was used to identify the Rocky Mountain subgroup with less serotinous cones. This technique was employed because of its potential for revealing groups or trends based on a combination of the soil variables which could be related to the groups based on cone characteristics.

The results of the principal components analysis, which are given in appendix G, show that the first three principal components account for 96% of the variance. The first component has a very large positive correlation (.95) with soil phosphorus and a large negative correlation (-.67) with magnesium. The second component has large positive correlations (ranging from .69 to .86) with all of the soil variables except phosphorus. The third component has a moderately large positive correlation (.52) with pH.

Examination of the stereogram of the sites plotted in terms of the first three soil principal components (figure 5.ii) reveals that although there is not a sharp group structure based on soil variables corresponding to the groups based on cone characteristics; nevertheless, there exists a definite ordering of the previously identified groups along a trend line which is roughly parallel to the first principal axis but also inclined towards the second principal axis. This trend line goes from the coastal group with serotinous cones through the coastal group with non-serotinous cones, the Rocky Mountain group with more serotinous cones, the Rocky Mountain group with less serotinous cones to the Sierra Nevada group. The extremely high positive correlation of the first principal axis with soil phosphorus, which also has a positive correlation (.29) with the second principal axis, confirms the important relationship of soil phosphorus levels to the groupings based on cone characters. The importance of the correlation of the first principal axis with magnesium is negated by the inclination of the trend towards the second principal axis:

since the level of magnesium is negatively correlated with the first principal axis but has a positive correlation of about the same magnitude with the second principal axis, therefore the direction of a trend which lies between the directions of these axes will have approximately no correlation with magnesium levels.

Based on this conclusion that the trend corresponding to group membership is essentially perpendicular to the direction corresponding to the variation in magnesium, it was decided to plot ~~a~~ stereogram of a direct ordination of the sites in terms of the other three soil variables: phosphorus, potassium, and pH (figure 5.12). It was felt that this direct approach might be useful not only in providing easy interpretation of the axes, but also in removing "noise" caused by wide variations in magnesium which apparently bear little relationship to the group structure. Examination of this stereogram confirms the preceeding conclusions concerning a well-defined trend in group membership associated with soil phosphorus, and emphasizes the absence of any noticeable relationship of the overall group structure to the other measured soil variables.

In conclusion, geographic location is clearly the most important of the extrinsic variables discussed in terms of its obvious relationship to the group structure, but this variable is unable to account for the division of the populations of the coastal region into two groups nor does it account for the subdivision of the Rocky Mountain group into two subgroups. Based on the preceeding results and discussion, the most likely underlying factor considered which could account for these divisions is available soil phosphorus. However, as Jenny, Arkley, and Schultz(1969) point out in discusssing possible "edaphic" causes for the pygmy vegetation near Mendocino, "There is an enormous multiplicity of 'causes', for thousands of soil properties are interrelated among each other, and with countless properties of the root system, and with enzymatic reactions and metabolic pathways inside the plant." All that this investigation has done is focus on a likely candidate for inclusion in further investigations.

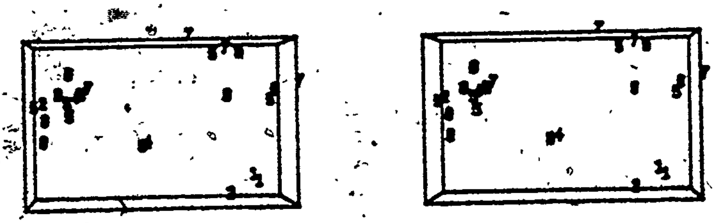


Figure 5.9 Stereogram showing ranks for potassium.

Figure 5.10 Stereogram showing ranks for magnesium.

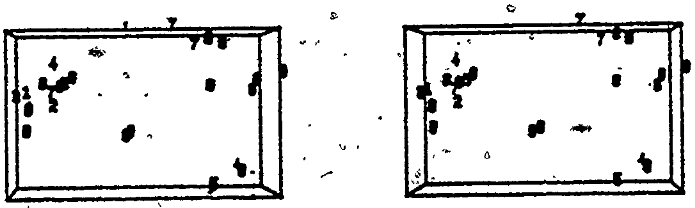


Figure 5.11 Stereogram relating group structure to principal components based on soil variables.

The numbers identify the groups which were formed on the basis of cone characters:

1 refers to the coastal group with serotinous cones,

2 refers to the coastal group, with non-serotinous cones,

3 refers to the Sierra Nevada group,

4 refers to the Rocky Mountain group with more serotinous cones,

5 refers to the Rocky Mountain group with less serotinous cones.

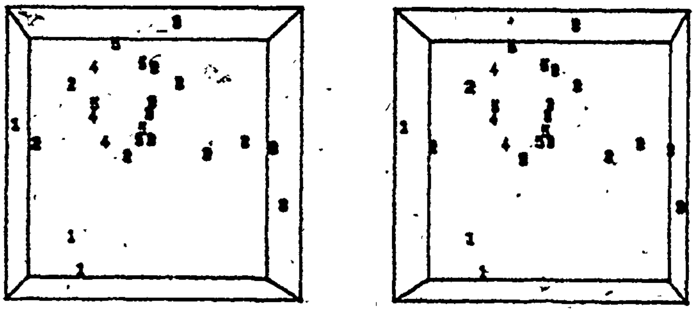
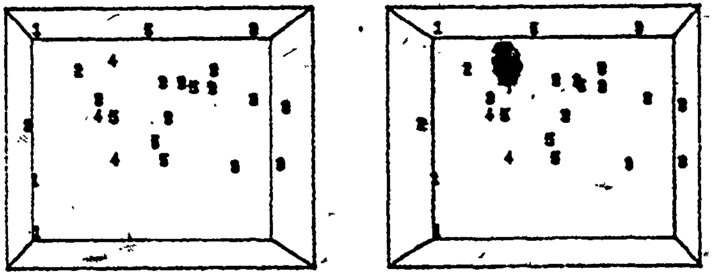


Figure 5.12 Direct ordination of sites based on three of the soil variables.

The horizontal and vertical axes in the plane of the page represent the levels of phosphorus and pH, respectively; while the axis perpendicular to the page represents potassium. The numbers identify the groups as in figure 5.11.



CHAPTER 6

VARIATION WITHIN GROUPS

1. The Sierra Nevada Group

In this section, the variation of the cone characters among the sites of the Sierra Nevada group is examined, and an attempt is made to relate this variation to extrinsic factors. Although figure 4.3 provided an excellent three-dimensional representation of the overall resemblance relationships among the sites, it would be expected that an improved three-dimensional display of the resemblances among the sites within a particular group could be obtained by examination of the stereogram based on a principal components analysis within that group by itself. The degree of improvement would depend on the extent to which the main trends of variation within the particular group correspond to the main trends of variation in the total collection of sites. Although the overall correlation of the resemblances among sites depicted by figure 4.3 with the resemblances based on the total dimensions of the data was .993; nevertheless, when the comparison was restricted to the matrices of resemblances among the Sierra Nevada sites, the correlation was found to be only .762. This suggests that there are significant differences between the overall trends in the cone characters and the trends within the Sierra Nevada group. Therefore, a principal components analysis of the Sierra Nevada sites was performed, and the resemblance matrix among the sites based on the first three components was compared to the resemblance matrix based on the total dimensions to reveal a much improved correlation of .989.

Figure 6.1 provides the three-dimensional stereogram of the Sierra Nevada sites based on the first three principal axes obtained from the principal component analysis within the Sierra Nevada group. The sites which have previously been referred to (table 3.3) as sites 6 to 16 are labelled on the stereogram with the letters A to K, consecutively. It should be noted that the two axes displayed in the plane of the paper are not the first two principal axes, but rather the first and third principal axes, with the second principal axis being portrayed in the direction perpendicular to the page. The reason for this is that the computer program used to produce the stereograms plots the axes in the order of their greatest difference between the maximum and minimum values of the points plotted along the axes rather than in terms of the greatest variance along the axes, which is the criterion used to order the axes in a principal components analysis.

The detailed results of this principal components analysis are presented in Appendix H. Examination of these results, and of figure 6.1 reveals that, as for the principal components analysis of all of the sites, almost all of the variance is accounted for by the first three principal components (87%); however, the results differ in that the shape of the Sierra Nevada cluster is more spherical, with the first principal component accounting for only 38% of the variance, while the second principal component accounts for 28%, and the third component accounts for 21%. Thus, there is not a strong directional trend in cone characteristics evident within the Sierra Nevada group such as was evident based on the principal components analysis which included all of the sites, in which case the first principal component accounted for 75% of the variance.

The first principal axis has large positive correlations (.81 to .84) with three cone characters: cone volume, apophysis height, and the ratio of apophysis height to apophysis length; thus, this direction corresponds to increasing cone size accompanied by increasing prominence of the apophyses. The second principal axis has a large positive correlation (.88) with the ratio of cone width to cone length; while the third principal axis has a large positive correlation with cone specific gravity and large negative correlations (-.70 to -.74) with cone symmetry and the ratio of apophysis height to apophysis width. The only two cone characteristics not noted as having high correlations with the first three principal axes are cone serotiny and the ratio of the volume of a cone to the volume of a cylinder of equivalent length and width. These two characters have their highest correlations (.70 and .77, respectively) with the fourth and fifth principal axes, which each account for only about 5% of the total variance. Thus, it is evident that these two characters are of relatively less importance in describing the variation within the Sierra Nevada group.

It is interesting to note the relative positions on the stereogram of the two sites which showed the most divergence from the main Sierra Nevada group according to the previous cluster analyses. These sites are the site at 2400 meters elevation near Bishop, California, (represented on the stereogram by the letter A) and the extreme southern site near Big Bear Lake (represented on the stereogram by the letter K). These two sites not only show a separation from the main spherical cluster of Sierra Nevada sites, but also are the most dissimilar pair of all pairs of Sierra Nevada sites, and are at opposite ends of the first principal axis. Thus, site A has unusually small values for those cone characteristics which have a high positive correlation with the first principal axis (i.e. cone volume, apophysis height, and the ratio of apophysis height to apophysis length); whereas, site K has unusually large values of these cone characters. A possible explanation for the divergence of these two sites from the main group of Sierra Nevada sites is that each of these sites occupies an "outlying" position relative to the geographic range of the Sierra Nevada group; whereas, the other Sierra Nevada sites are, by comparison, more "interior" to the geographic range of the group. That is, site K represents an isolated southern occurrence; while site A is on the extreme eastern edge of the range adjacent to the desert. (Although other Sierra Nevada sites have more easterly longitudes than site A; nevertheless, because the boundary between the desert and the mountains follows a northeasterly trend, these other sites are further from the desert.) The divergence of these two sites from the main group would thus seem to be a result comparable to that described by Beshir(1975) for Pinus banksiana, for which he found a single essentially homogeneous group except for the divergence of those sites at the periphery of the geographic range.

To provide a visual assessment of the degree of overlap in cone characteristics among the Sierra Nevada sites, a principal components analysis was performed based on the 110 individual cones of the Sierra Nevada group, and the first three principal components for each cone were plotted in figure 6.2 using the previously defined site labels, A to K. Recall that the comparable procedure applied to the total set of 240 cones labelled by geographic region displayed a clear separation into four groups with almost no overlap (figure 4.2). In contrast, figure 6.2 shows a great deal of overlap among the sites with no evidence of any separation of subgroups of sites.

The locations at which cones were collected within the Sierra Nevada region were particularly chosen to provide insight into the variation of the cone characteristics with respect to elevation and latitude. Figure 6.3 displays the elevations of the Sierra Nevada sites on the stereogram of their first three principal components, using the same numerical ranks to represent elevation as were used in a previous section. Examination of this stereogram does not provide clear evidence of a trend in cone characters corresponding to changes in elevation except that the two lowest elevation sites have the largest values on the second principal axis. To investigate a possible relationship between the second principal component and elevation, some advantage may be gained from the particular pattern of sampling within the Sierra Nevada; that is, two or three sites at different elevations were sampled at each of four general locations, with very little geographic separation between the sites of different elevation at each general location. Table 6.1 gives the values of the second principal component for each of the sites of these four geographic locations with the rows of the table corresponding to the four general locations presented in the order of decreasing latitude from the top to the bottom of the table, and the columns corresponding to increasing elevation from the left side to the right side of the table.

Figure 6.1 Stereogram of Sierra Nevada sites.

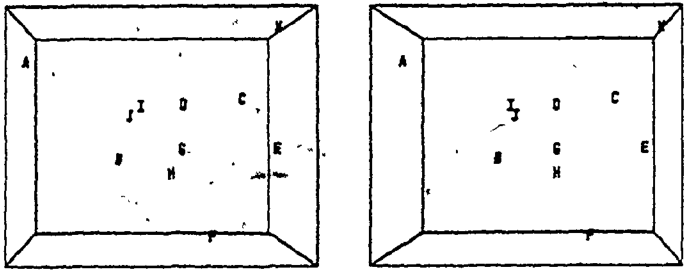


Figure 6.2 Stereogram of Sierra Nevada cones.

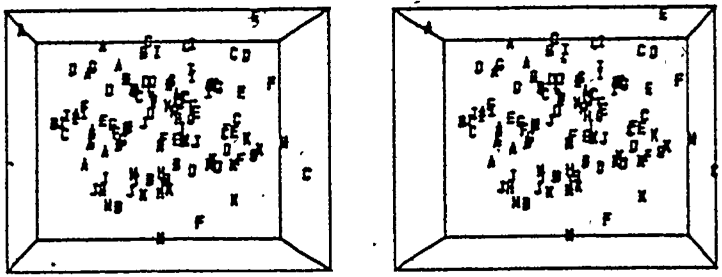


Figure 6.3 Stereogram relating variation within the Sierra Nevada to elevation.

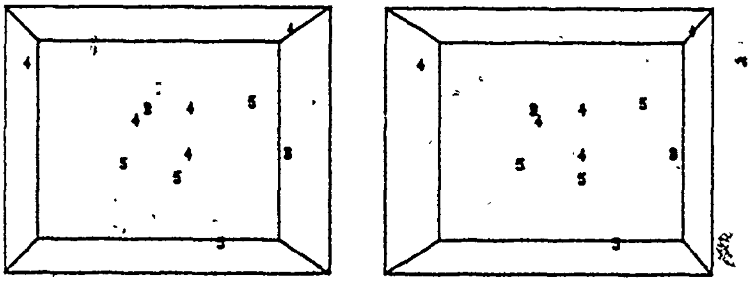


Table 6.1 Second principal component of Sierra Nevada sites related to elevation and latitude.

	elevation 3	elevation 4	elevation 5
north	.39	.17	
central		.09	-.05
south (east)		.06	-.05
south (west)	.37	-.36	-.47

The interesting result which can be observed in table 6.1 is that for all four groups of sites the higher elevation sites have a smaller value on the second principal axis. This suggests that there is a consistent decrease with elevation in those cone characters with high positive correlations with the second principal axis, and a consistent increase with increasing elevation in those cone characters with high negative correlations with the second principal axis. Recall that the cone character having the greatest magnitude of correlation with the second principal axis was the ratio of cone width to cone length, with a correlation of .88.

To further examine the possible relationship of cone characters to elevation, the ranking program developed by Jancey(1979) was applied to the Sierra Nevada cone data in order to compute "F-values" for each character for the pairs of nearby sites at differing elevations. The relevant results of this program are presented in table 6.2, and will be interpreted with reference to the preceeding principal components analysis, and the summary of cone characters for each site which is contained in Appendix B.

Table 6.2 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN CONES FROM NEARBY SITES OF DIFFERING ELEVATIONS IN THE SIERRA NEVADA.

(a). BP2400 versus BP3050

RANK	CHARACTER	NUMBER	F VALUE
1	apoph.ht.	3	16.6997
2	symmetry	7	7.09576
3	vol/cylvol	6	6.82656
4	apoph.h/w.	9	4.42309
5	volume	2	2.22213
6	apoph.h/l.	8	1.68429
7	sp.gr.	4	0.834312
8	serotiny	1	0.766774
9	cone.wid/l.	5	0.081981

Table 6.2 (continued)

(b) TRUCKEE versus MT.ROSE

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	5.46552
2	apoph.h/l.	8	4.90881
3	cone.wid/l.	5	2.5664
4	symmetry	7	2.1851
5	volume	2	1.67145
6	apoph.h/w.	9	1.26581
7	vol/cylvol	6	0.080198
8	apoph.ht.	3	0.057834
9	sp.gr.	4	0.004820

(c) UP.HORSE versus SADDLBAG

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	4.83129
2	apoph.ht.	3	2.48605
3	apoph.h/w.	9	2.15175
4	serotiny	1	1.45956
5	vol/cylvol	6	1.37032
6	volume	2	0.646241
7	apoph.h/l.	8	0.591116
8	cone.wid/l.	5	0.22051
9	symmetry	7	0.040879

Table 6.2 (continued)

(d) DINKEY versus HUNTING.

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	10.9592
2	cone.wid/l.	5	10.7344
3	apoph.ht.	3	9.01255
4	volume	2	6.7972
5	serotiny	1	1.99578
6	apoph.h/l.	8	0.175825
7	symmetry	7	0.12605
8	vol/cylvol	6	0.00518
9	apoph.h/w.	9	0.001108

(e) HUNTING versus KAISER

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	17.3812
2	sp.gr.	4	2.14108
3	apoph.h/l.	8	1.23867
4	symmetry	7	1.23305
5	apoph.ht.	3	1.17594
6	volume	2	1.10049
7	apoph.h/w.	9	0.469809
8	cone.wid/l.	5	0.188114
9	vol/cylvol	6	0.062223

Table 6.2 (continued)

(f) DINKEY versus KAISER

RANK	CHARACTER	NUMBER	F VALUE
1	cone.wid/l.	5	11.4682
2	serotiny	1	7.84958
3	sp.gr.	4	6.62903
4	volume	2	5.38894
5	apoph.ht.	3	5.26193
6	apoph.h/l.	8	1.25801
7	symmetry	7	0.96695
8	apoph.h/w.	9	0.343421
9	vol/cylvol	6	0.170621

Since the ratio of cone width to cone length had the greatest magnitude of correlation of any character with the second principal axis, this character will be examined first. From table 6.2, it can be seen that the F-values for this character are comparitively large only for those comparisons involving the "DINKEY" site; this implies the lack of any consistent general relationship between elevation and the ratio of cone width to cone length.

A procedure for possibly identifying those cone characters which have a consistent relationship with elevation is to look for those characters which have the highest rankings for discrimination between each of the "elevation-pairs" of sites, and observe whether any of the characters are consistently highly-ranked. For example, although apophysis height is the highest ranked character for discrimination between the pair of sites "BP2400" and "BP3050", nevertheless, this character is not highly-ranked for discrimination between any of the other pairs of sites. Only two characters show any indication of consistently high ranking for discrimination between the elevational pairs; namely, cone serotiny and cone specific gravity, and even for these characters, the high ranking occurs only for 3 out of the 6 pairs of sites. Thus, any relationship between cone characters and elevation within the Sierra Nevada is not particularly strong.

