MORPHOLOGICAL AND ANATOMICAL VARIATION OF <u>PICEA</u> IN SOUTHWESTERN

BRITISH COLUMBIA.

By

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ABSTRACT.

Relations between individual trees hypothesized to be
representative of Picea engelmannii and P. sitchensis and
putative hybrids in southwestern British Columbia were examined
using several morphological and anatomical variables measured on
cones, needles, and twigs. 36 variables were selected that had
an inter-individual variation that exceeded intra-individual
variation. Such relative variation suggested that the variables
selected were more genetically than developmentally variable.
These variables were measured on 640 trees.

Patterns of inter- and intra-individual variation of these
variables were examined with multivariate analyses. Similar
patterns of intra-individual variation with respect to position
in the canopy were detected regardless of the age of the tree or
the species, suggesting that intra-individual variation in Picea
is not necessarily a function of the environment extrinsic to
the individual. Further, the two hypothesized taxa were not
especially different with respect to the pattern of
intra-individual variation. In an inter-individual context, the
intra-taxonomic variation was shown to be larger than
inter-taxonomic variation. Inter-individual variation
attributed to the hypothesized taxa was smaller than
intra-population variation. Inter-taxonomic variation was only
25 percent larger than intra-individual variation. Further, the
hypothesized taxonomic polarity of the data was not co-incident
with the actual polarity of the data. What taxonomic structure
emerged was evident only as the extremes of a continuum of

variation over a large geographic area reflecting large
environmental variation, suggesting that recognition of two taxa
of _Picea_ in southwestern British Columbia may not be appropriate
or practically feasible. From the evidence available here, it
is not possible to attribute the pattern of variation to
hybridization followed by introgression or to the
differentiation of a single, large polymorphic taxon.

The pattern of inter-individual variation was only
partially correlated with regional and local scales of
geographic and environmental variation. Local patterns of
variation were not co-incident in 16 separate geographic areas.
The relation of the pattern of variation in nursery grown trees
with respect to regional scales of geographic variation was not
co-incident with the patterns of variation in naturally grown
trees from the same area of origin. This variability of
relations suggests that inter-individual variation is probably
attributable to processes operating at an extremely local scale.

Implications from these conclusions are presented and
discussed with respect to the systematics of _Picea_ and the
utilization of _Picea_ in forestry and tree improvement
programmes.

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ACKNOWLEDGEMENTS.

PREFACE.

There are reasons for conducting a scientific study that go beyond science. Regardless of the objectivity of any study these reasons invariably impact on the study. I cannot say what has attracted me to study trees, especially spruces. In conducting this research and writing the thesis three events occurred which effectively limited or coloured the conclusions that were drawn. As a result of studying the consequences of sample size on the results of multivariate analyses, the number of analytic approaches that could be used in the study were reduced. Consequently, the presentation of results is not as parsimonious a summarization as I would have liked. Furthermore, certain issues which, at the outset, I had wanted to investigate, simply could not be addressed because of deficiency in sample size. I have tried to indicate where such limitations have occurred.

Second, the realization of the analytic and biological deficiency resulting from ignoring intra-individual variation in the traditional approach to this type of study, came too late to be addressed effectively. This realization occurred during the reflective process of measuring, long after I had thought data collecting was finished. A quick field trip and some extremely fortuitous collections provided some data that proved critical in presenting insight into the nature of intra-individual variation. The failure to capitilize on intra-individual variation as a source of information represents a source of dissatisfaction. I have endeavoured to indicate a better

design in sampling and analyis which would effectively
incorporate such intra-individual information in future studies.

The third event, the one that I am most bitter about,
concerns my changing perception of the relation of forest
genetics to forestry and forest biology. In the last few weeks
of writing the thesis I attended a conference on forest
genetics. These meetings were pervaded by a concern for the
continuation of legislative and administrative programmes that
met political and industrial commitments rather than scientific
principles or the biology of the organisms being studied. There
were few instances where there was any recognition of the
problems, situations, and operational conditions under which
foresters work and forestry is conducted. It is as an
antithesis to this perceived disinterest that I offer the
epilogue. For any research to be of value, the results and
recommendations must be communicated to potential users;
otherwise, the research is a total loss (Young 1972; Secretariat
on Forestry Research Development 1984).

I.   INTRODUCTION.

Picea A. Diet. is a genus of widely distributed northern
hemisphere coniferous trees that includes between 35 and 40
species that have been variously grouped into several informal
supraspecific taxa (Flous 1936; Wright 1955; Gaussen 1966;
Bobrov 1971, 1973; Schmidt-Vogt 1977). Most of these species
occur at montane and subalpine elevations. It is an ancient
genus dating from late Cretaceous times in Asia (Florin 1963).

Species in the genus have been distinguished traditionally
on the basis of three morphological traits: nature of the cone
scale - stiff or flexuous; needle shape - rhomboid or flattened;
and the presence or absence of pubescence on twigs. All
possible combinations of these traits can be used to define only
nine taxa. Other features used to distinguish taxa are cone
size, crown form, and geographic or edaphic habit. Evaluation
of more morphological and anatomical variables (Wright 1955;
Colleau 1968; Sudo 1968) as well as chemical variables
(Wellendorf and Kaufmann 1977; Wellendorf and Simonsen 1979; see
review in La Roi and Dugle 1968) have been utilized, and these
tend to support the recognition of species on the basis of the
traditional variables. Chromosomal variation and DNA content
vary little between the various species (Pravdin, _et al_. 1976;
Moir and Fox 1977; Burley 1965c; Price, _et al_. 1973).
Evaluation of other variables in particular groups of species
have further substantiated the distinctness of taxa and have
clarified relationships in the genus (Duman 1957; Daubenmire
1968, 1972, 1974; Garman 1957; Marco 1931, 1939; von Rudloff

1975; Taylor and Patterson 1980; La Roi and Dugle 1968; Lee and
Sih-kin 1966). As well as attempts to understand relationships
based on these variables, a large number of controlled crosses
between species have been performed (Johnson 1939; Wright 1955;
Gordon 1976b, 1978, 1980, 1982; Fowler, et al. 1980, 1982;
Mikkola 1969). Bongarten and Hanover (1982) and Santamour
(1967) however, have called attention to some inadequacies in
the earlier work on controlled crosses owing to the inadequate
isolation and identification of parents as well as the small
number of parent trees used in these crosses.

Two groups in the genus have been subjected to intensive
systematic investigation: the P. abies - P. obovata complex in
Europe (Schmidt-Vogt 1977; Pravdin, et al. 1976; Lindquist 1948;
Andersson 1965), and the P. glauca complex ("Glaucoides", Fowler
1983) of North America. Such intensive research has been
conducted because of the importance of some of these species to
forestry. Investigation of the the P. glauca complex has
focused on the diversity shown by the species in western North
America: P. sitchensis (Bong.) Carr.; P. glauca (Moench.) Voss;
P. engelmannii Parry ex Engelm. (= P. glauca ssp. engelmannii
(Parry ex Engelm.) Taylor) P. pungens Engelm.; and, P. mexicana
Martinez (= P. engelmannii ssp. mexicana (Martinez) Taylor and
Patterson). The various taxa of the P. glauca complex are
separated from each other primarily on the three morphological
criteria traditionally used to distinguish the other species of
the genus. P. sitchensis is the only species in the complex
with flattened leaves, P. engelmannii and P. mexicana are the
only species in the complex with pubescent branches, and

P. glauca is the only species in the complex with stiff cone scales.

The most ancient fossils from western North America referable to Picea are of Miocene age (Florin 1963) and resemble the extant P. chihuahuana Martinez (Gordon 1968) of the Sierra Madre Occidentale of Mexico and P. breweriana S. Wats. of the Klamath region of Oregon and California. Tertiary and more recent macrofossils and microfossils of Picea are widely scattered in western North America (Crabtree 1983). These findings suggest the existence of three major groups of Picea in North America dating from the late Tertiary to the present: the P. breweriana - P. chihuahuana lineage, the remnants of a more widely distributed temperate and montane elevation forest in western North America; the P. mariana - P. rubens lineage of arcto-boreal latitudes in eastern North America and, the P. glauca complex, widespread at arcto-boreal latutudes. These three groups are generally considered to have migrated separately from Asia (Taylor and Patterson 1980), the P. glauca complex being the most recent migrant in the late Cretaceous or early Tertiary. The relationships among these three groups of spruces remain obscure as does the relation to fossils from a late Tertiary Picea from the southeastern United States (Critchfield 1984).

The similarity of extant forms of the P. glauca and P. abies complex to the Miocene P. banksii of arctic North America (Hills and Ogilvie 1970) lends weight to Hustich's (1953) hypothesis concerning a common derivation of the P. abies

and P. glauca complexes. Ogilvie (1972) contends that the extant species of the P. glauca complex were all differentiated by the Pleistocene and that the hybridization, so characteristic of this lineage (Wright 1955; Bobrov 1972, 1973), has been a post-glacial phenomenon (see also Critchfield 1984). Crabtree (1984) citing La Motte's (1939) collections, suggests that P. sitchensis may have been differentiated much earlier during the Oligocene. P. engelmannii appears to have been differentiated by the mid-Tertiary following mountain building (Taylor and Patterson 1980). Wright (1955) suggests that differentiation of these species was by geographic isolation rather than by the evolution of breeding barriers or through strong morphological differentiation. La Roi and Dugle (1968) counter Wright's (1955) comments, and suggest instead that Picea has been subjected to liberal taxonomy rather than to conservative evolution.

Research on the systematics of the taxa in the western area of the P. glauca complex reached a hiatus during 1968 with the coincident publication of the work of Daubenmire, La Roi and Dugle, and Ogilvie and von Rudloff followed in 1969 by Roche's work. This abundance of research was an elaboration on the earlier work of Taylor (1959), Garman (1957), and Horton (1959). More recent research has been conducted. This recent work has emphasized the relations of P. glauca and P. engelmannii. A latent assumption of this work is the recognition of P. sitchensis as a distinct species in the P. glauca complex. Indeed, this assumption continues a tradition of recognizing P. sitchensis as a distinct species in the genus based on its

flattened leaves and its occurrence at low elevations. Where hybrids have been observed with either P. glauca (Copes and Beckwith 1977; Hanover and Wilkinson 1970; Roche 1969; Daubenmire 1968) or P. engelmannii (Klinka, et al. 1982) they have been regarded as a local phenomenon that does not influence the validity of the assumed discreteness of P. sitchensis from the rest of the P. glauca complex. This position is held in spite of Roche's (1969) observations concerning the clinal variation between P. sitchensis and P. engelmannii.

This presumed discreteness of P. sitchensis from the rest of the P. glauca complex has resulted in investigations of patterns of variation within P. sitchensis that have generally proceeded independent of any consideration for other species in the P. glauca complex. Where other species of the P. glauca complex have been considered, they are identified merely as a source of comparison (Pollard, et al. 1976; von Rudloff 1975). By contrast, P. engelmannii is generally felt to be subsumed entirely in the variation demonstrated for P. glauca (Taylor 1959; Hanover and Wilkinson 1970); La Roi and Dugle 1968; Daubenmire 1974; Ogilvie and von Rudloff 1968; Roche 1969). The nomenclatural conventions remain to be resolved: continued recognition of P. engelmannii as a species (Daubenmire 1974; La Roi and Dugle 1968); subsumed as a subspecies of P. glauca (Taylor 1959; Ogilvie and von Rudloff 1968); or reduced to varietal status (Hustich 1953; Love and Love 1966). The presumed lack of discreteness between P. engelmannii and P. glauca has been adopted in forestry applications in British Columbia where the complex is referred to as simply "Interior

spruce" (Kiss 1976).

Contrary to the assumption that P. sitchensis is discrete
in the P. glauca complex are the remarks cited by Garman (1957)
that suggest that P. engelmannii be considered more closely
related to P. sitchensis than to P. glauca. Franklin (1961), on
the basis of seedling morphology, corroborates this impression
(see however Jeffers 1974). Alternatively, Moir and Fox (1977)
suggest a similarity of P. glauca to P. sitchensis on the basis
of the presence of a β-chromosome complement[1].

Observations made in conjunction with work associated with
that reported in Klinka, et al. (1982) and other observations in
areas of the coast mainland of southwestern British Columbia
suggested that hybridization of P. sitchensis with
P. engelmannii may not have been as local a phenomenon as
previously suggested. Although Garman (1957) called for special
attention to collecting materials of P. sitchensis and
P. engelmannii [2] from this area, the isolation of the area has
generally prevented extensive collection (Daubenmire 1968;
Falkenhagen and Nash 1978; Roche 1969; others in Ching and
Sziklai 1978b). An investigation of the variation of
P. sitchensis and P. engelmannii in this particular area would
seem to be necessary to better circumscribe the range of
variation in the P. glauca complex. The study presented here

[1] Guyla Kiss, British Columbia Ministry of Forests, Vernon
confirms the observations of Moir and Fox (1977) and offers the
observation that P. engelmannii lacks a β-chromosome complement.

[2] For the sake of brevity, P. sitchensis and P. engelmannii will
be referred to collectively as Picea unless otherwise noted.

addresses this issue of variation of _Picea_.

Conceptually, such a study involves examining and explaining the variation in the trees of the two hypothesized taxa. Analytically, such research is carried out by describing and correlating patterns of variation at various scales. There are two scales of variation: intra- and inter-individual variation. Effective description of inter-individual variation must be based on an estimate of intra-individual variation.

Explanations for intra-individual variation in conifers have not commonly been proposed. Where they have been tendered they have been related to the environment, although developmental considerations have been made for certain conifers. Analytic attention to intra-individual variation has not been considered generally in conifers. Where analytic consideration has been made it provides a convenient scale against which inter-individual variation can be compared. A developmental view of intra-individual variation potentially offers further explanations concerning the nature of inter-individual variation in addition to the results of numerical comparisons.

A plethora of specific explanations for emergent patterns of inter-individual variation could be tendered, but they fall under two general processes: hybridization and differentiation. Neither hypothesized process need be mutually exclusive. If hybridization constitutes a valid explanation, then the present study will add to our knowledge concerning this process and its evolutionary consequences in _Picea_ (Wright 1955; Bobrov 1972,

1973). If differentiation seems a plausible hypothesis, then
the results of such a study may address ecological and
evolutionary considerations in Picea. The essential contrast
and generalizations are: single species differentiation versus
two, or more, species merging.

Owing to the geographic scale upon which this study is
conducted and, that in sexually reproducing organisms every
individual is to some degree unique, one cannot present specific
explanations for relationships with respect to immediate
parentage and selection. Only more distant ancestry and larger
scale selection can be considered. Such parentage-specific
explanations would require detailed sampling and controlled
crosses - labour intensive procedures that are
counter-productive in examing the general variation over such a
large geographic area.

Independent patterns of variation have been observed and
described previously in both taxa for several scales of
variation based on several types of variables. Over the
geographic range of the species several patterns have been
observed: discontinuous variation (Falkenhagen 1974; Daubenmire
1968; Burley 1965a, 1966c; Forrest 1975b,c, 1980b; Mikshe 1971;
Pollard, et al. 1976; Moir and Fox 1977); clinal variation
(Pollard, et al. 1976; Burley 1966b,c; O'Driscoll 1976a;
Falkenhagen 1977, 1978; Illingworth 1976; Mergen and Thielges
1967; El-Kassaby and McLean 1983; Daubenmire 1968); deviations
from clinal variation (Moir and Fox 1977; Forrest 1980b; Lewis
and Lines 1976; Daubenmire 1968; Burley 1965b, 1966b; Cannell

and Willett 1975; Falkenhagen 1978; Pollard, et al. 1975;
Hanover and Wilkinson 1970); uniformity (Yeh and El-Kassaby
1980; Falkenhagen 1976; Hanover and Wilkinson 1970; Burley
1966a,c; Forrest 1980b). Other observation on variation are
reported in Burley (1966a), Harris (1978); and others in Ching
and Sziklai (1978b) and O'Driscoll (1976b). Explanations for
these patterns invoke several causes: glacial refugium;
migration; selection; differentiation; hybridization; isolation
and drift; and, evolutionary bottlenecks. The major source of
variation in P. sitchensis is correlated with latitude, whereas
in P. engelmannii it is correlated with elevation.

Most of the explanations for the observed patterns have
been tendered under the assumed validity that natural selection
is the principal operative process and the theoretical
expectations taken from the presumed distribution and occurrence
of the two species, (Fowells 1965; Hosie 1975; Krajina, et
al 1982; Griffin and Critchfield 1976; Little 1971). The
occurrence of Picea in the study area is far more sporadic than
the continuity suggested by the maps in these publications
(Klinka, et al. 1982). Assumptions need to be reconsidered when
based on the presumption that large inter-breeding populations
are continuuous.

On a local scale where observations have been reported
concerning the nature of population variation in these taxa, the
largest source of variation is invariably contained within the
populations. These studies of populations have been based on
seedling populations rather than mature individuals, as have

most others studies on conifers (Falkenhagen 1974). The observed high intra-population variation is consistant with observations reported for the majority of other coniferous species. Explanations for high intra-population variation in Picea, as well as other conifer genera have not been tendered. Furthermore, specific local explanations cannot be presented here owing to a concern for circumscribing the general variation of Picea - however it may be possible to provide an estimate of the magnitude of intra-population variation compared to inter-population variation.

Studies of the variation serve an economic as well as a systematic purpose. Both species are landscape dominants in various parts of their range and are important commercial tree species. Furthermore, they are potentially valuable in reforestation programmes as both species occur as primary successional species. P. engelmannii is particulary important in reforestation in the central interior of British Columbia. Additionally, both species are used as exotics in European reforestation and aforestation. It is worth noting that the latitudes of this study in southwestern British Columbia are comparable to those of southern Britain, and that observations made in the present study may prove to have relevance to forestry in that part of Britain. The significance of P. sitchensis to forestry has been realized since it is the most widely planted commercial species in Britain (Pearce 1976). Hybrids between P. sitchensis and P. glauca are also of interest (Faulkner 1982). Dietrichson (1971) suggests that more consideration be given to P. engelmannii in Norway. Various

provenances of P. engelmannii also may prove useful as an exotic
in some places in western North America[1] (Shepperd,
et al. 1981).   Alternative explanations for species
differentiation or coalescence may have implications for
forestry relating to the feasability of production and use of
"inter-specific" crosses.

Owing to the economic importance of these species, further
information pertaining to the occurrence and ecology of the taxa
can be found in various bibliographies (Krajina 1969; Fowler and
Roche 1977; Roche and Folwer 1975; Christensen and Hunt 1965;
Phelps 1973; Harris and Ruth 1970; Dobbs 1972; Krajina,
et al. 1982).   Where relevant, specific conclusions from this
corpus of literature have been detailed in the succeeding
chapters. Additionally, specific observations are also given
from more recent literature and further discussion is provided
of the conceptual and analytic framework.

In summary, the present study is concerned with the nature
of variation in naturally occurring individuals of
P. engelmannii and P. sitchensis in a portion of the range of
these species that has not been described previously. The
hypothesis being tested is that there are two taxa:
P. sitchensis and P. engelmanii. The inference derived is: if
this hypothesis is appropriate then an examination of trees from
areas not sampled previously will continue to support the
recognition of two taxa. Such a study seeks to uncover and

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[1] Helmar Hahn, British Columbia Ministry of Forests ,Vancouver
Forest Region, pers. comm.

describe patterns of inter-individual variation at various
geographic scales and offer explanations for the patterns
described. To assess inter-individual variation, conceptual and
analytic attention must be given to aspects of intra-individual
variation. The primary question being addressed is whether
variation is a consequence of the hybridization and subsequent
introgression and differentiation of the two taxa, or simply the
consequence of the differentiation of a single polymorphic
taxon. The secondary concern is to present possible
explanations for these patterns of differentiation.

II. MATERIALS AND METHODS.

1. Introduction.

The phenomena requiring explanation are various aspects of phenotypic variation of <u>Picea</u> in southwestern British Columbia. The identification of a given phenomenon represents a major step towards proposing an explanation for that phenomenon. Quantification and subsequent description of that phenomenon and the conditions under which it is manifest are required prior to tendering explanations. However, the very act of quantification focuses attention on only a portion of the potential information available about the specific phenomenon and the conditions surrouding its occurrence; in this case, the characteristics of an organism. Since, quantification is an estimate of the phenomenon, explanations must be tendered that respect the bias inherent in these estimates. This amounts to carefully considering the nature of these characters, the nature of sampling, and how the measurement error associated with quantifying characters can be minimized during analysis so that explanations are not emburdened by an observational bias.

As one can never describe an organism completely by its characters, so too is it impossible to measure a character completely. Indeed, there are probably an infinite number of characters by which an organism can be described - so too are there an infinite number of ways to measure a character. Measurements or descriptions are simply rules used to assign a number to an object (O'Grady 1982). It is important to realize that characters are the manifestations of individual organisms

by which we describe, communicate, and draw inferences about
individual organisms. A character does not exist as an
independent manifestation of an organism (Davis and Heywood
1973; O'Grady 1982). Although we see organisms, their parts,
and characters, it is specific variables in a limited
multivariate perspective that we actually measure. The
distinction between character and variable serves the same
epistemological purpose as recognizing the difference between
population and sample, or estimand and estimator. It is crucial
here, as elsewhere, to acknowledge clearly the methodologically
and conceptually constrained preceptions of the world around us
and how we bring these perceptions to bear on a subject of
study. Merely acknowledging the intuitive usage of a
fundamental concept, such as a character (Wiley 1981), does
little to alleviate ambiguities that may arise from such usage.

Measuring variables, collecting samples, and determining
sources of error associated with measuring and collecting are
inextricably intertwined with the selection of an appropriate
analytic synthesis. Several aspects of sampling are unique to
trees, but the analysis and conceptual framework used is that
appplied in any systematic investigation of a biological system.
An analytic technique well suited to resolving a problem on
theoretical grounds may be inadequate or inappropriate with
respect to resolving that problem for a given collection of
samples and variables. Understanding the nature of variable
variation and covariation, sampling limitations, and associated
measurement error for a given set of data as well as the caveats
for a given analytic protocol allows one to select an

appropriate analytic methodology. To this end considerable effort was spent in defining variables, sampling, and determining associated error so that an appropriate analytic method could be employed.

In addition to explicitly recognizing the perceptive constraints that are brought to bear on a subject of study, it is equally important to state clearly the nature of the inferences to be drawn from such a study. Specifically, the central inference to be drawn here is that, besides the effect of the environment, individuals that look alike are assumed to share a large number of genes in common and are thus capable of interbreeding (Solbrig 1968).

2. Characters.

Phenotypic variables are regarded as an expression of genetic information and the interaction of that information with the internal environment and the immediate external environment of the organism, and the surrounding environment. Variables that are more variable within an individual (intra-individual) than inter-individually (inter-individual) are regarded as being less buffered against the local environment than are those that are more variable between individuals. Both types of variables are genetic, albeit at different extremes of a continuum of the degree of buffering.

Assessing differences between taxa is, analytically, a relativistic exercise. There must be information about variation within a taxon (intra-specific) as well as between

taxa (inter-specific). Traditionally, in defining taxa, variables that have an inter-taxonomic variation larger than intra-taxonomic variation are preferred. However, one must contend with individuals, and, analytically, variable variation and co-variation expressed intra- and inter-individually. If variables that have a higher inter-individual than intra-individual variation are more variable between hypothesized taxa, and these variables are inter-correlated in their variation, then, and only then, can an inference be made concerning taxonomic relationships (Davis and Heywood 1973). Davis (1983) provides further information with respect to this view and gives an example. Similarly, Newhan and Jancey (1983) provide an example with respect to population differentiation.

2.1 Variables selected.

The central aspect of this study is to provide a quantification of phenotypic variation of _Picea_ in southwestern British Columbia. Specifically, interest is in distinguishing between individual trees. As the objective is to understand the relationships of individual trees and a character is the product of the necessity to describe and communicate information about a particular phenomenon, out of an infinite number of characters by which it is possible to describe a given individual, only certain of these characters may be of value.

The characters selected for this study had to circumscribe the general form of parts of the organism. The variables selected had to meet two criteria. First, the accuracy and

precision (Cochran 1977) of the measurement of these variables was assessed and only those variables with a high degree of measurement repeatability (= "measurement error") were selected. Second, as interest was in inter-individual variation, only those variables displaying greater inter-individual than intra-individual variation were used.

The characters used in this study are morphological and anatomical. Morphological characters refer to the external form of a structure (e.g. leaf length). Anatomical characters define the internal form of a structure (e.g. number of endodermal cells in cross-section).

The characters selected can be regarded as a sample of the genome of the plant. Developmentally, the more characters selected from more portions of an individual, the better the representation of the genome. The selection criteria adopted are fundamentally those adopted by other workers when dealing with other morphological and chemical variables. Some workers would attach more specific genetic interpretations to certain of these variables than others, depending upon the objectives and theoretical predisposition of the researcher.