For cone serotiny, in one of the cases where it is highly-ranked, the results in Appendix B show that the higher elevation site has greater cone serotiny than the lower elevation site; whereas, in the other two cases the lower elevation site has greater cone serotiny than the higher elevation site. This contradiction implies that the relatively high ranking for cone serotiny does not correspond to a consistent trend related to elevation.

For cone specific gravity, for those three cases for which this character is highly-ranked for its ability to discriminate between the "elevation-pairs", the higher elevation sites all have cones with lower specific gravity than the lower elevation sites with which they are paired. Thus, the only relationship between elevation and cone characters which could be supported based on the results discussed above is a tendency for cones from higher elevations to have lower specific gravity. This decrease in specific gravity with elevation was also noted by Critchfield(1957) for cones from sites in the Sierra Nevada, Cascade Mountains of Washington and Oregon, and Blue Mountains of Oregon, although the pairs of sites on which he based his inference were not as close geographically as the pairs are in the present study. This relationship between elevation and specific gravity will be examined further in the subsequent discussion of variation within the Rocky Mountain group.

Table 6.1 does not suggest any clear trend of variation in the second principal component with latitude; to search for other possible trends with latitude, figure 6.4 was created by plotting the previously defined ranks for latitude on the stereogram of the first three principal components for Sierra Nevada sites, but no trends are evident.

Another comparison of interest for the Sierra Nevada group is the comparison of the three sites from the west side of the Sierra Nevada with the sites from the east side. Figure 6.5, which was created by plotting on the stereogram of Sierra Nevada sites the letter W to represent the sites from the west side of the Sierra Nevada and the letter E to represent the sites from the east side of the Sierra Nevada, does not demonstrate any segregation of the western sites from the eastern sites, but rather the western sites occupy an "interior" position on the stereogram.

Ranks for the climatic and edaphic variables considered in the previous section were also plotted on the stereogram of the first three principal components for the Sierra Nevada sites. Examination of these stereograms, which are included in Appendix J, did not reveal any trends for any of these variables in relation to the cone characters for the Sierra Nevada sites.

In conclusion, the Sierra Nevada sites appear to represent an essentially homogeneous group with some divergence from the group occurring only for two sites on the periphery of the geographic range; also, there are no evident trends in cone characters related to any of the extrinsic factors considered except for a tendency for cone specific gravity to decrease with elevation.

Figure 6.4 Stereogram relating variation within the Sierra Nevada to latitude.

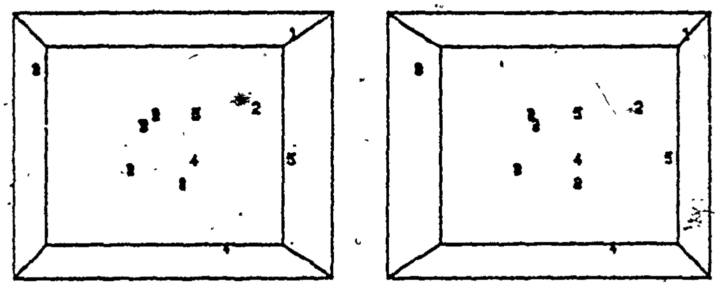
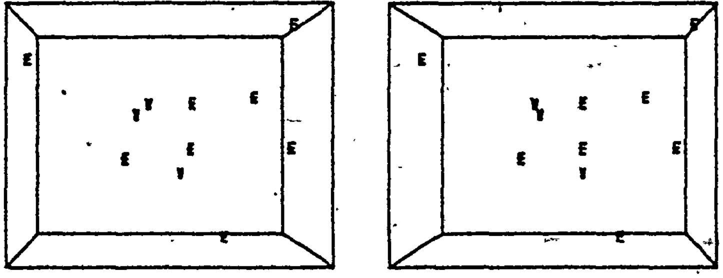


Figure 6.5 Comparison of sites on the eastern and western sides of the Sierra Nevadas.



2. The Rocky Mountain Group

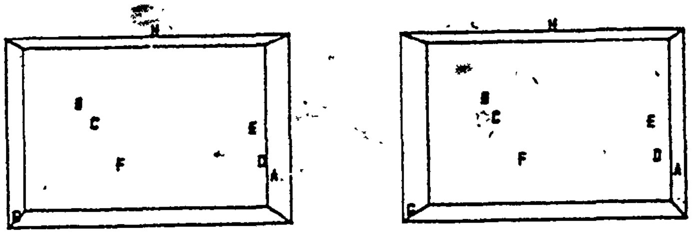
In this section, the variation of the cone characters among the sites of the Rocky Mountain group is examined, and an attempt is made to relate this variation to extrinsic factors. The analysis parallels that done for the Sierra Nevada group, and comparisons will be made where appropriate between the results for the two groups.

For the Sierra Nevada group, it was shown that a considerable improvement in portraying the resemblances among the sites within that group could be obtained if the sites were plotted on the first three axes derived from a principal components analysis within that group, rather than using the first three principal axes derived by a principal components analysis of the total set of sites. The corresponding comparison for the Rocky Mountain group showed only a slight improvement in the portrayal of the resemblances among the sites within the Rocky Mountain group by using the first three principal axes derived by principal components analysis within the group. The corresponding correlations of the resemblance matrices with the resemblance matrix based on all cone characters were .958 for the case where the three principal axes were obtained by principal components analysis of the total set of sites, and .992 for the case where the three principal axes were obtained by principal components analysis within the Rocky

Mountain group. Thus, the trends within the total set of sites show a closer relationship to the trends within the Rocky Mountain group than they did to the trends within the Sierra Nevada group.

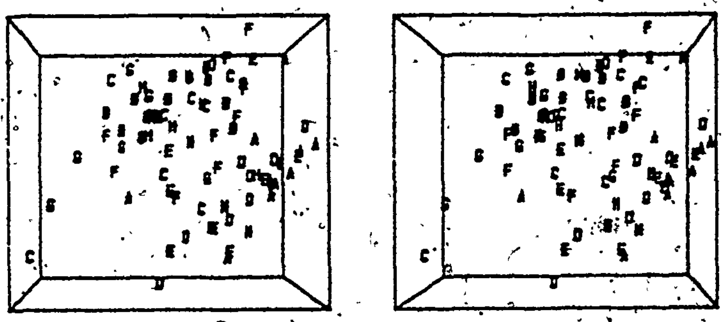
Figure 6.6 provides the three-dimensional stereogram of the Rocky Mountain sites based on the first three principal axes obtained from the principal component analysis within the Rocky Mountain group. The sites which have previously been referred to (table 3.3) as sites 17 to 24 are labelled on the stereogram with the letters A to H, consecutively. The detailed results of the principal components analysis are presented in Appendix I. The first three principal components account for 92% of the total variance, with 62% accounted for by the first principal component which thus represents a major trend within the group. The cone characters with the largest magnitude of correlation with the first principal axis are: cone serotiny (.94), cone specific gravity (.92), and apophysis height (.86). Thus, the major trend within the Rocky Mountain group consists of increases in cone serotiny, specific gravity, and apophysis height along the direction of the first principal axis. For the other principal axes, the largest magnitudes of correlation with cone characters are -.86 between the second principal axis and the ratio of cone width to cone length, +.74 between the third principal axis and cone symmetry, and -.71 between the third principal axis and the ratio of apophysis height to apophysis length.

Figure 6.6 Stereogram of Rocky Mountain sites.



Since a difference in cone serotiny, which is highly correlated with the first principal axis, was previously found to be the major difference between the two Rocky Mountain subgroups, it is not surprising that these subgroups are seen, upon inspection of figure 6.6, to be clearly separated along the direction of the first principal axis. The stereogram reveals not only a close grouping of three sites with more serotinous cones and another close grouping of three sites with less serotinous cones, but also a divergence of two of the sites with less serotinous cones from the other sites. These two divergent sites are site H, the Utah site, and site G, the high elevation site on the west side of the Front Range in Colorado. The divergence of the Utah si[illegible] is not unexpected, since it has a comparatively large geographic separation from the other Rocky Mountain sites. The divergence of the high elevation site on the west side of the Front Range could be related to the extremely low average annual temperatures at that site, which is the coldest of all the sites sampled. Thus, as for the Sierra Nevada group, divergence of cone characters occurs at those sites whose location or environmental conditions are "extreme" relative to the main group.

Figure 6.7 Stereogram of Rocky Mountain cones.



To provide a visual assessment of the degree of overlap in cone characteristics among the Rocky Mountain sites, a principal components analysis was performed based on the 80 individual cones of the Rocky Mountain group, and the first three principal components for each cone were plotted in figure 6.7 using the previously defined site labels, A to H. This stereogram reveals two main subgroups of cones, with very little overlap, corresponding to the two subgroups of sites previously identified. It also shows a definite separation between the cones from the Utah site and the other sites in the direction perpendicular to the page.

From figure 6.6, it can be seen that the main separation between the Utah site and the other Rocky Mountain sites occurs in the direction of the second principal axis. The large magnitude of correlation of the ratio of cone width to cone length with this axis suggests that a closer examination be made of the variation of this character between the Utah sites and the other Rocky Mountain sites. Appendix K presents the results of applying the Jancey(1979) ranking algorithm to the comparison of the cone characters of the Utah site with each of the other Rocky Mountain sites. The only character which is consistently highly-ranked for its ability to discriminate between the Utah site and the other Rocky Mountain sites is the ratio of cone width to cone length. Recall, that it was shown in a previous section that this character was one of the most highly-ranked for its ability to discriminate between the cones of the California groups and the Rocky Mountain group. Appendix B shows that the ratio of cone width to cone length for cones from the Utah site is much less than it is for cones from the other Rocky Mountain sites and, in fact, is about half-way between the values for the California sites and the Rocky Mountain sites in Colorado. Thus, with respect to this particular character, the Utah site is intermediate between the California sites and the Colorado sites; however, as shown by the clustering results and the stereogram of all of the sites, the much greater similarity of the cones from the Utah site to those from Colorado with respect to other characters clearly places the Utah site within the Rocky Mountain group.

Figure 6.8 displays the ranks for elevation of the Rocky Mountain sites on the stereogram of these sites. All except two of the sites were at high elevations, and no obvious pattern relating cone characters to elevation is apparent from this stereogram. Four of the Rocky Mountain locations were chosen to provide information on variation of the cones with elevation between nearby pairs of sites of equivalent topographic situations; these two pairs are depicted on figure 6.6 as sites D and C at low and high elevations, respectively, on the east side of the Front Range of the Rocky Mountains in Colorado, and sites F and G at low and high elevations on the west side of the Front Range. From this stereogram, it can be seen that in both cases the lower elevation site of each pair has a larger value along the first principal axis; this suggests a decrease with elevation in those characters with high positive correlations with the first principal axis (i.e. cone serotiny, cone specific gravity, and apophysis height). The application of the Jancey(1979) ranking algorithm to the cone characters for the two pairs of sites produced the results shown in table 6.3.

Examining table 6.3, it is obvious that the only cone character which is highly-ranked based on its ability to discriminate between the high and low elevation sites for comparisons on both the east and west sides of the Front Range is cone specific gravity; this is true even for sites F and G, for which there is little difference in cone serotiny, which Critchfield(1957) had assumed to be highly correlated with cone specific gravity. From Appendix B, it is seen that cone specific gravity is lower at the high elevation sites. Thus, the data for the Rocky Mountain sites confirm the trend suggested by the Sierra Nevada sites of a decrease in specific gravity with higher elevation.

Figure 6.8 Stereogram relating variation within the Rocky Mountains to elevation.

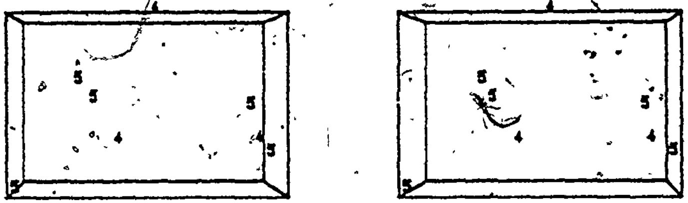


Table 6.3 CHARACTER RANKING BASED ON THEIR ABILITY TO DISCRIMINATE BETWEEN CONES FROM NEARBY SITES OF DIFFERING ELEVATIONS IN THE ROCKY MOUNTAINS.

(a) VALL2540 versus VALL3100

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	23.493
2	sp.gr.	4	16.9414
3	cone.wid/l.	5	0.731536
4	volume	2	0.499088
5	vol/cylvol	6	0.398351
6	apoph.h/w.	9	0.137453
7	apoph.ht.	3	0.135891
8	apoph.h/l.	8	0.096972
9	symmetry	7	0.01759

(b) FRASER versus MEAD.CR.

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	10.3016
2	apoph.h/l.	8	5.69507
3	symmetry	7	2.15368
4	apoph.h/w.	9	1.81819
5	apoph.ht.	3	1.2051
6	serotiny	1	1.00862
7	vol/cylvol	6	0.736915
8	cone.wid/l.	5	0.324469
9	volume	2	0.111732

The Rocky Mountain sites were chosen not only to provide insight into variation in cone characters with respect to elevation, but also to provide information on the variation in cone characters among nearby sites of varying topographic situations at the same elevation. The four sites chosen for this purpose are depicted on figure 6.6 by the letters A, B, C and E, where:

A is a ridge top site,

B is a valley bottom site,

C is on a south-facing slope,

E is on a north-facing slope.

From figure 6.6, it can be seen that there are relatively large differences between these nearby sites compared to the amount of variation within the Rocky Mountain group. In particular, two of the four sites are part of the subgroup with more serotinous cones, while the other two are part of the subgroup with less serotinous cones. Referring back to table 3.4 which summarized the climate for the sites, and recalling also the discussion of the variation of soil temperature with topography, there is no evident pattern relating the variation in climatic factors which accompany the variation in topographic situations to the subdivision of the sites from different topographic situations between the subgroups with more and less serotinous cones.

The extrinsic variable which has been shown, in the previous analysis of variation between the groups, to be most closely related to the divisions into more and less serotinous groups was available soil phosphorus. Figure 6.9, which displays the ranks for exchangeable soil phosphorus on the stereogram of the Rocky Mountain sites, shows a decrease of soil phosphorus in the direction of the first principal axis, which has been shown to be highly correlated with cone serotiny, and thus this figure provides additional evidence of a relationship between these variables.

The stereograms relating the other soil variables and the climatic variables to the cone characteristics of the Rocky Mountain sites are given in Appendix L, and do not reveal any evident trends, except that the stereogram which displays the ranks for average annual temperature suggests a trend of increasing temperature in the direction of the first principal axis. However, this apparent trend could be largely attributed to the extremely low temperature at the site at 3050 meters elevation on the west side of the Front Range which occupies an outlying position on the stereogram.

In conclusion, there exists a major trend within the Rocky Mountain group, which is expressed by the first principal axis, of an increase in cone serotiny, specific gravity, and apophysis height. The extrinsic factor most closely related to this trend in cone characters is soil phosphorus. Along the direction of this trend, the Rocky Mountain group splits into two subgroups with more and less serotinous cones. There are also two sites which tend to diverge from the other sites of the Rocky Mountain group; as was the case with the two divergent Sierra Nevada sites, these two Rocky Mountain sites occupy extreme positions relative to the environmental and geographic range of the group. The cones from the Utah site show a consistent significant difference from the cones of the Colorado sites only in the ratio of cone width to cone length; for this character, the cones of the Utah site have values about half-way between the values for the cones from California and the cones from Colorado. In agreement with the results for the Sierra Nevada group, there is a consistent decrease of cone specific gravity with elevation.

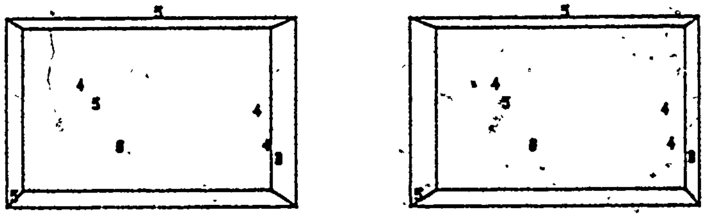


Figure 6.9 Stereogram relating variation within the Rocky Mountains to soil phosphorus.

CHAPTER 7

SUMMARY

Two preliminary studies were undertaken to optimize the allocation of the effort required to measure the cone characters, so that a maximum possible number of sites could be included in the study. These preliminary studies were carried out prior to the field work, using cones provided by Rall and Illingworth. The first study demonstrated that a sample of one cone from each of ten trees at each location provided an adequate basis for the computation of a matrix of resemblances among locations. The second study selected a set of cone characters for measurement through the application of an algorithm which ranked characters on the basis of a comparison of their variation between locations to their variation within locations (Jancey,1979). The characters selected were cone volume, the ratio of cone width to cone length, cone specific gravity, cone taper as measured by the ratio of the volume of the cone to the volume of a cylinder of equal length and diameter, cone serotiny, cone symmetry as measured by the ratio of the length from the point of attachment of the peduncle to the tip of the cone to the total length of the cone, apophysis height, the ratio of apophysis height to apophysis length, and the ratio of apophysis height to apophysis width.

Several of these characters have definitions which are original to this study, and might be of use in other studies of geographic variation in cones. In particular, cone serotiny is defined as a continuous variable measuring the proportion of the total length of the cone for which the scales are closed. This definition for cone serotiny not only expresses this variable on a scale which is more compatible than the previously used binary or interval scales with the scale used for the measurements of the other cone characters, but also this new definition is more informative concerning the degree of serotiny expressed by a cone.

Cones and data were collected from 24 locations in California, Utah, and Colorado. These locations were selected to provide information on the variation of the cones of Pinus contorta among the four geographic subspecies recognized by Critchfield(1957), and to compare the magnitude of the variation between geographic regions to the variation with respect to changes in elevation, latitude, topographic situation, climate and soil.

Preliminary analyses of the data structure were performed by using principal component analyses followed by the plotting of stereograms of the first three principal components. By correlating resemblance matrices, it was shown that there was very little distortion in these three-dimensional displays. The stereograms revealed a clear group structure corresponding to the four subspecies defined by Critchfield(1957), with the addition that the population with serotinous cones from the serpentine soil of northwest California was grouped with the populations with serotinous cones from the highly-acid soil near Mendocino.

A wide range of clustering algorithms (clustering by neighbourhoods, single linkage clustering, complete linkage clustering, and average linkage clustering) were applied to the data and confirmed the basic structure of four groups. They also revealed two subgroups within the Rocky Mountain group separated on the basis of the degree of cone serotiny, and a tendency for two sites within the Sierra Nevada group to diverge from the main group; however, these differences within the groups were not large enough to influence the clustering into four main groups.

The Jancey(1979) character ranking algorithm was used to identify those cone characters which showed the most significant differences between the four groups and between the two Rocky Mountain subgroups. The following paragraphs summarize the main conclusions based on this procedure.

The difference between the two Rocky Mountain subgroups with respect to cone serotiny was found to be much greater than their differences with respect to any other cone character; whereas, for the two coastal groups, the difference in cone serotiny is accompanied by differences of comparable magnitude in specific gravity and apophysis shape, with the more serotinous cones having higher specific gravity and "knobbier" apophyses.

The cones of the two coastal groups do not show significant differences in their size, overall shape, symmetry, or the height of their apophyses.

The most useful of the characters for distinguishing between cones from the California groups and cones from the Rocky Mountain group is the ratio of cone width to cone length, with the California cones being narrower relative to their length than the Rocky Mountain cones. All of the California groups also have significantly shorter apophyses than the Rocky Mountain group. The shape of the apophyses of the coastal group with non-serotinous cones and of the Sierra Nevada group differs significantly from the shape of the apophyses of the Rocky Mountain group; whereas, the shape of the apophyses of the coastal group with serotinous cones does not differ significantly from those of the Rocky Mountain group.

A unique distinction between the cones of the Sierra Nevada group and the cones of any other group is that the Sierra Nevada cones are much more symmetric.

The use of a continuous measure of cone serotiny reveals significant differences between the degree of serotiny of the Sierra Nevada cones and the "non-serotinous" cones of the coast, with the Sierra Nevada cones being more open.

Critchfield(1957) regarded cone specific gravity as being the most useful character for distinguishing between the cones of the four groups. The results of the present study show that although there are significant differences in specific gravity between some of the groups; nevertheless, other characters are generally more highly-ranked based on their ability to distinguish between the groups.

The variation in cone characters between the groups was related to various extrinsic factors, with the main technique employed being the plotting of ranks for the extrinsic factors on stereograms of the first three principal components of the sites. The main conclusions from this part of the study were that geographic location was clearly the most important of the extrinsic variables considered in terms of its obvious relationship to the group structure, but this variable was unable to account for the division of the populations of the coastal region into two groups nor did it account for the subdivision of the Rocky Mountain group into two subgroups. The extrinsic variable which showed the greatest potential for explaining these divisions within the geographic regions was the amount of available soil phosphorus.

The variation of the cone characters among the sites within the Sierra Nevada group, and within the Rocky

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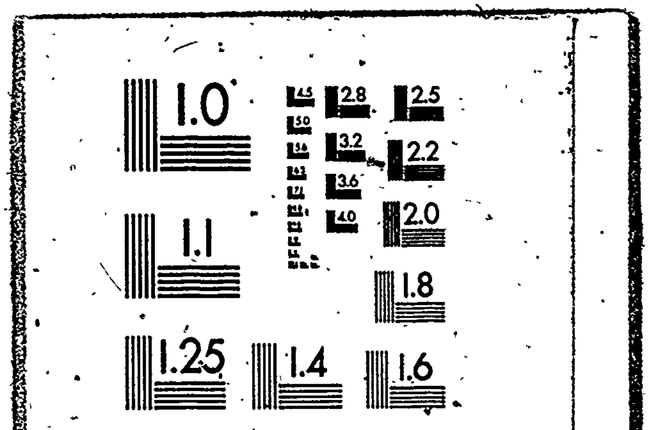

Mountain group, was examined and an attempt was made to relate this variation within groups to extrinsic factors. The main techniques used were principal component analyses within groups, the plotting of environmental ranks on stereograms based on these principal component analyses, and the application of the Jancey(1979) ranking algorithm to compare the ability of cone characters to discriminate between certain pairs of sites of particular interest.

The Sierra Nevada group did not show any strong trends in cone characters, but appeared to be a relatively homogeneous spherical group except for the divergence of two of the sites from the main group. These two divergent sites were the site at 2400 meters elevation near Bishop, California which was on the extreme eastern edge of the mountain range adjacent to the desert, and the site from the extreme southern location near Big Bear Lake.

The Rocky Mountain group showed a strong trend in cone characters consisting of an increase in cone serotiny, cone specific gravity, and apophysis height in the direction of the first principal axis. The extrinsic factor most closely related to this trend in cone characters was soil phosphorus. Along the direction of this trend, the Rocky Mountain group split into two subgroups with more and less serotinous cones. There were also two sites which tended to diverge from the other sites of the Rocky Mountain group; as was the case with the two divergent Sierra Nevada sites, these two Rocky Mountain sites occupied extreme positions relative to the environmental and geographic range of the group. The cones from the Utah site showed a consistent significant difference from the cones of the Colorado sites only in the ratio of cone width to cone length; for this character, the cones of the Utah site had values about half-way between the values for the cones from California and the cones from Colorado.

For both the Sierra Nevada sites and the Rocky Mountain sites the only character which showed a consistent variation with elevation was cone specific gravity which decreased with elevation.

This summary of the research has shown that the objectives presented in an earlier section have been satisfied. The patterns of variation in the southern part of the range of _Pinus contorta_ have been identified in terms of clusters related primarily to geographic location and available soil phosphorus, with a trend within the mountain regions related to elevation. The clusters identified correspond to the four subspecies defined by Critchfield(1957), with the addition that the population with serotinous cones from the serpentine soil of northwest California was grouped with the populations with serotinous cones from the highly-acid soil near Mendocino. In spite of the great variation in environment within the geographic regions, the strong group structure related to these regions demonstrates that the variation in cones within the regions is of much less magnitude than the variation in cones between the regions. It is recommended that this study be extended to cover the entire geographic range of _Pinus contorta_, with special attention given to the sampling of areas of possible transition between the groups identified in this study; for example, the Siskiyou Mountains of California and Oregon, the Blue Mountains of Oregon, and some river valleys in British Columbia which may provide a transition between coastal and inland groups.

APPENDICES

APPENDIX A: Data Before Transformation

The first number in each row identifies the location.

Cone Length (MM.)

1	43.000	42.000	39.000	39.000	39.000
1	34.000	35.000	43.000	43.000	37.000
2	38.000	36.000	38.000	35.000	48.000
2	39.000	53.000	44.000	46.000	42.000
3	42.000	39.000	43.000	51.000	43.000
3	47.000	43.000	42.000	44.000	48.000
4	54.000	37.000	35.000	36.000	36.000
4	36.000	36.000	39.000	44.000	39.000
5	42.000	34.000	36.000	38.000	39.000
5	34.000	32.000	38.000	37.000	43.000
6	45.000	38.000	40.000	45.000	48.000
6	48.000	39.000	44.000	47.000	36.000
7	42.000	52.000	38.000	47.000	36.000
7	42.000	50.000	41.000	37.000	55.000
8	42.000	49.000	60.000	54.000	44.000
8	37.000	39.000	47.000	35.000	48.000
9	42.000	54.000	40.000	44.000	41.000
9	52.000	37.000	39.000	38.000	50.000
10	44.000	45.000	46.000	49.000	41.000
10	44.000	38.000	41.000	44.000	42.000
11	40.000	45.000	40.000	44.000	49.000
11	51.000	58.000	40.000	37.000	41.000
12	41.000	53.000	40.000	41.000	46.000
12	42.000	51.000	42.000	47.000	42.000
13	54.000	42.000	51.000	54.000	50.000
13	45.000	57.000	56.000	54.000	44.000
14	34.000	38.000	43.000	40.000	45.000
14	42.000	37.000	44.000	49.000	42.000
15	48.000	46.000	53.000	43.000	45.000
15	53.000	52.000	51.000	45.000	49.000
16	58.000	54.000	58.000	52.000	50.000
16	62.000	61.000	61.000	54.000	55.000
17	34.000	48.000	42.000	37.000	33.000
17	34.000	46.000	38.000	34.000	39.000
18	39.000	39.000	34.000	41.000	41.000
18	39.000	39.000	39.000	37.000	41.000
19	40.000	38.000	40.000	34.000	34.000
19	44.000	50.000	46.000	43.000	47.000
20	41.000	40.000	38.000	47.000	40.000
20	33.000	36.000	48.000	35.000	40.000
21	50.000	39.000	37.000	36.000	37.000
21	39.000	36.000	41.000	35.000	42.000
22	34.000	35.000	36.000	38.000	36.000
22	41.000	39.000	29.000	37.000	37.000
23	32.000	40.000	38.000	36.000	32.000
23	30.000	33.000	34.000	44.000	39.000
24	36.000	54.000	50.000	46.000	48.000
24	41.000	39.000	40.000	44.000	44.000

Cone weight (g.)

1	6.100	5.600	3.800	4.300	4.500
1	3.400	3.200	6.200	6.000	4.500
2	4.600	3.700	3.600	3.400	5.700
2	4.500	8.000	5.200	5.400	5.800
3	6.000	3.100	3.200	7.400	3.400
3	5.200	3.600	4.200	4.700	5.300
4	5.800	2.800	2.400	2.800	2.400
4	2.900	2.300	2.600	4.500	3.100
5	5.900	3.800	3.700	3.500	4.400
5	4.000	3.600	4.000	4.800	7.700
6	2.800	2.800	3.400	3.100	4.800
6	4.200	2.400	3.700	3.600	2.100
7	2.700	6.200	3.300	4.000	4.100
7	3.200	4.800	2.400	2.800	5.100
8	14.000	4.600	8.400	7.000	4.100
8	3.600	3.500	5.800	3.200	4.600
9	3.500	6.200	3.300	5.100	3.900
9	6.200	2.300	3.200	3.000	6.300
10	5.500	5.200	5.900	6.000	3.500
10	4.900	4.600	4.600	4.100	3.600
11	2.700	3.900	3.100	3.200	4.400
11	4.900	7.000	3.300	1.700	3.100
12	4.300	7.200	3.800	3.800	3.500
12	3.300	4.900	3.400	5.100	3.800
13	5.900	3.100	3.500	4.100	3.000
13	3.500	6.700	4.500	7.100	3.600
14	2.600	3.200	3.400	3.300	4.200
14	4.300	3.700	3.400	7.000	3.700
15	4.200	4.200	4.700	3.500	4.100
15	5.000	4.500	3.700	4.300	3.300
16	10.300	6.700	5.900	6.200	8.000
16	6.600	8.600	9.500	7.600	6.300
17	5.400	7.200	6.500	5.000	5.900
17	4.400	7.700	5.500	4.200	5.600
18	4.600	5.600	3.700	6.200	6.200
18	4.400	5.600	3.400	4.100	4.900
19	5.200	5.000	5.200	4.500	3.600
19	5.100	8.100	6.700	5.400	7.100
20	8.100	6.000	6.800	6.100	6.300
20	2.700	3.700	6.900	4.900	6.400
21	8.700	4.900	4.200	4.400	5.500
21	5.300	3.500	6.500	4.600	8.500
22	3.600	5.200	3.900	3.800	3.600
22	5.200	4.700	2.500	3.300	4.200
23	3.100	5.000	3.600	3.500	2.700
23	2.600	2.800	2.100	5.600	5.300
24	4.100	7.300	8.900	6.300	6.900
24	4.800	6.100	5.100	5.100	5.700

Cone weight (g.)

1	6.100	5.600	3.800	4.300	4.500
1	3.400	3.200	6.200	6.000	4.500
2	4.600	3.700	3.600	3.400	5.700
2	4.500	8.000	5.200	5.400	5.800
3	6.000	3.100	3.200	7.400	3.400
3	5.200	3.600	4.200	4.700	5.300
4	5.800	2.800	2.400	2.800	2.400
4	2.900	2.300	2.600	4.500	3.100
5	5.900	3.800	3.700	3.500	4.400
5	4.000	3.600	4.000	4.800	7.700
6	2.800	2.800	3.400	3.100	4.800
6	4.200	2.400	3.700	3.600	2.100
7	2.700	6.200	3.300	4.000	4.100
7	3.200	4.800	2.400	2.800	5.100
8	14.000	4.600	8.400	7.000	4.100
8	3.600	3.500	5.800	3.200	4.600
9	3.500	6.200	3.300	5.100	3.900
9	6.200	2.300	3.200	3.000	6.300
10	5.500	5.200	5.900	6.000	3.500
10	4.900	4.600	4.600	4.100	3.600
11	2.700	3.900	3.100	3.200	4.400
11	4.900	7.000	3.300	1.700	3.100
12	4.300	7.200	3.800	3.800	3.500
12	3.300	4.900	3.400	5.100	3.800
13	5.900	3.100	3.500	4.100	3.000
13	3.500	6.700	4.500	7.100	3.600
14	2.600	3.200	3.400	3.300	4.200
14	4.300	3.700	3.400	7.000	3.700
15	4.200	4.200	4.700	3.500	4.100
15	5.000	4.500	3.700	4.300	3.300
16	10.300	6.700	5.900	6.200	8.000
16	6.600	8.600	9.500	7.600	6.300
17	5.400	7.200	6.500	5.000	5.900
17	4.400	7.700	5.500	4.200	5.600
18	4.600	5.600	3.700	6.200	6.200
18	4.400	5.600	3.400	4.100	4.900
19	5.200	5.000	5.200	4.500	3.600
19	5.100	8.100	6.700	5.400	7.100
20	8.100	6.000	6.800	6.100	6.300
20	2.700	3.700	6.900	4.900	6.400
21	8.700	4.900	4.200	4.400	5.500
21	5.300	3.500	6.500	4.600	8.500
22	3.600	5.200	3.900	3.800	3.600
22	5.200	4.700	2.500	3.300	4.200
23	3.100	5.000	3.600	3.500	2.700
23	2.600	2.800	2.100	5.600	5.300
24	4.100	7.300	8.900	6.300	6.900
24	4.800	6.100	5.100	5.100	5.700

Cone volume (cc.)

1	8.200	6.900	5.000	5.300	5.700
1	4.400	4.200	8.100	7.300	5.300
2	5.700	4.700	4.500	4.100	6.200
2	5.200	11.200	6.800	7.000	7.900
3	8.000	4.100	5.400	9.300	6.100
3	8.800	6.400	6.700	6.400	7.600
4	8.900	4.000	4.100	4.400	4.500
4	4.000	4.000	3.900	7.100	5.000
5	7.000	4.900	5.000	5.000	5.900
5	5.600	4.500	5.200	6.500	9.600
6	6.800	4.800	6.400	5.800	8.300
6	7.400	4.200	6.600	6.400	3.700
7	5.200	11.400	5.700	7.800	7.000
7	6.100	9.200	5.500	5.200	10.300
8	7.200	9.100	15.800	13.500	7.000
8	6.000	6.000	10.400	5.800	8.300
9	7.400	10.100	6.000	8.000	7.000
9	11.900	4.600	5.700	5.700	11.000
10	9.800	9.300	9.900	10.900	6.900
10	9.300	7.800	8.200	8.200	6.400
11	5.700	7.000	6.600	6.900	9.500
11	10.800	12.700	6.800	4.100	6.400
12	8.300	15.000	6.900	6.800	7.200
12	6.900	8.800	6.800	9.000	7.600
13	11.800	6.800	7.200	8.200	6.600
13	7.200	12.300	9.800	11.900	8.000
14	4.500	5.500	6.300	6.300	6.800
14	8.200	5.900	6.800	10.400	7.200
15	8.000	8.000	9.000	6.800	7.400
15	9.400	8.900	8.100	8.000	6.700
16	17.700	11.200	11.800	11.100	13.800
16	12.300	14.200	19.000	12.200	11.000
17	7.100	11.800	9.200	8.000	8.200
17	6.500	10.200	8.000	6.100	7.800
18	7.400	8.800	6.500	9.900	10.200
18	8.000	10.000	6.200	5.800	8.100
19	7.900	8.800	7.800	7.800	6.000
19	7.400	14.700	11.500	9.000	11.500
20	12.100	9.000	10.000	9.400	8.700
20	4.200	5.500	10.100	7.000	9.000
21	13.300	6.900	5.800	6.100	8.500
21	7.400	5.600	8.100	6.400	11.700
22	5.600	7.800	8.300	6.300	5.900
22	8.500	7.900	3.800	5.600	6.000
23	5.900	11.000	6.500	6.300	5.100
23	4.900	5.300	4.900	10.000	10.300
24	5.800	12.300	14.000	9.200	9.900
24	7.200	9.500	7.100	6.800	8.000

Cone width (mm.)

1	21.500	20.500	20.500	19.500	20.000
1	19.000	17.500	23.500	23.000	23.000
2	20.000	18.500	18.000	19.000	20.500
2	19.500	24.500	21.000	21.000	23.000
3	24.000	18.000	18.500	22.000	19.000
3	24.000	20.500	21.000	20.500	23.000
4	23.500	17.500	18.500	19.000	19.500
4	18.500	17.500	16.000	22.500	19.000
5	20.000	18.500	19.000	20.000	20.000
5	19.000	18.500	19.000	21.500	23.500
6	20.000	18.500	20.500	17.000	20.500
6	20.500	17.500	21.000	18.500	17.000
7	17.500	24.000	18.000	19.000	21.000
7	20.500	20.500	18.000	18.500	20.500
8	21.000	23.000	28.500	28.000	21.000
8	20.500	21.500	24.500	20.500	20.500
9	21.000	22.000	19.500	21.000	23.500
9	24.500	18.500	19.500	19.500	23.500
10	24.500	23.000	21.500	24.000	19.000
10	24.000	25.000	22.500	22.500	21.000
11	20.000	21.000	21.000	21.000	23.500
11	24.500	22.000	23.000	17.000	19.000
12	23.000	28.000	21.000	21.000	20.500
12	19.000	22.000	19.000	22.500	21.500
13	23.000	21.000	18.000	21.000	18.000
13	20.500	24.500	20.000	25.500	21.000
14	18.500	19.500	19.000	21.500	19.000
14	22.500	19.500	20.000	23.500	21.000
15	21.500	23.000	20.500	19.500	20.500
15	21.500	21.000	20.000	21.500	18.500
16	28.000	23.500	24.000	24.500	27.500
16	24.000	26.500	29.000	25.000	24.500
17	22.500	28.500	24.000	27.000	26.500
17	22.500	26.500	24.500	22.500	24.000
18	24.000	26.500	24.000	27.500	28.500
18	26.500	27.500	23.000	23.000	25.500
19	25.500	26.000	23.500	26.500	21.000
19	24.500	30.000	27.500	25.500	28.000
20	26.500	27.500	30.000	29.000	26.500
20	19.000	21.500	27.500	23.500	26.500
21	31.000	21.500	23.500	23.000	25.000
21	24.000	22.000	25.500	23.000	28.500
22	22.000	24.500	26.000	22.000	24.500
22	27.000	28.000	20.000	21.500	23.000
23	22.500	27.500	22.000	24.000	22.000
23	22.500	20.500	23.000	27.000	29.500
24	22.500	27.000	30.500	26.000	26.000
24	24.000	26.500	24.500	21.500	25.000

Length to peduncle (MM.)