To provide a general description of a large, architecturally complex organism, characters were selected that represent the reproductive and vegetative portions of the organism. Owing to the size of the organism, vegetative and reproductive characters could not be examined from the same portion of the canopy. Similary the preparatory techniques employed did not allow for a one-to-one correspondence to be

made between certain vegetative variables.

Characters are grouped together in "character suites" as there exists a one-to-one developmental correspondence between the characters for any given sample. Developmentally, a one-to-one correspondence does not exist between individual samples from different character suites. For example, although characters of cones, cone scales and bracts, twig morphology, twig anatomy, needle morphology, and needle anatomy all could be examined for each individual tree, they are measured as variables on separate parts of the same tree. Thus one cannot analyze for variable inter-correlations between suites of variables except as it applies to mean values calculated for these characters for separate trees. Correlation between, say, aspects of needle morphology and cones within the canopy of a single tree are analytically possible, but are not meaningful in a developmental sense.

The initial selection of a character and description of variables was based upon previous work on Picea (see Table 1; Facey 1956; Jansson and Bornmann 1981; Duman 1957; de Laubenfels 1953; Dalgas 1973; Jeffree, et al. 1971; Gordon 1976a; Parker, et al. 1983; Martinez 1961 in Taylor and Patterson 1980; Colleau 1968; Stover 1944) and other conifers (Fulling 1934; Carlson and Blake 1969) and examination in the field and herbarium (UBC, V, WS; acronyms according to Holmgren and Keuken 1974) of many samples. Cone scale phyllotaxis (Daubenmire, 1968) was not used because of the high error associated with measuring this variable (see also Cannell and Bowler 1978).

Table 1. Characters used in previous studies. Ratio variables
    excluded. Studies: 1 - Daubenmire 1968; 2 - Daubenmire 1972; 3 -
    Daubenmire 1974; 4 - Falkenhagen and Nash 1978; 5 - Funsch 1975; 6 -
    Garman 1957; 7 - Horton 1959; 8 - Khalil 1974; 9 - Klinka, et al.
    1982; 10 - La Roi and Dugle 1968; 11 - Mitton and Andalora 1981; 12 -
    Ogilvie and von Rudloff 1968; 13 - Parker and McLachlan 1978; 14 -
    Reed and Freytag 1949; 15 - Roche 1969; 16 - Strong 1978; 17 - Taylor
    and Patterson 1980; 18 - Taylor, et al. 1975; 19 - Taylor 1959.

VARIABLES	STUDIES
CONE SIZE.	
largest cone length	1,2,3,6,10,17,18
median cone length	1,2,3,17,18
median cone width	1,2,3,17,18
mean cone length	4,5,8,9,13,19
mean cone width	8,9,13,19
cone texture	6,10
cone apex shape	6,10
cone weigth	8
CONE SCALE MEASUREMENTS.	
scale phyllotaxy	1,2,3
scale shape	10
scale margin thickness	13
scale texture	10
scale apex shape	7,10,13,19
scale margin form	7,10,12,13,19
scale length	1,2,3,5,6,8,9,10,12,15,16,17,18
scale width	1,2,3,5,6,8,9,10,12,15,16,17,18
scale taper	2,7,9,12,13,16
scale width 2mm below apex	15
free scale	2,3,9,13,16,17,18
seed impression length	15,16
seed impression width	9
BRACT MEASUREMENTS.	
bract apex shape	6,7,10,13
bract margin form	10
bract length	6,9,13,15
bract width	9
bract taper	9
SEED MEASUREMENTS.	
seed wing length	4
seed wing width	4
seed length	4
seed width	4
TWIG MEASUREMENTS.	
branch diameter	5
sterigmata projection	1,2,3,6,10
sterigmata angle	1,2,3,6,10
pulvinus length	5
pulvinus shape	13
pubescence	1,2,3,5,6,10,11,12,13,17,18,19
twig colour	13
BUD MEASUREMENTS.	
bud scale length	13
bud scale width	13
bud scale apex shape	13
bud scale margin form	13
bud scale form	11
LEAF MEASUREMENTS.	
leaf sharpness	5,11,13
longest leaf length	1,2,3,17
average leaf length	5,13,14,19
stomatal lines	1,2,3,6
("dorsiventrality")	
resin sac position	11,14
resin sac length	11,14
leaf weight	13
leaf colour	5
leaf orientation	5
leaf odour	5

Ratio variables calculated by others were not calculated because
of the poor statistical properties associated with ratios (see
review in Phillips 1983).

The translation of variables from characters may be done in
a number of different manners. Characters can be expressed as
continuous, categorical, or counts. Continuous variables offer
an analytic flexibility that other types of variables do not
generally allow. Continuous variables are also more in keeping
with the continuous nature of variation of characters and the
hypothesized genetic control over their expression (Falconer
1981)

2.2 Variable measurement repeatability.

Samples used in determining measurement repeatability were
selected randomly from the total number of samples available
(Appendix II). Measurement repeatability is an estimate of the
precision of measuring. The initial assessment of measurement
repeatability of these variables was carried out using replicate
measurements made by two different observers. Assessment of
measurement repeatability was made with an analysis of variance
model of the form:

(MODEL 1.)

$$y = A + e.$$

where y is a measurement for a given variable by a given
observer, A is the hypothesized effect of an observer, and e is
residual variation.

Variables displaying greater than 10 percent variation attributed to observers were subjected to re-specification and re-measured on another sample. Re-specification sought to make the description of a variable less ambiguous. Quantitative variables which appeared to be invariate were re-measured on another sample by two observers at a higher magnification.

Following re-measurement, those variables still possessing greater than 10 percent variation between observers were again re-specified and re-examined on yet another sample. Variables proving invariate were re-examined over several samples to determine whether in fact they varied at all.

Following this second re-examination, measurement repeatability was measured at four separate times during the course of the year spent in measuring. Average repeatability estimates over these four estimates are given in Table 2. Table 2 also gives the average repeatability for each variable suite. In general, those variables with a larger number of reference points and assumed symmetry of form proved to be the variables that showed the largest amount of measurement error.

Figure 1 illustrates the variables eventually selected. Appendix I contains the full descriptions for the variables and includes the method of sampling, specimen preparation, and measurement technique for each variable suite.

Table 2. Average variable and variable suite measurement repeatability, inter-individual variability, and inter-population variability. Measurement repeatability based on ANOVA in MODEL 1, averaged over four replicates performed during the coarse of measurement. Inter-individual and population variability based on same form of ANOVA (MODEL 1). Repeatability and variability expressed as a percentage of the total sums of squares ($\%SS_A$). No.taxonomic circumscription.

VARIABLE	MEASUREMENT REPEATABILITY	INTER-INDIVIDUAL	INTER-POPULATION
LEAF MORPHOLOGY SUITE			
NEEDLEN	4.3	78.47	31.05
ABXSTOM	3.2	82.33	41.48
ADXSTOM	0.0	65.06	38.03
RESCYNO	0.0	75.29	46.68
RESCYLOC	1.8	64.87	40.21
RESCYLEN	0.8	76.68	38.23
$\bar{x}$	1.7	72.94	39.28
TWIG MORPHOLOGY SUITE			
PULVLEN	7.0	89.47	54.90
TIPWID	3.2	76.33	36.51
TIPDEP	6.3	66.36	14.79
PULVPUB	0.0	97.17	74.19
$\bar{x}$	4.1	82.33	45.10
LEAF ANATOMY SUITE			
NEEDWID	1.1	91.28	56.51
NEEDEP	7.6	91.63	58.06
ABXANG	2.0	87.26	73.69
ADXANG	3.0	71.20	44.92
CENCYWID	7.5	91.09	46.40
CENCYLAT	2.0	91.33	59.46
CENCYABX	1.2	92.93	73.91
CENCYADX	1.6	81.77	38.36
ENDONUM	3.0	84.68	39.20
PHLEND	9.8	88.53	53.22
XYLEND	4.6	85.68	47.08
$\bar{x}$	4.0	87.72	53.71
CONE MORPHOLOGY SUITE			
CONLEN	0.0	66.75	54.12
CONWID	0.0	72.82	36.92
SCALEN	5.2	62.18	40.18
SCALWID	4.3	76.76	48.30
SCALTAP	9.6	58.76	35.38
WINGWID	6.7	69.61	32.05
WINGTAP	6.2	52.23	19.92
FREESCAL	4.8	67.31	35.87
BRACTLEN	9.2	79.22	67.21
BRACTWID	6.2	67.02	41.82
BRACTAP	7.7	82.38	67.99
$\bar{x}$	5.5	68.64	74.19
TWIG ANATOMY SUITE			
PITHDIA	8.3	32.14	70.84
CORTHIK	4.2	13.35	68.77
PERITHIK	2.3	36.49	79.33
VBTHIK	6.2	35.76	77.83
$\bar{x}$	5.3	29.44	74.19
CONE COLLECTION SUITE			
SHCOLEN	-	-	50.97
SHCOWID	-	-	44.23
LOCOLEN	-	-	55.96
LOCOWID	-	-	48.91
$\bar{x}$	-	-	50.02
TOTAL (without twig anatomy)			
$\bar{x}$	4.1	62.14	46.34

Figure 1. Illustrations of variables used. Abbreviations given in
Appendix I. Triangles, _P. engelmannii_: squares, _P. glauca_:
circles, _P. sitchensis_. Numbers beside figure are sample numbers
(Appendix II). Not illustrated: SHCOLEN, SHCOWID, LOCOLEN, LOCOWID,
CONLEN, CONWID, LEAFLEN. Schematic representation of leaf
cross-section follows the convention of Colleau 1968.
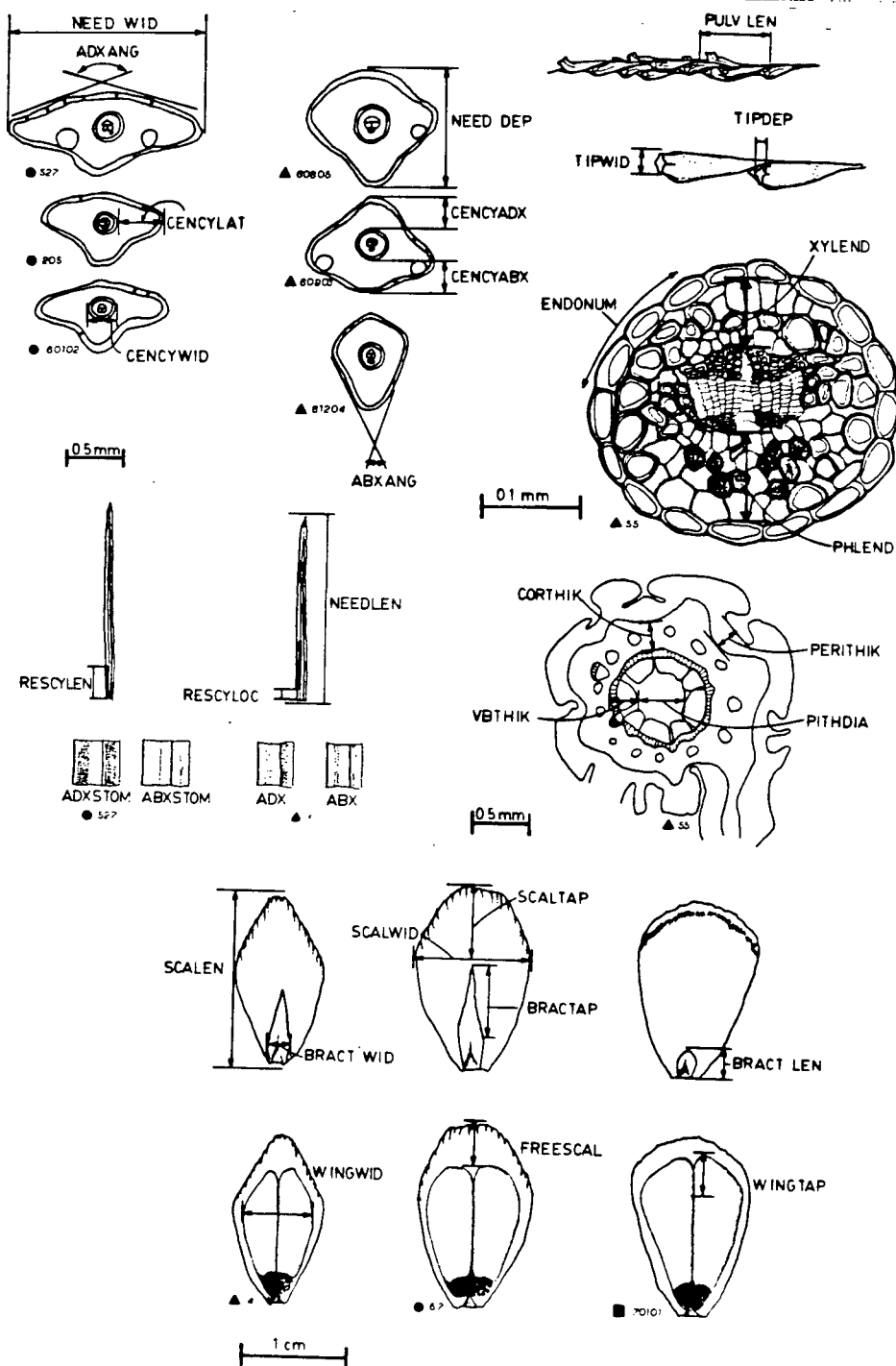
2.3 Variable variation between individuals.

The variables selected were measured on representative
samples of the two taxa. The nature of variable variation was
examined with an ANOVA of the same form as given above in MODEL
1; however, here y is a measurement for a given variable made on
a given sample from an individual, A is the hypothesized effect
of the individual tree (inter-individual variation), and e is
residual variation or, in this case, intra-individual variation.
Those variables with an inter-individual variation that exceeded
the the intra-individual variation were retained for further
measurement. Application of this rule removed twig anatomy
variables from further consideration. Table 2 gives the amount
of inter-individual variation for the variables selected.
Figure 2 summarizes inter-individual variation and
inter-population variation[1]. Figure 3 illustrates some of the
variation in leaf anatomy encountered in this study. Daubenmire
(1968, 1972, 1974) and others (Garman 1957; Horton 1959)
illustrate some of the variation encountered in cone morphology.
As an aside, Pravdin, et al. (1978) illustrate the range of
variation for the P. abies complex.

Estimates of inter-individual variation based on the
results of this form of ANOVA are also known as repeatability
estimates (Falconer 1981). As a statistic from ANOVA,

_____

[1] Between population variation is assessed with a model of the
same form as in MODEL 1 given above for inter-individual
variation, the exception here being that "A" is the effect of
the population (inter-population variation).

Figure 2. Summary of variable variation based on all individuals
without reference to taxonomic circumscription. %SS$_{individual}$ -
amount of variation between individual trees. %SS$_{population}$ -
amount of variation between individual populations. Variable suites:
T - twig anatomy; C - cone collection; P - twig morphology; S - cone
scale morphology; N - leaf morphology; A - leaf anatomy. Values
given are those in Table 2.
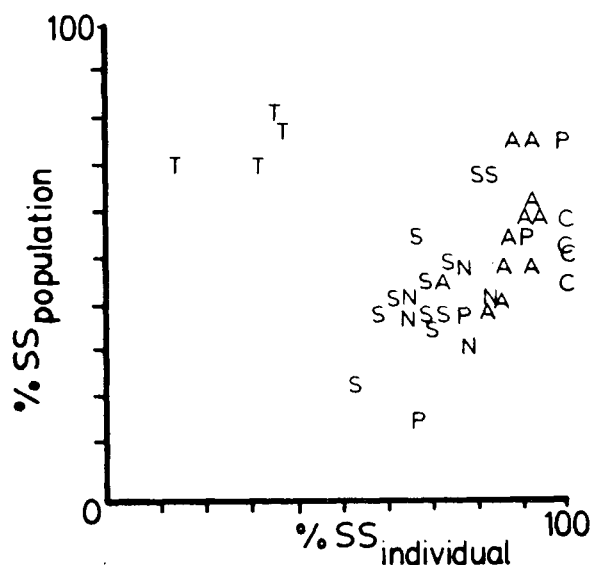
repeatability is interpreted as a sample-specific estimate of

the heritability of a trait. As an approximation of broad sense

heritability, repeatability is subject to cautious

interpretation (Falconer 1981; Zobel 1961); however, this does

not negate its comparative utility. Owing to the size and

perennial nature of conifers, repeatability is the most

practical means of estimating the heritability of traits.

Indeed, considering the statistical (Sokal and Rohlf 1969),

biological (Falconer 1981; Robinson 1963; Jacquard 1983) and

philosophical (Kempthorne 1978) assumptions engendered by the

"components of variance" use of ANOVA, repeatability may be the

only appropriate means of assessing heritabiity. Rather than

stressing the specific genetic aspects that some researchers

Figure 3. Illustration of range of variation encountered for leaf
anatomy. Numbers identify individual trees listed in Appendix II.

P. engelmannii

P. sitchensis

0.5mm
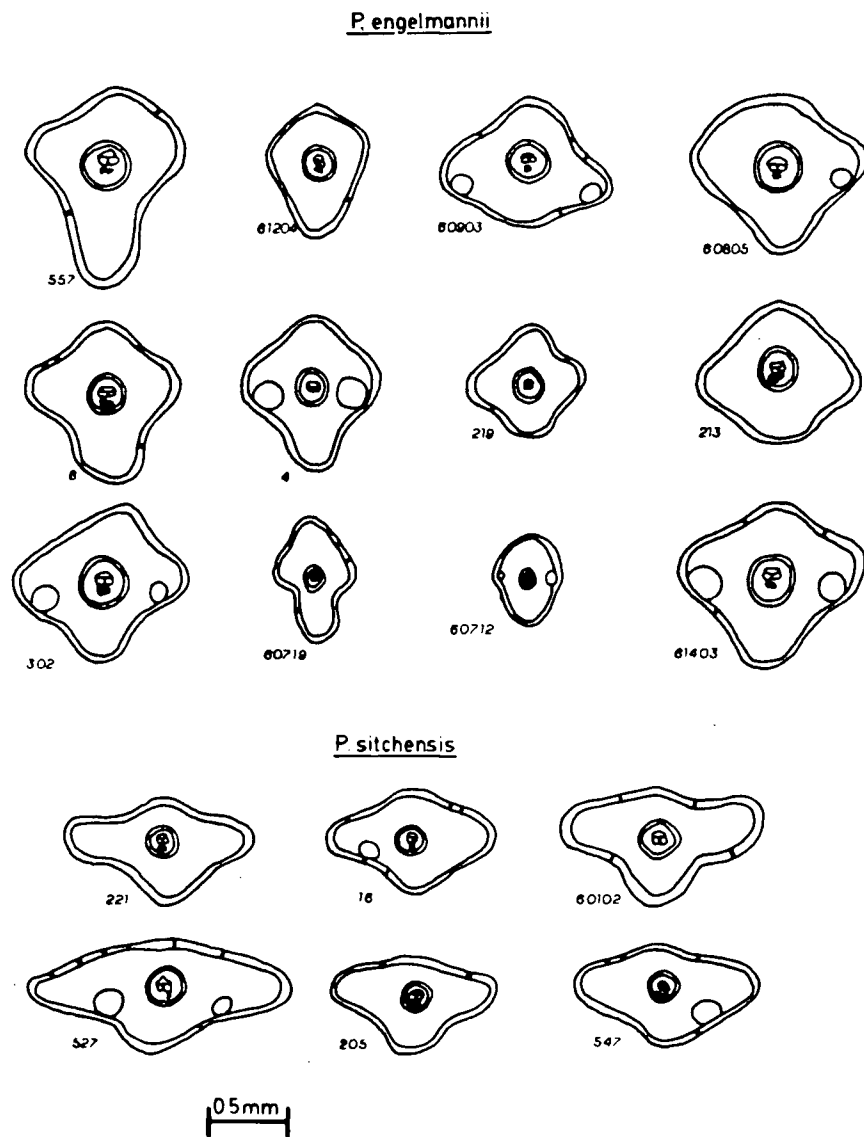
associate with heritability, repeatability will be used here
simply as a relative expression of the amount of
inter-individual variability.

The inter-individual variation values given in Table 2 are
comparable to those given for repeatability estimates shown by
other morphological characters in other coniferous species

(Table 3). These repeatability estimates are generally larger than published heritabilities for other variables in tree species (Hattemer 1963) and probably reflect the over-estimation of heritability considered in the broad sense. However, as heritabilities are most commonly calculated for growth and physiological variables it could reflect basic genetic differences between morphological and physiological variables. Additionally, the size of the heritability estimate could be interpreted as simply the result of a more heterogenous sample than other studies - the fact that hypothesized trans-individual effects have not been considered in Table 3.

Andersson's (1965) results, presented in Table 3, are particularly large, but it should be noted that these samples were from a very large geographic area. Sorensen's data for Pinus elliottii Engelm. may be small as a result of selection imposed in sampling (Sorensen 1964). These may serve as a convenient example of Zobel's (1961) remarks concerning the population-specific nature of the genetic interpretation of such estimates.

As a group, the cone characters measured here (Table 2, Fig. 2) are more variable within an individual than are vegetative variables. The inference drawn is that, in Picea of southwestern British Columbia, the reproductive characters selected are subject to less genetic control than are the vegetative characters. This conclusion is contradictory to the general expectation that reproductive characters are less subject to environmental perturbation than are vegetative

Table 3.   Inter-individual variation, repeatability estimates, reported
   for morphological characters in other coniferous tree species.
   Values reported in the table are percentage of total variation due to
   differences between individual trees. Values are calculated from
   cited authorities and refer to the total inter-individual variation
   without respect to hypothesized trans-individual sources or
   variation.

Picea glauca (Khalil 1974)
   cone weight   86.16
   cone length   95.07
   cone width   71.33
   scale length   78.74
   scale width   62.11
        x̄   78.68

Picea mariana
      (Parker et al . 1983)
   cone length   67.30
   cone diameter   68.70
   scale length   70.90
   scale width   71.90
   scale concavity   61.40
   dark band width   70.00
   light band width   67.60
   seed length   73.80
   seed+wing length   70.60
   leaf width   48.40
   leaf thickness   49.20
   twig pubescence   60.60
   leaf apex shape   30.30
   resin canal
      separation   70.00
   vascular bundle
      diameter   36.80
   longest bud
      scale length   75.80
   lateral bud
      length   71.30
        x̄   62.59

Pseudotsuga menziesii
      (Chen, et al., unpubl.)

   x̄ needle anatomy 86.32

Abies balsamea (Lester 1968)
   cone length   70.00
   scale length   85.00
   seed length   77.00
   bract length   85.00
   stalk length   76.00
        x̄   77.80

Picea abies (Andersson 1965)

   cone weight   90.01
   cone length   91.67
   #seeds/ cone   81.22
   seed weight/ cone   85.29
        x̄   86.17

Pinus elliottii (Sorensen 1964)
   leaf length   48.67
   fasicle volume   54.95
   leaf divergence   41.83
   sheath length   78.74
   bud scale length   77.83
        x̄   60.40

Pinus kesiya
      (Burley and Barrow 1972)
   leaf length   76.84
   % 3-leaf fasicle   67.96
   leaf/ fasicle   67.88
        x̄   70.89

Picea mariana (Khalil 1975)
   cone length   65.93
   cone width   64.91
        x̄   65.42

(Stebbins 1950; Davis and Heywood 1973). This also contradicts the observations of Parker et al. (1983) (see Table 3) and Taylor (1959). The general trend in Table 3 of cone morphology variables is that they have a larger inter-individual variation than vegetative variables.

3. Samples and sampling.

Once variables were selected, it was necessary to direct attention to the origin of the samples and how these samples relate to the various a priori trans-individual levels of organization that have been hypothesized, i.e. populations and taxa.

3.1 Study area.

The main area of study is mainland southwestern British Columbia including both the Coast and Cascade Mountain Ranges (Fig. 4A). The area included in the study was expanded to address specific situations arising in the main portion of the study area. These supplemental areas were selected to circumscribe better the variation of both species and to consider the existence and effect of a possible third species, P. glauca. Such supplemental sampling permits a better understanding of the variation in the study area.

Specifically, the inclusion of samples from these additional areas sought to: identify the relation between

Figure 4. Maps of locations of samples and study area. A - study area:
B - common garden samples of P. sitchensis: C - naturally growing
collections from southern portion of range of P. sitchensis: D -
samples of P. engelmannii outside of study area. Tree and population
numbers correspond to those given in Appendix II.
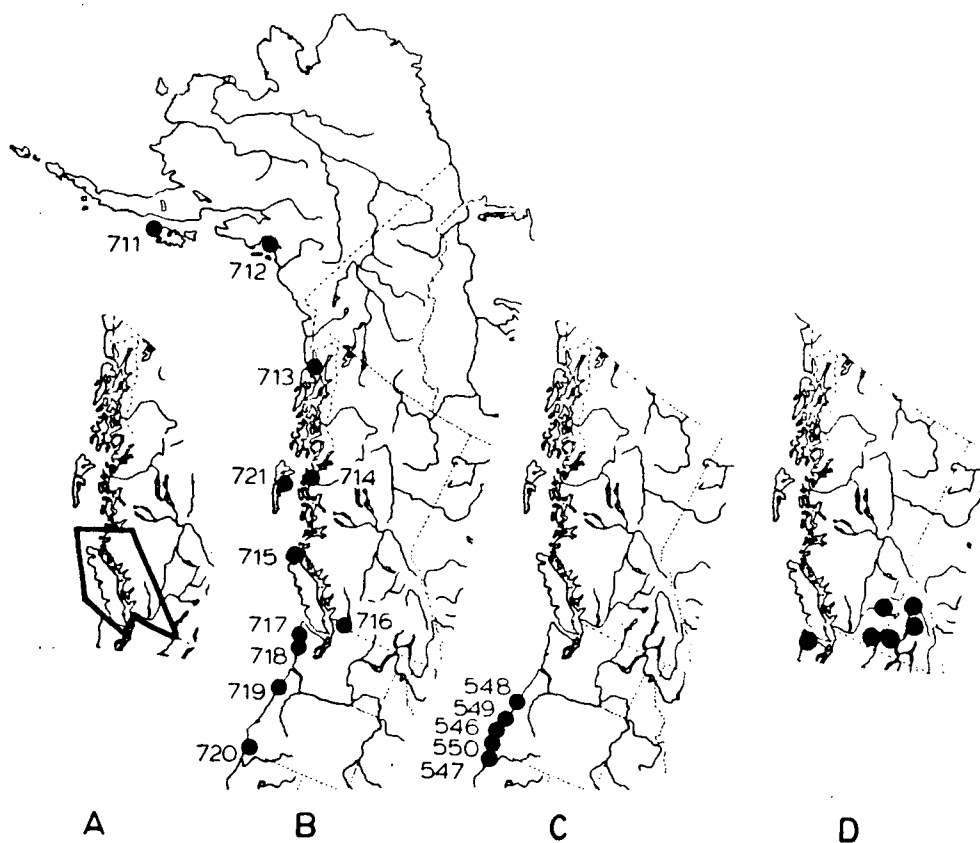
P. engelmannii and P. glauca; identify the relation between

P. engelmannii in the study area to that reported for a disjunct

location of the P. engelmannii on the Olympic Peninisula (Sharpe

1970; Hitchcock, et al. 1969) (Fig. 4D); identify the relation

between P. engelmannii in the study area to that in the wettest

and driest portions of the interior of British Columbia

(Fig. 4D); and, identify the relation between P. sitchensis in

the study area and that in more southerly locations (Fig. 4B, C)

The possibility of the occurrence and/ or introgression of
P. glauca Knight Inlet could not be denied a priori. As such it
was necessary to examine the relation between P. engelmannii and
P. glauca, albeit superficially. The suspected occurrence of
P. glauca in Knight Inlet is based on the crown form and cone
morphology for trees east of Remote Creek along the Klinkaklini
River. Additionally, personal reconnaissance during previous
research[1] west of Tatla Lake indicated the presence of P. glauca
in the relatively low elevation pass to Knight Inlet along the
Klinaklina River. Such an occurrence is not unexpected since
similar situations have been reported for more northerly inlets:
Skeena River (Daubenmire 1968; Garman 1957; Roche 1969; Coupé,
et al. 1982; Hanover and Wilkinson 1970; Copes and Beckwith
1977; Falkenhagen and Nash 1978); Dean River (Pojar[2]); Bella
Coola River (Pojar[2]); Nass River (Garman 1957; Roche 1969); and
Bulkley River (Roche 1969).

Several specific collections were made to describe the
nature of intra-individual variation. These are described more
fully in Chapter III.

Samples were collected under natural situations as well as
from a variety of common garden situations. First,
representatives of P. sitchensis from throughout the natural
range of the species were sampled in a common garden situation

in the Chilliwack Valley[3] (Fig. 4B). The trees had been grown
from seed. Comparison of naturally occurring trees to nursery
grown trees may provide insight into the factors surrounding
population differentiation. Further, this comparison may prove
useful in relating the results reported from other common garden
research to the results presented here based on plants collected
under natural conditions. More exact locations and information
are given in Appendix II.

Two other common gardens were sampled; one at Red Rock,
south of Prince George, British Columbia[1] and the other at
Fredericton, New Brunswick[2]. In both of these nurseries,
individuals of known hybrid parentage were sampled. Such
collections provide information concerning the description of
hybrids. Secondly these collections provide information
regarding the practicality of recognizing naturally occurring
hybrids. More specific information about the parentage of these
trees is provided in Appendix II.

In addition to the trees specifically sampled for this
study, data from specimens sampled previously in Klinka, et
al. (1982) were also used[3].

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[1] British Columbia Ministry of Forests, Vancouver Forest Region,
Research Branch - Vancouver 1981.
[2] British Columbia Ministry of Forests, Prince Rupert Forest
Region, Smithers.
[3] Ulf Bitterlick; British Columbia Ministry of Forests

[1] Gyula Kish; British Columbia Ministry of Forests.
[2] Dan Fowler; Canadian Forestry Service.
[3] permission of Karel Klinka; British Columbia Ministry of
Forests.

3.1.1 Climate.

In the study area samples came from elevations between sea level and 2100 m ASL. Some of the range of climatic conditions reported within the study area are indicated in Table 4. Owing to the extreme topographic variation and local climatic alteration associated with such topography, actual climatic values can well be expected to differ substantially from those reported. The values presented in Table 4 give an impression of climatic variation rather than providing an accurate description of the climate at any given sample location. However these climatic variables should not be interpreted as being the only factors responsible for limiting growth and survival of Picea at a given site. Further, the variation of the climate corresponds roughly with elevation, latitude, and longitude. Climate in the range of P. sitchensis is summarized briefly by Fletcher (1976). Schaeffer (1978a,b) and O'Driscoll (1976b) provide a general overview of climatic variation for the study area.

Figure 5 illustrates the range of distribution of samples with respect to longitude, latitude, and elevation. These figures serve to corroborate the impression from the literature that P. sitchensis is a low elevation, coastal species whereas P. engelmanii is a high elevation, interior species; however, any edaphic discontinuity (Wright 1955; Daubenmire 1968) is not apparent. Predictably, the "hybrids" occur in intermediate areas. It should be noted that the collections of P. sitchensis from the highest elevations came from more northerly areas - an observation that corroborates Daubenmire's (1968) report that

Table 4. Summary of some annual average climatic variables reported for the study area and adjacent areas. SSS - standard P. sitchensis; SSP - putative P. sitchensis; SXE - "hybrid"; ESP - putative P. engelmannii; ESS - standard P. engelmannii; WSS - standard P. glauca. - no data available. Sources: U.S. Dept. of Commerce (1975); Environment Canada (1973; 1975a, 1975b).

STATION	ID	ELEV (m)	RAIN (mm)	SNOW	x̄ T (C)	min T (C)	maxT (C)	FROST (day)
STUDY AREA								
BRITTANIA BEACH	SSS	50	1985	782	10.0	6.4	13.5	43
PORT ALICE		20	3152	587	9.4	5.7	13.1	33
PORT HARDY		25	1660	706	7.9	4.7	11.2	67
RIVER JORDAN		5	1962	218	9.0	5.2	12.8	44
SQUAMISH		2	1916	1455	8.9	4.7	13.3	84
TOFINO		30	3020	417	9.2	5.7	12.7	49
VANCOUVER - UBC		95	1258	490	9.8	6.6	13.1	33
CHILLIWACK	SSP	10	1636	1029	10.2	5.7	14.8	57
HANEY RESEARCH FOR.		190	2101	1107	8.9	4.7	13.2	80
HOPE		50	1448	1621	9.7	5.1	14.3	77
ALTA LAKE	SXE	730	837	5936	5.7	0.4	10.9	176
PEMBERTON MEADOWS	ESP	240	742	2825	7.2	2.1	12.3	128
SKAGIT RIVER		560	802	3228	7.8	1.9	13.8	165
ALLISON PASS	ESS	1470	486	9652	1.8	-3.7	7.5	255
OUTSIDE STUDY AREA								
HEDLEY	ESP	570	218	752	7.9	1.7	14.1	158
KEREMEOS		470	189	602	9.7	4.2	15.1	114
KLEENA KLEENE		980	204	1669	1.8	-5.8	9.5	258
MICA DAM		630	717	7364	4.2	-0.9	9.3	184
REVELSTOKE		500	703	4115	7.2	1.7	12.6	150
CHUTE LAKE	ESS	1305	302	3106	3.2	-3.3	9.6	228
HEDLEY MINE		1930	214	3297	2.2	-3.4	7.7	231
SEQUIM, WASH.	SSS	60	-	-	9.8	7.3	17.1	-
ELWHA STATION, WASH.		120	1413	-	-	-	-	-
BROOKINGS, ORE.	SSS	30	2056	-	11.8	8.3	15.3	-
BANDON, ORE.		30	1519	-	10.8	7.4	14.3	-
CANARY, ORE.		30	2097	-	11.2	6.3	16.3	-
OTTAWA, ONTARIO	WSS	-	663	193	5.8	0.8	10.8	162
CHILLIWACK RIVER NURSERY SAMPLES								
KODIAK IS. ALASKA	SSS	10	1440	-	4.8	-1.2	12.7	-
CORDOVA BAY		15	2350	-	3.4	-5.0	11.9	-
JUNEAU		10	1389	-	6.0	-2.6	14.1	-
TERRACE, B.C.		70	917	1816	6.7	2.7	10.8	137
SANDSPIT		10	1182	785	7.9	5.1	10.6	63
BELLA COOLA		20	1358	1750	7.4	2.8	12.0	124
CHILLIWACK					< SEE ABOVE >			
FORKS, WASH.		120	2956	-	9.5	3.6	15.6	-
CLOVERDALE, ORE.		5	2147	-	10.9	5.9	15.7	-
CANARY					< SEE ABOVE >			
BROOKINGS					< SEE ABOVE >			

Figure 5. Elevational, latitudinal, and longitudinal distribution of samples. SSS - standard P. sitchensis; SSP - putative P. sitchensis; SXE - "hybrid"; ESP - putative P. engelmannii ; ESS - standard P. engelmannii; IESP - putative P. engelmannii interior; IESS - standard P. engelmannii interior.
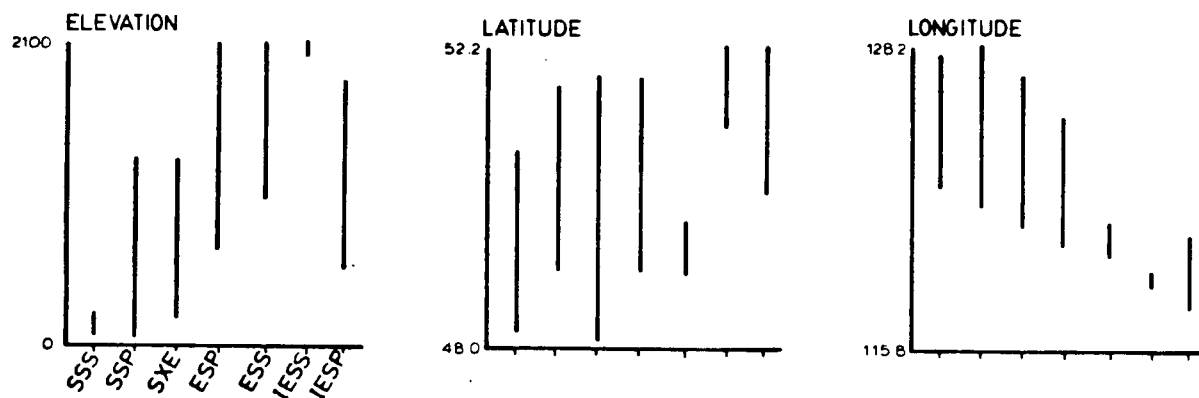
this species occupies a wider elevation range at higher latitudes.

3.1.2 Edaphic environment.

Parent materials in the study area are primarily coarse textured quartz- and grano-diorites (Holland 1976). Notable exceptions are the limestone and sedimentary parent materials of the Chilliwack Valley and some of its associated drainages. In all areas these parent materials are overlain, to various degrees, by an accumulation of glacial tills and colluvial materials (Ryder 1978).

Soils where Picea occur are primarily those associated with fluvial and alluvial landforms. Well aerated and pervious cumulic regosols and less aerated and saturated gleysols are the most frequent. On the outer coast, Picea may occur in brackish conditions associated with sandy soils of advancing beach fronts (Cordes 1972).

Picea occurs on a variety of soil types on more upland

sites. In the northerly coastal portion of the study area,

Picea occurs on various degrees of humified podsols and

"folisols" (Pojar 1982). In the interior portion of the study

area, Picea may be found on various degrees of illuviated

luvisols. With increasing elevation on both the coast and the

interior, Picea is found on poorly developed podsols and

brunisols.

Like climate, edaphic variation corresponds roughly with

geographic location. Further, the descriptions of the edaphic

environment given here are not meant to be accurate for any

given site - they simply serve to describe the possible

variation in the study area.

An approximation of the edaphic environment is provided by

an indication of the relative availabity of moisture for each

collection site. Such quantification is provided by the

classification outlined in Walmsley, et al. (1980). Briefly,

this classification of moisture availability is a landscape

classification with secondary attention paid to textural

properties of the specific soil. The disposition of samples

with respect to moisture regime is given in Table 5. The

disposition of individual samples with respect to moisture

regime is given in Appendix II. Table 5 serves to illustrate

the wider edaphic amplitude of P. engelmannii and "hybrids"

compared with P. sitchensis. It should be noted that this

moisture index is not entirely independent of local climate.

For example, what constitutes a subxeric site on the outer coast

Table 5. Distribution of samples with respect to moisture regime. Moisture regime scheme follows Walmsley, et al. (1980).

IDENTIFICATION	XERIC	SUB-XERIC	SUB-MESIC	MESIC	SUB-HYGRIC	HYGRIC	TOTAL
P. sitchensis							
STANDARDS			1	4	36	21	62
PUTATIVES	1		5	13	38	8	65
"HYBRIDS"	1	2	10	25	51	44	133
P. engelmannii							
STANDARDS			10	51	10		71
PUTATIVES	1	16	27	18	36	7	105
SELKIRK MTNS.							
STANDARDS		10					10
PUTATIVES		10	5	27	12	15	69
							** 515 **

might well be subhygric in the interior.

A description of the edaphic environment present today does not necessarily reflect the edaphic environment that was critical to the establishment and early growth of the trees sampled for this study. Additionally, the lateral variability of edaphic variables is such (Courtin, et al. 1983) that more detailed description besides that given here is liable to be subject to a large measurement error.

3.1.3 Associated vegetation.

In addition to climatic and edaphic variation, there are many documented descriptions of vegetation found growing with Picea. References specific to the study area and auxiliary sample sites can be found in: Krajina, et al. (1978); Krajina, et al. (1982); Krajina (1969); Krajina (1965); Klinka, et al. (1982); Klinka, et al. (1980); Klinka, et al. (1979); Jones

and Annas (1978); Franklin and Dyrness (1973); Rowe (1977).

As with climate there is a strong interdependence of vegetation and elevation, longitude, and latitude. An approximation of associated forest vegetation, primarily forest trees, is provided in this study by assigning each sample to a "biogeoclimatic zone" (Krajina 1969). More precise biogeoclimatic circumscription is possible (Mitchell, et al. 1981a, b; Utzig, et al. 1983; Courtin, et al. 1981; Klinka, et al. 1979), however the wide geographic distribution of the samples makes assignment to these aerially smaller syntaxa impractical. The biogeoclimatic disposition of samples is indicated in Table 6. The disposition of individual samples is given in Appendix II.

Like the edaphic environment, contemporary associated vegetation may not be necessarily that contributing to the survival and characteristics of the individual today. The effect of a given herb species on a large tree may be vastly different from the effect of the same herb species upon the establishment and development of seedlings.

3.1.4 Geological, vegetation, and climatic history.

Evidence of recent glaciation is pervasive throughout the study area. The majority of upland soils have developed from glacial tills and the landscape is dominated by the effects of glaciation (Ryder 1978). Holland (1976) and Ryder (1978) provide a review and summary of the geomorphic history of the study area. With the exception of the trees sampled in Oregon

Table 6. Distribution of samples with respect to biogeoclimatic zones. CDF - coastal douglas-fir zone; CWH - coastal western hemlock zone; MH - mountain hemlock zone; ESSF - engelmann spruce subalpine fir zone; IDF - interior douglas-fir zone; IWH - interior western hemlock zone. Assignment to biogeoclimatic zone based on Courten, et al. (1981); Klinka, et al. (1979, 1980); Mitchell, et al. (1981a, b); and, Utzig, et al. (1983).

| | | BIOGEOCLIMATIC ZONES | | | | |
IDENTIFICATION	CDF	CWH	MH	ESSF	IDF	IWH
P. sitchensis						
STANDARDS	13	49				
PUTATIVES	1	64				
"HYBRIDS"		116	15		2	
P. engelmannii						
STANDARDS				71		
PUTATIVES		7	7	56	35	
SELKIRK MTNS.						
STANDARDS				10		
PUTATIVES				50	5	14

and California, all trees sampled came from an area covered by ice during the last continental glaciation (Ryder 1978).

Daubenmire (1978) and Wolfe (1969) provide reviews and summary of the pre-Quaternary vegetation of the area. Hebda (1983) provides a summary of the post-glacial vegetation change for the coast. Mack, et al. (1976), Hansen (1955), and Hebda (1982) provide summaries of vegetation changes for the interior.

Following the most recent glaciation the climate is assumed to have become warmer and drier than at present. This xerothermic or hypsithermal period occurred around 6000 yBp and was most pronounced in the interior (Alley 1976; Mack, et al. 1976; Hansen 1955; Daubenmire 1975; Hebda 1982) and in the rainshadow areas of the coast (Barnosky 1981). The hypothesis

of the existence of the xerothermic period remains enigmatic for more coastal areas (Mathewes 1973).

The vegetation and re-vegetative history of the study area has been discussed by numerous workers. The vegetation history constitutes the basis for derived inferences concerning climatic history. The accounts differ in respect to actual dates but the trends reported are similar.

3.1.5 History of *Picea* in western North America.

In examining the variation of the two hypothesized taxa in the study area it is necessary to place the occurrence of *Picea* today into some sort of historical perspective, especially if inferences regarding relationships are to be forthcoming. Particularly important in considering the Quaternary history of *Picea* in the study area, is the post-glacial period. These interpretations are generally based on palynologic evidence. As separation of *P. sitchensis* and *P. engelmannii* on pollen size is tenuous (Mathewes 1973; Wilson 1963), it is impossible to retrace the history of both taxa during this period. It is generally agreed that these species, like many others, retreated south during glacial episodes and that more montane species descended to lower elevations. For the coastal area where investigations have been made primarily at low elevations, *Picea* pollen has been assumed to be that of *P. sitchensis* . In the interior, *Picea* pollen has been assumed to be either *P. engelmannii* or *P. glauca*, depending upon the proximity of contemporary species. The sanctity of these interpretations has

been challenged by the recent findings of macrofossils in the Puget lowlands identified as P. engelmannii (Barnosky 1981). Daubenmire (1968) provides a further review of the nature of Picea in the Puget lowlands.

An important issue in the Quaternary history of Picea in western North America concerns the hypothesis of a glacial refugia of the species. Such an hypothesis has been tendered for P. sitchensis (reviewed in Daubenmire 1968) and P. glauca (reviewed in Critchfield 1984). In both cases conclusions concerning this hypothesis remains enigmatic. The hypothesis is frequently invoked to explain apparent discontinuities in the variation of P. sitchensis. A similar hypothesis has been tendered by Porsild (in Garman 1957) for P. engelmannii. A related issue is the hypothesized intra-glacial genetic depauperization of P. sitchensis (Yeh and El-Kassaby 1980) and subsequent differentiation during post-glacial migration (Illingworth 1976). Post-glacial differentiation of P. engelmannii during migration has also been hypothesized by Daubenmire (1974).

For the coast and interior, Picea pollen is generally present and abundant in the oldest sequences. For the coastal areas, Picea pollen declines gradually to the present. In the interior and rain shadow areas, Picea initially declines and then increases after 5000 yBP, tending to support the hypothesized occurrence of a hypsithermal interval.

3.2 Trans-individual circumscription of samples

Regardless of the hypothesized sources of trans-individual variation, often stipulated by theoretical considerations or convention rather than biological reality, the nature of the occurrence of _Picea_ in southwestern British Columbia is such that systematic and balanced sampling for all sources of trans-individual variation was not possible.

3.2.1 Population circumscription of samples.

Where there were a number of individual trees at a particular location a population was defined if individuals were within 30m of each other, approximately the same age (+/- 10 years), and were growing in similar physiographic and edaphic conditions. This spatial part of this definition of a population is based upon the available literature pertaining to pollen (Wright 1953; Colwell 1951; Ibe 1983; Silen 1962; Wang, et al. 1969) and seed dispersal (Mair 1973; Stern and Roche 1974) in forest trees. This spatial restriction minimizes long distance pollination and dispersal.

Trees were cored as a check that obviously different aged individuals had not been sampled. Under collection situations where increment coring was not possible, diameter at breast height was used as an age estimator. Such sampling reduces the potential heterogeneity in the data related to different ages and meso-topographic environmental conditions. The restricted distance between trees also confines the definition of population to those individuals that are potentially able to

cross-pollinate with each other ("neighbourhood size" - Ledig 1974) and probably represent the progeny from a restricted parental generation. As a consequence of adopting such a narrow definition of a population, intra-population variation is expected to be lower than that observed for studies with broader operational definitions of a population.

As a result of such stringent definitions of a population, the populations sampled could be represented by two or more individuals. In some areas there were, potentially, a large number of trees that could be assigned clearly to a single population. Under such conditions where there were such large numbers of individuals, samples from five to ten trees were made. A larger number of individual trees could have been sampled in such populations, but only at the expense of a large investment of time spent in sampling. Such population-intensive sampling would have resulted in a concomitant decline in the distribution of sampling over the geographic extent of the study area. As a result, sampling at a population level was unbalanced thereby complicating analysis. The distribution of samples into populations is indicated in Table 7. Specific distribution of individual samples is given in Appendix II.

In most cases populations were even-aged and lacked a complex stand age-structure such as found in Abies amabilis stands (Herring and Etheridge 1976). Similarly the edaphic and physiographic environment were well circumscribed - individuals were lacking on adjacent physiographically or edaphically different sites. In some situations it was possible to define

Table 7. Distribution of samples as populations and single occurrences.
Populations - total number of samples: total # populations
{# populations * # samples per population}.

IDENTIFICATION	POPULATIONS	SINGLES
P. sitchensis		
STANDARDS	44: 6{16;2*10;2*3;2}	18
PUTATIVES	21: 7{6;4;3;4*2}	44
"HYBRIDS"	82: 13{16;15;13;10;7;5;2*3;5*2}	51
P. engelmannii		
STANDARDS	66: 7{21;11;10;2*7;2*5}	5
PUTATIVES	84: 13{22;15;13;2*6;6*3;2*2}	21
SELKIRK MTNS.		
STANDARDS	10: 2*5	
PUTATIVES	66: 19{10;2*5;4;12*3;3*2}	3
TOTAL	373:67{22;21;2*16;2*15;2*13; 11;5*10;3*7;3*6;7*5; 2*4;23*3;15*2}	142

populations and collect samples from spatially adjacent sites
where there were obvious environmental differences or age
differences. Stand age differences (i.e. comparing mature and
saplings) were associated with obvious edaphic perturbation of
one form or another. Seedling and sapling samples collected
were growing in recently exposed mineral soil, agreeing with the
general observations by Dobbs (1972) and others.

Along the coast, populations, in the sense defined above,
were difficult to find as a consequence of logging or simply
edaphic conditions (i.e. relatively restricted edaphic amplitude
of Picea coupled with its early successional occurrence).
Approximatly 40 percent of the collections made were sampled
from lone trees. Indeed, this inability to satisfy the
hypothesized populational level of trans-individual variation
causes questions to be asked as whether or not a "population" is

indeed a viable, naturally occurring subject worthy of study in coastal <u>Picea</u> collected in this study.