1	40.000	35.000	32.000	34.000	32.000
1	32.000	30.000	35.000	34.500	32.000
2	31.500	31.500	31.000	31.000	41.000
2	35.500	48.000	39.500	39.000	35.500
3	39.500	36.000	38.500	48.500	35.500
3	39.000	36.500	40.000	41.000	41.500
4	48.000	32.500	29.500	32.000	31.000
4	31.000	28.500	34.500	37.500	32.000
5	34.000	29.000	28.500	31.000	33.000
5	31.000	27.000	31.000	29.500	34.000
6	45.000	34.500	36.500	43.000	44.000
6	43.000	35.500	42.500	43.500	32.000
7	40.000	49.000	37.000	47.500	35.500
7	40.000	47.000	38.000	36.000	54.000
8	42.000	47.000	56.500	52.500	42.500
8	36.000	35.500	46.000	33.500	45.000
9	40.000	51.500	38.000	42.500	39.000
9	50.000	33.500	38.500	37.000	44.000
10	42.500	44.500	46.000	47.500	39.000
10	42.000	35.500	40.500	42.000	40.000
11	37.000	42.500	39.500	42.000	46.500
11	47.000	57.000	36.000	36.000	40.500
12	39.000	51.000	37.000	39.500	45.000
12	40.500	45.500	40.000	45.000	40.000
13	52.000	39.500	49.000	51.000	48.000
13	44.500	56.500	52.000	48.000	43.500
14	31.000	36.000	41.500	38.500	43.000
14	38.500	36.000	41.500	47.500	40.500
15	45.500	43.500	50.000	41.000	42.000
15	50.500	48.500	49.000	42.000	45.500
16	51.500	51.500	54.000	47.000	48.000
16	59.000	55.000	59.000	48.500	48.000
17	31.000	39.000	36.500	30.500	27.000
17	30.500	36.500	33.000	30.500	33.000
18	29.500	30.500	27.500	36.000	34.500
18	31.500	32.000	33.000	30.000	31.500
19	34.000	34.000	35.000	27.000	33.000
19	36.000	47.000	40.500	36.500	41.500
20	37.000	32.500	35.000	40.000	35.500
20	29.000	29.500	40.500	33.000	36.000
21	41.500	31.500	31.000	31.500	34.500
21	32.000	31.500	38.000	31.000	35.000
22	29.000	32.500	31.000	34.500	29.000
22	35.500	30.500	25.000	32.000	29.500
23	29.500	39.000	31.500	33.000	25.500
23	27.000	31.000	28.000	38.000	35.500
24	27.500	45.000	41.500	40.000	42.500
24	34.000	32.000	34.000	39.000	37.500

Apophysis length (MM.)

1	7.100	7.100	5.800	7.000	9.400
1	6.700	5.600	7.600	6.000	6.100
2	6.000	6.100	5.700	5.600	7.100
2	5.200	6.800	6.300	6.400	6.200
3	7.700	6.500	7.400	7.400	8.100
3	6.800	8.000	6.900	6.300	8.800
4	7.800	6.300	5.600	7.900	7.800
4	6.800	6.200	6.100	8.400	8.700
5	7.300	7.000	5.900	8.000	6.100
5	6.500	6.400	6.200	6.200	7.000
6	6.600	5.400	7.800	7.000	6.600
6	7.000	5.400	6.300	7.000	6.700
7	8.100	11.000	6.000	7.900	7.900
7	8.100	6.300	8.100	6.800	7.200
8	7.700	6.800	8.600	9.500	7.300
8	6.600	8.300	7.800	7.800	6.800
9	5.700	8.300	7.700	6.500	6.200
9	7.800	7.700	7.100	6.300	8.900
10	6.100	6.400	6.700	5.100	5.500
10	6.500	5.500	6.500	6.200	6.000
11	6.000	8.800	6.100	5.000	7.500
11	7.700	7.200	7.900	6.700	7.800
12	7.000	7.400	6.100	6.000	7.300
12	6.600	6.700	4.800	6.300	7.100
13	8.100	8.000	7.200	8.300	6.600
13	7.400	7.800	9.600	9.200	7.800
14	5.300	5.400	7.400	7.200	7.000
14	6.400	5.800	5.600	5.900	6.100
15	6.600	7.200	8.200	7.500	7.700
15	8.700	8.500	8.200	8.200	8.000
16	8.700	8.000	8.200	10.400	8.600
16	8.000	8.000	9.300	7.000	7.000
17	5.800	7.000	8.300	9.800	7.200
17	6.000	8.000	7.200	7.000	7.000
18	7.100	7.200	6.200	6.600	7.100
18	7.000	7.800	6.300	7.000	9.000
19	7.300	7.900	8.500	8.300	5.200
19	7.100	7.500	8.000	7.800	8.900
20	8.100	8.900	9.400	8.000	6.600
20	7.000	7.000	7.400	7.200	7.900
21	9.000	7.500	7.500	7.600	8.800
21	8.000	8.100	7.600	7.100	8.000
22	6.500	6.000	6.200	5.300	7.700
22	6.500	8.900	6.000	6.400	7.400
23	5.300	10.400	8.100	5.100	7.100
23	6.400	6.800	7.600	9.800	7.400
24	8.000	8.500	9.100	9.200	6.400
24	8.000	9.000	9.100	6.700	7.200

Apophysis width (mm.)

1	7.600	7.400	5.900	7.900	8.300
1	6.900	5.500	7.400	6.300	7.300
2	6.200	5.700	6.600	6.200	6.300
2	6.200	6.800	6.400	6.200	7.500
3	8.000	7.000	7.500	6.200	7.100
3	7.100	7.600	6.900	6.500	8.500
4	7.900	6.300	6.600	6.800	7.700
4	6.400	6.500	5.600	8.300	8.400
5	6.900	6.500	5.900	6.700	5.700
5	6.300	7.100	6.400	6.000	6.700
6	7.200	6.200	8.900	7.700	7.600
6	7.700	5.400	7.000	7.800	9.000
7	9.700	9.100	7.000	8.900	8.600
7	6.500	8.500	8.700	7.100	6.800
8	8.500	7.800	9.200	9.500	8.100
8	7.500	9.300	9.400	11.000	8.000
9	8.500	8.700	8.000	9.000	7.500
9	8.700	8.900	7.100	7.600	10.800
10	8.000	8.200	7.700	7.400	8.200
10	7.600	6.900	8.200	7.300	8.200
11	6.800	10.500	6.100	6.900	7.200
11	7.600	7.500	9.100	6.400	7.800
12	8.000	8.600	5.700	6.000	7.800
12	6.700	9.300	7.100	7.200	7.900
13	8.000	8.500	7.500	9.800	7.200
13	8.400	9.500	10.000	8.900	7.000
14	5.800	6.000	6.400	6.700	7.100
14	7.200	7.000	6.600	7.100	7.800
15	8.400	7.400	8.500	8.000	7.700
15	8.700	8.500	8.200	8.200	8.000
16	10.500	10.100	9.600	13.600	10.100
16	8.600	8.600	11.700	8.400	8.900
17	7.900	7.000	8.300	8.900	8.300
17	7.000	9.100	7.200	7.700	7.000
18	6.900	7.200	9.200	9.400	7.800
18	8.200	7.800	7.500	8.400	8.100
19	7.800	6.300	8.500	8.300	6.100
19	8.000	8.500	7.700	8.200	9.800
20	8.000	8.800	10.300	9.600	7.900
20	7.000	9.100	9.800	7.100	8.000
21	10.100	7.200	8.000	7.800	8.800
21	8.400	8.500	7.600	8.200	9.400
22	7.900	8.000	7.500	6.300	8.100
22	8.000	9.500	6.000	7.800	8.100
23	5.400	8.800	8.800	6.900	8.200
23	6.400	7.200	10.000	9.000	8.200
24	8.500	8.900	9.200	9.000	7.200
24	8.600	7.100	8.200	6.100	7.500

Apophysis height (mm.)

1	3.900	2.800	2.900	3.500	3.200
1	2.700	2.300	2.800	3.200	3.700
2	2.600	2.500	2.400	1.900	3.300
2	2.300	3.100	2.800	2.700	2.800
3	2.800	2.200	2.500	2.100	2.400
3	3.700	2.600	2.700	2.100	3.400
4	3.300	2.000	2.500	2.300	2.400
4	2.600	2.000	2.100	3.400	2.600
5	3.600	2.200	3.200	4.000	2.800
5	2.500	2.100	3.200	2.600	4.000
6	2.000	1.600	1.900	2.100	1.800
6	1.700	1.700	2.300	2.000	1.500
7	2.000	3.000	2.300	2.800	2.300
7	2.100	2.600	2.500	2.100	2.100
8	2.300	2.000	4.000	3.000	2.600
8	2.400	3.200	3.200	2.500	1.700
9	2.200	2.900	2.100	2.100	2.800
9	3.100	2.600	1.700	2.200	3.400
10	2.800	2.300	2.500	2.600	1.900
10	2.100	2.500	2.700	2.500	2.700
11	2.100	2.900	2.500	2.800	2.300
11	3.200	2.900	3.800	1.800	2.300
12	1.700	3.200	2.500	2.100	2.200
12	1.900	2.600	1.800	2.400	2.500
13	2.600	2.800	2.300	2.500	2.100
13	2.200	2.500	3.300	3.700	2.500
14	2.300	2.300	1.700	2.500	1.800
14	2.500	2.100	1.600	2.100	2.200
15	2.800	2.400	2.500	1.800	2.700
15	2.800	2.500	2.200	2.400	2.300
16	3.000	3.100	2.700	3.200	2.400
16	2.300	2.600	3.500	2.900	3.200
17	3.300	5.600	4.700	4.900	5.200
17	5.100	5.000	4.400	2.800	4.100
18	3.300	3.900	3.700	5.000	2.800
18	4.000	3.400	2.800	3.900	4.300
19	4.100	3.600	3.500	4.100	1.700
19	4.300	4.300	3.600	3.600	6.200
20	4.100	4.000	5.100	4.600	3.700
20	2.900	4.600	5.500	2.500	3.300
21	5.800	4.000	4.300	3.200	3.200
21	4.100	3.700	3.200	3.200	5.300
22	4.100	3.300	2.800	2.500	4.800
22	3.500	5.800	4.300	3.200	4.500
23	3.500	3.500	3.800	2.700	3.500
23	3.200	2.300	3.900	3.900	3.900
24	3.700	3.700	4.400	4.500	3.000
24	3.500	3.400	3.700	3.200	3.100

Specific gravity

1	0.744	0.812	0.760	0.811	0.789
1	0.773	0.762	0.765	0.822	0.849
2	0.807	0.787	0.800	0.829	0.919
2	0.865	0.714	0.765	0.771	0.734
3	0.750	0.756	0.593	0.796	0.557
3	0.591	0.563	0.627	0.734	0.697
4	0.652	0.700	0.585	0.636	0.533
4	0.725	0.575	0.667	0.634	0.620
5	0.843	0.776	0.740	0.700	0.746
5	0.714	0.800	0.769	0.738	0.802
6	0.412	0.583	0.531	0.534	0.578
6	0.568	0.571	0.561	0.563	0.568
7	0.519	0.544	0.579	0.513	0.586
7	0.525	0.522	0.436	0.538	0.495
8	0.556	0.505	0.532	0.519	0.586
8	0.600	0.583	0.558	0.552	0.554
9	0.473	0.614	0.550	0.638	0.557
9	0.521	0.500	0.561	0.526	0.573
10	0.561	0.559	0.596	0.550	0.507
10	0.527	0.590	0.561	0.500	0.563
11	0.474	0.557	0.470	0.464	0.463
11	0.454	0.551	0.485	0.415	0.484
12	0.518	0.480	0.551	0.559	0.486
12	0.478	0.557	0.500	0.567	0.500
13	0.500	0.456	0.486	0.500	0.455
13	0.486	0.545	0.459	0.597	0.450
14	0.578	0.582	0.540	0.524	0.618
14	0.524	0.627	0.500	0.673	0.514
15	0.525	0.525	0.522	0.515	0.554
15	0.532	0.506	0.457	0.538	0.493
16	0.582	0.598	0.500	0.559	0.580
16	0.537	0.606	0.500	0.623	0.573
17	0.761	0.610	0.707	0.625	0.720
17	0.677	0.755	0.688	0.689	0.718
18	0.622	0.636	0.569	0.626	0.608
18	0.550	0.560	0.548	0.707	0.605
19	0.658	0.568	0.667	0.577	0.600
19	0.689	0.551	0.583	0.600	0.617
20	0.669	0.667	0.680	0.649	0.724
20	0.643	0.673	0.683	0.700	0.711
21	0.654	0.710	0.724	0.721	0.647
21	0.716	0.625	0.802	0.719	0.726
22	0.643	0.667	0.470	0.603	0.610
22	0.612	0.595	0.658	0.589	0.700
23	0.525	0.473	0.569	0.571	0.549
23	0.551	0.547	0.449	0.580	0.524
24	0.707	0.593	0.636	0.685	0.697
24	0.667	0.642	0.718	0.750	0.713

Cone width/length

1	0.500	0.488	0.526	0.500	0.513
1	0.559	0.500	0.547	0.535	0.622
2	0.526	0.514	0.474	0.543	0.427
2	0.500	0.462	0.477	0.457	0.548
3	0.571	0.462	0.430	0.431	0.442
3	0.511	0.477	0.500	0.466	0.479
4	0.435	0.473	0.529	0.528	0.542
4	0.514	0.486	0.410	0.511	0.487
5	0.476	0.544	0.528	0.526	0.513
5	0.559	0.578	0.500	0.581	0.547
6	0.444	0.487	0.513	0.378	0.427
6	0.427	0.449	0.477	0.394	0.472
7	0.417	0.462	0.474	0.404	0.583
7	0.488	0.410	0.439	0.500	0.373
8	0.500	0.469	0.475	0.519	0.477
8	0.554	0.551	0.521	0.586	0.427
9	0.500	0.407	0.488	0.477	0.573
9	0.471	0.500	0.500	0.513	0.470
10	0.557	0.511	0.467	0.490	0.463
1[illegible]	0.545	0.658	0.549	0.511	0.500
11	0.500	0.467	0.525	0.477	0.480
11	0.480	0.379	0.575	0.459	0.463
12	0.561	0.528	0.525	0.512	0.446
12	0.452	0.431	0.452	0.479	0.512
13	0.426	0.500	0.353	0.389	0.360
13	0.456	0.430	0.357	0.472	0.477
14	0.544	0.513	0.442	0.538	0.422
14	0.536	0.527	0.455	0.480	0.500
15	0.448	0.500	0.387	0.453	0.456
15	0.406	0.404	0.392	0.478	0.378
16	0.483	0.435	0.414	0.471	0.550
16	0.387	0.434	0.475	0.463	0.445
17	0.662	0.594	0.571	0.730	0.803
17	0.662	0.576	0.645	0.662	0.615
18	0.615	0.679	0.706	0.671	0.695
18	0.679	0.705	0.590	0.622	0.622
19	0.638	0.684	0.588	0.779	0.618
19	0.557	0.600	0.598	0.593	0.596
20	0.646	0.688	0.789	0.617	0.663
20	0.576	0.597	0.573	0.671	0.663
21	0.620	0.551	0.635	0.639	0.676
21	0.615	0.611	0.622	0.657	0.679
22	0.647	0.700	0.722	0.579	0.681
22	0.659	0.718	0.690	0.581	0.622
23	0.703	0.688	0.579	0.667	0.688
23	0.750	0.621	0.676	0.614	0.756
24	0.625	0.500	0.610	0.565	0.542
24	0.585	0.679	0.613	0.489	0.568

Cone volume divided by volume of cylinder of the same length and width

1	0.413	0.391	0.305	0.357	0.365
1	0.358	0.392	0.341	0.321	0.271
2	0.375	0.381	0.365	0.324	0.307
2	0.351	0.352	0.350	0.345	0.356
3	0.331	0.324	0.367	0.377	0.393
3	0.325	0.354	0.362	0.346	0.299
4	0.298	0.353	0.342	0.339	0.329
4	0.325	0.363	0.391	0.319	0.355
5	0.417	0.421	0.385	0.329	0.378
5	0.456	0.411	0.379	0.380	0.404
6	0.378	0.369	0.381	0.446	0.411
6	0.367	0.352	0.340	0.398	0.356
7	0.404	0.381	0.463	0.460	0.441
7	0.346	0.438	0.414	0.411	0.446
8	0.389	0.351	0.324	0.319	0.361
8	0.386	0.333	0.369	0.394	0.411
9	0.400	0.386	0.394	0.412	0.309
9	0.381	0.363	0.384	0.394	0.398
10	0.371	0.391	0.466	0.386	0.466
10	0.367	0.328	0.395	0.368	0.346
11	0.356	0.353	0.374	0.356	0.351
11	0.353	0.452	0.321	0.383	0.432
12	0.383	0.361	0.391	0.376	0.372
12	0.455	0.357	0.448	0.378	0.391
13	0.413	0.367	0.436	0.344	0.407
13	0.381	0.359	0.438	0.339	0.412
14	0.387	0.381	0.406	0.341	0.419
14	0.386	0.419	0.386	0.384	0.389
15	0.361	0.329	0.404	0.416	0.391
15	0.384	0.388	0.397	0.385	0.400
16	0.389	0.376	0.353	0.356	0.365
16	0.344	0.331	0.370	0.361	0.333
17	0.412	0.303	0.380	0.297	0.354
17	0.378	0.316	0.351	0.354	0.347
18	0.329	0.321	0.332	0.319	0.306
18	0.292	0.339	0.301	0.296	0.304
19	0.304	0.343	0.353	0.327	0.400
19	0.280	0.327	0.331	0.322	0.312
20	0.420	0.298	0.292	0.238	0.310
20	0.353	0.331	0.278	0.362	0.320
21	0.277	0.383	0.284	0.320	0.368
21	0.329	0.321	0.304	0.346	0.343
22	0.340	0.371	0.341	0.343	0.273
22	0.284	0.258	0.328	0.327	0.307
23	0.364	0.364	0.353	0.304	0.329
23	0.323	0.382	0.272	0.312	0.303
24	0.318	0.312	0.301	0.296	0.305
24	0.305	0.347	0.296	0.334	0.291