3.2.2 Taxonomic circumscription of samples.

A pre-requisite for investigating the similarity of taxa is that reference samples, designated as "standards", are required. For the purposes of this study three groups of standards were choosen: standards, putatives, and hybrids.

Trees growing along the immediate coast and coast-mainland that occurred below 100m ASL and were growing in alluvial sites, fluvial terraces, <u>Lysichiton</u> swamps, or beach fronts were declared as standards representing <u>P. sitchensis</u>. Individual trees growing at the tree-line and within 500m of tree line in the Cascade Range and the more easterly mountain ranges were, regardless of edaphic habitat, considered as standards of <u>P. engelmannii</u>. Owing to the taxonomic confusion between <u>P. engelmannii</u> and <u>P. glauca</u> in British Columbia (Garman 1957; Daubenmire 1974; Roche 1969; Taylor 1959) standards representative of <u>P. glauca</u> were obtained from the Ottawa Valley[1].

Trees which were growing at intermediate elevations and displayed "characteristic" crown and morphological characters of the two taxa were declared to be putative representatives of the taxa being investigated. The description of "hybrids" was

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[1] Samples collected courtesy of Daniel Gagnon, Université du Quebec à Montréal.

applied to those trees that had an "intermediate" crown form and
morphological characters. Such an identification of hybrid
individuals separated, as a group, trees found growing at
intermediate elevations on the coastal side of the Cascades and
Coast Mountains along alluvial fans, fluvial terrances, and
along steep colluvial slopes with seepage. This
characterization of the "hybrid" habitat coincides with that
expected to favour hybridization and survival of hybrids. The
disposition of samples as standards, putatives, and hybrids is
given in Table 5. The latitudinal, longitudinal, and elevation
of separation of standards of the two taxa should be noted in
Figure 5. More specific disposition of individual samples is
given in Appendix II.

3.2.3 Local geographic circumscription of samples.

In examining the relationship between morphological and
anatomical variation with local geographic variation it was
necessary to assign samples, somewhat arbitrarily, to 16
geographic areas. The general location of these geographic
areas are given in Figure 6. The distribution of samples into
the geographic areas in given in Table 8. The distrubition of
individual trees is given in Appendix II.

These geographic areas circumscribe the occurrence of
samples and can be divided into three broad areas: coast,
transition, and interior. These broad areas roughly correspond
to the physiography of the study area (Holland 1976). The 16
geographic areas are not meant to reflect climatic, ecological,

Figure 6. Location of geographic areas circumscribing samples. General
geographic areas: C - coast; T - transition; I - interior. Specific
geographic locations: 1 - southern Vancouver Is. and Olympic
Penninsula (SVIOLY); 2 - Howe Sd. and Whistler (HOWHIS); 3 - lower
Fraser Valley (LOFRAV); 4 - Toba Inlet (TOBA); 5 - Bute Inlet (BUTE);
6 - Knight Inlet (KNIGHT); 7 - northern Vancouver Is. (NVANCI); 8 -
Chilliwack Valley (CHILLI); 9 - Fraser Canyon (HOPLYT); 10 - upper
Lillooett River (PEMBRA); 11 - Sumalo and Skagit Rivers (HOPMAN); 12
- Similkameen River (MANPRI); 13 - Okanagan (OKAN); 14 - Mt.
Revelstoke (MTREV); 15 - Rogers' Pass (ROGPAS); 16 - Mica Creek
(MICA).
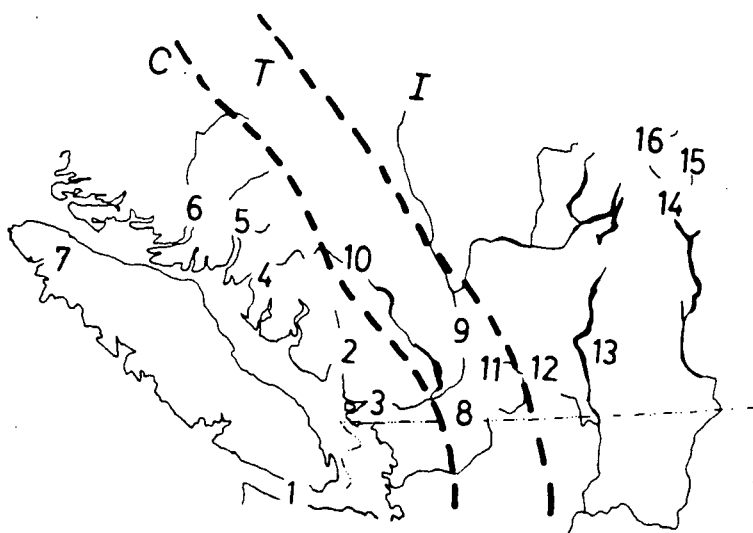
edaphic, or taxonomic groups. They simply group together

samples in a given geographic area and are generally

circumscribed by a major drainage and attempt to illustrate the

local morphological and environmental variation that might be

encountered in such an area. Table 8 illustrates the variety of

identifications that can be found in a narrowly defined area.

3.3 Selection of samples.

The arborescent habit of Picea made for specific problems

in systematic sampling of foliage, branches, and cones. Foliage

and branches were often not easily obtained even with a 3m long

pole pruner. The lowest whorl branches were often over 6m above

the ground. Cones in the two species are usually restricted to

Table 8. Distribution of samples into geographic areas. Numbers and abbreviations for geographic areas given in caption to Figure 6. SSS - *P. sitchensis* standard; SSP - *P. sitchensis* putative; SXE - "hybrid"; ESP - *P. engelmannii* putative; ESS - *P. engelmannii* standard; IESP - Selkirk Mtns. *P. engelmannii* putative; IESS - Selkirk Mtns. *P. engelmannii* standard. Note, not all trees collected were assigned to a geographic area.

GEOGRAPHIC AREA	(#)	SSS	SSP	SXE	IDENTIFICATION ESP	ESS	IESP	IESS	TOTAL
SVIOLY	1	9		15					24
HOWHIS	2	38	2	47	2				89
LOFRAV	3	5	6						11
TOBA	4	1	14	1					16
BUTE	5		3	5					8
KNIGHT	6		18	30	2				50
NVANCI	7	7	11						18
CHILLI	8		3	21					24
HOPLYT	9		2		8				10
PEMBRA	10				66				66
HOPMAN	11			14	4				18
MANPRI	12				28	44			72
OKAN	13				1	27			28
MTREV	14						5	24	29
ROGPAS	15							24	24
MICA	16						5	16	21

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the top third of the canopy of the tree (Owens and Molder 1976b; Harrison and Owens 1983) and collections of cones usually had to be made from cones that had fallen to the ground. Cones were not always available as a result of poor or sporadic cone-set, insect damage, or squirrel predation.

Those trees five years old or younger were not sampled owing to the diminutive size of the foliage and problems encountered with the manipulation of such small structures during measurement. As well, such young trees appear to display juvenille foliage that is distinct from mature trees (Jeffers 1974). Similar relations between age and size have been reported by Funsch (1975), although he claims that the effect of age is most pronounced for trees younger than 15 years. Another aspect of immature trees that was observed regards pubescence.

It appears that young trees may lack pubescence whereas the mature trees in the same stand have pubescence. Based on observations at the Chilliwack River Nursery, species that are described as pubescent, are glabrous when young. Lindquist (1948) reports similar observations for P. abies. For these reasons twig morphology was not recorded for immature trees.

Wherever possible, vegetative and reproductive materials were collected from each individual. Cones were collected from around the base of the individual in such a manner that possible contamination by cones from neighbouring trees was minimized. It was assumed that this manner of collecting cones represented a random sample from the canopy. Cone collections made directly from the upper canopy of trees were made by climbing, or sampling standing trees from a helicopter or from fallen trees. Following collection, the cones were examined and, on the basis of the amount of decomposition, only those cones obviously belonging to the most recent cone crop were retained for measurement.

Branch and foliage collections were made from the lowermost whorl primary branches (Fig. 7). Twig and needles were sampled from the middle of a two year old increment. Such collections were not always available and other orders of branches from different canopy positions had to be collected. The true order of branching was often difficult to identify owing to previous damage to branches collected. For trees growing at tree line, where annual extension growth was very small, it was not possible to measure characters associated with twig morphology.

Figure 7. Schematic representation of sources of intra-individual
variation associated with branch architecture in P. engelmannii and
P. sitchensis. A) Four-year old stem (O) with whorl (W) and
interwhorl (I) primary (1) branches. B) Three-year old whorl primary
branch with whorl and interwhorl secondary (2) branches. Circles
represent whorl nodes. Ordering scheme is acropetal.
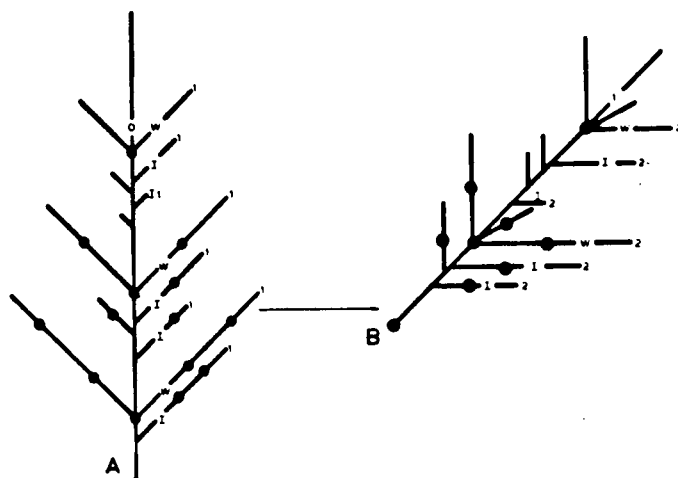
Generally, vegetative materials were more difficult to obtain
than were reproductive materials (Table 9). More complete
collections could be made in the interior where the trees were
smaller and had narrower crown forms..

The patchiness of the sampling from individuals created
unbalanced variable suites for separate trees (i.e. not all
trees could have the same number of variable suites measured).
Such an unbalanced availability of samples complicates any pure
statistical evaluation of the data. A general summary of the
number of complete variable suites is given in Table 9.
Specific disposition of individuals with respect to variable
suites is given in Appendix II.

Table 9. Summary of samples with complete measurements for various variable
suites. p - # variables per variable suite. Note, cone morphology includes
cone collection variables.

| IDENTIFICATION | VARIABLE SUITES | | | | | |
	MORPHOLOGY CONE (p=15)	TWIG (p=4)	LEAF (p=6)	ANATOMY LEAF (p=11)	TOTAL (p=36)	TOTAL AVAILABLE
P. sitchensis						
STANDARDS	42	46	46	44	24	62
PUTATIVES	59	35	35	19	16	65
"HYBRIDS"	102	99	100	77	50	133
P. engelmannii						
STANDARDS	45	53	53	65	37	71
PUTATIVES	63	60	52	71	38	105
SELKIRK MTNS.						
STANDARDS	10	10	10	10	10	10
PUTATIVES	55	45	45	41	29	69

4. Analyses.

The data analyses conducted here are primarily exploratory
rather than confirmatory in nature (Mosteller and Tukey 1977).
Precise statistical inferences, although an experimental ideal,
are frequently difficult to make owing to the necessity of
satisfying attendant assumptions. Such an approach focuses more
on the utilization of statistical techniques for purposes of
general indication and determination rather than precise
statistical inferences. The analytic and biological assumptions
associated with such heuristic approaches are less stringent
than those associated with purely confirmatory statistical
approaches. It is worth noting that exploratory data analysis
is an integral part of a confirmatory data-analytic protocol.
Further, this approach in biology and systematics is not new,
merely a rephrasing of the informal data-analytic methodology of
Anderson (1941, 1949, 1956).

4.1 Mathematical notation and formulation

The mathematical notation and formulation given here has been intentionally simplified and minimized to allow for an appreciation of the translation of the biological situation under investigation into the actual analytic model employed in the investigation. Such brevity allows for the communication of analytic intuition, and does not encumber the reader with the complexity and detail of the analysis.

Similarly, owing to the length of various analytic results, the notation and detail presented in the body of the text is intentionally minimized. However, as the discussion of many of the results are based upon details excluded in these tables in the text, the complete tables are presented in Appendix III.

4.2 Statistical techniques.

Data were subjected to a variety of univariate (analysis of variance (ANOVA), regression, and correlation) and multivariate techniques (principal components analysis (PCA)). Univariate techniques (UVA) estimate various population parameters from the data whereas multivariate techniques (MVA) are typically used to maximize various parameters and minimize the dimensionality of the data. MVAs produce summary statistics and variables which are linear composites of the original variables and are used to explore further the relations among samples where the original variables would not ordinarily permit such exploration because of variable inter-correlations.

MVA methods have been used most commonly as the basis for tendering evolutionary inferences. Making more direct genetic inferences, aside from controlled hybridization (Sharik and Barnes 1971; Tai and Tarn 1980; Tai and De Jong 1980; Williamson 1977; Goodman 1967; Neff and Smith 1979), are comparatively rare and recent (Lande 1979; Leamy 1977; Morishima and Oka 1968; Oka and Morishima 1968; Smith, et al. 1962; Wright 1954; Hashiguichi and Morishima 1969; Atchley, et al. 1982; Chevrud, et al. 1983). Most genetic inferences have been based on UVA (see however Becker 1967, regarding "selection indices"). Although genetic inference derived from UVA are often appropriate for specific breeding purposes, they generally ignore the multivariate nature of character variation and covariation (Arnold 1981; Sterns 1984). To ignore such aspects of genetic variation ignores, for example, the potential effect of intra-chromosomal linkage, inter-chromosomal effects, multi-genic effects, and cytoplasmic effects in accounting for observed patterns of phenotypic variation.

It is the inter-relation of variables that is fundamental to studies of biological systems. Development and evolution can be viewed as changing variable inter-relations with respect to different time scales. Maze, et al. (1984) and Scagel, et al. (1984) demonstrate such changes for ovule development of Nothofagus antarctica. Mitton, et al. (1980) demonstrate similar changes between populations of Pinus ponderosa. Maze (1983) demonstrates such changes between population and species of Abies. Most structured multivariate systematic studies rely on these variable inter-correlations (Adams 1982; Campbell and

Dearn 1980; Scagel and Maze 1984).

MVA methods are used throughout the study as they provide for simultaneous quantification of variation and linear inter-independance of variables. By contrast, UVA methods provide for quantification of only single variables one at a time and neglect the inter-dependance of variables. Quantification and statistical attention to variable inter-dependance respects the integrated nature of biological systems. In the case of whole organisms, developmental and evolutionary interdependance.

4.2.1 Conformity to distributional assumptions.

Utilization of UVA and MVA often require satisfaction of specific sampling and distributional assumptions about the data. A common distributional assumption is that the data be normally distributed. In assessing normality of variable distributions D'Agostino's test of normality (Zar 1974) was used. Variables not falling within the specified confidence limits calculated for D'Agostino's D were further characterized using cumulative frequency distribution plots (CFDs, Univ. of Michigan, Statistical Research Lab. 1976), measures of skewness (g_1) and kurtosis (g_2). Such characterization allows inferences to be drawn concerning the nature of the distribution (Bock 1975), suggests transformations appropriate to minimize departures from normality, and aids in the detection of outliers (Barnett and Lewis 1978). Transforming data to approximate normality or symmetrize the data (Tukey 1977), although useful for drawing

statistical conclusions, may make interpretation difficult.

For the various data sets examined the variables did not have to be transformed. Most variables appeared to be slightly skewed to the right from that expected for normally distributed data. This is the same situation reported by Barkworth, et al. (1979). Such skewed distributions may be attributed either to the consequence of increased developmental variability at larger sizes or to increased measurement error.

Multivariate normality is assumed for statistical applications of MVA. The assessment of multivariate normality is most easily approached by assuring that the marginal distributions of the variables are normally distributed (Bock 1975; Pimentel 1979). Generally, if the marginal distributions approximate normality, so will the conditional and component distributions, thereby approximating multivariate normality (Pimentel 1979). However, marginal normality by itself is not sufficient to indicate multivariate normality. Purely statistical assessments of multivaiate normality are available (Mardia 1970, 1974; Wagle 1968; Day 1969; Mardia and Zemrock 1975; Machado 1983; Malmgren 1979; Reyment 1971; Cox and Small 1978; Andrews, et al. 1972) ,however statistical elegance is achieved at the expense of computational cost and restriction to dimensionally small sets of data. An heuristic assessment of the conformity to multivariate normality is provided by the CFD technique proposed by Campbell (1980). Gnanadesikan (1977) provides many examples of the use of CFD techniques for characterizing multivariate data prior to MVA.

For most heuristic applications of MVA, multivariate normality does not have to be assumed, merely that the data not contain wild outliers or groups of outliers. Some MVA, such as canonical variates analysis (CVA), may be sensitive to departures from multivariate normality, especially with repect to individual group covariance matrices (Gower 1972).

The data sets examined here were all indicated as being multivariate normally distributed. Single or groups of outliers were apparantly non-existent, and there was little in the way of departure from the curve expected for a multivariate normal distribution.

4.2.2 Sample size.

Fundamental to any study of variation is the establishment of an adequate sample size (n) for a specific purpose. Such concerns refer to the sample accuracy. Previous investigations in Picea have generally used an n based on criteria relating more to the economics of the study rather than respecting the variability of the organism. No information is provided in any of these studies as to the adequacy of the sample sizes used (see Table 1 for citation of specific studies).

Concern for the economics of conducting research may well constitute a valid criterion for deciding upon a given n. However, without some information concerning the adequacy of n in estimating a desired population parameter there can be little confidence placed in the value of the sample statistic. Sample

size directly influences the sample statistic - the larger n is the more reliable is the statistic that estimates the parameter. Any estimate of n is, by definition, sample specific. The more variable a collection of samples, the larger an n will be required to estimate reliably a given parameter.

The sample size estimation technique employed here is based upon the methodology outlined in Scagel, et al. (1984). This approach seeks to select an n at which the determinant of the correlation matrix ($|\underline{R}|$) stabilizes, thereby providing a stable n for MVA. A similar sample size estimation methodology is used for individual variables where one selects an n at which the standard error of the mean is less than the accuracy of the measuring device.

During the initial sampling for this study a univariate sample size estimation technique illustrated by Green (1972) in concert with a graphical technique illustrated by Wood (1972) was used. The technique illustrated by Green (1972) requires that an estimate of the population coefficient of variation be made. In contrast, Wood's (1972) technique is a sequential, sample-specific graphical technique. Sample sizes suggested by these techniques were used as the basis for selecting sample size for separate variable suites. However, utilizing the less parameter- and sample-specific methodology of Scagel, et al. (1984) indicated that these initial sample size estimates were generally too small (Table 10). In arriving at the multivariate extension of the sample-size estimation a similar underestimation of multivariate sample size was observed for the

Table 10. Sample size estimates for intra-individual variation (n) and inter-individual variation (t). Estimates based on standards of both taxa. Univariate estimates based upon the n or t at which s.e.$\bar{x}$ declines below measurement accuracy. Multivariate estimates based upon n or t at which |R| or D' stabilize. Inter-individual variation based on averaging n based on sample-size estimation of Green (1972) and Wood (1972) (n/t USED) n_{est} - n based on larger of Green or Wood's technique. p - number of variables per variable suite.

VARIABLE	(n_{est})	n P. sitchensis	P. engelmannii	n/t USED	t P. sitchensis	P. engelmannii
NEEDLEN	(8)	10	5	5	20	15
ABxSTOM	(9)	5	5	"	25	20
ADxSTOM	(7)	10	5		10	10
RESCYNO	(35)	1	1		1	1
RESCYLOC	(19)	10	20		10	20
RESCYLEN	(47)	10	20		10	15
PULVLEN	(8)	20	30	5	40	40
TIPWID	(2)	7	15	"	20	10
TIPDEP	(2)	5	10		15	20
PULVPUB	(1)	1	1		1	1
NEEDWID	(2)	25	30	5	50	45
NEEDEP	(1)	20	30	"	45	40
ABXANG	(1)	5	10		10	20
ADXANG	(3)	8	20		20	15
CENCYWID	(1)	20	30		45	45
CENCYLAT	(2)	25	35		70	50
CENCYABx	(2)	20	35		30	40
CENCYADx	(8)	25	35		50	45
ENDONUM	(2)	5	10		5	25
PHLEND	(4)	20	40		50	45
XYLEND	(11)	25	30		45	30
CONLEN	(3)	30	20	5	25	25
CONWID	(2)	20	1	5	10	10
SCALEN	(7)	1	5	10	5	10
SCALWID	(6)	20	25	"	20	30
SCALTAP	(12)	25	30		25	35
WINGWID	(8)	30	30		20	30
WINGTAP	(10)	20	30		20	20
FREESCAL	(28)	15	35		25	35
BRACTLEN	(20)	25	25		30	35
BRACTWID	(12)	10	5		10	15
BRACTTAP	(30)	25	10		25	20
SHCOLEN	(3)	-	-	>5	25	25
SHCOWID	(2)	-	-	"	15	10
LOCOLEN	(3)	-	-		25	20
LOCOWID	(2)	-	-		5	10

VARIABLE SUITE

LEAF ANATOMY: |R|		30	35	5	40	30
(p=11) D'		25	30		30	20
CONE COLLECTION: |R|		-	-	1	30	35
(p=11) D'		-	-		25	20
LEAF MORPHOLOGY: |R|		30	25	5	30	40
(p=6) D'		20	10		9	15
TWIG MORPHOLOGY: |R|		10	25	5	25	20
(p=4) D'		20	15		12	10
CONE MORPHOLOGY: |R|		35	30	10	35	35
(p=4) D'		15	25		20	20

technique proposed by Newhan and Jancey (1981).

In addition to the stabilization of the determinant of the correlation matric, the stabilization of Mahalanobis' D^2 was also examined. The determinant of the correlation matrix is an essential statistic for the multivariate application of MVA. Mahalanobis' D^2 is an essential statistic in the statistical application of a structured MVA such as multivariate analysis of variance (MANOVA) and its further extension to CVA and discriminant function analysis (DFA). Assessment of the stabilization of Mahalanobis' D^2 is a pre-requisite to performing a structured MVA.

Univariate and multivariate sample size estimates are given for all variables and variable suites in Table 10. The sample sizes reported here for both intra- and inter-individual levels of variation are based upon standards of each species. Sample sizes (n or t) and degrees of freedom (df) have been given explicitly in all tables and figures. The actual sample sizes employed were smaller than those indicated by Table 10 as the tests were performed after sampling was completed.

4.2.3 Discrete variables.

Pulvinus pubescence, unlike the other variables is a qualitative rather than quantitative variable (Appendix I). The inclusion of such a variable along with quantitative continuous variables in a multivariate analysis may contribute more to inter-sample differences than the quantitative variables, even when standardized (Barkworth, et al. 1979; Sneath and Sokal

1973). Realizing that the inclusion of such a qualitative variable may bias the results of a multivariate analysis, it is critical to determine the degree that such a variable may be assoicated with other variables prior to being submitted to an analysis. If the variation of such a variable is similar to that of the other variables then it is permissable to include the two types of variables in the same analysis.

A measure of partial correlation could address the problem of the contribution of the categorical variable in a bivariate situation; however, it does not address the multivariate nature of the situation nor does it address the question of whether the qualitative variable-state is associated with the quantitative variables. Rephrasing, a bivariate approach does not allow one to determine if, assuming a quantitative variable is taxonomically significant, the qualitative variable is similarily significant.

Barkworth, et al. (1979) addressed this problem by way of MANOVA. Briefly, the groups of samples they submitted to MANOVA were determined by the state of a qualitative character and only quantitative characters were employed. Employing Wilk's λ to test the multivariate differences between the group centroids enabled them to determine whether a specific qualitative variable-state used to calibrate the groups was indeed taxonomically significant (i.e. shared variation with quantitative variables). Such an approach to the evaluation of the contribution of the qualitative variable to the relationships amongst the two species was taken here. It should

be pointed out that as only two variable states were involved
here (pubescence: present or absent), the MANOVA approach
employeed by Barkworth, et al. (1979) simplifies to Hotelling's
T^2 test of the difference between two centroids (Morrison 1976).

A summary of the T^2s performed is given in Tables 11. In

Table 11. Summary of Hotelling's T^2 for twig morphology based on
    variable state for discrete (presence/ absence) variable: pulvinus
    pubescence. *, T^2 significant @ $p \leq 0.01$; D^2 values given in body of
    table. P.s - P. sitchensis; P.g - P. glauca; P.e - P. engelmannii.

COMPARISON	df (3,x)	D^2
INTRA-INDIVIDUAL		
ADVENTITIOUS vs. WHORL	8	invariate
PRIMARY vs. SECONDARY	98	invariate
1979 vs. 1981	9	invariate
INTERWHORL P. sitchensis	52	2.97
INTERWHORL P. engelmannii	58	invariate
INTER-INDIVIDUAL		
P. sitchensis	530	1.97
P. engelmannii	385	0.37
P. glauca	61	11.50
INTER-SPECIFIC		
P.s x P.e x P.g	984	1.14*
P.s x P.e	919	1.59*

only two instances were the continuous variables of twig
morphology indicated as showing significant differences between
the groups being compared. For those comparisons where the
variable was either invariate or the attained T^2 was not
significant, the variable was excluded from further analysis for
that source of variation.

4.2.4 Univariate analyses.

ANOVA was used both as a means of testing the differences between means as well as examining the structure of the data. ANOVA was used as a means of partitioning the variation on the basis of the percentage of the total sums of squares into various hypothesized sources ($\%SS_{SOURCE}$ (uva)). The use of ANOVA for both heuristic and statistical purposes is consistant with the data-explorative purpose of ANOVA (Tukey 1962; Tukey and Wilk 1966; Kempthorne 1978; Wilkinson 1978; O'Grady 1982). Bartlett's test (Zar 1974) was used in testing the equality of the group variances when the ANOVA model employed was balanced or near-balanced. The specific forms of the ANOVA models used are given explicitly in the text as "nude" models (Nooney 1965).

The partitioning of variation on the basis of sums of squares is, in comparison with the "variance component analysis" (Sokal and Rohlf 1969), less dependent upon the assumptions of the homogeneity of group variances. Additionally, partitioning by a sums of square criterion rather than a mean square criterion allows one to compare the variation of individual groups for a specific hypothesized source of variation. At the time of completion of this study it was observed that the two methods of partitioning variance from an hypothesized source gave approximately equal results.

For most of the MVAs performed, UVAs of the individual variables involved were also performed and the results presented along with the MVA. Although these UVAs are often unneccessary for the purpose of the points raised here, they are a valuable

adjunct for two reasons. First, under situations where a reader
may not be familiar with the MVA techniques used, such UVA will
allow an appreciation for the situation being described.
Secondly, for readers interested in extending the results given
here to independent research, such UVA may be useful in
designing a sampling technique and considering specific
variables (i.e. Newman and Jancey 1983).

4.2.5 Multivariate analyses.

PCA was the principal MVA technique used. The summary
variables provide the basis for most of the UVA. PCA maximizes
the between sample variance in the data and allows a comparison
of the individual samples without a priori stratification of
variables (as in canonical correlation analysis) or samples (as
in canonical variates analysis (CCA)). In all cases PCA was
performed upon a correlation matrix, R, of some p variables.
The correlation matrix was preferred rather than the dispersion
matrix, or variance-covariance matrix, as interest was in
relative rather than absolute variation. As many variables were
not commensurable, R provides a scale-independent means of
examining character variation and covariation (see also Noy-Meir
1973; Noy-Meir, et al. 1975 for succinct discussion on the
nature of the dispersion matrix to be submitted to an
eigenvalue-eigenvector extraction technique). Individual
elements of R, correlation coefficents, r_{jk}, are intuitively more
meaningful in the context of morphological variation than other
measures of dispersion, such as variance and covariance.
Considerable detail and discussion of PCA is provided here as it

is the most generalized of the eigenvector-eigenvalue extraction techniques used and the interpretative techniques are readily extended to the other MVA used.

PCA, like other MVA eigenvector-eigenvalue extraction techniques results in i vector-variables. These vector-variables are linear composites of the original variables and are independent or orthogonal with respect to each other. These vector-variables are referred to as components (="principal variables", Dempster 1969) or, more colloquially, "axes". Associated with each component is an eigenvalue (λ_i) and eigenvector ($\underline{v}_i$). λ_i is the variance of samples for that component. $\underline{v}_i$ is a vector of coefficients relating the original variable values to the new vector-variable. For a "stable" PCA solution the number of samples, n, must exceed the number of original variables, p, forming $\underline{R}$ (see also remarks above with respect to sample size; Karr and Martin 1981; Scagel, et al. 1984).

PCA maximizes the variance of the n samples on which the p variables have been measured. The value of each sample for each component is referred to as the component score for that sample. The linear independence of the individual components is shown in that the correlation of the scores from separate components is 0.0. Cooley and Lohnes (1971) provide a readable account of the calculation of component scores for a particular PCA.

The component scores serve as a summarization of the initial data. As each of the original p variables contributes to each component, the component scores have the desirable

property of providing a reduction in dimensionality of the
original data. For the same reason component scores are also
more normally distributed than the original p variables on the
same sample (Morrison 1976; Pimentel 1979; Chatfield and Collins
1980; the "central limit theorem").

Statistical inference based on PCA assumes multivariate
normality of the original data and that $\underline{R}$ is derived from a
single population. However, Chatfield and Collins (1980) and
Morrison (1976) provide evidence for the statistical robustness
of PCA and associated interpretative techniques under non-normal
situations. Satisfaction of multivariate normality is seen as
being important where results are marginal in their
significance. PCA can be used for heuristic appreciation of the
variation in the data even if the distributional caveats cannot
be satisfied provided the data do not contain radical outliers
(Ruymgaart 1981). It is the heuristic application of PCA
(ordination, clustering, and UVA or MVA statistical analyses of
component scores) that the method is most frequently
encountered. The reader is referred to Pimentel (1979), Gittins
(1969), and Isebrands and Crow (1975) for a more detailed
discussion of the caveats associated with the method and
application to biological situations.

Prior to performing PCA, the correlation matrix to be
factored was evaluated to determine whether in fact PCA was
necessary. Estimates of the overall structure of $\underline{R}$ are provided
by test of equicorrelation (Bartlett's or Lawley's test of
equality, Chatfield and Collins 1980) and independence

(Anderson's test of sphericity, Chatfield and Collins 1980) of r_{jk} of $\underline{R}$. If the r_{jk} are equal but non-zero there is no unique component possible to extract. If the original variables are independent (i.e. all r_{jk} are statistically equal to zero) there is no reason to perform a PCA as the original variables already can be considered linearly independent and reduction of dimensionality is not necessary. Unless otherwise noted, all PCAs reported here have been based upon an $\underline{R}$ where the r_{jk} were statistically neither the same nor equal to zero.

The interpretation of the results of PCA has been made with a number of techniques. Component-specific interpretations of $\underline{R}$ are based upon considering the porportion of the total variation (=intra-set redundancy, Gittins 1979) of the data attributed to the component (%var.), and a test of the independence of the extracted component from residual structure in $\underline{R}$ (Anderson's test of equality, Morrison 1976; Cooley and Lohnes 1971). Unless otherwise noted all components from PCAs reported here are significantly different from residual variation and have an eigenvalue greater than 1.0.

Eigenvalues have not been presented in the tables of the results of the PCAs as the percent variance is just as meaningful provided that the PCA is derived from a correlation matrix. For a correlation matrix:

$$\% \, var. = 100 \cdot \left(\lambda_i / p\right) = 100 \cdot \left(\lambda_i \Big/ \sum_{i=1}^{i=p} \lambda_i\right)$$

The eigenvector values, a_{il} , (=component loadings) of the
original variables provide an estimate of the significance of
the contribution of each of the original variables to a
particular component. An alternate, and more stable (Gittins
1979), way to interpret the contribution of the original
variables to the scores of the separate components is to
calculate product-moment correlations between the original
variables and the component scores ("component correlations",
Pimentel 1979; "component structure", Cooley and Lohnes 1971).
For a correlation matrix the relationship of the component
correlations to the eigenvalue of that component is the average
square of the component correlations for a given component
equals the percentage of the total variance extracted by that
component. The reliance upon component correlation is
especially necessary under conditions where the original data
may have been transformed. Additionally, such product-moment
correlations have an advantage over eigenvector values in that
their significance can be tested.

An additional inference derived from the relative sizes and
signs of eigenvector values concerns the form of variation
described by a given component (Pimental 1979). If the
eigenvector values are approximately the same size and sign
(i.e. approximating a vector of isometry, Pimentel 1979), then
the form of variation for that component is said to reflect,
primarily, differences in size among samples. If the
eigenvector values are markedly different in magnitude and are
of opposite signs, then the component reflects size and shape
differences. The distinction between these two forms of

variation is important as it serves to reflect, respectively, the differences between simple and complex variable variation and inter-correlation.

Correlation among eigenvector values of separate PCAs (Atchley, et al. 1982; Pimentel 1979, "theoretical vectors"; Blackith and Reyment 1971) provides an assessment of the similarity between these PCAs. Such comparisons are valid only where the PCAs share the same variables but not necessarily the same samples. The correlation of correlation matrices or comparisons of |R| may also suffice as an alternative means of comparing R (Newman and Jancey 1981; Scagel and Maze 1984; Scagel, et al. 1984).

The component scores can be used to provide ordinations that illustrate the pattern of variation of samples. Unless otherwise indicated all ordinations presented here are drawn in such a manner that the scales of the co-ordinate axes are equal. The length of the axes correspond to the maximum dispersion of sample submitted to the analysis for the first component. This graphical convention emphasizes the decreasing variance extracted by succeeding components. Where means of several samples are illustrated, the scale of the ordination emphasizes the dispersion of the means in the space of the original samples from which the means were calculated. In all ordinations the amount of variation accounted for by a given component is given parenthetically to emphasize the decreasing variance associated with sequentially smaller eigenvectors.

In addition to ordination, component scores are also

utilized in subsequent univariate analyses. Univariate

techniques allow a component-specific interpretation and provide

a further method of assessing the significance of a component.

Utilizing component scores in correlation and regression

analyses is a common practise. ANOVA of component scores has

not received the same attention (but see Moore 1965; Pimentel

1979; Maze and Parker 1983; Scagel and Maze 1984; Wheeler and

Guires 1979). Total multivariate variation is referred to here

as "$\%SS_{SOURCE}$ (mva)". Owing to the additive nature of the

components from PCA, the utilization of ANOVA may provide an

assessment of the total multivariate variation over some p

components (Scagel and Maze 1984; Wheeler and Guires 1979).

Although tests of significance associated with %SS (uva) are

given, no similar tests of significance are provided for %SS

(mva).

During the completion of this study it was observed that

the value obtained for total multivariate variation (v_c, Scagel

and Maze 1984) of a given source is equal to the average

variation of each variable for the same hypothesized source.

For example, given a simple situation where variation is

hypothesized to be due to a single source, A, and samples have

been measured for three variables, $\underline{x}_j$: x_1, x_2, x_3.

The calculation of total multivariate variation due to source A would be (<u>sensu</u> Scagel and Maze 1984):

$$\frac{1}{3}\left[\sum_{i=1}^{i=3}\left(\lambda_i \middle/ \sum_{i=1}^{i=3}\lambda_i\right)\cdot\left(SS_{A_i}\middle/ SS_{iTOTALi}\right)\right] = V_c$$

V_c can also be calculated by:

$$\frac{1}{3}\left[\sum_{j=1}^{j=3}\left(SS_{A_j}\middle/ SS_{TOTALj}\right)\right] = V_c$$

This relation simplifies the analytic steps necessary to calculate %SS (mva). Indeed, this relation provides a means by which multivariate variation can be calculated when a PCA cannot be performed owing to either the structure of <u>R</u> or dimensionality of the data. It also provides a way that previous univariate studies can be compared to multivariate studies. Additionally, the same empirical relation exists for r^2 values from regression of individual variables and r^2 values from regression of component scores. This relation between multivariate and univariate variation serves to further justify the inclusion of UVA results with the results of MVA and increases the utility of these results for future independent analyses.

Although reduction of dimensionality is an essential feature of PCA, Orloci (1973, 1975, 1978) provides an independent means of assessing dimensionality. Orloci's technique of ranking variables on a sums of squares criterion and specific variance (=redundancy) was employed here as a means

of providing a summarization of the data used and to suggest a
reduced character set for utilization if further sampling is
undertaken (i.e. an independent corroboratory study). Beshir
(1975) provides an illustration of the use of this technique
with respect to Pinus banksiana.

4.3 Computation and tests of significance.

Mention has been made of various tests of statistical
significance employed in different analyses. Unless otherwise
stated in the text, all tests indicated as being significant are
judged to be so at a probability of $p \leq 0.01$. Levels of
significance are explicitly referenced in all tables and
figures.

All analyses were performed using the computing facilities
available at the University of British Columbia. Statistical
programmes used were: ANOVAR (Greig and Osterlin 1978); GENLIN
(Greig and Bjerring 1980); MIDAS (Fox and Guire 1976); and,
NTSYS (Rohlf, et al. 1980). Multivariate and univariate sample
size estimation and Orloci's ranking of characters by a
dispersion criterion were performed using a programme developed
by John Emanuel of the Faculty of Forestry at the University of
British Columbia. Gary Bradfield of the Botany Department at
the University of British Columbia provided a two-dimensional
plotting routine which accommodated identification of plotted
points. As well, several programmes developed as system
sub-routines at the University of British Columbia were used.

III. INTRA-INDIVIDUAL VARIATION.

1. Introduction.

In morphologically small and simple organisms, the perception and assessment of intra-individual and inter-individual variation is, for systematic purposes, often readily apparent. In morphologically large and anatomically complex organsims, such as spruce trees, intra-individual variation is not as apparent nor, as a result, is inter-individual variation as easy to assess. Intra-individual variation of trees is most commonly considered with respect to statistical accuracy (Zobel and Talbert 1984).

As intra-individual variation is, by classical definition (Falconer 1981), not a result of genetic variation but localized environmental and developmental variation, such variation serves as a comparative yardstick against which suspected genetic variation can be compared. Implicit in the recognition of genetic and developmental sources of variation is the assumption that heritable differences between individuals are genetic, whereas differences amongst parts of an individual are the result of somatic mutations, or other "non-genetic" causes or the result of genotype-environment interaction. However, such assumptions ignore the genetic basis of development. As mentioned earlier (Chapt. II), developmental variation is better considered as simply another level of genetic variation, albeit a less environmentally buffered one.

The nature of intra-individual variation in an

inter-individual context is important to consider for the reasons outlined here. Having been satisfied that the variables being used in this study have a larger inter-individual than intra-individual variation (Table 2) one could ignore intra-individual variation, or in the words of Mosteller and Tukey (1977), "sweep it under the rug". However, to ignore intra-individual variation assumes random intra-individual variation. That intra-individual variation may not be random suggests that sampling and interpretation could be influenced by developmental variation. In P. sitchensis, these points and others have been emphasized by Forrest (1975b, 1980a).

Reference has been made earlier to the sampling problems necessitated by the size, form, and occurrence of individual trees. As well, the attendant structural complexity in even those positions of the tree that could be easily sampled, necessitated very specific sampling strategies. Evidence in the literature available on Picea substantiates the impressions based on field observations of differences between orders, positions, and ages in the canopy. Addressing the issue of intra-individual variation of the selected variables avoids critsicms such as those directed at Parker, et al. (1981) by Hunt and von Rudloff (1983).

A number of morphological and anatomical studies of intra-individual variation of Picea have been conducted. Denne (1979) and France and Mexal (1980) have related the variability of wood anatomy in P. sitchensis to position in the canopy and bole. Garman (1957) related variation of scale morphology to

position in the cone. This variation is seen readily in
longitudinal cone sections. Taylor (1959) reported on cone and
needle morphology within the canopy. Ewers (1982) and Sifton
(1965) have reported on age-related variation of needle anatomy
in P. abies (L.) Krast. and P. pungens. In addition to
positional variability of morphological variables, Funsch (1975)
also examined intra-individual variability related to compass
direction in the canopy of P. engelmannii. Wilson (1963)
reported on the variability of pollen of P. glauca.

Generally, the most apical and lowest orders of branches
have the largest structures; they also develop more quickly
(Harrison and Owens 1983). Taylor (1959) could not detect
intra-individual variation in Rocky Mountain P. englmannii.
Similarly, Funsch (1975) could not detect intra-individual
variation related to compass direction of the canopy. Variation
that has been observed in P. sitchensis has been attributed to
competition for nutrients and light, growth regulation
associated with apical dominance, and the external environment
(Larsen 1927; Stover 1944; Wardle 1968; Leverenz and Jarvis
1980a,b; Grace, et al. 1975).

More recently interest has focused on the intra-individual
variability of physiological and growth variables in Picea.
Structural variation sometimes has been reported in conjunction
with these physiological studies (Leverenz and Jarvis 1980a,b;
Lewandowska and Jarvis 1978). Intra-individual physiological
variation has been related to order of branching (Norman and
Jarvis 1974), position (Baxter and Cannell 1978; Fraser, et

al. 1964; Leverenz and Jarvis 1979, 1980a,b; Lewandowska and
Jarvis 1978), and age (Freeland 1952; Fry and Phillips 1977;
Soikkeli 1978). Schulze, et al. (1977) working on P. abies and
Leverenz and Jarvis (1980a) working on P. sitchensis have
reported variation within a single increment of growth.

Intra-individual physiological variation, like structural
variation, has been hypothesized to be effected by competition
for light and nutrients, growth regulators, the
micro-environment surrounding the structure, and the environment
of the tree. Of special interest has been the relation of
intra-individual variation to incident sunlight ("sun and shade"
positions, Kramer and Kozloski 1979; Zimmerman and Brown 1971)
as reported by Leverenz and Jarvis (1980a,b) in P. sitchensis,
and Fuchs, et al. (1977) and Schulze, et al. (1977) in P. abies.
With the advent of commercial scale grafting programmes
attention has also been directed to cyclo-, peri-, and
topophysis.

Some of the most elegant studies of intra-individual
variation in conifers and Picea in particular are the
contributions of Hrutfiord, et al. (1974), Forrest (1975a,b;
1980a), von Rudloff (1967, 1975), Ogilvie and von Rudloff
(1968), and Kaufmann, et al. (1974). These studies have
emphasized both the spatial and temporal variation of volatile
chemical compounds. It should be noted that intra-individual
variability, at least in P. sitchensis, is not restricted to the
aerial portions of the tree, but also occurs in the root
system (Ford and Deans 1977; Eis and Long 1972).

In the present study there are several obvious sources of
intra-individual variation that can be quantified. These relate
to the age of the increment of growth, the position, and order
of branches. These sources of variation are common in other
coniferous species owing to the similar architecture (Tomlinson,
1983: "Massart's model"). Indeed, studies of intra-individual
variation of P. sitchensis have formed the basis for entire
studies (Denne 1979; France and Mexal 1980; Schulze, et
al. 1977; Fraser, et al. 1964; von Rudloff 1967; Forrest 1975a,
b, 1980a). Since interest here is in the variation associated
with material from a variety of positions that are commonly
encountered during collecting, emphasis has been placed on
assessing variation in vegetative materials associated with:
adventitious and whorl primary branches of the same age from the
lowest primary branch (Fig. 7); primary and secondary whorl
primary branches of the same age from the lowest primary
branches (Fig. 7); the year of collection of primary whorl
branches from the lowest whorl primary branches; and, whorl
primary branches from different positions in the canopy. The
variation of cone morphology with respect to positions in the
canopy was also examined. Although addressing these sources of
intra-individual variation may not allow the assignment of
statistical confidence limits to inter-individual variation due
to the unbalanced nature of sampling, it will permit an
heuristic appreciation of this source of variation.

Adventitious branching in P. sitchensis is thought to be a
result of environmental inducement by either physical damage to

the tree (Herman 1964) or stand damage (Issac 1940). Based on
observations made in the field, the same would appear to be the
case for P. engelmannii although there has not been explicit
citation to this effect in the literature. There is also no
literature indicating whether there are morphological or
anatomical differences between the two positions. As these two
positions of branches are often in markedly different
environments, it would be reasonable to expect the existence of
morphological and anatomical differences. Adventitious
branches, although not uniformly present, are easier to sample
than whorl branches.

Orders of branches have been more intensively investigated
by a number of workers. It is an obvious source of variation.
The nature of branching of the tree is interpreted as a
determinant of the form of the tree. Some research has
suggested significant differences between orders of branching.
Where these differences are observed they are attributed
invariably to growth regulation associated with apical
dominance.

With respect to temporal variation in conifers, the
literature is very extensive with both observations and tendered
explanations for such variation (Stover 1944; Andersson 1965).
Explanations for this source of variation have been attributed
to extrinsic factors (climatic changes, pathogen infestation,
physical damage) and intrinsic controls (mast seeding, Silverton
1980). As sampling was carried out over several years it would
appear that this source of variation could easily influence the

results.

By temporal variation reference is made to variation
between two year old twigs and needles initiated and elongating
during separate years. For example, a two year old vegetative
collection made in 1979 would have been initiated at the end of
1977 and elongated during 1978. Such material may differ from
two year old material collected during 1980 owing to the
specific extrinsic and intrinsic conditions surrounding
initiation and elongation during 1978 and 1979 (see Harrison and
Owens 1983; Owens and Molder 1976a, 1976b, 1977, 1979,1980;
Owens, et al. 1977; Singh and Owens 1981, regarding sequence and
timing of vegetative and reproductive events). It should be
noted that because of the perennial habit of the organism that
there is a temporal component associated with whorl, position,
and order of branching (Fraser 1976). Additionally the temporal
variation could be assessed for eight years growth in Picea
because the leaves persist that long. ·

Perhaps the single most obvious source of variation in
large arborescent organisms is that associated with the position
in the canopy from which a sample comes. Indeed, it is height
that most characterizes tree architecture. Certainly this is
the most extensively documented source of intra-individual
variation. Explanations for within-canopy variation,
"heterophylly", are attributed to environmental ("sun and shade"
leaf morphology) and developmental ("juvenile and mature"
foliage, "vegetative and fertile" positions) causes.

Quantifying intra-individual variation in P. engelmannii

and P. sitchensis provides a description of this variation for
more taxa. Addressing aspects of this variation in mature and
immature individuals may allow for explanations of this
variation with respect to various competing hypotheses
concerning environmental or developmental control. In addition,
such information may be of value in tree-breeding programmes
where grafting and rooting projects are being carried out
(Klaehn 1963; Rouland 1973), although graft incompatibility
problems have not been reported for P. sitchensis or
P. engelmannii (Bower 1982). Further such investigations may be
useful in understanding the interaction of trees with various
pathogens (Whitham 1981).

Attention to intra-individual variation serves more than
just the pragmatic objectives demanded by a systematic study and
silvicultural practises. It is essential for an understanding
of the development and functioning of morphologically and
anatomically complex organisms. For this reason
intra-individual variation in trees has been related to crown
form. Although crown form is poorly understood and quantified,
it has been assumed to be important based on the demonstration
of patterns of intra-individual variatiation.

Crown form is reportedly under genetic control in many
species of Picea (Grant and Mitton 1976, 1977; Alexandrov 1971;
Roche 1965; Lindquist 1948; Jankiewicz and Stecki 1976) although
there is a diversity of opinion as to the degree of genetic
control. Some have attributed taxonomic significance to crown
form in Picea (Schmidt-Vogt 1977; Jones and Bernard 1977) and

have speculated on adaptation of various crown forms of P. abies to heavy snow packs (Alexandrov 1971; Lindquist 1948). Other researchers have emphasized the adaptation of the crown of P. sitchensis to the interception of precipatation and light (Ford and Deans 1978; Cochrane and Ford 1976; Ford and Diggle 1980), competition for nutrients, competition with other trees (Ford 1976), and optimization of mechanical properties associated with support (McMahon and Konauer 1976). Both intrinsic (Cannell 1974) and extrinsic (Cannell, et al. 1976; Pollard and Logan 1979) controls have been proposed. The most frequently tendered speculation concerns adapatation for optimization of photosynthetic efficiency (Leverenz and Jarvis 1980a,b; Norman and Jarvis 1974; Horn 1971; Fisher and Honda 1979a,b; Fisher and Hibbs 1982).

Regardless of the hypothesized adaptation, crown form is generally agreed to influence stand structure, composition, regeneration, and reproduction (Brunig 1976; Jankiewicz and Stecki 1976). Crown form is recognized to consist of a hierarchy of units (Fraser, et al. 1964; Cochrane and Ford 1978) in which slight internal and external changes during development may result in substantial alterations to the crown form (Pearce and Moore 1962; Honda 1971; Tomlinson 1982), which, in turn may affect the stand characteristics mentioned above. These explanations of crown form respect the development of individual trees and physical interaction amongst trees in the stand.

2. Materials and methods.

2.1 Materials.

All investigations were restricted to individuals
considered to be standards for the two species (see Chapt. II).
Such a limitation simplifies the nature and expected degree of
inter-individual variation, permitting a more constrained
situation under which intra-individual variation can be
examined.

All the sources of intra-individual variation being
considered could not be assessed for any single tree or at any
one site encountered during the course of the field collections.
To do so would have necessitated whole tree sampling.
Adventitious and whorl primary branches were compared from an
individual of P. engelmannii (Tree 218, Appendix II). Primary
and secondary whorl branches were compared from an individual
representative of P. sitchensis (Tree 527, Appendix II). Year
to year comparisons were made for an individual representative
of P. engelmannii (Tree 60705, Appendix II).