Cone symmetry

1	0.930	0.833	0.821	0.872	0.821
1	0.941	0.857	0.814	0.802	0.865
2	0.829	0.875	0.816	0.886	0.854
2	0.910	0.906	0.898	0.848	0.845
3	0.940	0.923	0.895	0.951	0.826
3	0.830	0.849	0.952	0.932	0.865
4	0.889	0.878	0.843	0.889	0.861
4	0.861	0.792	0.885	0.852	0.821
5	0.810	0.853	0.792	0.816	0.846
5	0.912	0.844	0.816	0.797	0.791
6	1.000	0.908	0.913	0.956	0.917
6	0.896	0.910	0.966	0.926	0.889
7	0.952	0.942	0.974	1.011	0.986
7	0.952	0.940	0.927	0.973	0.982
8	1.000	0.959	0.942	0.972	0.966
8	0.973	0.910	0.979	0.957	0.938
9	0.952	0.954	0.950	0.966	0.951
9	0.962	0.905	0.987	0.974	0.880
10	0.966	0.989	1.000	0.969	0.951
10	0.955	0.934	0.988	0.955	0.952
11	0.925	0.944	0.988	0.955	0.949
11	0.922	0.983	0.900	0.973	0.988
12	0.951	0.962	0.925	0.963	0.978
12	0.964	0.892	0.952	0.957	0.952
13	0.963	0.940	0.961	0.944	0.960
13	0.989	0.991	0.929	0.889	0.989
14	0.912	0.947	0.965	0.963	0.956
14	0.917	0.973	0.943	0.969	0.964
15	0.948	0.946	0.943	0.953	0.933
15	0.953	0.933	0.961	0.933	0.929
16	0.888	0.954	0.931	0.904	0.960
16	0.952	0.902	0.967	0.898	0.873
17	0.912	0.813	0.869	0.824	0.818
17	0.897	0.793	0.868	0.897	0.846
18	0.756	0.782	0.809	0.878	0.841
18	0.808	0.821	0.846	0.811	0.768
19	0.850	0.895	0.875	0.794	0.971
19	0.818	0.940	0.880	0.849	0.883
20	0.902	0.813	0.921	0.851	0.888
20	0.879	0.819	0.844	0.943	0.900
21	0.830	0.808	0.838	0.875	0.932
21	0.821	0.875	0.927	0.886	0.833
22	0.853	0.929	0.861	0.908	0.806
22	0.866	0.782	0.862	0.865	0.797
23	0.922	0.975	0.829	0.917	0.797
23	0.900	0.939	0.824	0.864	0.910
24	0.764	0.833	0.830	0.870	0.885
24	0.829	0.821	0.850	0.886	0.852

Apophysis height/length

1	0.549	0.394	0.500	0.500	0.340
1	0.403	0.411	0.368	0.533	0.607
2	0.433	0.410	0.421	0.339	0.465
2	0.442	0.456	0.444	0.422	0.452
3	0.364	0.338	0.338	0.284	0.296
3	0.544	0.325	0.391	0.333	0.386
4	0.423	0.317	0.446	0.291	0.308
4	0.382	0.323	0.344	0.405	0.299
5	0.493	0.314	0.542	0.500	0.459
5	0.385	0.328	0.516	0.419	0.571
6	0.303	0.296	0.244	0.300	0.273
6	0.243	0.315	0.365	0.286	0.224
7	0.247	0.273	0.383	0.354	0.291
7	0.259	0.413	0.309	0.309	0.292
8	0.299	0.294	0.465	0.316	0.356
8	0.364	0.386	0.410	0.321	0.250
9	0.386	0.349	0.273	0.323	0.452
9	0.397	0.338	0.239	0.349	0.382
10	0.459	0.359	0.373	0.510	0.345
10	0.323	0.455	0.415	0.403	0.450
11	0.350	0.330	0.410	0.560	0.307
11	0.416	0.403	0.481	0.269	0.295
12	0.243	0.432	0.410	0.350	0.301
12	0.288	0.388	0.375	0.381	0.352
13	0.321	0.350	0.319	0.301	0.318
13	0.297	0.321	0.344	0.402	0.321
14	0.434	0.426	0.230	0.347	0.257
14	0.391	0.362	0.286	0.356	0.361
15	0.424	0.333	0.305	0.240	0.351
15	0.322	0.294	0.268	0.293	0.288
16	0.345	0.388	0.329	0.308	0.279
16	0.288	0.325	0.376	0.414	0.457
17	0.569	0.800	0.566	0.500	0.722
17	0.850	0.625	0.611	0.400	0.586
18	0.465	0.542	0.597	0.758	0.394
18	0.571	0.436	0.444	0.557	0.478
19	0.562	0.456	0.412	0.494	0.327
19	0.606	0.573	0.450	0.462	0.697
20	0.506	0.449	0.543	0.575	0.561
20	0.414	0.657	0.743	0.347	0.418
21	0.644	0.533	0.573	0.421	0.364
21	0.513	0.457	0.421	0.451	0.663
22	0.631	0.550	0.452	0.472	0.623
22	0.538	0.652	0.717	0.500	0.608
23	0.660	0.337	0.469	0.529	0.493
23	0.500	0.338	0.513	0.398	0.527
24	0.463	0.435	0.484	0.489	0.469
24	0.438	0.378	0.407	0.478	0.431

Apophysis height/width

1	0.513	0.378	0.492	0.443	0.386
1	0.391	0.418	0.378	0.508	0.507
2	0.419	0.439	0.364	0.306	0.524
2	0.371	0.456	0.438	0.435	0.373
3	0.350	0.314	0.333	0.339	0.338
3	0.521	0.342	0.391	0.323	0.400
4	0.418	0.317	0.379	0.338	0.312
4	0.406	0.308	0.375	0.410	0.310
5	0.522	0.338	0.542	0.597	0.491
5	0.397	0.296	0.500	0.433	0.597
6	0.278	0.258	0.213	0.273	0.237
6	0.221	0.315	0.329	0.256	0.167
7	0.206	0.330	0.329	0.315	0.267
7	0.323	0.306	0.287	0.296	0.309
8	0.271	0.256	0.435	0.316	0.321
8	0.320	0.344	0.340	0.227	0.213
9	0.259	0.333	0.263	0.233	0.373
9	0.356	0.292	0.239	0.289	0.315
10	0.350	0.280	0.325	0.351	0.232
10	0.276	0.362	0.329	0.342	0.329
11	0.309	0.276	0.410	0.406	0.319
11	0.421	0.387	0.418	0.281	0.295
12	0.213	0.372	0.439	0.350	0.282
12	0.288	0.280	0.254	0.333	0.316
13	0.325	0.329	0.307	0.255	0.292
13	0.262	0.263	0.330	0.416	0.357
14	0.397	0.383	0.266	0.373	0.254
14	0.347	0.300	0.242	0.296	0.282
15	0.333	0.324	0.294	0.225	0.351
15	0.322	0.294	0.268	0.293	0.288
16	0.286	0.307	0.281	0.235	0.238
16	0.267	0.302	0.299	0.345	0.360
17	0.418	0.800	0.566	0.551	0.627
17	0.729	0.549	0.611	0.364	0.586
18	0.478	0.542	0.402	0.532	0.359
18	0.488	0.436	0.373	0.464	0.531
19	0.526	0.571	0.412	0.494	0.279
19	0.538	0.506	0.468	0.439	0.633
20	0.513	0.455	0.495	0.479	0.468
20	0.414	0.505	0.561	0.352	0.413
21	0.574	0.556	0.538	0.410	0.364
21	0.488	0.435	0.421	0.390	0.564
22	0.519	0.413	0.373	0.397	0.593
22	0.438	0.611	0.717	0.410	0.556
23	0.648	0.398	0.432	0.391	0.427
23	0.500	0.319	0.390	0.433	0.476
24	0.435	0.416	0.478	0.500	0.417
24	0.407	0.479	0.451	0.525	0.413

APPENDIX B: Data Summarization and Standardization

1. Data Summary Prior to Transformation and Standardization

CHARACTER: serotiny

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.87	0.274712	0.31	1
MENDO2	0.81	0.306014	0.35	1
MENDOSHOR	0.284	4.45221E-2	0.21	0.36
CRESCENT	0.294	5.18973E-2	0.22	0.37
GASQUET	1	0	1	1
BISHOP2400	0.166	3.56526E-2	0.11	0.22
BISHOP3050	0.186	5.08156E-2	0.1	0.28
COTTONWOOD	0.19	5.01110E-2	0.1	0.25
MT.ROSE	0.159	3.95671E-2	0.1	0.21
TRUCKEE	0.2	3.85861E-2	0.16	0.27
SADDLEBAG	0.19	4.16333E-2	0.13	0.24
UPPER.HORSE	0.167	4.37290E-2	0.1	0.22
KAISER	0.195	5.40062E-2	0.11	0.29
DINKEY	0.163	4.59589E-2	0.11	0.27
HUNTINGDON	0.121	2.46982E-2	0.1	0.18
BIG.BEAR	0.171	4.77144E-2	0.1	0.25
RIDGE3050	0.882	0.251608	0.33	1
SOUTH3100	0.335	7.51665E-2	0.26	0.5
VALLEY3100	0.383	0.230268	0.13	1
VALLEY2540	0.93	0.221359	0.3	1
NORTH3050	0.815	0.298189	0.35	1
FRASER	0.444	0.203044	0.3	1
MEADOW.CR.	0.386	0.217879	0.28	1
UTAH	0.499	0.348535	0.23	1
ALL STANDS	0.41	0.166438		

CHARACTER: volume

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	6.04	1.47588	4.2	8.2
MENDO2	6.33	2.09552	4.1	11.2
MENDOSHOR	6.88	1.57537	4.1	9.3
CRESCENT	4.99	1.67495	3.9	8.9
GASQUET	5.92	1.50614	4.5	9.6
BISHOP2400	6.04	1.4362	3.7	8.3
BISHOP3050	7.34	2.25596	5.2	11.4
COTTONWOOD	8.91	3.40505	5.8	15.8
MT.ROSE	7.74	2.48202	4.6	11.9
TRUCKEE	8.67	1.41582	6.4	10.9
SADDLEBAG	7.65	2.57391	4.1	12.7
UPPER.HORSE	8.33	2.48866	6.8	15
KAISER	8.98	2.27293	6.6	12.3
DINKEY	6.79	1.61138	4.5	10.4
HUNTINGDON	8.03	0.898208	6.7	9.4
BIG.BEAR	13.43	2.82333	11	19
RIDGE3050	8.29	1.72011	6.1	11.8
SOUTH3100	8.09	1.62306	5.8	10.2
VALLEY3100	9.24	2.58423	6	14.7
VALLEY2540	8.5	2.33	4.2	12.1
NORTH3050	7.98	2.59007	5.6	13.3
FRASER	6.57	1.50558	3.8	8.5
MEADOW.CR.	7.02	2.43027	4.9	11
UTAH	8.98	2.58018	5.8	14
ALL STANDS	7.78083	2.13731		

CHARACTER : apoph.ht.

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	3.1	0.494413	2.3	3.9
MENDO2	2.64	0.400555	1.9	3.3
MENDOSHOR	2.65	0.535931	2.1	3.7
CRESCENT	2.52	0.491709	2	3.4
GASQUET	3.02	0.694102	2.1	4
BISHOP2400	1.86	0.245854	1.5	2.3
BISHOP3050	2.38	0.33599	2	3
COTTONWOOD	2.69	0.672392	1.7	4
MT.ROSE	2.51	0.53427	1.7	3.4
TRUCKEE	2.46	0.283627	1.9	2.8
SADDLEBAG	2.66	0.583476	1.8	3.8
UPPER.HORSE	2.29	0.44833	1.7	3.2
KAISER	2.65	0.499444	2.1	3.7
DINKEY	2.11	0.317805	1.6	2.5
HUNTINGDON	2.44	0.302582	1.8	2.8
BIG.BEAR	2.89	0.384274	2.3	3.5
RIDGE3050	4.51	0.882484	2.8	5.6
SOUTH3100	3.71	0.674042	2.8	5
VALLEY3100	3.9	1.10353	1.7	6.2
VALLEY2540	4.03	0.955743	2.5	5.5
NORTH3050	4	0.92376	3.2	5.8
FRASER	3.88	1.00863	2.5	5.8
MEADOW.CR.	3.42	0.545283	2.3	3.9
UTAH	3.62	0.505085	3	4.5
ALL STANDS	2.9975	0.62335		

CHARACTER: sp.gr.

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.788733	3.35457E-2	0.74	0.85
MENDO2	0.799286	6.08514E-2	0.71	0.92
MENDOSHOR	0.666379	8.98907E-2	0.55	0.80
CRESCENT	0.632722	5.79102E-2	0.53	0.72
GASQUET	0.762819	4.37655E-2	0.7	0.84
BISHOP2400	0.546882	5.04005E-2	0.41	0.58
BISHOP3050	0.525687	4.22541E-2	0.44	0.59
COTTONWOOD	0.55439	3.00247E-2	0.51	0.6
MT.ROSE	0.551293	4.97213E-2	0.47	0.64
TRUCKEE	0.551413	3.16591E-2	0.5	0.6
SADDLEBAG	0.481664	4.30692E-2	0.41	0.56
UPPER.HORSE	0.519548	3.53976E-2	0.48	0.57
KAISER	0.493319	4.64955E-2	0.45	0.6
DINKEY	0.567921	5.72479E-2	0.5	0.68
HUNTINGDON	0.516534	2.69305E-2	0.46	0.55
BIG.BEAR	0.56563	4.21240E-2	0.5	0.62
RIDGE3050	0.694757	4.90665E-2	0.61	0.76
SOUTH3100	0.603155	4.89937E-2	0.55	0.71
VALLEY3100	0.611021	4.60964E-2	0.55	0.69
VALLEY2540	0.679903	2.58482E-2	0.64	0.72
NORTH3050	0.704572	5.08576E-2	0.62	0.80
FRASER	0.614663	6.21882E-2	0.47	0.7
MEADOW.CR.	0.533927	0.042944	0.45	0.58
UTAH	0.680744	4.65603E-2	0.59	0.75
ALL STANDS	0.61029	4.83015E-2		

CHARACTER: cone.wid/l.

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.52884	3.98310E-2	0.48	0.62
MENDO2	0.492751	3.98670E-2	0.42	0.54
MENDOSHOR	0.476889	4.27498E-2	0.43	0.57
CRESCENT	0.491497	4.25125E-2	0.41	0.54
GASQUET	0.535177	3.34485E-2	0.47	0.58
BISHOP2400	0.446756	4.19971E-2	0.37	0.51
BISHOP3050	0.454932	6.06218E-2	0.37	0.58
COTTONWOOD	0.507959	4.76753E-2	0.42	0.58
MT.ROSE	0.489966	4.14979E-2	0.40	0.57
TRUCKEE	0.525203	5.67760E-2	0.46	0.65
SADDLEBAG	0.480611	4.99635E-2	0.37	0.57
UPPER.HORSE	0.489889	4.35422E-2	0.43	0.56
KAISER	0.421978	5.45486E-2	0.35	0.5
DINKEY	0.495574	4.37774E-2	0.42	0.54
HUNTINGDON	0.430075	4.22096E-2	0.37	0.5
BIG.BEAR	0.455824	4.44041E-2	0.38	0.55
RIDGE3050	0.651944	7.16310E-2	0.57	0.80
SOUTH3100	0.658454	4.22596E-2	0.58	0.70
VALLEY3100	0.624968	6.39931E-2	0.55	0.77
VALLEY2540	0.648266	6.40669E-2	0.57	0.78
NORTH3050	0.630514	3.68431E-2	0.55	0.67
FRASER	0.659763	5.22508E-2	0.57	0.72
MEADOW.CR.	0.674147	5.70625E-2	0.57	0.75
UTAH	0.577606	5.81429E-2	0.48	0.67
ALL STANDS	0.535399	4.97767E-2		

CHARACTER: vol/cylvol

STAND.NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.351443	4.33311E-2	0.27	0.41
MENDO2	0.350759	2.20566E-2	0.30	0.38
MENDOSHOR	0.347819	2.82604E-2	0.29	0.39
CRESCENT	0.341299	2.58490E-2	0.29	0.39
GASQUET	0.396015	3.40873E-2	0.32	0.45
BISHOP2400	0.379715	3.15287E-2	0.34	0.44
BISHOP3050	0.420221	3.69571E-2	0.34	0.46
COTTONWOOD	0.363674	3.17143E-2	0.31	0.41
MT.ROSE	0.38236	2.88400E-2	0.30	0.41
TRUCKEE	0.38838	4.55454E-2	0.32	0.46
SADDLEBAG	0.373219	4.01302E-2	0.32	0.45
UPPER.HORSE	0.391316	3.38294E-2	0.35	0.45
KAISER	0.389659	3.63842E-2	0.33	0.43
DINKEY	0.389694	2.24145E-2	0.34	0.41
HUNTINGDON	0.385353	2.46855E-2	0.32	0.41
BIG.BEAR	0.357956	1.83480E-2	0.33	0.38
RIDGE3050	0.349161	3.63439E-2	0.29	0.41
SOUTH3100	0.314003	1.63440E-2	0.29	0.33
VALLEY3100	0.329765	3.19621E-2	0.28	0.40
VALLEY2540	0.320156	5.04091E-2	0.23	0.42
NORTH3050	0.327453	3.39211E-2	0.27	0.38
FRASER	0.317252	3.57194E-2	0.25	0.37
MEADOW.CR.	0.330683	3.44094E-2	0.27	0.38
UTAH	0.310535	1.80203E-2	0.29	0.34
ALL STANDS	0.358662	3.28365E-2		

CHARACTER: symmetry

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.855585	4.80447E-2	0.80	0.94
MENDO2	0.866632	3.29968E-2	0.81	0.91
MENDOSHOR	0.896287	5.02766E-2	0.82	0.95
CRESCENT	0.85703	3.18145E-2	0.79	0.88
GASQUET	0.827537	3.72795E-2	0.79	0.91
BISHOP2400	0.927904	3.50215E-2	0.88	1
BISHOP3050	0.963913	2.55041E-2	0.92	1.01
COTTONWOOD	0.959558	2.50043E-2	0.91	1
MT.ROSE	0.948102	3.19773E-2	0.88	0.98
TRUCKEE	0.965889	2.06654E-2	0.93	1
SADDLEBAG	0.952558	3.04716E-2	0.9	0.98
UPPER.HORSE	0.949881	2.44311E-2	0.89	0.97
KAISER	0.955488	3.18044E-2	0.88	0.99
DINKEY	0.95088	2.14532E-2	0.91	0.97
HUNTINGDON	0.9432	1.08282E-2	0.92	0.96
BIG.BEAR	0.922786	3.39071E-2	0.87	0.96
RIDGE3050	0.853799	4.09460E-2	0.79	0.91
SOUTH3100	0.812026	3.71142E-2	0.75	0.87
VALLEY3100	0.875488	5.26224E-2	0.79	0.97
VALLEY2540	0.87594	4.32143E-2	0.81	0.94
NORTH3050	0.862435	4.36683E-2	0.80	0.93
FRASER	0.852821	4.66255E-2	0.78	0.92
MEADOW.CR.	0.887618	5.71145E-2	0.79	0.97
UTAH	0.842062	3.60968E-2	0.76	0.88
ALL STANDS	0.900226	3.70130E-2		

CHARACTER : apoph.h/l.