Inter-positional variation was compared under three
conditions. Single, mature trees representative for both of the
taxa were sampled at regularly spaced intervals throughout the
crown (Fig. 8). This sampling was possible since the trees had
been either blown over during a storm (Tree 221, Appendix II) or
struck down by a truck (Tree 557, Appendix II). Six, eleven
year old saplings representing a single half-sib family[1] of
P. sitchensis were sampled at each whorl in their canopies where
weevil damage had not obscured the ordering of branches.

Figure 8. Schematic representatin of individual trees of P. engelmannii and P. sitchensis from which intra-individual sampling conducted. T1 - T6, 11-year old immature P. sitchensis from nursery: lateral branch increments shown are averaged per whorl, circles represent whorl nodes. T7, mature P. sitchensis (SXP 221). T8, mature P. engelmannii (SXP 527). Triangles mark position at which samples taken from mature trees. Not all whorl primary branches marked for immature trees due to measurement problems associated with weevil damage. *, positions cones collected from.
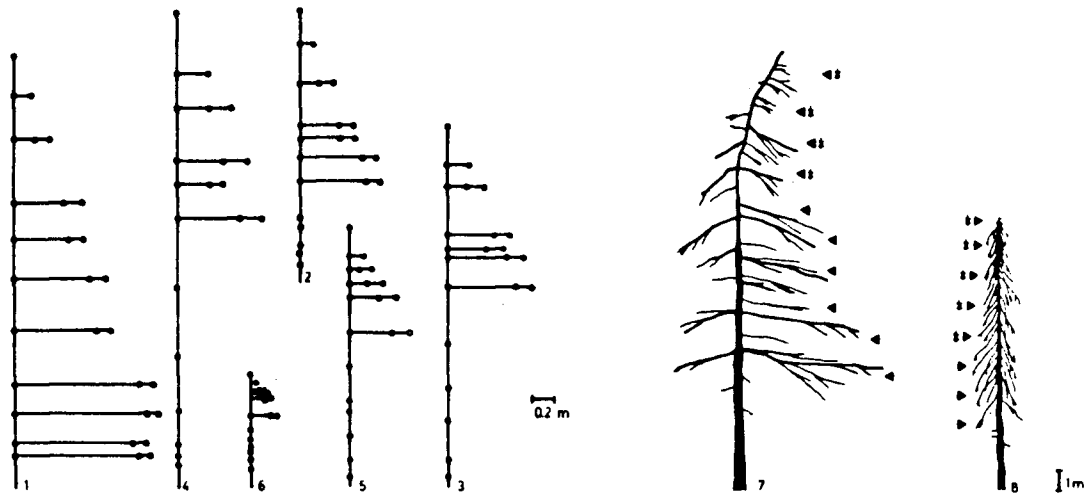
Including immature trees allows a test of whether inter-positional variation may be environmental or developmental. If variation is a result of environmental causes, then mature and immature trees would not be expected to display similar patterns of intra-individual variation. Including immature individuals also allows a comparison of their morphology and anatomy with that of mature trees and test whether, within the circumscription of a given taxon, there are substantial differences that could result from the age of the

trees.

The mature trees collected appeared similar in age, form, and edaphic disposition to neighbouring trees in the populations. The trees were sampled in late autumn before there had been severe loss of the current year's cone crop. The saplings sampled were growing at the Chilliwack River Nursery of the British Columbia Ministry of Forests (Appendix II: trees 71601, 71602, 71603, 71604, 71605, 71606). Relevant information concerning the height, age, form, and sampling positions of the individuals is given in Figure 8.

For examining the nature of intra-individual variation in the context of inter-individual variation, individual trees were included that were standards of P. engelmannii and P. sitchensis.

2.2 Analyses.

PCAs based upon correlation matrices of separate suites of variables were performed. Owing to the restricted number of samples available, combining separate suites of variables by averaging could not be used without invalidating the dimensionality constraints of PCA. All data submitted to PCA were first tested for independence of correlation coefficients. Where independence was accepted and PCA therefore not necessary, univariate analyses of the individual variables was performed.

Evaluating differences between various positions was based upon ANOVAs of original variables or component scores. The

ANOVA models used are given in Table 12. It should be noted
that owing to the paucity of materials, that there is no term
that refers to differences among taxa. The lack of samples
prevented a structured MVA, such as MANOVA and subsequent CVA,
from being performed; although such a structured MVA would have
been analytically appropriate.

Differences between positions in the canopy were examined
in two manners. Mahalanobis' D^2 distances between apical- and
basal-most positions were calculated as a means of comparing
these positions in the various trees. Although the sample sizes
available per position are suboptimal (Table 10), the behavior
of the sample size estimation of D^2 was such that such a
utilization of D^2 may suffice in giving an impression of the
general trend rather than specific detail. Preliminary
inspections of scatter plots of component scores against whorl
or position were also made to determine whether a general trend
were present in the data. If a trend were apparent, regression
was performed provided that dispersion of samples around the
regression line could be considered normally distributed
(Chatterjee and Price 1977).

Mahalanobis' D^2 distances were also calculated as a means
of determining overall similarity of the individual trees
sampled for inter-positional variation. The sample sizes
available per individual tree appeared (Table 10) to be adequate
for allowing such use D^2.

It was impossible to quantify intra-individual variation in
an inter-individual or inter-taxonmic context using a single

Table 12. ANOVA models used in assessing various aspects of intra-individual variation. y - variable values or component scores for a given sample; e - residual variation.

SOURCE	MODEL	TERMS	VARIABLE SUITE
ADVENTITIOUS/ WHORL	$y = A + e.$	A - branch position: adventitious whorl	TWIG MORPHOLOGY LEAF MORPHOLOGY LEAF ANATOMY
PRIMARY/ SECONDARY	$y = A + B(A) + e.$	A - branch order: primary secondary B(A) - branch within order.	TWIG MORPHOLOGY LEAF MORPHOLOGY LEAF ANATOMY
YEAR/ YEAR	$y = A + e.$	A - collection year	TWIG MORPHOLOGY LEAF MORPHOLOGY LEAF ANATOMY
INTER-POSITIONAL	$y = A + B(A) + e.$	A - tree B(A) - position in tree	TWIG MORPHOLOGY LEAF MORPHOLOGY LEAF ANATOMY
	$y = A + B(A) + C(AB) + e.$	A - tree B(A) - position in tree C(AB) - cone in position	CONE MORPHOLOGY

ANOVA as systematic sampling of all individuals could not be
undertaken. A comparison was made between two different ANOVAs
based on component scores from PCAs including and excluding the
source of intra-individual variation of interest. Differences
between these ANOVAs were assessed on the basis of the change in
the sums of squares. The exact nature of the ANOVAs are given
is Table 13. Without respect to the taxonomic circumscription
of the individual trees, suites of variables whose
intra-individual variation did not markedly decrease the amount
of inter-individual variation were to be preferred to those
suites that were drastically altered by the inter-individual
variation. It would be predicted that adding sources of

Table 13. ANOVA models used in assessing the contribution of
intra-individual variation in the context of inter-individual
variation. y - variable value for component score for a given
sample; e - residual variation.

MODEL	TERMS	VARIABLE SUITES
y = A + e.	A - individual	TWIG MORPHOLOGY
		LEAF MORPHOLOGY
	or	CONE MORPHOLOGY
		LEAF ANATOMY
	A - taxa:	
	P. sitchensis	
	P. engelmannii	

intra-individual variation should decrease the amount of
variation due to hypothesized inter-individual sources. Where
possible, specifying the ANOVA in terms of individuals, rather
than taxa, prevented the unwarranted imposition and reification
of a priori taxonomic hypotheses.

To serve as an heuristic appreciation of intra-individual variation, ordinations of component scores were made to provide an heuristic appreciation for the intra-individual variation in such an inter-individual context. In those analyses that compared separate PCAs of separate trees, the scales of the ordinate and the abscissa were determined by the largest dispersion of samples over all separate analyses. Such ordination facilitates comparison among individual analyses.

3. Results.

3.1 Adventitious versus whorl primary branches.

The sample sizes (Table 10) were not sufficient to perform a reliable PCA. Further, tests of the independence of correlation coefficients indicated that there was no significant co-variation among the groups of variables in the various $\underline{R}$s, indicating that all variables could be considered independent, thus making PCA unnecessary.

ANOVAs, Table 14, indicated that only the average length of the resin cysts (RESCYLEN) could be considered significantly different between whorl and adventitious branches - those of the whorl branches being longer (2.6 mm) than those of the adventitious branches (1.2 mm). Bartlett's test of the equality of variances did not indicate heteroscedacity of variances among the two positions.

With the exception of the single significant difference,

Table 14. ANOVAs of individual variables comparing adventitious and whorl primary branches of P. engelmannii. *, significant F-values @ p ≤ 0.01. Other symbology given in Table 12.

VARIABLES SUITE	%SS$_A$	VARIABLE SUITE	%SS$_A$
LEAF MORPHOLOGY (n=10)		LEAF ANATOMY (n=10)	
NEEDLEN	38.38	NEEDWID	7.93
ABXSTOM	0.50	NEEDEP	7.49
ADXSTOM	0.67	ABXANG	20.41
RESCYNO	9.09	ADXANG	2.11
RESCYLOC	0.58	CENCYWID	2.14
RESCYLEN	53.68*	CENCYLAT	22.17
$\bar{x}$	17.58	CENCYABX	2.72
		CENCYADX	20.29
TWIG MORPHOLOGY (n=10)		ENDONUM	26.60
PULVLEN	1.45	PHLEND	18.55
TIPWID	0.00	XYLEND	9.35
TIPDEP	2.44	$\bar{x}$	12.71
PULVPUB	invariate		
$\bar{x}$	1.30		

TOTAL $\bar{x}$ 10.53

the average amount of variation resulting from differences between the two orders of branches for all suites of variables accounted for only about 10 percent of the total intra-individual variation – twice as large as the measurement repeatability (Table 2). As a group, leaf morphology variables provided the best separation of the two positions of branches. Twig morphology appeared to vary little with respect to branch position.

3.2 Primary versus secondary whorl branches.

ANOVAs, Table 15, indicated that differences between orders of branches, although significant, consistently accounted for less variation in the data than differences between individual branches. The variation attributed to differences between orders of branches was extracted primarly by the first component of the PCAs, an interpretation supported by ordinations in

Table 15. Multivariate apportionment of variation for separate variable
    suites due to differences between orders of branches. Abbreviation
    of PCAs and ANOVAs in Table 39, Appendix III. Symbols given in
    Table 12. Ordination of resultant component scores given in
    Figure 9.

VARIABLE SUITE	A	%SS (mva) B(A)	E
LEAF ANATOMY	18.37	35.32	46.31
LEAF MORPHOLOGY	7.67	36.97	55.36
TWIG MORPHOLOGY	33.42	44.95	21.65
$\bar{x}$ VEGETATIVE	19.82	39.08	41.11

Figure 9. Component correlations and mean values suggest that
variables measured on primary whorl branches were consistently
larger than those of the secondary branches. However, leaf
anatomy appears to vary in more than just size of variables as
evidenced by the very low and negative component correlations
for angles of the leaf surface (ABXANG, ADXANG). Differences
between the two orders of branches was most emphasized by twig
morphology.

Figure 9. Ordinations of first two components of PCAs of separate
    variable suites of whorl primary and secondary branches of
    P. sitchensis. Scores from PCA given in Table 39, Appendix III.
    Open circles - whorl primary branch; filled circles - whorl secondary
    branch. Glyphs represent individual samples.
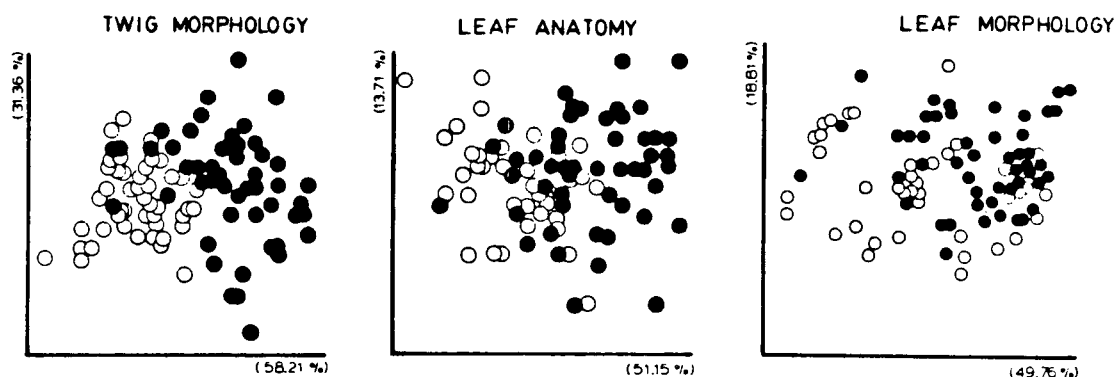
The total variation for all variables over all suites of

variables as a result of differences between branch orders was about 20 percent and that attributed to differences between branches within an order was nearly twice (i.e. 40%) as large. The difference between orders was twice as large as the mean difference between adventitious and whorl branches (Table 14).

With the exception of the twig morphology variable suite, intra-branch (residual) variation accounted for a much larger proportion of the total variation than any other hypothesized source of variation.

Ordinations of individual branch means (Fig. 9) showed no consistent relation between the secondary branch subtending a given primary (i.e. primary and secondary branches from the same whorl primary branch did not appear more similar than secondaries from other branches). The ordinations re-inforce the results obtained from ANOVAs of component scores (Table 15) that there was little separation between the two orders of branches, except in the case of twig morphology. Figure 9 also emphasizes that the variation among samples from secondary branches based on twig morphology were more variable than samples from primary branches.

3.3 Year to year variation.

The sample sizes were insufficient to allow a PCA (Table 10). Additionally, tests of the independence of correlation coefficients of $\underline{R}$ indicated that the pulvinus, leaf morphology, and cone morphology variable suites had no significant overall variation in the data, suggesting that

variables in these groups were independent.

One-way ANOVA (Table 16) tested whether some of the
variables distinguished between the two different years. The
results indicate that there were significant differences between
the years for only 7 variables: RESCYNO, PULVLEN, TIPWID,
NEEDWID, CENCYLAT, CONWID, AND SCALEN. The average amount of

Table 16. ANOVAs comparing year to year variation of variables in
P. engelmannii.

VARIABLES SUITE	%SS$_A$	VARIABLE SUITE	%SS$_A$
LEAF MORPHOLOGY (n=10)		LEAF ANATOMY (n=10)	
NEEDLEN	12.90	NEEDWID	59.37*
ABXSTOM	10.11	NEEDEP	13.45
ADXSTOM	4.00	ABXANG	3.80
RESCYNO	51.02*	ADXANG	7.40
RESCYLOC	38.33	CENCYWID	0.38
RESCYLEN	3.82	CENCYLAT	73.35*
$\bar{x}$	20.03	CENCYABX	0.26
		CENCYADX	26.44
		ENDONUM	0.00
TWIG MORPHOLOGY (n=10)		PHLEND	11.36
PULVLEN	81.09*	XYLEND	5.77
TIPWID	55.17*	$\bar{x}$	18.33
TIPDEP	7.44		
PULVPUB	invariate	CONE MORPHOLOGY (n=34)	
$\bar{x}$	47.90	CONLEN	1.50
		CONWID	46.04*
		SCALEN	27.54*
		SCALWID	2.35
		SCALTAP	2.11
		WINGWID	2.82
		WINGTAP	1.34
		FREESCAL	3.27
		BRACTLEN	0.84
		BRACTWID	3.10
		BRACTAP	0.17
		$\bar{x}$	31.01

TOTAL $\bar{x}$ 29.34

variation between years accounted for 30 percent of the total
intra-individual variation. This amount of intra-individual
variation is, in comparison with measurement repeatability,
branch position (11%), and branch order (20%) a large source of

variation. However, it is not as large a source of intra-individual variation as within increment variation (Table 15). Examination of mean variable values for the two years of growth suggested that there were no consistent trends (i.e. one year did not have consistently larger variable values than the other, even those variables which were significantly different over the two years).

3.4 Inter-positional variation.

Overall eigen-structure indicated significant variation amongst all variables in each variable suite. ANOVA of component scores indicated that the largest single source of variation was attributed to inter-individual differences (Table 17). However, considering all intra-individual sources of

Table 17. Multivariate apportionment of variation for separate variable suites due to differences between positions of branches. Abbreviation of PCAs and ANOVAs in Table 40, Appendix III. Symbols given in Table 12. Ordinations of resultant component scores given in Figure 10.

VARIABLE SUITE	A	%SS (mva) B(A)	C(AB)	E
LEAF ANATOMY	55.30	22.90		21.57
LEAF MORPHOLOGY	44.96	23.90		31.14
TWIG MORPHOLOGY	46.23	46.59		7.18
CONE MORPHOLOGY	27.64	11.91	42.97	17.49
$\bar{x}$ VEGETATIVE	48.91	31.13		19.96
$\bar{x}$ TOTAL	43.59	26.33		30.09

variation, only leaf anatomy had an inter-individual variation that exceeded intra-individual. The largest variation was hypothesized to be the result of inter-positional effects

manifest by twig morphology. The largest source of variation of cone morphology (Table 17) was attributed to differences between cones at a single position in the canopy. Differences between cones from different whorls provided the second largest source of variation.

Mahalanobis' D^2 distances between apical- and basal-most branches (Table 18) indicate that there were greater differences in leaf anatomy within mature trees than immature trees. The

Table 18. Mahalanobis' D^2 distances between apical- and basal-most branches and cones of P. engelmannii and P. sitchensis. Diagonal elements (+), intra-individual distances between apical- and basal-most branches. Lower off-diagonal elements, distances between basal branches. Upper off-diagonal elements, distances between apical branches. Is, immature P. sitchensis (T1 - T6); Ms, mature P. sitchensis (T7); Me, mature P. engelmannii (T8). P.engelmannii and P. sitchensis. Note: D^2 values could not be calculated for twig morphology due to matrix singularity.

LEAF ANATOMY

	Is	Ms	Me
Is	3.10	34.50	77.82
Ms	5.23	41.98	44.23
Me	205.92	199.41	73.90

LEAF MORPHOLOGY

	Is	Ms	Me
Is	10.81	18.82	18.04
Ms	2.89	20.53	19.28
Me	20.12	11.83	2.39

CONE MORPHOLOGY

	Ms	Me
Ms	43.76	65.30
Me	43.47	8.80

individual of P. engelmannii was decidedly different from both the mature and immature P. sitchensis , but only with respect to

leaf anatomy.

These distances also indicate that there were greater differences between the basal branches than between the apical branches.   Leaves from the basal most branches of P. engelmannii were less similar to those of P. sitchensis than were leaves from the apical most branches.Differences between the two taxa were most emphasized by comparing leaf anatomy of basal branches.   Inter-individual differences of both taxa were most conspicuous when apical-most positions were compared on the basis of leaf and cone morphology.   Inter-individual differences in P. sitchensis are most obvious when comparing apical branches.

Figure 10, indicates that there exists a discrete difference between the apical- and basal-most branches. Further, Figure 10 indicates that there is consistently a greater dispersion amongst the apical-most needles than among the basal-most needles.   This pattern is evident in both mature and immature trees.

The overall assessment of differences based on Mahalanobis' D^2 is given in Table 19.   These results indicate that the largest inter-individual differences exist between the single individual of P. engelmannii and all individuals of P. sitchensis .   By contrast, the differences among individuals of P. sitchensis are trivial and there appears to be no difference resulting from the age except, perhaps, in considering leaf morphology.   That is, the mature individual of P. sitchensis is no less different from immature trees than

Figure 10. Ordinations of first two components of PCAs of separate
variable suites of whorl branch positions from P. engelmannii and
P. sitchensis. Scores from PCAs given in Table 40, Appendix III.
Open glyphs, apical-most branches; filled glyphs, basal-most
positions. Circles - P. sitchensis; triangles - P. engelmannii.
Intervening sampled positions omitted from ordination to emphasize
polarity. Glyphs represent individual samples.
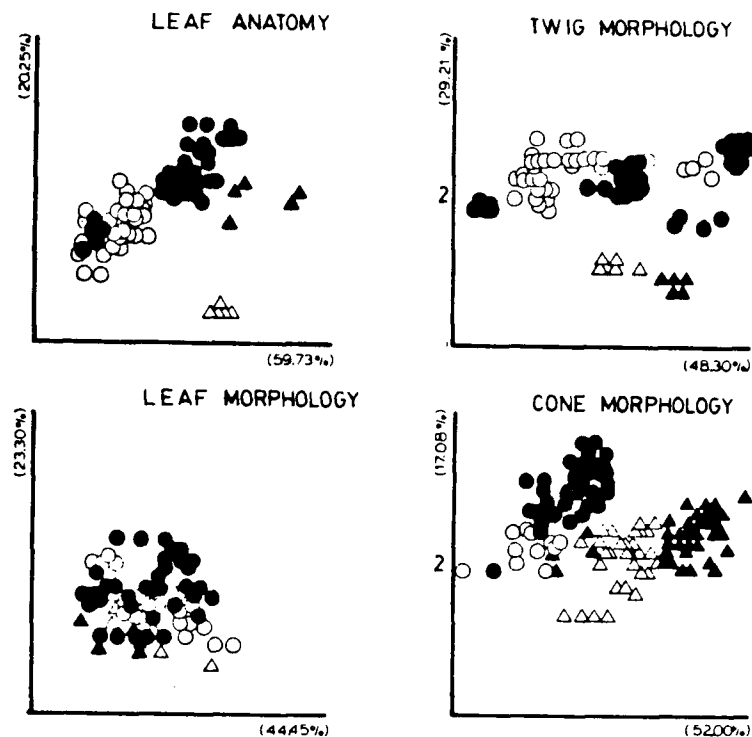
differences between individual immature trees.

With respect to branch pubescence, it was observed that the

apical-most branches of the sampled mature individual of

P. sitchensis had pubescent pulvinii. This same situation

existed for the apical-most branches from a putative

P. sitchensis (Tree 532, Appendix II). Similarly, pubescent

branches were also observed on an individual of P. glauca (Tree

70301, Appendix II) from the Ottawa Valley. Observations made

on fallen branches from other trees in the study area suggested

that this situation was more frequent than the samples available

Table 19. Average Mahalanobis' D² distances between individual trees in Table 18.
   D² values below diagonal (---.--) - distances between individual trees.
   Symbols given in Figure 8 and Table 18.

LEAF ANATOMY

		T1	T2	T3	T4	T5	T6	T7	T8
Is	T1	---.--							
	T2	3.06	---.--						
	T3	5.61	4.22	---.--					
	T4	7.66	3.59	7.61	---.--				
	T5	6.88	2.85	9.42	2.39	---.--			
	T6	10.01	6.33	11.69	11.94	7.18	---.--		
Ms	T7	6.99	5.74	13.23	11.61	5.81	8.55	---.--	
Me	T8	56.38	51.49	47.06	66.23	56.28	59.18	53.77	---.--

LEAF MORPHOLOGY

		T1	T2	T3	T4	T5	T6	T7	T8
Is	T1	---.--							
	T2	5.88	---.--						
	T3	0.95	6.08	---.--					
	T4	2.18	6.02	0.87	---.--				
	T5	3.77	3.37	4.20	2.69	---.--			
	T6	11.66	6.88	9.41	6.62	7.68	---.--		
Ms	T7	20.77	19.84	22.40	22.24	15.14	22.16	---.--	
Me	T8	38.05	25.65	39.73	39.39	31.54	24.38	13.31	---.--

TWIG MORPHOLOGY

		T1	T2	T3	T4	T5	T6	T7	T8
Is	T1	---.--							
	T2	3.67	---.--						
	T3	3.16	0.56	---.--					
	T4	0.32	3.76	3.72	---.--				
	T5	1.24	2.83	1.59	1.38	---.--			
	T6	8.54	1.97	1.87	9.87	6.85	---.--		
Ms	T7	4.81	2.14	2.11	4.02	2.26	6.12	---.--	
Me	T8	88.95	90.41	87.61	88.02	83.54	95.99	71.46	---.--
		T1	T2	T3	T4	T5	T6	T7	T8

would suggest. In these situations where the apical branches were pubescent, the basal branches appeared glabrous.

As the PCA of all trees may have convoluted patterns of intra-individual variation, and the ANOVAs suggested significant differences between individual trees, separate PCAs were performed for each tree for each variable suite. The component scores from these PCAs were then examined by ANOVA (Table 20). The first component from each of these PCAs indicates that the largest source of variation was attributed to differences between whorl positions for twig morphology, leaf anatomy, and leaf morphology (averaging 74%, 53%, and 51% respectively over all trees). Inter-positional differences were less than intra-positional differences for cone morphology, averaging 17 percent over all trees. Intra-position cone morphology variation was much larger (83%) than inter-positional variation for any other variable suite.

The relative magnitude of the component correlations (Table 21) suggested that the first components were reflecting size and shape differences between samples. ANOVAs suggested that inter-branch differences generally exceeded intra-branch variation only for the first components. Examples of the type of variation shown by leaf anatomy are given in Figure 11 which emphasizes the striking variation within and between trees. An initial scatter of component scores against position or whorl suggested a common trend for each tree (Fig. 12). However as the variances of component scores for each position could not be considered equal, based on Bartlett's test, regression and

Table 20. Multivariate apportionment of variation for separate variable suites of separate trees due to whorl positions. Abbreviation of Table 41 in Appendix III. Symbols given in Table 12 and Figure 8. Ordinations of resultant component scores given in Figures 12 and 13.

VARIABLE SUITE		Is T1	T2	T3	%SS (mva) T4	T5	T6	Ms T7	Me T8	x̄
LEAF ANATOMY	A	67.89	53.39	60.72	67.82	53.21	35.16	59.05	29.90	53.39
	e	32.11	46.61	39.28	32.20	46.79	64.84	40.95	70.10	46.61
LEAF MORPHOLOGY	A	43.01	41.89	42.93	42.92	72.89	52 47	82.79	27.30	50.78
	e	56.69	58.11	57.07	57.08	27.11	47.53	17.21	72.70	49.23
TWIG MORPHOLOGY	A	94.25			96.55			74.84	30.90	74.14
	e	5.75			3.45			25.16	69.10	25.87
CONE MORPHOLOGY	A							24.85	8.92	16.89
	B(A)							62.72	63.87	63.30
	e							12.42	27.21	19.82
x̄ VEGETATIVE	A	68.38			69.10			72.22	29.07	59.44
	e	31.62			30.90			27.87	70.93	40.56
x̄ TOTAl	A							60.38	24.03	48.80
	e							39.63	75.97	51.20

Table 21. Correlations amongst component correlations for first components from PCAs in Table 20. *, correlations significant @ p ≤ 0.01. Other symbols as in Figure 8.

LEAF ANATOMY

		T1	T2	T3	T4	T5	T6	T7	T8
Is	T1	.---							
	T2	.599	.---						
	T3	.726*	.912*	.---					
	T4	.749*	.905*	.967*	.---				
	T5	.389	.849*	.754*	.704	.---			
	T6	.509	.863*	.722	.781*	.719	.---		
Ms	T7	.435	.808*	.827	.702	.847*	.516	.---	
Me	T8	.709	.689	.829	.847*	.550	.377	.611	.---

LEAF MORPHOLOGY

		T1	T2	T3	T4	T5	T6	T7	T8
Is	T1	.---							
	T2	-.671	.---						
	T3	.688	-.490	.---					
	T4	.924*	-.878	.562	.---				
	T5	.790	-.323	.884	.563	.---			
	T6	.975*	-.594	.751	.877	.831	.---		
Ms	T7	.955*	-.713	.763	.909	.837	.955*	.---	
Me	T8	.938*	-.774	.693	.941*	.758	.928*	.991*	.---

TWIG MORPHOLOGY

		T1	T4	T7	T8
Is	T1	.---			
	T4	.574	.---		
Ms	T7	.519	.519	.---	
Me	T8	.438	.438	.438	.---

Figure 11. Examples of intra-individual variation of leaf anatomy for some trees shown in Figure 8.
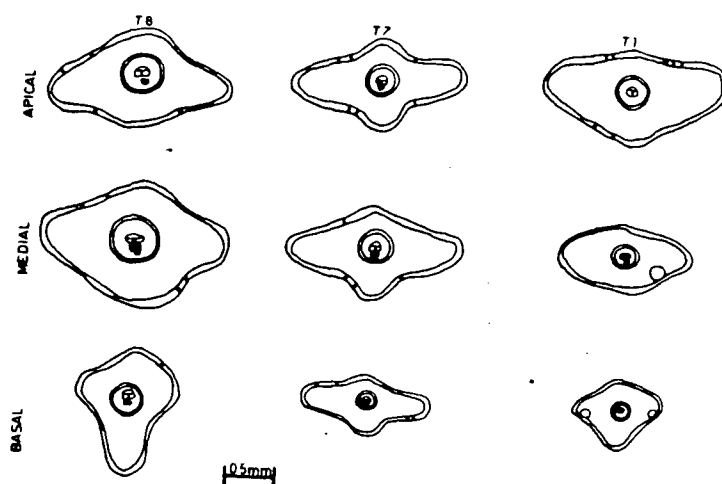
statistical comparison of slopes was not considered appropriate.

These diagrams (Fig. 12) further emphasize the continuous nature of variation in the trees. The diagrams also emphasize the similarity of intra-individual variation of all the individuals regardless of age with the exception of the necrotic and stunted individuals (Fig. 8: T5, T6). Table 21 presents correlations among the eigenvector-values from separate PCAs indicating a striking similarity in the contribution of leaf anatomy variables to the pattern of intra-individual pattern.

PCAs of individual trees and subsequent scatters of component scores indicated that variation inter-positional variation was the largest source of variation in each tree, except for P. engelmannii. Correlations amongst component correlations (Table 21) from PCAs in Table 20, suggest a general similarity of the variables contributing to the pattern of

Figure 12. Scatters of means and standard deviations of scores of first
components of PCAs for individual branches of individual trees
against whorl branch positions. Scores based on PCAs given in
Table 41, Appendix III. Symbols as in Figure 8. All first
components drawn to same scale.

LEAF ANATOMY

LEAF MORPHOLOGY

TWIG MORPHOLOGY
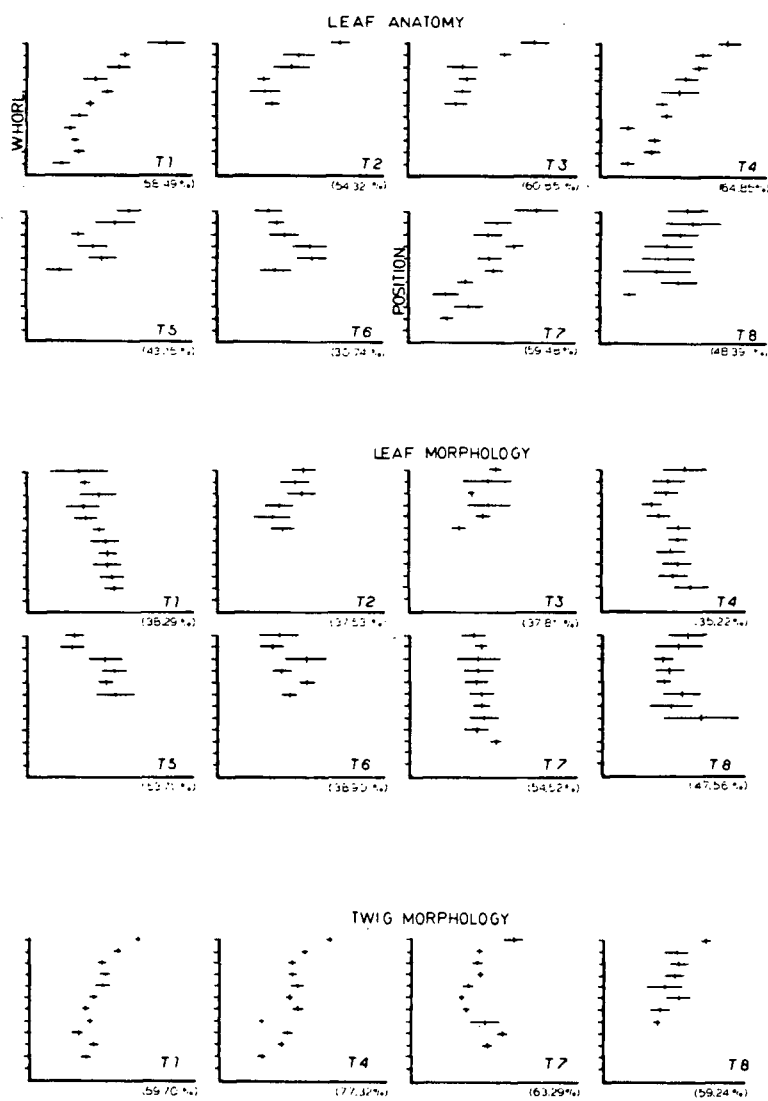
intra-individual variation amongst all trees. The component correlations indicated that the pattern of inter-positional variation of leaf anatomy of individals of P. sitchensis was, regardless of maturity, a result of the apical leaves being wider (NEEDWID) and deeper (NEEDEP) and having larger central cylinders (or measurements associated with the location of the central cylinder; CENCY....) than the more basal leaves. Variation among leaves of the individual of P. engelmannii was more dependent upon aspects of the central cylinder and vascular bundle than the variables contributing to the variation in P. sitchensis.

Unlike leaf anatomy, leaf and twig morphology, although showing significant differences between positions, did not show a consistent trend that was highly correlated with position in the canopy. There was no consistent trend in inter-whorl variation, except for leaf anatomy, that suggested that the more apically disposed leaves were more variable. Of the variable suites that were examined with PCA, twig morphology showed the least intra-position variation.

PCAs of cone morphology variation within the canopy of individual trees were also performed (Table 20). Although there was significant variation in the data, preliminary scatters of PCA component scores against position in the canopy did not appear to be related linearly as in the case of leaf anatomy. Figure 13 presents an ordination of the first two components from these separate PCAs, and indicates a virtual overlap amongst cones of apical- and basal-most cone bearing branches.
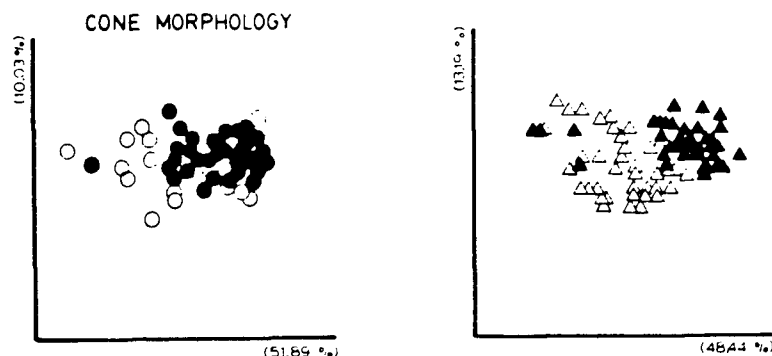
Like twig and leaf morphology, cone morphology variation of the
two trees were not significantly correlated (r=0.345).

3.5 Intra-individual variation in the context of
   inter-individual variation.

Without including sources of specific intra-individual
variation, all evaluation of correlation matrices indicated that
there was significant variation in the data (Table 22).   ANOVAs
(Table 22) suggested that the largest source of variation was
attributed to differences between individuals.   Eigen-vector
values for the components of the separate PCAs suggested that
the patterns of variation were significantly correlated.

Interjecting intra-individual variation only minimally
altered the results of ANOVA, suggesting that these
intra-individual sources of variation were not highly
significant in an inter-individual context, thereby
corroborating the conclusion from earlier analyses.   Adding

Table 22. Multivariate apportionment of variation for separate variable suites due to differences between individual trees or taxa, emphasizing different sources of intra-individual variation in an inter-individual context. Abbreviation of the PCAs and ANOVAs in Table 42, Appendix III. $\underline{WO}$ - without any other intra-individual variation besides intra-increment; $1°/2°$ - with primary and secondary orders of branching and branches within order; POS - with inter-positional variation; %WO - change from %SS $\underline{WO}$. Other symbols given in Table 13. Ordination of resultant component scores given in Figure 14.

| | | | %SS | (mva) | | |
| | | TAXA | | | INDIVIDUAL | |
VARIABLE SUITE	A	E	%WO	A	E	%WO
LEAF ANATOMY $\underline{WO}$	31.87	68.13	0.0	87.72	12.82	0.0
$1°/2°$	36.49	63.51	-4.62	86.96	13.04	0.02
POS	30.27	69.27	1.14	79.89	20.11	7.29
LEAF MORPHOLOGY $\underline{WO}$	26.58	73.42	0.0	79.60	20.40	0.0
$1°/2°$	21.80	78.20	4.78	75.52	24.48	4.08
POS	23.00	77.00	3.58	77.09	22.91	2.51
TWIG MORPHOLOGY $\underline{WO}$	35.42	64.58	0.0	93.68	6.32	0.0
$1°/2°$	35.05	64.95	0.37	90.63	9.37	3.05
POS	31.27	68.73	4.15	87.41	12.59	6.27
CONE MORPHOLOGY $\underline{WO}$	19.02	80.98	0.0	67.73	32.27	0.0
$\overline{POS}$	17.87	82.13	1.15	63.50	35.50	3.23
x VEGETATIVE $\underline{WO}$	31.29	68.71	0.0	87.00	13.00	0.0
$1°/2°$	31.11	68.89	0.18	84.37	15.63	2.63
POS	28.18	71.82	-3.11	81.46	18.54	5.54
x TOTAL $\underline{WO}$	28.22	71.78	0.0	82.18	17.82	0.0
$\overline{POS}$	25.60	74.40	2.62	76.97	23.03	5.18

intra-individual sources of variation generally decreased the amount of variation between individuals. Such a decrease is expected. However, for leaf anatomy the variation between hypothesized taxa increased suggesting that the inclusion of intra-individual sources of variation could alter a taxonomic hypothesis.

These ANOVAs suggest that differences between taxa are much less than differences between individuals. Further, the inter-individual and inter-taxonomic differentiation was lower for cone morphology than for the other variable suites.

Ordinations, Figure 14, corroborate the impression of small

inter-taxonomic differences. Indeed, bearing in mind that the open glyphs represent means of individual trees (i.e. on average 18% of the total varition in the data has been removed from the ordination during the calculations of means) there is a large degree of overlap between point-swarms assignable to the two taxa.

The results presented in Tables 14 to 17 have been averaged and summarized in Figure 15. This summarization assumes that the three hypothesized sources of variation are independent. Compared to the other hypothesized sources of intra-individual variation, the variation within a single increment is indicated as being larger than both the specified inter-increment sources of variation.

4. Discussion.

Other sources of intra-individual variation are possible to investigate and, perhaps, should have been investigated. Consideration of the size and pattern of just these few sources of intra-individual variation leads to considerations concerning how these patterns may affect the understanding and interpretation of patterns of inter-individual variation. Such consideration of the patterns of intra-individual variation calls into question the assumed efficacy of extrinsic processes in accounting for intra-crown patterns of variation and the development of crown form.

As these results are based on only a few trees and a few positions, the conclusions must be regarded as being more

Figure 14. Ordinations of first two components of PCAs of separate
variable suites for intra-individual variation in the context of
inter-individual variation. Scores based on PCAs given in Table 42,
Appendix III. Open glyphs represent means of individual trees; solid
glyphs are individual samples from a single tree for the source of
variation indicated. Other glyphs as in Figure 10.

LEAF MORPHOLOGY

TWIG MORPHOLOGY

LEAF ANATOMY

CONE MORPHOLOGY
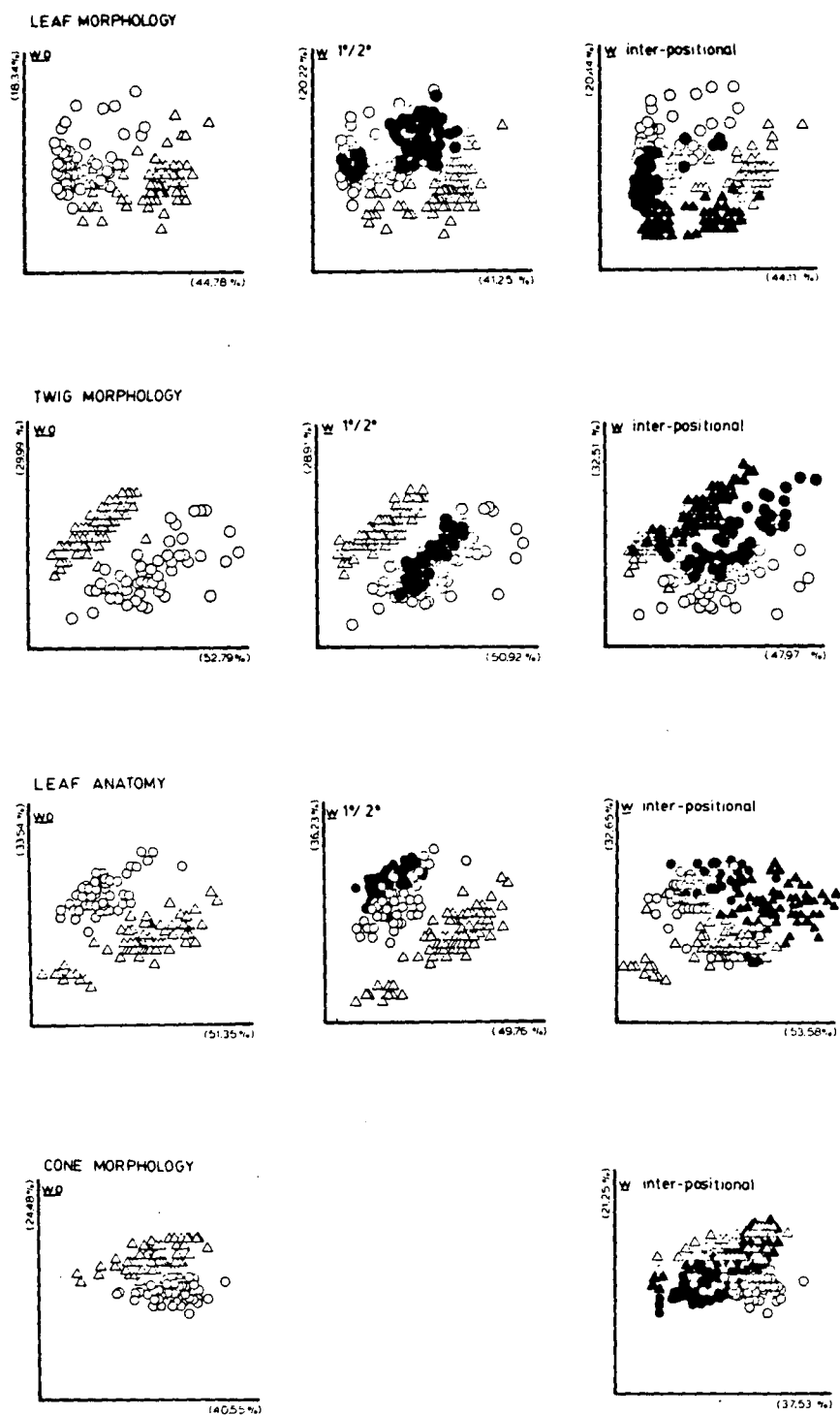
Figure 15. Summary of partioning of sources of intra-individual
variation. Summary based on total %SS (mva) Tables 14 to 17.
Stipled border of pie indicates region that is referred to in all
subsequent analyses as "intra-individual variation".
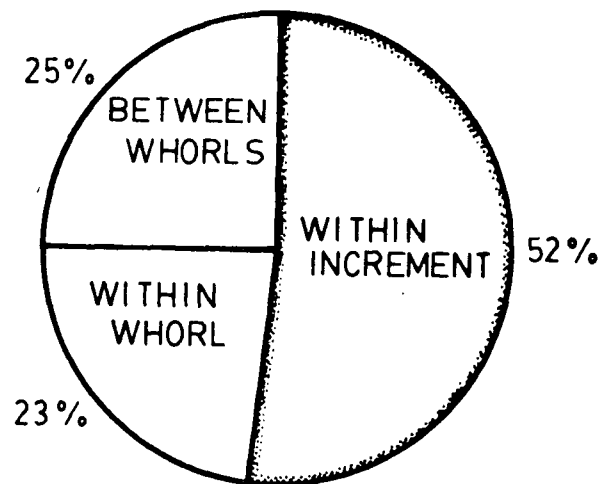
tentative than conclusive in nature. Regardless, these results

suggest the need for new research directions and approaches to

research in seeking to understand the integration of

developmental, ecological and evolutionary processes. As

forestry interests become increasingly concerned with

physiological and yield variables (Campbell 1975), particularly

phenology (Dietrichson 1964), investigations of the

developmental assumptions underlying these variables (Burley

1965; Campbell 1974; Rehfeldt and Lester 1969; Rehfeldt 1983;

and Cannell, et al. 1976) should be undertaken.

4.1 Sampling implications.

These results suggest that, in <u>Picea</u>, provided that the sampling of vegetative materials is restricted to the lower branches of individuals, there should not be a great deal of difference as to whether a whorl or adventitious branch is sampled. Further, the order of branching and year of collection may be unimportant to understanding inter-individual variation. However, as these estimates are sample and variable specific, it seems appropriate to suggest that extending sampling and increasing the present sample sizes and making critical observations on other aspects of crown form may well uncover previously unreported and significant sources and patterns of intra-individual variation. Where obvious environmental and developmental differences between positions in the canopy appear to exist, it would seem advisable to note these features and to take them into consideration when making interpretations.

The results suggest three specific situations in which sources of intra-individual variation should be taken into consideration when examining patterns of inter-individual variation and deriving inferences. First, where patterns of inter-individual variation based on leaf morphology are strongly correlated with resin cyst lengths (RESCYLEN), then the disposition of samples with respect to whorl or adventitious branches should be taken into consideration. Second, anomalies in inter-individual variation based on twig morphology might be explainable by the order of branch sampled. Third, where collections have been made over several years, inter-individual

variation of twig morphology could reflect differences in the year of collection. Similarly, patterns of inter-individual variation based on cone morphology that are strongly correlated with cone width (CONWID) should be examined for artifacts created by the year of collections.

The lack of discrete differences between juvenile and mature individuals of P. sitchensis (Table 21) suggests that, for the ages and environmental conditions sampled here, all ages of individuals could be used when examining patterns of inter-individual variation. The situation remains unclear with respect to P. engelmannii owing to a lack of immature samples. Not withstanding the observations of age-related variation demonstrated in other species of Picea (Lindquist 1948; Funsch 1975) and the observations reported in Chapter II with respect to pubescence and needle morphology, the analyses presented here indicate that age-related differences are not especially large. However they do differ in intra-individual variation - mature trees are more variable than immature. With respect to the variables examined here, in an inter-individual context, age-related variation appears to be a trivial source of variation.

The demonstrated lack of identifiable pattern of intra-individual variation of cone morphology suggests that the assumption (Chapt. II) that cone collections represent a random collection from the crown is not necessary. The data presented suggest that disposition of cones in the tree will probably not be of serious consequence in understanding patterns of

inter-individual variation.

On an inter-individual note, considering that the trees used in this analysis represent standards of the two taxa, and probably represent the most morphologically and anatomically polarized data available, the discreteness of the two taxa requires comment. That intra-individual sources of variation generally exceed inter-individual sources of variation (Table 17) is a somewhat unexpected result considering that these individuals supposedly represent two taxa. The individuals in question are separated by 6° longitude and 1400m elevation. Further, inter-specific variation is much less than inter-individual variation (Table 22) suggesting that the points raised here with respect to the pattern and degree of intra-individual variation should be taken into careful consideration when exploring patterns of inter-individual variation. This opinion is further re-inforced upon considering the spread of samples from individual trees in these ordinations (Fig. 14).

These results question the paleobotanical significance of the findings of macrofossils of P. engelmannii in the Puget lowlands (Barnosky 1981). This reported finding of P. engelmannii could simply be of needles from the upper canopy of P. sitchensis rather than needles of P. engelmannii. Other findings of Picea macro-fossils (e.g. Hills and Ogilvie 1970; see also citations in Critchfield 1984) should be carefully re-examined in light of these findings. Wilson (1963) echoes these same remarks with respect to microfossils.

These results on inter-specific variation contradict those
of other researchers (Garman 1957; Roche 1969; Daubenmire 1968;
Klinka, et al. 1982). The values presented in Table 22 suggest
that intra-individual variation may be as large as
inter-specific variation. This observation of the relative size
of inter-specific and intra-individual variation lends support
to the incorporation of information about intra-individual
variation into research on trans-individual sources of
variation. The demonstration of smaller differences between
taxa based on cone morphology as compared to vegetative
variables (Table 22) suggests that the conclusion of previous
work relying primarily on aspects of cone morphology (Coupé, et
al. 1982; Strong 1978; Roche 1969; Critchfield 1984; Horton
1959) should be re-considered. These conclusions and
considerations have been integrated into subsequent
interpretations of patterns of inter-individual variation.