STAND NAME	MEAN	STD. DEV.	MIN.	MAX.
MENDO1	0.46061	8.86310E-2	0.34	0.60
MENDO2	0.428442	3.57085E-2	0.33	0.46
MENDOSHOR	0.360014	7.32923E-2	0.28	0.54
CRESCENT	0.353861	5.60255E-2	0.29	0.44
GASQUET	0.452848	8.85056E-2	0.31	0.57
BISHOP2400	0.284799	4.13069E-2	0.22	0.36
BISHOP3050	0.312963	5.42112E-2	0.24	0.41
COTTONWOOD	0.345984	6.32478E-2	0.25	0.46
MT.ROSE	0.348854	6.14225E-2	0.23	0.45
TRUCKEE	0.409302	5.93121E-2	0.32	0.50
SADDLEBAG	0.381895	9.04989E-2	0.26	0.56
UPPER.HORSE	0.35205	5.87584E-2	0.24	0.43
KAISER	0.329407	3.01949E-2	0.29	0.40
DINKEY	0.344898	6.80902E-2	0.22	0.43
HUNTINGDON	0.311754	5.06420E-2	0.24	0.42
BIG.BEAR	0.350863	5.72654E-2	0.27	0.45
RIDGE3050	0.622928	0.135497	0.4	0.85
SOUTH3100	0.524186	0.105437	0.39	0.75
VALLEY3100	0.503714	0.106761	0.32	0.69
VALLEY2540	0.521339	0.120402	0.34	0.74
NORTH3050	0.503935	9.95088E-2	0.36	0.74
FRASER	0.574238	8.56165E-2	0.45	0.66
MEADOW.CR.	0.47648	9.79001E-2	0.33	0.71
UTAH	0.446923	3.60259E-2	0.37	0.66
ALL STANDS	0.416762	7.85096E-2		0.48

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CHARACTER:    apoph.h/w.

STAND NAME     MEAN           STD. DEV.         MIN.        MAX.

MENDO1          0.441429       5.82022E-2       0.37        0.51
MENDO2          0.412502       6.05952E-2       0.30        0.52
MENDOSHOR       0.365197       6.12756E-2       0.31        0.52
CRESCENT        0.3572         4.51367E-2       0.30        0.41
GASQUET         0.471377       0.103208         0.29        0.59
BISHOP2400      0.254614       4.81440E-2       0.16        0.32
BISHOP3050      0.296739       3.72491E-2       0.20        0.32
COTTONWOOD      0.304284       6.52867E-2       0.21        0.43
MT.ROSE         0.295351       4.83632E-2       0.23        0.37
TRUCKEE         0.317786       4.16177E-2       0.23        0.36
SADDLEBAG       0.352152       6.09648E-2       0.27        0.42
UPPER.HORSE     0.31217        6.46638E-2       0.21        0.43
KAISER          0.313578       4.96021E-2       0.25        0.41
DINKEY          0.313964       5.66591E-2       0.24        0.39
HUNTINGDON      0.299186       3.59748E-2       0.22        0.35
BIG.BEAR        0.292052       4.04262E-2       0.23        0.35
RIDGE3050       0.579954       0.12857          0.36        0.80
SOUTH3100       0.460518       6.63555E-2       0.35        0.54
VALLEY3100      0.486409       9.69093E-2       0.27        0.63
VALLEY2540      0.465533       6.00499E-2       0.35        0.56
NORTH3050       0.473972       7.92768E-2       0.36        0.57
FRASER          0.502474       0.114225         0.37        0.71
MEADOW.CR.      0.441421       8.79712E-2       0.31        0.64
UTAH            0.452095       4.12995E-2       0.40        0.52
ALL STANDS      0.385915       6.91456E-2
```

2. Ordered Lists of Stand Means, Following Logarithmic Transformation and Standardization

STANDS ORDERED BY: serotiny

STAND	STANDARDIZED MEAN
HUNTINGDON	-2.83691
MT.ROSE	-2.06403
DINKEY	-1.99181
UPPER.HORSE	-1.92638
BISHOP2400	-1.9066
BIG.BEAR	-1.86324
BISHOP3050	-1.6085
COTTONWOOD	-1.5453
SADDLEBAG	-1.50925
KAISER	-1.47152
TRUCKEE	-1.33518
MENDOSHOR	-0.272439
CRESCENT	-0.178897
SOUTH3100	0.191846
VALLEY3100	0.296021
MEADOW.CR.	0.426978
UTAH	0.858992
FRASER	0.907603
MENDO2	2.62114
NORTH3050	2.65974
MENDO1	2.8896
RIDGE3050	2.97645
VALLEY2540	3.16104
GASQUET	3.52062

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STANDS ORDERED BY:  volume

STAND           STANDARDIZED MEAN

CRESCENT        -1.65352
GASQUET         -0.940802
BISHOP2400      -0.877332
MENDO1          -0.872301
MENDO2          -0.755987
FRASER          -0.548506
DINKEY          -0.413434
MEADOW.CR.      -0.384168
MENDOSHOR       -0.36989
BISHOP3050      -0.177738
SADDLEBAG       -5.32912E-2
MT.ROSE          4.36572E-3
NORTH3050        0.136115
SOUTH3100        0.274289
HUNTINGDON       0.295458
UPPER.HORSE      0.341568
RIDGE3050        0.36892
VALLEY2540       0.378679
COTTONWOOD       0.49245
TRUCKEE          0.562532
UTAH             0.610727
KAISER           0.638332
VALLEY3100       0.730201
BIG.BEAR         2.21333
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STANDS ORDERED BY: apoph.ht.

STAND          STANDARDIZED MEAN

BISHOP2400     -2.25047
DINKEY         -1.62298
UPPER.HORSE    -1.23668
BISHOP3050     -0.998538
HUNTINGDON     -0.865892
TRUCKEE        -0.818999
MT.ROSE        -0.788823
CRESCENT       -0.745424
SADDLEBAG      -0.497105
MENDOSHOR      -0.494272
KAISER         -0.481549
MENDO2         -0.481401
COTTONWOOD     -0.473602
BIG.BEAR       -7.04212E-3
GASQUET         0.13597
MENDO1          0.333063
MEADOW.CR.      0.825751
UTAH            1.139
SOUTH3100       1.23131
VALLEY3100      1.34766
FRASER          1.38127
NORTH3050       1.57817
VALLEY2540      1.59053
RIDGE3050       2.20006
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STANDS ORDERED BY:  sp.gr

STAND           STANDARDIZED MEAN

SADDLEBAG       -2.8153
KAISER          -2.52152
HUNTINGDON      -1.9192
UPPER HORSE     -1.85701
BISHOP3050      -1.72277
MEADOW.CR.      -1.53024
BISHOP2400      -1.24909
MT.ROSE         -1.13964
TRUCKEE         -1.11038
COTTONWOOD      -1.04129
BIG.BEAR        -0.807273
DINKEY          -0.780619
SOUTH3100       -1.32315E-2
VALLEY3100       0.152287
FRASER           0.19492
CRESCENT         0.569619
MENDOSHOR        1.15879
UTAH             1.49915
VALLEY2540       1.50253
RIDGE3050        1.75051
NORTH3050        1.9242
GASQUET          2.92189
MENDO1           3.34514
MENDO2           3.48854
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STANDS ORDERED BY:  cone.wid/l.

STAND            STANDARDIZED MEAN

KAISER           -2.47336
HUNTINGDON       -2.23377
BISHOP2400       -1.82321
BISHOP3050       -1.66752
BIG.BEAR         -1.60909
MENDOSHOR        -1.11715
SADDLEBAG        -1.0503
UPPER.HORSE      -0.829869
MT.ROSE          -0.825121
CRESCENT         -0.794515
MENDO2           -0.761206
DINKEY           -0.706994
COTTONWOOD       -0.44637
TRUCKEE          -9.83605E-2
MENDO1            2.40439E-3
GASQUET           0.136953
UTAH              0.924541
VALLEY3100        1.77227
NORTH3050         1.89647
VALLEY2540        2.16586
RIDGE3050         2.21616
SOUTH3100         2.35803
FRASER            2.36845
MEADOW.CR.        2.59568
```

```
STANDS ORDERED BY:  vol/cylvol

STAND               STANDARDIZED MEAN

UTAH                -1.4939
SOUTH3100           -1.37109
FRASER              -1.3105
VALLEY2540          -1.26765
NORTH3050           -0.957085
VALLEY3100          -0.872629
MEADOW.CR.          -0.851844
CRESCENT            -0.484588
MENDOSHOR           -0.284716
RIDGE3050           -0.263672
MENDO1              -0.217894
MENDO2              -0.181032
BIG.BEAR             4.55234E-2
COTTONWOOD           0.192326
SADDLEBAG            0.456435
BISHOP2400           0.663992
MT.ROSE              0.740921
HUNTINGDON           0.834539
TRUCKEE              0.876135
KAISER               0.932951
DINKEY               0.960188
UPPER.HORSE          0.987171
GASQUET              1.11386
BISHOP3050           1.75256
```

```
STANDS ORDERED BY:  symmetry

STAND          STANDARDIZED MEAN

SOUTH3100      -2.42218
GASQUET        -1.97071
UTAH           -1.5557
FRASER         -1.26559
RIDGE3050      -1.23085
MENDO1         -1.18941
CRESCENT       -1.13137
NORTH3050      -0.99382
MENDO2         -0.866739
VALLEY3100     -0.647651
VALLEY2540     -0.623165
MEADOW.CR.     -0.326703
MENDOSHOR      -8.46305E-2
BIG.BEAR        0.628311
BISHOP2400      0.759463
HUNTINGDON      1.16206
MT.ROSE         1.27434
UPPER.HORSE     1.32419
DINKEY          1.35093
SADDLEBAG       1.38736
KAISER          1.45943
COTTONWOOD      1.5653
BISHOP3050      1.67291
TRUCKEE         1.72424
```

```
STANDS ORDERED BY:  apoph.h/l.

STAND              STANDARDIZED MEAN

BISHOP2400         -1.97611
HUNTINGDON         -1.48066
BISHOP3050         -1.46856
KAISER             -1.12998
DINKEY             -0.960526
COTTONWOOD         -0.919062
MT.ROSE            -0.872953
BIG.BEAR           -0.822866
UPPER.HORSE        -0.815112
CRESCENT           -0.771378
MENDOSHOR          -0.703386
SADDLEBAG          -0.419531
TRUCKEE             5.00899E-2
MENDO2              0.339355
GASQUET             0.564323
UTAH                0.577679
MENDO1              0.66976
MEADOW.CR.          0.842356
VALLEY3100          1.14749
NORTH3050           1.16864
VALLEY2540          1.32164
SOUTH3100           1.39133
FRASER              1.93871
RIDGE3050           2.32875
```

```
STANDS ORDERED BY:  apoph.h/w.

STAND           STANDARDIZED MEAN

BISHOP2400      -2.28562
BIG.BEAR        -1.44271
MT.ROSE         -1.39695
BISHOP3050      -1.34825
HUNTINGDON      -1.29319
COTTONWOOD      -1.27466
UPPER.HORSE     -1.11784
DINKEY          -1.0582
KAISER          -1.0438
TRUCKEE         -0.953313
SADDLEBAG       -0.389645
CRESCENT        -0.268967
MENDOSHOR       -0.162257
MENDO2           0.547982
MEADOW.CR.       0.903393
MENDO1           0.952555
UTAH             1.11456
SOUTH3100        1.18637
GASQUET          1.23921
VALLEY2540       1.2598
NORTH3050        1.33537
VALLEY3100       1.43794
FRASER           1.61754
RIDGE3050        2.44068
```

APPENDIX C: Results of Principal Component Analysis for 240 Cones

```
COVARIANCE MATRIX USED

ROOT 1 = 14.7937                PERCENT OF VARIANCE = 59
VECTOR 1
 0.491637 -1.51513E-2  0.30643  0.388325  0.349271 -0.207161
-0.324799 0.328371  0.367614

ROOT 2 = 3.97959                PERCENT OF VARIANCE = 16
VECTOR 2
-0.390927  0.313669  0.35486 -0.583612  0.32819 -0.259499
 3.43780E-2  0.258864  0.19753

ROOT 3 = 1.88297                PERCENT OF VARIANCE = 7
VECTOR 3
-5.20446E-2 -0.567522 -0.308662 -0.16894  0.654109 -0.172563
-0.142813 -0.172856 -0.208532

ROOT 4 = 1.55606                PERCENT OF VARIANCE = 6
VECTOR 4
-0.45867 -0.100627  2.79852E-2  0.204504 -0.350835 -0.486817
-0.606476 -9.14566E-2 -2.52420E-2

ROOT 5 = 1.17765                PERCENT OF VARIANCE = 5
VECTOR 5
-0.254315  0.426392 -4.76836E-2  0.568947  0.359979 -0.28459
 0.365416 -0.158704 -0.24134

ROOT 6 = 0.850239               PERCENT OF VARIANCE = 3
VECTOR 6
-0.407733 -0.505998 -2.79816E-2  0.262019 -8.69871E-2
 2.68056E-2 0.428346  0.428962  0.364019

ROOT 7 = 0.602658               PERCENT OF VARIANCE = 2
VECTOR 7
-0.396139  0.145984  5.72624E-3  0.199879  0.280517  0.72580
-0.413072  6.31922E-2  4.09688E-2

ROOT 8 = 0.224781               PERCENT OF VARIANCE = 1
VECTOR 8
-6.26355E-2 -0.104559  0.274119  2.47012E-2  5.64447E-2
 4.91625E-2 0.104061 -0.756342  0.566488

ROOT 9 = 0.195788               PERCENT OF VARIANCE = 1
VECTOR 9
-2.47354E-2 -0.314782  0.778389  7.29500E-2 -1.81396E-2
 0.109808 8.15409E-2 -4.09522E-2 -0.518051
```

```
CORRELATION OF EIGENVECTORS WITH VARIABLES

VECTOR 1
 0.860466 -4.78434E-2  0.792864  0.731423  0.724544 -0.60334
-0.775368  0.842271  0.886431

VECTOR 2
-0.354866  0.513715  0.476217 -0.570135  0.353108 -0.391987
 4.25651E-2  0.344381  0.247039

VECTOR 3
-3.24973E-2 -0.639346 -0.284927 -0.113524  0.484099 -0.17930
-0.121631 -0.158181 -0.179394

VECTOR 4
-0.260354 -0.103053  2.34839E-2  0.124925 -0.236036 -0.45983
-0.469549 -7.60809E-2 -1.97402E-2

VECTOR 5
-0.125583  0.379883 -3.48102E-2  0.302353  0.210693 -0.23386
 0.246122 -0.114854 -0.164192

VECTOR 6
-0.171079 -0.383047 -1.73569E-2  0.118314 -4.32602E-2
 1.87160E-2 0.245143  0.263777  0.21043

VECTOR 7
-0.139937  9.30410E-2  2.99043E-3  7.59866E-2  0.117451
 0.426649 -0.199028  3.27150E-2  1.99390E-2

VECTOR 8
-1.35130E-2 -4.06981E-2  8.74274E-2  5.73498E-3  1.44333E-2
 1.76494E-2  3.06211E-2 -0.239136  0.168377

VECTOR 9
-4.98037E-3 -0.11435  0.231696  1.58071E-2 -4.32897E-3
 3.67911E-2 2.23935E-2 -1.20842E-2 -0.143707
```

(At this point, the computer program printed component scores for each of the 240 cones for each of the 9 components; to save space, these have been omitted from this appendix.)

APPENDIX D: Results of Principal Component Analysis for 24 locations

```
COVARIANCE MATRIX USED

ROOT 1 = 13.3167                           PERCENT OF VARIANCE = 75
VECTOR 1
 0.522523 -3.70577E-2  0.270497  0.417455  0.364093 -0.18728
-0.325494  0.295997  0.341991

ROOT 2 = 2.61851                           PERCENT OF VARIANCE = 15
VECTOR 2
-0.301705  0.243334  0.312726 -0.596541  0.513674 -0.213564
 6.03593E-2  0.247319  0.147726

ROOT 3 = 0.650339                          PERCENT OF VARIANCE = 4
VECTOR 3
 0.327514  0.620286  0.288894  6.27035E-2 -0.203411  0.31504
 0.512705  0.12765  2.83424E-2

ROOT 4 = 0.568756                          PERCENT OF VARIANCE = 3
VECTOR 4
 0.365781 -0.524702 -0.205121 -0.319476  0.282152  0.473031
 0.339966 0.124392  0.111052

ROOT 5 = 0.289556                          PERCENT OF VARIANCE = 2
VECTOR 5
-0.152713  6.58109E-2 -0.270343  0.463531  0.547674 -0.19393
 0.469205 1.97112E-3 -0.355932

ROOT 6 = 0.169896                          PERCENT OF VARIANCE = 1
VECTOR 6
-0.458663  0.171842 -0.136421  0.261785  0.15957  0.666675
-0.298894 0.295174  0.163015

ROOT 7 = 0.113911                          PERCENT OF VARIANCE = 1
VECTOR 7
-0.358605 -0.322779  0.105603  0.218828 -0.311485 -0.221548
 0.439546 0.31125  0.521532

ROOT 8 = 4.77004E-2                        PERCENT OF VARIANCE = 0
VECTOR 8
 0.168305  0.201748 -0.594866 -0.173593 -0.208768 -0.240732
-8.65088E-2  0.652632 -0.109652

ROOT 9 = 2.40243E-2                        PERCENT OF VARIANCE = 0
VECTOR 9
-6.53109E-2 -0.317173  0.496776  4.95990E-2 -0.128735
 8.49024E-2 -4.23135E-2  0.457729 -0.640939
```

```
CORRELATION OF EIGENVECTORS WITH VARIABLES

VECTOR 1
 0.944158 -0.1742  0.847348  0.826908  0.818794 -0.731359
 -0.895737 0.913718  0.955821

VECTOR 2
-0.24174  0.507227  0.434401 -0.523981  0.512246 -0.369812
 7.36562E-2  0.338541  0.183083

VECTOR 3
 0.13078  0.644368  0.19999  2.74480E-2 -0.10109  0.271868
 0.3118 8.70800E-2  1.75053E-2

VECTOR 4
 0.136592 -0.509739 -0.132793 -0.130783  0.131133  0.381751
 0.193347 7.93561E-2  6.41435E-2

VECTOR 5
-4.06896E-2  4.56179E-2 -0.124877  0.135392  0.181615
 -0.11167 0.1904  8.97231E-4 -0.146688

VECTOR 6
-9.36108E-2  9.12419E-2 -4.82694E-2  5.85714E-2  4.05328E-2
 0.294058 -9.29068E-2  0.102919  5.14614E-2

VECTOR 7
-5.99293E-2 -0.140333  3.05955E-2  4.00898E-2 -6.47863E-2
-8.00160E-2  0.111873  8.88624E-2  0.134811

VECTOR 8
 1.82012E-2  5.67600E-2 -0.111527 -2.05798E-2 -2.80989E-2
-5.62629E-2 -1.42482E-2  0.120574 -1.83417E-2

VECTOR 9
-5.01246E-3 -6.33275E-2  6.60976E-2  4.17298E-3 -1.22966E-2
 1.40822E-2 -4.94587E-3  6.00150E-2 -7.60860E-2
```

```
COMPONENT 1 COMPONENT SCORES

0.830219 -0.636061 -7.67689E-2 -3.05728E-2 0.87671  -0.937455
-0.875518 -0.584779  -0.70017  -0.516262 -0.682525 -0.76537
-0.879342 -0.690912  -0.991918  -0.611024  1.17777  0.654509
0.501822 0.989614 0.9614 0.749885 0.331774 0.632857

COMPONENT 2 COMPONENT SCORES

-0.561547 -0.718573 -0.327312 -0.317928 -0.616259  -0.303551
-0.111507 9.75086E-2 2.70076E-2 0.142619 0.261018 9.62186E-2
2.86857E-2  -8.80151E-2  -2.26255E-3  7.61316E-2  0.186084
0.475215  0.411364  0.124724  3.77854E-2  0.426811  0.580943
7.48390E-2

COMPONENT 3 COMPONENT SCORES

3.01976E-2  3.78404E-2  -8.11182E-2   -0.404742   4.41620E-2
-0.25954  0.10213  8.29298E-2  -0.014397 0.159479 3.26638E-2
2.71548E-2   0.206061   -9.18046E-2   -6.03268E-3   0.256027
0.239902  -0.282406  3.51414E-2  0.181174 0.108911 -0.183887
-0.164012 -5.58341E-2

COMPONENT 4 COMPONENT SCORES

1.25090E-2  -3.17638E-2   -0.158171   -3.97757E-2   0.192547
3.79162E-2 0.178272 -3.18010E-2 1.16351E-2 0.127699 0.161194
8.76905E-2 2.97899E-3 0.114194 -0.118894 -0.430576  0.109985
-0.17181   -8.97511E-2   5.32113E-2   2.44030E-4  6.52805E-2
0.229515 -0.312329

COMPONENT 5 COMPONENT SCORES

0.022857   6.55394E-2   3.08724E-2   -8.20991E-2   -0.164219
6.28701E-2  -5.96079E-2 0.170633 0.103909 0.181886 -0.170677
3.37490E-2   -0.26134   0.164538    -0.122074    -5.31362E-3
-8.14043E-2   -7.27619E-2   7.40937E-3  0.104778  7.36077E-2
-1.50584E-2 1.88850E-2 -6.97653E-3

COMPONENT 6 COMPONENT SCORES

-1.69682E-2  -3.06107E-2  -3.01667E-2  -6.97485E-2  0.144284
-6.82688E-2  2.94956E-2  -6.34985E-2  5.26947E-2  9.22738E-2
-9.41313E-2   6.92079E-2   -0.108925   0.109905   3.59468E-2
2.75840E-2    0.101615    0.120512    6.53604E-2    -0.193123
-8.00411E-2 1.47054E-2 -9.07564E-2 -1.73461E-2

COMPONENT 7 COMPONENT SCORES

5.05631E-2   6.34444E-2   0.101916   2.52274E-2    -0.133201
-0.124392    -2.96186E-2  -1.02303E-2  1.22623E-2  1.68020E-2
8.17189E-2  -3.57121E-2  5.86906E-3  5.33682E-2   6.19131E-2
-9.69364E-2  5.29125E-2   -9.87952E-2  6.20334E-2 -7.47203E-2
-3.44753E-2 0.100803 -6.39793E-2 1.32276E-2
```

```
COMPONENT 8 COMPONENT SCORES

3.96897E-3 8.51323E-2  -3.33170E-2  -2.34980E-2  -1.65152E-2
3.62197E-2  -9.22896E-2  -5.14623E-2  -4.42705E-2 7.64001E-2
5.79583E-2  4.46993E-2  3.08185E-2  -6.03243E-3  -4.77965E-2
3.52492E-2  -1.62126E-2  3.81000E-2  -2.99540E-2  6.82964E-3
-5.44218E-2 4.27439E-2 -1.85768E-2 -2.37732E-2

COMPONENT 9 COMPONENT SCORES

3.06262E-2 -1.54557E-2  -3.07964E-2  2.55222E-2  -1.97451E-2
8.80465E-3   1.34599E-2   1.28589E-2  6.17236E-2  1.97842E-2
-2.04650E-2 -4.39963E-2  3.54695E-3  -4.79171E-2  5.54419E-3
2.26465E-2  2.38456E-2  1.46967E-2  -5.11122E-2  -5.10442E-3
1.21423E-2 6.22595E-2 -3.29096E-2 -4.99597E-2
```

Appendix E: Euclidean dissimilarity between locations based on 9 cone characters.

Stands are identified by their code names, and followed by an ordered series of standardized Euclidean distances from that stand to subsequent stands.

```
MENDO01
1.31565   4.6176   4.81365   1.76529   8.72813   8.5383    7.54091
7.89007   7.40264   8.35772   8.31553   8.83614   7.74158 9.19851
7.96269 4.17708   5.44536   4.98365   3.63835   3.03425   4.88937
6.18209 3.60935


MENDO02
4.03617 4.39318   2.40334  7.99794   7.97017   7.10607   7.39826
7.01874   8.01988   7.82989   8.3121   7.17067   8.62007   7.47827
5.30535 6.10231   5.52095   4.59298   4.05902   5.67698   6.65124
4.11999


MENDOSHOR
1.82274 5.37366   4.47768   4.46252   3.44795  3.64097   3.75559
4.5029   4.18313   4.76071   3.55543   4.75061   3.97739   6.86331
5.46897 4.57568 5.91363 5.46283 5.53315 5.21085 4.01139


CRESCENT
5.35633 4.54216   4.98224   4.24568   4.21885   4.55077   4.82527
4.69931   5.36818   4.04144   5.26268   5.06477   7.08468   5.2237
4.90218 6.16159 5.6847 5.35469 5.01106 4.30199


GASQUET
9.10646 8.80441   8.12459   8.36917   7.86423   8.72599   8.67767
9.17182   8.17557   9.61738   8.53953   4.35533   5.86265 5.57491
4.26363 3.69995 5.41805 6.5559 4.48669


BISHOP2400
2.35582 3.18028   2.49489   3.78147   3.66287   2.64673   3.23693
2.24881   2.4894   4.15551   10.7801   8.63258   7.95214   9.72543
9.4417 8.91249 7.50657 8.03454


BISHOP3050
2.33187   1.6952   2.59331   2.37323   1.52795   1.77878   1.86452
1.7935   3.46954   9.99854   8.28707   7.22408   9.15639   8.92012
8.39767 6.84962 7.71976
```

```
COTTONWOOD
1.07819  1.35263  2.2239  1.51263  2.64274  1.77794  2.59177
2.37147  8.65284  6.68075  5.54717  7.62123  7.4393  6.84079
5.32506 6.10417

MT.ROSE
1.6255 2.13745  0.996114  2.39491  1.09307  1.91872  2.67612
9.18361  7.11122  6.12316  8.27884  8.02432  7.31284 5.84393
6.6384

TRUCKEE
2.27024 1.61659  3.04044  1.92042  3.21238  2.98831  8.24786
6.51738 5.29937 7.39124 7.2328 6.5415 5.04065 6.11849

SADDLEBAG
1.67816 1.93813  2.62349  2.52191  3.44443  9.05694  7.00516
5.97936 8.25293 8.12622 7.07914 5.33544 6.85298

UPPER.HORSE
2.03315 1.38687  1.86193  2.86447  9.42242  7.34296  6.34887
8.5576 8.35676 7.56103 5.92451 7.01351

KAISER
2.97859  1.68317  2.8769  10.0032  8.19593  7.12033  9.16699
8.99759 8.38567 6.86251 7.63708

DINKEY
2.40718 3.44496  9.27834  7.32203  6.35703  8.39129  8.10658
7.44498 6.04263 6.79866

HUNTINGDON
2.89015  10.5761  8.39032  7.46989  9.74978  9.47779  8.7231
7.26175 7.89181

BIG.BEAR
9.02419 7.00088  5.97521  8.12035  7.89654  7.51499  6.39397
6.21869

RIDGE3050
4.11461 3.72894 2.06294 1.94376 3.18779 5.05955 3.72065

SOUTH3100
2.0305 3.81417 3.5327 1.7556 2.83782 2.51834
```

```
VALLEY3100
3.25387 3.04734 1.8972 2.35001 2.13242

VALLEY2540
0.907537 2.94204 4.31762 2.93145

NORTH3050
2.76804 4.35813 2.40583

FRASER
2.52948 2.72286

MEADOW.CR.
3.90919

UTAH
```

Appendix F: Euclidean dissimilarity between locations based on first three principal components.

Stands are identified by their code names, and followed by an ordered series of standardized Euclidean distances from that stand to subsequent stands.

```
MEND01
0.249826  0.943337  0.994729  7.31425E-2   1.80975   1.76557
1.56184  1.64027  1.52498  1.72192  1.72585  1.81711  1.5978
1.90638 1.59211 0.850717 1.09703  1.02685  0.720533  0.61855
1.01446 1.26153 0.671819


MEND02
0.821805 0.894872 0.261572 1.65428 1.63019  1.46917  1.53106
1.44371  1.64265  1.62111  1.69798  1.47488  1.77914 1.49478
1.07363 1.23613 1.13789 0.925578  0.826423  1.17219  1.34984
0.798929


MENDOSHOR
0.327039  1.00415  0.879306   0.847438   0.682245   0.720155
0.686933   0.852067   0.815643   0.923759  0.659203  0.97406
0.749575 1.39302 1.10423 0.945477  1.18756  1.11678  1.12366
0.999353 0.816048


CRESCENT
1.05531 0.918545 1.00671 0.847087 0.848357 0.87541  0.975471
0.947618  1.10165  0.766053 1.08757 0.963754 1.45934 1.05517
1.00439 1.25699 1.17234 1.10115 0.998607 0.846252


GASQUET
1.8658  1.8244  1.62693  1.70405  1.59046  1.78912   1.79007
1.87773  1.65981  1.96756  1.65458  0.879037 1.16075 1.09391
0.761955 0.662676 1.07521 1.33176 0.739649


BISHOP2400
0.414152  0.63444  0.475046   0.742999   0.684916   0.521175
0.574928  0.367933 0.397501 0.718697 2.22786 1.77239 1.63385
2.02268 1.96416 1.84018 1.54997 1.62805


BISHOP3050
0.358588  0.252015  0.443772  0.425261   0.246787   0.174557
0.268778  0.192828  0.358956 2.07931 1.68318 1.47477 1.88169
1.84299 1.73595 1.41699 1.52803
```

```
COTTONWOOD
0.166607  0.112202  0.197018  0.189012  0.326596  0.276071
0.428522  0.176376  1.77174  1.34609 1.13203 1.57769 1.54755
1.40034 1.06525 1.22573

MT.ROSE
0.278246  0.239347  0.103768  0.28409   0.138953  0.293332
0.288945  1.90174  1.45185  1.26292  1.70387 1.66617 1.51368
1.18074 1.33453

TRUCKEE
0.240299 0.285863 0.383377 0.383195 0.524055 0.150738 1.6965
1.29483 1.06027 1.50614 1.48224 1.34231 1.00794 1.17108

SADDLEBAG
0.184533 0.350402 0.370657 0.408091 0.298641 1.8733  1.39026
1.19385 1.68424 1.66076 1.45814 1.08159 1.33144

UPPER.HORSE
0.222616 0.231597 0.249247 0.276783 1.95682 1.50184  1.30582
1.76196 1.72969 1.56519 1.21459 1.40085

KAISER
0.37128 0.242105 0.277024  2.0634  1.67054  1.44335  1.87159
1.84333 1.7219 1.38157 1.5354

DINKEY
0.324523 0.392827 1.91758 1.47096  1.29927  1.71579  1.66921
1.53278 1.22418 1.33423

HUNTINGDON
0.468936  2.19169  1.7364  1.5505  1.9944  1.95711  1.80267
1.45508 1.62737

BIG.BEAR
1.79224 1.43204  1.18305  1.60312  1.57976  1.47261  1.14897
1.28238

RIDGE3050
0.793854  0.741339  0.206438   0.293201   0.648562  1.01724
0.629893

SOUTH3100
0.358087 0.670854 0.662311 0.145415 0.359657 0.460548
```

```
VALLEY3100
0.584319 0.596837 0.331281 0.311986 0.372419

VALLEY2540
0.116517 0.531033 0.871804 0.431204

NORTH3050
0.530858 0.875178 0.369397

FRASER
0.446059 0.3924

MEADOW.CR.
0.598744

UTAH
```

APPENDIX G: Results of Principal Component Analysis of Sites based on Soil Variables

```
COVARIANCE MATRIX USED

ROOT 1 = 1.19168                 PERCENT OF VARIANCE = 51
VECTOR 1
 0.8771  5.27243E-2 -0.475179 -4.60499E-2

ROOT 2 = 0.867359                PERCENT OF VARIANCE = 37
VECTOR 2
 0.30783  0.53691  0.576026  0.534006

ROOT 3 = 0.177684                PERCENT OF VARIANCE = 8
VECTOR 3
-8.36057E-2 -0.470141 -0.286966  0.830439

ROOT 4 = 9.05881E-2              PERCENT OF VARIANCE = 4
VECTOR 4
-0.359091  0.698509 -0.600042  0.151949


CORRELATION OF EIGENVECTORS WITH VARIABLES

VECTOR 1
 0.951842  9.91725E-2 -0.667385 -8.21461E-2

VECTOR 2
 0.285  0.861591  0.690208  0.812688

VECTOR 3
-3.50344E-2 -0.341469 -0.15563  0.572018

VECTOR 4
-0.107442  0.362249 -0.232357  7.47327E-2


COMPONENT 1
COMPONENT SCORES
-0.197025 -0.223071 -0.226807 -0.356523 -0.37863  0.135618
 3.90656E-2  0.253888  4.80843E-2  5.89915E-2 -3.70430E-2
 0.141044  0.49602  0.455027  0.352539  4.67641E-2 -0.155248
-0.150672 5.28465E-3 -0.151034 -0.116756  1.89213E-2
 2.00802E-2 -0.078521

COMPONENT 2
COMPONENT SCORES
-0.497178 -0.374881  0.133493 -6.65005E-2 -1.97601E-2
0.34554
 3.48156E-2 -9.29182E-2  7.29009E-2  0.200143 -0.107683
 0.137672 -0.264717 -7.64840E-2 -5.81936E-2 -4.98886E-2
 3.15455E-2  7.51043E-2 -4.56011E-2  0.196896 -5.49990E-2
 0.217177 -5.43394E-3  0.268953
```

```
COMPONENT 3
COMPONENT SCORES
-8.73146E-2  4.74097E-3 -6.09217E-4 -1.47566E-2  0.296173
-1.21511E-3  5.91598E-2 -8.45717E-2  5.04153E-2 -5.26902E-2
 6.93838E-2  0.018405  4.09163E-2  7.36165E-2  8.14704E-2
 3.15324E-2 -5.10599E-2 -6.90905E-2 -5.40009E-2 -1.33404E-2
-0.10539 -7.67708E-2 -0.135485  2.04818E-2

COMPONENT 4
COMPONENT SCORES
 1.48750E-2  3.46628E-2  6.00969E-2 -2.24029E-2 -0.108726
-2.30612E-2  2.35834E-2 -4.91455E-2 -5.97389E-2 -7.73395E-2
 0.170984  5.29734E-2 -5.78219E-2  5.01050E-2  4.90682E-2
-7.43174E-2  2.96580E-2 -2.34957E-2 -4.61750E-2  6.70456E-2
-4.37330E-2 -1.77393E-2 -1.19751E-2  6.26194E-2
```

APPENDIX H: Results of Principal Components Analysis of sites within the Sierra Nevada

```
COVARIANCE MATRIX USED

ROOT 1 = 1.14132                  PERCENT OF VARIANCE = 38
VECTOR 1
 0.146612  0.599457  0.484905  7.88759E-2  0.313286 -0.21834
 4.87529E-2  0.416365  0.237157

ROOT 2 = 0.840596                 PERCENT OF VARIANCE = 28
VECTOR 2
 0.116944 -0.380069 -0.29294  0.386002  0.732127  4.48364E-2
 0.143409 0.219394  1.84551E-2

ROOT 3 = 0.649418                 PERCENT OF VARIANCE = 21
VECTOR 3
-0.189667  0.323288 -9.36352E-2  0.689191 -5.02558E-2
 -0.233268 -0.29876 -0.230436 -0.420073

ROOT 4 = 0.165976                 PERCENT OF VARIANCE = 5
VECTOR 4
 0.2249  0.230688  0.10151  0.313105 -0.139903  0.780347
 0.383766 -7.20740E-2 -8.29327E-2

ROOT 5 = 0.125853                 PERCENT OF VARIANCE = 4
VECTOR 5
 0.902235 -1.61507E-2 -6.29465E-2 -8.45805E-2 -7.24468E-2
 -0.244074-4.89874E-2 -9.40747E-2 -0.313886

ROOT 6 = 6.54338E-2               PERCENT OF VARIANCE = 2
VECTOR 6
-5.42624E-2 -0.373675  0.668957  0.146954  7.87925E-2
 -0.234102 0.367038 -0.432521 -7.42987E-2

ROOT 7 = 2.69014E-2               PERCENT OF VARIANCE = 1
VECTOR 7
 0.188729 -0.272522 -1.07465E-3  0.491717 -0.480403 -0.13673
-7.96375E-2  0.193739  0.595791

ROOT 8 = 1.41451E-2               PERCENT OF VARIANCE = 0
VECTOR 8
 6.83775E-2  0.343157 -0.360905 -2.83517E-2  0.16955 -0.1647
 0.25949 -0.617185  0.492334

ROOT 9 = 1.17367E-2               PERCENT OF VARIANCE = 0
VECTOR 9
-0.144941  8.10001E-2 -0.279754  2.05777E-2 -0.269728
 -0.356028 0.727825  0.325322 -0.242225
```

```
CORRELATION OF EIGENVECTORS WITH VARIABLES

VECTOR 1
0.378 0.812559 0.839877 0.123451 0.44099 -0.513978  0.151067
0.819438 0.55735

VECTOR 2
0.258757 -0.442129  -0.43544  0.518477  0.884433  9.05789E-2
0.381362 0.370558 3.72218E-2

VECTOR 3
-0.36887 0.330557 -0.122337 0.813669  -5.33622E-2  -0.414209
-0.698317 -0.342099 -0.74469

VECTOR 4
0.221122 0.119245 6.70486E-2 0.186879  -7.50991E-2  0.700509
0.453479 -5.40929E-2 -7.43254E-2

VECTOR 5
0.772449  -7.26971E-3  -3.62042E-2  -4.39590E-2  -3.38638E-2
-0.19079 -5.04062E-2 -6.14813E-2 -0.244958

VECTOR 6
-0.033498 -0.12128 0.277432 5.50718E-2  2.65565E-2  -0.13195
0.27232 -0.20382 -4.18091E-2

VECTOR 7
7.47042E-2  -5.67129E-2  -2.85767E-4   0.118154   -0.103819
-4.94165E-2 -3.78855E-2 5.85387E-2 0.214966

VECTOR 8
1.96261E-2  5.17801E-2  -6.95909E-2  -4.94000E-3  2.65697E-2
-4.31668E-2 8.95138E-2 -0.135225 0.12881

VECTOR 9
-3.78951E-2 1.11340E-2  -4.91366E-2  3.26600E-3  -3.85021E-2
-8.49883E-2 0.2287 6.49270E-2 -5.77272E-2
```

```
COMPONENT 1 COMPONENT SCORES

-0.687363 -0.269295 0.263088  1.27380E-2  0.372846  0.164787
8.31731E-3 -8.01679E-3 -0.17045 -0.219158 0.532509

COMPONENT 2 COMPONENT SCORES

6.16852E-2   -5.15793E-2    0.199036    0.165091    0.388534
-5.27303E-2    9.38703E-2   -0.472589    0.368905   -0.357944
-0.342279

COMPONENT 3 COMPONENT SCORES

0.270202 -0.147037 0.106701 8.17398E-2 -8.78654E-2 -0.484226
-9.92170E-2 -0.232893 7.37350E-2 4.68277E-2 0.472032

COMPONENT 4 COMPONENT SCORES

-0.119695    0.282266    -4.65768E-2    -1.99533E-2    0.097669
-0.224526    -1.25817E-2  8.08392E-2  1.47640E-2  -5.04196E-2
-1.78501E-3

COMPONENT 5 COMPONENT SCORES

0.164096  2.34456E-2   7.98409E-2    -7.51521E-2   2.42145E-2
3.43315E-2   -5.85938E-2   0.114169    -9.72467E-2  -0.240201
3.10956E-2

COMPONENT 6 COMPONENT SCORES

-4.06982E-2  5.22135E-2  0.171204   7.92737E-2   -8.05686E-2
3.29236E-3   -0.118043  -1.19662E-2  -3.27521E-2  3.12283E-2
-5.31838E-2

COMPONENT 7 COMPONENT SCORES

-1.30608E-2 -1.56641E-2 -3.16693E-2 -1.[illegible]8212E-2  -2.31383E-3
2.38268E-2    -0.102113    3.91457E-2    0.110706    -1.21307E-2
1.80948E-2

COMPONENT 8 COMPONENT SCORES

-1.60232E-2 1.18152E-3  5.13753E-2  -7.67424E-2  -3.94753E-2
-8.92130E-3  4.35432E-2  4.13990E-3  4.24947E-2  -9.38716E-4
-6.33635E-4

COMPONENT 9 COMPONENT SCORES

8.57571E-3  -4.61893E-2  2.37035E-2  -2.00909E-2  5.09724E-2
-3.69701E-2  -1.40856E-2  4.08901E-2  -1.00631E-2 3.78380E-2
-3.45808E-2
```

APPENDIX I: Results of Principal Components Analysis of sites within the Rocky Mountains.

```
COVARIANCE MATRIX USED

ROOT 1 = 2.95336                  PERCENT OF VARIANCE = 62
VECTOR 1
0.696775 8.89468E-2 0.202036 0.63987 -6.50538E-2  7.45625E-2
1.65743E-2 0.140551 0.182849

ROOT 2 = 0.886061                 PERCENT OF VARIANCE = 18
VECTOR 2
-0.359119 0.292304 -8.67833E-2 0.472628 -0.475681  -0.251953
-0.389162 -0.303977 -0.1452

ROOT 3 = 0.564916                 PERCENT OF VARIANCE = 12
VECTOR 3
0.251951   5.74238E-2   -0.208027   -3.42529E-2    -0.192496
-6.61696E-2 0.650908 -0.539858 -0.363612

ROOT 4 = 0.252676                 PERCENT OF VARIANCE = 5
VECTOR 4
-0.321587 0.441292 0.194945  6.31059E-3  -0.295753   0.480617
0.415948 9.76389E-2 0.403474

ROOT 5 = 9.28406E-2               PERCENT OF VARIANCE = 2
VECTOR 5
0.248218  0.696512  6.07977E-2  -0.265565  0.336157   0.22852
-0.340048 -0.234671 -0.207632

ROOT 6 = 4.07827E-2               PERCENT OF VARIANCE = 1
VECTOR 6
-7.70762E-2 0.437154 0.11494 3.06914E-3  0.177577  -0.699371
0.316058 0.407451 -5.63204E-2

ROOT 7 = 1.10851E-2               PERCENT OF VARIANCE = 0
VECTOR 7
-0.38535 -7.38345E-2  0.133299  0.513263  0.584739  0.251675
0.186273 -5.08339E-2 -0.349721
```

```
CORRELATION OF EIGENVECTORS WITH VARIABLES

VECTOR 1
0.941456  0.339237  0.8647   0.923684   -0.214522   0.321347
4.32735E-2 0.427538 0.598967

VECTOR 2
-0.265778 0.610635 -0.202739  0.373701  -0.859191  -0.594767
-0.556531 -0.506471 -0.29252

VECTOR 3
0.148887   9.57852E-2   -0.388043   -2.16253E-2    -0.277623
-0.124723 0.743257 -0.718214 -0.58491

VECTOR 4
-0.127095  0.492292  0.2432  2.66456E-3  -0.285267  0.605866
0.317649 8.68734E-2 0.434066

VECTOR 5
5.94636E-2 0.470991 4.59754E-2 -6.79694E-2 0.196541 0.174618
-0.157412 -0.126564 -0.135401

VECTOR 6
-1.22379E-2  0.195924   5.76075E-2   5.20629E-4   6.88122E-2
-0.354194 9.69689E-2 0.145645 -2.43424E-2

VECTOR 7
-3.18987E-2  -1.72522E-2  3.48309E-2   4.53924E-2   0.118134
6.64514E-2 2.97952E-2 -9.47340E-3 -7.88044E-2
```

```
COMPONENT 1 COMPONENT SCORES

0.862677  -0.543545  -0.40977  0.655663   0.626102   -0.2566
-0.926277 -8.24979E-3

COMPONENT 2 COMPONENT SCORES

[illegible]0.288308 0.227633 0.100654  -0.140807  6.29789E-2  -0.19248
-0.456514 0.686839

COMPONENT 3 COMPONENT SCORES

-0.325107 -0.405387 8.50399E-2  0.289879  0.173867  -0.25825
0.2904 0.149556

COMPONENT 4 COMPONENT SCORES

0.202729 -0.180374 0.356347  -0.162052  -0.107347  -0.115437
-1.84977E-2 2.46329E-2

COMPONENT 5 COMPONENT SCORES

3.59907E-2   0.16168   1.99761E-2   7.75517E-2   -2.80688E-2
-0.229706 2.99641E-2 -6.73873E-2

COMPONENT 6 COMPONENT SCORES

-5.75058E-2  6.12325E-3  8.16640E-2   0.116608  -7.85380E-2
5.40460E-2 -7.84031E-2 -4.39946E-2

COMPONENT 7 COMPONENT SCORES

-3.05891E-2  1.26060E-2  3.70051E-2  -2.49573E-2  7.28637E-2
1.24003E-3 -2.05911E-2 -4.75772E-2
```

APPENDIX J: Stereograms relating some edaphic and climatic variables to the Sierra Nevada sites

Figure J.1 Stereogram relating variation within the Sierra Nevada to temperature.

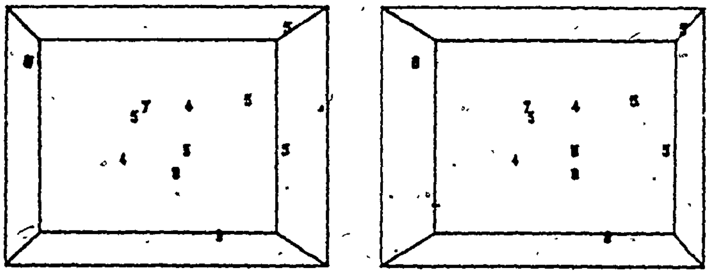


Figure J.2 Stereogram relating variation within the Sierra Nevada to precipitation.

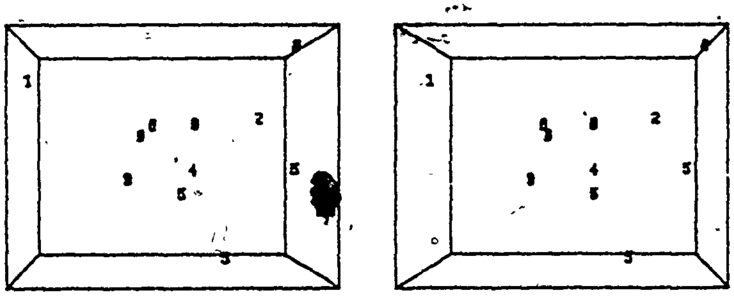


Figure J.3 Stereogram relating variation within the Sierra Nevada to pH.

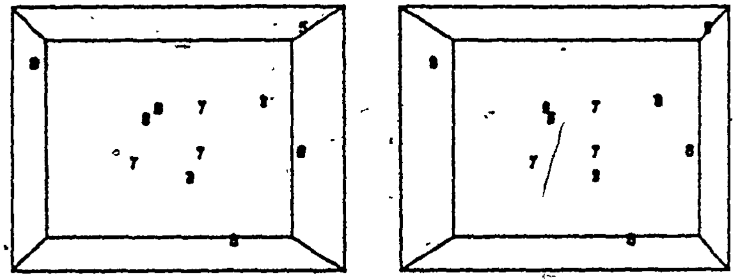


Figure J.4 Stereogram relating variation within the Sierra Nevada to phosphorus.

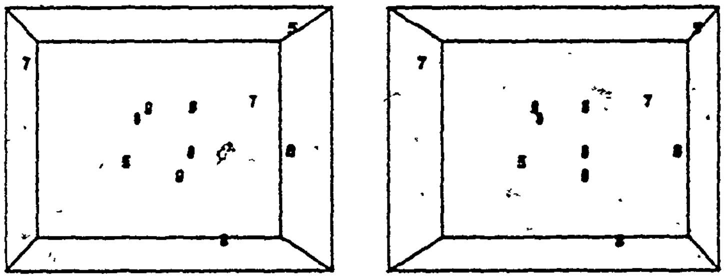


Figure J.5 Stereogram relating variation within the Sierra Nevada to potassium.

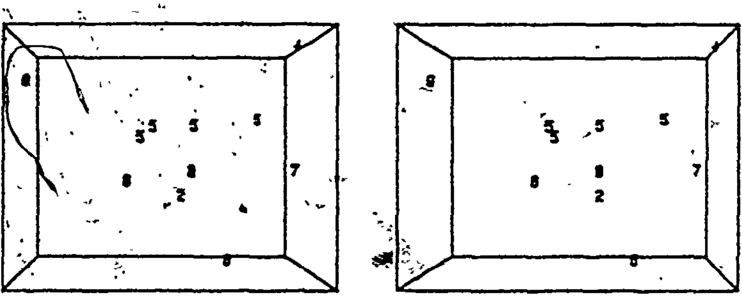
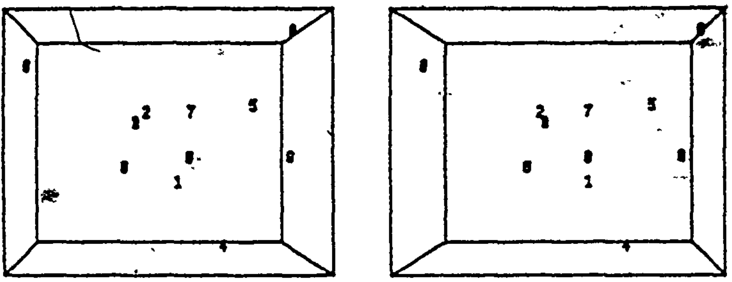


Figure J.6 Stereogram relating variation within the Sierra Nevada to magnesium.



APPENDIX K: Characters ranked on the basis of their ability to discriminate the Utah site from the other Rocky Mountain sites

(a) RIDG3050

RANK	CHARACTER	NUMBER	F VALUE
1	apoph.h/l.	8	17.5304
2	vol/cylvol	6	9.13698
3	serotiny	1	9.00655
4	apoph.h/w.	9	8.38983
5	cone.wid/l.	5	6.73356
6	apoph.ht.	3	6.52719
7	symmetry	7	0.44297
8	sp.gr.	4	0.408945
9	volume	2	0.346456

(b) SOU3100

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	13.2777
2	cone.wid/l.	5	12.3143
3	apoph.h/l.	8	4.90801
4	symmetry	7	3.32661
5	serotiny	1	1.11676
6	volume	2	0.657243
7	vol/cylvol	6	0.218974
8	apoph.ht.	3	0.063552
9	apoph.h/w.	9	0.051038

(c) VALL3100

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	11.3131
2	cone.wid/l.	5	3.20193
3	vol/cylvol	6	2.716
4	symmetry	7	2.65802
5	apoph.h/l.	8	1.93479
6	serotiny	1	0.547328
7	apoph.h/w.	9	0.528476
8	apoph.ht.	3	0.13624
9	volume	2	0.067290

(d) VALL2540

RANK	CHARACTER	NUMBER	F VALUE
1	serotiny	1	10.8666
2	cone.wid/l.	5	6.88082
3	symmetry	7	3.52681
4	apoph.h/l.	8	2.94353
5	apoph.ht.	3	0.968944
6	apoph.h/w.	9	0.241224
7	volume	2	0.209405
8	vol/cylvol	6	0.157718
9	sp.gr.	4	0.000192

(e) NOR3050

RANK	CHARACTER	NUMBER	F VALUE
1	cone.wid/l.	5	5.92814
2	serotiny	1	5.87746
3	apoph.h/l.	8	2.47018
4	vol/cylvol	6	1.75373
5	symmetry	7	1.26107
6	sp.gr.	4	1.16324
7	apoph.ht.	3	1.13576
8	volume	2	0.956587
9	apoph.h/w.	9	0.39696

(f) FRASER

RANK	CHARACTER	NUMBER	F VALUE
1	apoph.h/l.	8	20.0457
2	cone.wid/l.	5	10.7822
3	volume	2	6.72224
4	sp.gr.	4	6.65924
5	apoph.h/w.	9	1.32359
6	symmetry	7	0.302902
7	apoph.ht.	3	0.26321
8	vol/cylvol	6	0.174006
9	serotiny	1	0.005141

(g) MEAD.CR.

RANK	CHARACTER	NUMBER	F VALUE
1	sp.gr.	4	50.058
2	cone.wid/l.	5	13.7978
3	symmetry	7	4.35719
4	volume	2	3.77035
5	vol/cylvol	6	2.47107
6	apoph.ht.	3	0.762168
7	apoph.h/l.	8	0.433615
8	serotiny	1	0.384514
9	apoph.h/w.	9	0.310837

APPENDIX L: Stereograms relating edaphic and climatic variables to the Rocky Mountain sites

Figure L.1 Stereogram relating variation within the Rocky Mountains to temperature.

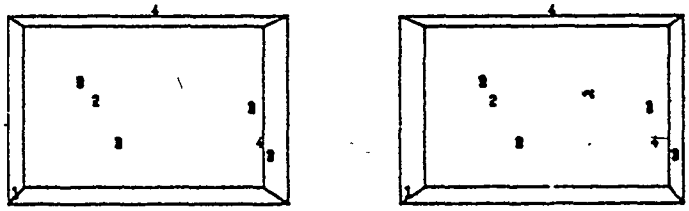


Figure L.2 Stereogram relating variation within the Rocky Mountains to precipitation.

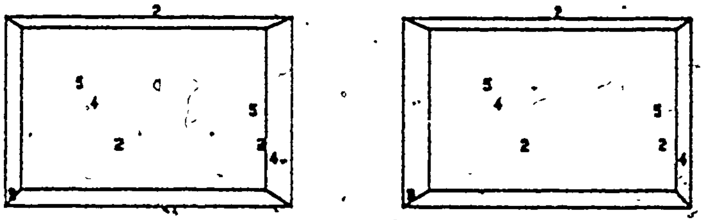


Figure L.3 Stereogram relating variation within the Rocky Mountains to pH.

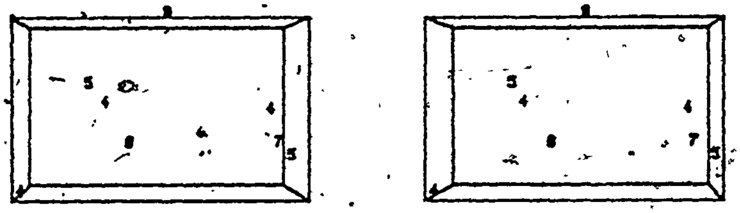


Figure L.4 Stereogram relating variation within the Rocky Mountains to potassium.

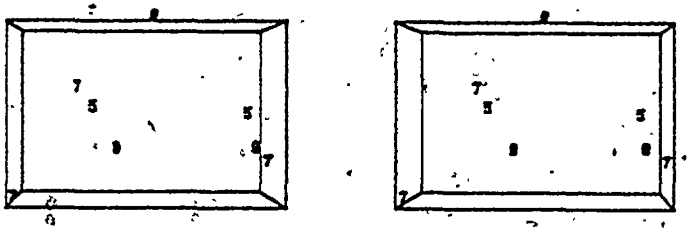
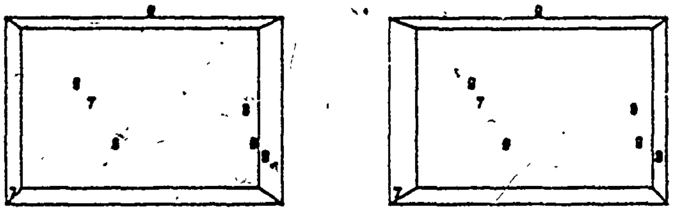


Figure L.5 Stereogram relating variation within the Rocky Mountains to magnesium.



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