4.2 Crown form morphogenesis.

The results presented here support those of previous
reports with respect to the significance between orders and
positions of branches in the canopy. If physiological
characteristics are strongly related to the patterns of
morphological variation shown here, then, even if they are as
slight as reported here, when extrapolated for the entire volume
of the living canopy of an individual tree these differences
could prove to be highly significant and especially relevant in
understanding the physiological maintenance of individual trees.

The morphological and anatomical variation shown here may also be important in understanding the nature of selective insect and fungal infestation.

Explanations for the observed consistency of larger variable values on primary branches and apical-most canopy positions could be ascribed to growth regulation associated with apical dominance. The high degree of variation attributed to differences between branches within an order could result from the local environment (i.e. direction, shading, surrounding vegetation, insect or physical damage). The observation of discrete differences between the apical- and basal-most branches suggests the manifestation of environmental variation described as "sun and shade" morphology. However, both mature and immature trees show the same pattern of clinal intra-canopy variation, thus suggesting that the pattern may not be caused by environmental factors. In this regard it is worth pointing out that, owing to the perennial duration of the leaves in Picea, that the leaf that appears today in the sun will, eventually, be in the shade. The discrete differences between apical- and basal-most branches must be regarded as a sampling artifact caused by sampling opposite poles of a continuum.

Figure 12 and Table 20 indicate a high degree of similarity of patterns of intra-individual variation over a small but diverse group of individaul trees in markedly different environments. Such an observation is unexpected if extrinsic controls are regarded as being important to tree form and intra-crown variation. Further the uniformity of the pattern of

intra-individual variation suggests similar controls. It is interesting to note that the maintenance of this uniformity in pattern appears to be affected by the vigour of the individual tree. These results suggest that, in P. sitchensis and P. engelmannii, crown form and intra-crown variation may be the result, primarily, of developmental as opposed to environmental processes. These results suggest that growth and development of saplings is under the same sort of developmental control as in mature trees although not to the same degree of intra-crown differentiation. Such suggestions lead directly to considering how known physiological processes associated with growth regulation can account for the continued co-ordinated and predictable growth, physiology, and development in such large, architecturally complex organisms as Picea. The known physiological processes may be adequate in addressing the development of young trees, however the co-ordination of growth and development in trees reaching over 30m in height remains enigmatic.

In support of the aforementioned necessity for an integration of developmental and evolutionary studies, are the results dealing with the assessment of inter-individual similarity based upon whether samples from apical or basal branches are examined. Similar observations have been made by Ogilvie and von Rudloff (1968) concerning the similarity of intra-crown variation of P. engelmannii to elevational variation. Stover (1944) cites a similarity of intra-crown variation of P. engelamnnii that corresponds to edaphic variation. The same applies for the observation made here and

reported elsewhere by Daubenmire (1968, 1974) with respect to the appearance of pubescent and glabrous branches on the same individuals well removed from possible sympatry with other pubescent species of Picea (e.g. P. engelmannii, P. mariana, or P. rubens). These results hint at shared and derived developmental differences between taxa that, instead of being expressed throughout the growth and development of an individual, are only manifest at particular stages during growth and then only at given positions. It is worth noting the similarity of the situation reported here with that reported for P. abies by Lindquist (1948).

4.3 Further research.

Having presented a thumbnail sketch of patterns of intra-individual variation in Picea it seems appropriate to suggest some direction for future research dealing with intra-individual variation. Specifically: research directed at exploring the dynamics and inter-relations of these sources of variation through the development and growth of individual trees; and, systematic sampling of these sources of intra-individual variation in an inter-individual and inter-taxonomic context. Tomlinson (1982) suggests such an approach is essential for understanding the form and variability of form in trees. This same suggestion has been made by Norman and Jarvis (1974) with respect to physiological variation. Riding (1976) provides an example with practical application in grafting programmes.

Dealing first with the dynamics of intra-individual variation, one would predict increased variability for more recently derived portions of the canopy than in older portions (Maze, et al. 1984). In fact, this hypothesis appears to have been upheld here, at least for leaf anatomy (Fig. 10) where there is increasing intra-individual variation with the age of the tree. Especially important in this regard would be research directed at unravelling the inter-dependence of position, age, and order with respect to growth and development of the canopy of individual trees. Such a study would address directly the growth and development of crown form variation and would provide a valuable extension of the dynamics described by Maillette (1982) and others, (Rehfeldt and Wykoff 1981; Namkoong, et al. 1972; Namkoong and Conkle 1976; Nicholls 1967) and the static descriptions of Fraser (Fraser, et al. 1964; Fraser and McGuire 1969; Fraser 1976). The changing proportion of sources of intra-individual variation over the course of development might be important to understanding the controls of this process. Such a study would require whole tree, systematic sampling with careful mapping of sampling locations, ages, and orders.

Extending a study, such as that outlined above, to several different populations of, say, several taxa, could be used to derive inferences concerning the integration of development in evolutionary processes. Additionally, as interest in such a study would be in intra-individual variation, variables in addition to those measured here might also be considered.

Another area of research, partially allied to that discussed above, is the matter of age-related variation. The issue of age-related variation is central to the inferences made concerning the physiology of establishing seedlings and any resultant selection. Age related variation has been addressed in several species of _Abies_ in the context of the differentiation of juvenile from mature populations (Maze, _et al_. 1981; Maze and Parker 1983). However, it should be pointed out that in these studies the effect of age-related variation and selection may not have been adequately separated. The apparently anomalous results of these studies of increasing variability with age could be simply a consequence of age-related variation rather than genetic differentiation between generations. Age-related variation is well known in _Juniperus_ (e.g. _Juniperus scopulorum_ Sarg.) as well as in other woody plants (Wareing and Phillips 1981; Zimmerman and Brown 1971; Kramer and Kozlowski 1979) and a truly morphogenetic study of age-related variation would have to involve sequential sampling of the same individuals over the course of development through to sexual maturity of the organism. In _Picea_ such a study would require many years. The development in conifers and _Picea_ have all been based on static analysis of crown form, a dynamic study may prove useful in understanding the perceptions of patterns of variation, as well it would provide information regarding the morphogenetic explanation for these patterns. Such a study may be especially important in understanding the degree that cumulative effects are responsible for crown form and examine the conformity of these descriptions with respect to

hypothesized models (Honda 1971; McMahon and Kroneuer 1976;

Fisher and Honda 1979a; Baker, et al. 1973) and reported

variations (Fisher and Hibbs 1982; Hibbs 1981).

IV. INTER-INDIVIDUAL VARIATION: TAXONOMIC CIRCUMSCRIPTION.

1. Introduction.

As P. engelmannii and P. sitchensis do not generally exhibit natural cloning (however see Cooper (1931) regarding layering in P. sitchensis), phenotypic differences between individuals are a function of genetic differences as well as developmental and environmental differences. Except for identical twins, all individuals are genetically unique. Specifically, we are interested in whether there are analytically emergent, trans-individual levels of variation that correspond to a priori genecological, populational, or taxonomic hypotheses: generations, ecotypes, populations, and species - P. engelmannii and P. sitchensis. By analytically emergent, reference is here made to examining for and detecting hypothesized sources of variation rather than a priori imposition of these hypotheses on the data. Good examples of the analytic emergence of a trans-individual source of variation are provided by Campbell and Dearn (1980) and Wells, et al. (1977).

If the emergence of trans-individual sources of variation can be demonstrated, then they require quantification and subsequent explanation. Quantification and explanation for hypothesized sources of variation without examining the validity of these hypotheses may bias conclusions regarding these levels of variation. Indeed, tendering explanations for sources of variation more conceptual than real may lead to unwarranted

reification and misrepresentation of biological reality. Burley
(1965a) and Langlett (1959,1962,1963) point out that a name
(i.e. a taxonomic hypothesis) confers a false sense of
importance on a named taxonomic group (hypothesis) and
automatically imparts an impression of homogeneity within and
heterogeneity between groups, or that there is more variability
between than within groups. Intra-individual, or developmental,
variation provides the scale against which patterns and scales
of trans-individual variation are compared. The intent of this
chapter is to examine the validity of the taxonomic hypothesis
of two taxa, as the acceptance of such a taxonomy will determine
the circumscription of the subspecific levels of
inter-individual variation.

For example, quantification and explanation for population
variation in a taxon that lacks genecological structure of
prevalent, selected genotype(s) may lead to erroneous
conclusions regarding explanation for the observed variation
between groups of sympatric individuals. Further, in a species
where a large number of individuals are not part of identifiable
populations, such as P. sitchensis, the tendering of
explanations based on populational assumptions would be
inappropriate. Similarly, quantification and explanations for
population variation in a poorly defined or polymorphic taxon
that has been subjected to arbitrary nomenclatural splitting may
lead to erroneous conclusions about that taxon unless the nature
of population variation in geographically juxtaposed and
sympatric "taxa" is also considered.

Such examples are especially easy to envisage for the two
taxa being investigated here. The reported lack of a pronounced
latitudinal trend in populations of P. sitchensis (Lewis and
Lines 1976) may serve as a convenient case in point. The
perceived narrow edaphic and geographic range of P. sitchensis
along a lengthy latitudinal range suggests that there should be
a pronounced latitudinal variation (Wright 1976). Such
latitudinal variation has been demonstrated by a number of
workers (see Ching and Sziklai 1978b; O'Driscoll 1976b).
However, as mentioned in previous chapters, the actual nature of
"populations" are somewhat different from expectations - perhaps
accounting for the lack of a pronounced trend. Additionally,
the reported hybridization of P. sitchensis with P. glauca
(Little 1953[1]; Daubenmire 1968; Roche 1969; Copes and Beckwith
1977), may serve to obscure the expected trend in variation or
suggest discontinuities in variation. By comparison the
variation of P. engelmannii has generally been related to
elevation (Habeck and Weaver 1969; Ogilvie and von Rudloff 1968;
Horton 1959; Garman 1957; La Roi and Dugle 1968).

If trans-individual sources of variation corresponding to
the two hypothesized taxa are indeed emergent, then the question
of potential natural hybridization needs to be addressed. The
results presented in Chapter III (Table 22) indicated that the
recognition of hybrids may be difficult as differences between
the two taxa are smaller than differences between trees.

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[1] Hultén (1968) considers this report to be based on a hybrid
between P. sitchensis and P. mariana rather than P. glauca.

Similarly, if these hypothesized trans-individual sources of variation are not manifest in an emergent manner, then the perceived discreteness of these taxa may be called into question. Further, such findings may indicate areas in which previous conclusions may have been deficient owing to acceptance of the questionable perception of discreteness of the two taxa.

Establishing whether there are such trans-individual levels of variation as generations, populations, discrete taxa, and hybrids between these taxa may, in themselves, offer explanations for the reported inconsistancy between expected and actual variation. Often populations and provenances are simply arbitrarily erected as being representative of individuals from a particular geographic area without reference to the edaphic and microgeographic variation or the actual phylogeny. Establishing the nature of these sources of variation provides a vital circumscription for the further detailed quantification and subsequent explanation. From a more practical viewpoint, documentation of such levels of variation may suggest alternate prescriptions and objectives in silvicultural and tree-breeding programmes.

2. Materials and methods.

2.1 Materials.

All of the trees sampled were used in examining trans-individual sources of variation (this included the samples of P. sitchensis from the Chilliwack River Nursery). Both

mature and immature trees were used as previous analyses
(Table 19) indicated little difference between the different
ages. In providing further inter-taxonomic comparison,
individuals of P. glauca were included in some analyses. To
assess the ability to recognize natural hybrids, samples of
known artifical hybridization were included in some analyses.
Additionally, artificial hybrids and samples of their maternal
parent were also compared.

2.2 Analyses.

The primary analytic technqiue was PCA. PCA respects the
unstructured form of the hypothesis being tested (Burley and
Barrow 1972) and the available sample size (Table 10). This
analytic approach allows any trans-individual sources of
variation to be emergent rather than imposed a priori.
Including intra-individual variation in these analyses allows
any emergent trans-individual source of variation to be assessed
relative to variation that is more intra-individual in nature
(i.e. developmental rather than genetic). Pragmatically, if
trans-individual sources of variation are indeed emergent, then
it would be worthwhile to be able to assign individuals to these
sources. The assignment of a given individual to a hypothesized
taxon is dependent upon intra-individual variation. Although
the inclusion of intra-individual variation could be
accommodated and would be appropriate for a structured MVA, the
available sample sizes mitigate against such an approach
(Table 10).

In quantifying trans-individual levels of variation of populations and taxa, ANOVA of PCAs based on separate variable suites of populations of standards were performed that used the nested design:

(MODEL 2.)

$$y = A + B(A) + C(AB) + e.$$

where A is an effect based on different taxa, B is the effect attributed to particular population in A, C is the effect of an individual in B, and e is intra-individual variation. This ANOVA was used in evaluating PCAs of P. engelmannii and P. sitchensis, as well as in evaluating PCAs that included populations of standards of P. glauca. The inclusion of a term for hypothesized populations serves a comparative purpose rather than a test on the differentiation among populations. It should be remembered that intra-individual variation refers to intra-increment variation, and that some of the populations are comparatively small.

Using just those standard samples that occurred in populations may unduly polarize the data leading to an inappropriate assessment of relationships of the two taxa. Additionally, it ignores a major source of variation in the data as a large number of trees are not present in recognizeable populations (Table 7). Increasing the number of samples representative of the two taxa without benefit of the circumscription by a population or restriction to extreme environmental and geographic locations may allow a less biased assessment of the differences between the two taxa.

A nested ANOVA:

$$Y = A + B(A) + e.$$

applied to PCAs of such data and compared to the previous ANOVAs on just populations of standards will indicate the degree of bias caused by dealing with recognizable morphological and environmental extremes. In this ANOVA, A is the effect attributed to different taxa, B the effect of different individuals in the taxa, and e is the intra-individual variation. As with populations of standards, this analysis was performed for P. engelmannii, P. sitchensis, and P. glauca.

Prior to addressing the question of naturally occurring hybrids, an evaluation of the morphology of known hybrids in the context of standards of both taxa was performed to determine whether the detection of natural hybridization was practical. This evaluation was made using an ordination from PCAs including populations of standards of P. engelmannii and P. sitchensis along with samples of known artificial hybrids. A further comparison of artificial hybrids and the putative hybrids was performed to determine the relation among hybrids without reference to parent taxa. These comparisons could be made only for the vegetative variable suites as the artificial hybrids were still immature and lacked cones. In this comparison between artificial and putative hybrids, the ANOVA used was that given in MODEL 3, except that A was the effect attributed to the different groups of hybrids: artificial or putative.

PCAs of separate variable suites for all trees were also performed. As well a PCA based on all 36 variables was also performed. For the analysis that used the artificial hybrids, all 21 vegetative variables were used. For those PCAs of all variables or all vegetative variables, values were averaged for each tree, thus ignoring intra-individual variation. Such averaging was necessary owing to the lack of an intra-individual one-to-one correspondance between variables of separate variable suites. The sample size was considered adequate to perform these PCAs on the basis of the sample size estimation technique outlined in Chapter II. ANOVAs based on these analyses had the hypothesized term attributed to individuals in MODEL 2 and MODEL 3 subsumed by the residual term as a result of averaging per tree.

3. Results.

3.1 Populations of standards.

3.1.1 P. engelmannii and P. sitchensis.

Polarizing the relation between P. engelmannii and P. sitchensis by examing only populations of standards indicated that there were significant, but small differences between the two taxa (Table 23). Figure 16 corroborates this impression of slight difference between the two taxa. For all variable suites, the amount of intra-taxonomic variation exceeds the inter-taxonomic variation. With the exception of cone morphology, inter-population variation accounts for less variation than inter-individual variation within populations. It should be noted (Table 23), that the largest amount of

Table 23. Multivariate apportionment of variation for separate
variable suites due to differences between taxa, populations, and
individual standards of P. engelmannii and P. sitchensis.
Abbreviation of PCAs and ANOVAs in Table 43, Appendix III. Symbols
given in MODEL 2. Ordination of resultant component scores given in
Figure 16.

VARIABLE SUITE	A	%SS (mva) B(A)	C(AB)	E
LEAF ANATOMY	29.21	24.49	33.61	12.69
LEAF MORPHOLOGY	29.09	16.16	33.50	21.26
TWIG MORPHOLOGY	41.81	16.74	36.84	4.62
CONE MORPHOLOGY	20.79	27.70	20.35	31.14
TOTAL	31.54	27.14	-	41.32
x VEGETATIVE	33.37	19.13	34.65	12.86

intra-individual variation is attributed to cone morphology and
leaf morphology and exceeds the corresponding variation between
taxa. The smallest amount of intra-individual variation is
attributed to twig morphology. Generally, there is more
variation between individual trees within a population than
between populations or between hypothesized taxa. ANOVAs of
separate variables in Table 23 indicated that there were only
six variables that had an inter-taxonomic variation that
exceeded intra-taxonomic variation (ABXANG, CENCYABX, ADXSTOM,
PULVPUB, BRACTLEN, BRACTAP). The diversity of climatic,
environmental, and geographic variation of these samples should
be considered in appreciating these results.

Ignoring intra-individual variation for all 36 variables
emphasized the distinction between the two taxa (Fig. 16).
However, it should be noted that as a result of the averaging by
tree that 17 percent of the total variation has been removed.
As Figure 16 illustrates, the primary difference between
ordinations of separate variable suites and that based on all
variables is one of rotation of co-ordinate axes rather than the

Figure 16. Ordinations of first two components of PCAs of separate
variable suites for populations of standards of P. engelmannii and
P. sitchensis. Scores based on PCAs given in Table 43, Appendix III.
Glyphs represent means for individual trees. Glyphs as in Figure 10.
Not all individual trees could be plotted.
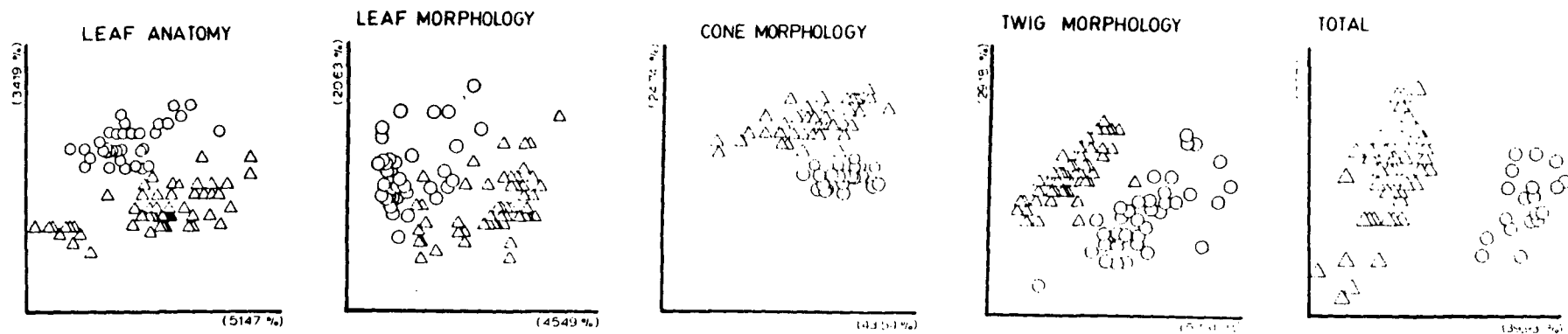
emergence of any fundamental new pattern.

Based upon the component correlations of the components which account for the largest difference between the hypothesized taxa it appears that ABXANG, ADXANG, CENCYABX, SCALWID, BRACTAP, ADXSTOM, RESCYNO, RESCYLOC, PULVPUB, and TIPWID are the variables that best describe the polarity in the data. Further, the size and sign of these component correlations suggest that polarity is not strictly a reflection of size differences. These are not all the same variables that account for the largest differences between hypothesized taxa. These results suggest that the hypothesized taxonomic polarity is not co-incident with the polarity of the data.

3.1.2 *P. engelmannii*, *P. sitchensis*, and *P. glauca*.

Adding the populations of *P. glauca* from western Quebec further polarizes the data, however there is still a larger intra-taxonomic variation than inter-taxonomic variation (Table 24). In addition to the six individual variables indicated that had an inter-taxonomic variation that exceeded intra-taxonomic variation, NEEDEP and FREESCAL were also considered important to distinguishing between the taxa. Component correlations suggest that the addition of two populations of *P. glauca* really only effected the first component, other components remained approximately the same with respect to sign and magnitude of component correlations and the variation accounted for. The addition of the two populations of

Table 24. Multivariate apportionment of variation for separate variable suites due to differences between taxa, populations, and individuals of standard P. engelmannii, P. glauca, and P. sitchensis. Abbreviation of PCAs and ANOVAs given in Table 44, Appendix III. Symbols given in MODEL 2. Ordinations of resultant component scores given in Figure 17.

VARIABLE SUITE	A	%SS (mva) B(A)	C(AB)	E
LEAF ANATOMY	35.68	27.39	20.75	16.18
LEAF MORPHOLOGY	29.98	13.90	32.68	21.78
TWIG MORPHOLOGY	41.70	16.48	35.92	5.91
CONE MORPHOLOGY	35.39	19.39	18.64	26.02
TOTAL	38.90	24.15	-	36.95
$\bar{x}$ VEGETATIVE	35.79	19.26	29.78	13.17

P. glauca increased the variability as a result of populations from that given in Table 23, but only for leaf anatomy and twig morphology. Like the results in Table 23, inter-individual variation based on vegetative variables were greater than that based on reproductive variables. The polarizing variables remained as above, with the substitution of BRACTLEN for BRACTAP and the addition of CENCYLAT. Again, there appears to be a lack of co-incidence between taxonomic and data polarity.

Ordinations (Fig. 17) emphasize the striking similarity among the three taxa. P. engelmannii is intermediate to the other two taxa with respect to leaf anatomy and cone morphology. P. glauca appears intermediate to the other two taxa for leaf morphology and twig morphology. The ordination of all 36 variables, like that in Figure 16, further emphasized the distinction between P. engelmannii and P. sitchensis. P. glauca however constitutes only a polar position with respect to the second component of variation and the samples fall within the range of variation shown for standards of P. engelmannii. It should be remembered that the standards of P. glauca and

Figure 17. Ordinations of first two components of PCAs of separate
variable suites for populations of standards of P. engelmannii,
P. glauca, and P. sitchensis. Scores based on PCAs given in
Table 44, Appendix III. Glyphs represent means of individual trees
and are as in Figure 16 except squares represent indviduals of
P. glauca. Not all individual trees could be plotted due to overlap.
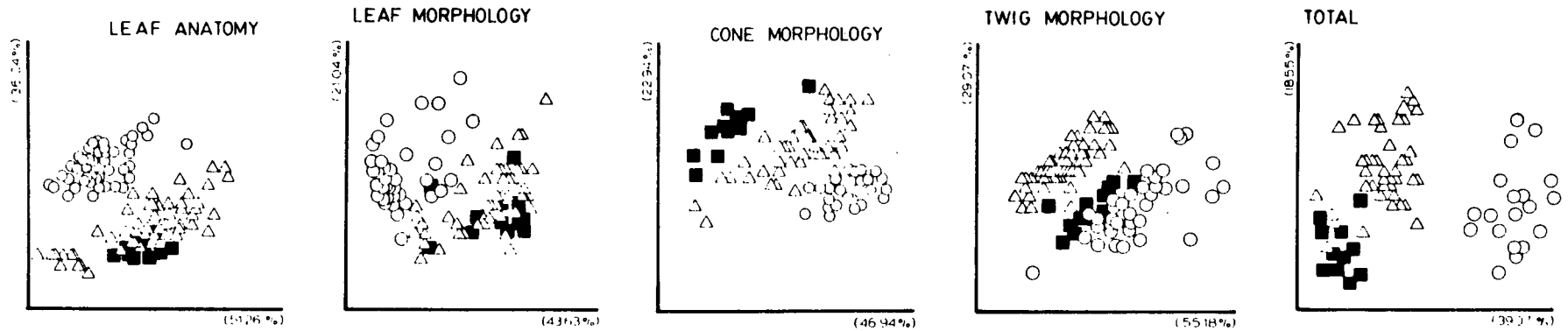
P. engelmannii came from populations on different sides of the
continent.

3.2 Individual standards and putative taxonomic representatives.

3.2.1 P. engelmannii and P. sitchensis.

The decreased morphological and anatomical polarity created
by considering more than just populations of standards was
reflected in the amount of variation accounted for by the first
few axes (Table 25) compared to those in Table 23. In spite of

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Table 25. Multivariate apportionment of variation for separate variable
suites due to differences between taxa and individuals of standard
and putative P. engelmannii and P. sitchensis. Abbreviation of PCAs
and ANOVAs given in Table 45, Appendix III. Symbols given in
MODEL 3. Ordinations of resultant component scores given in
Figure 18.

VARIABLE SUITE	%SS (mva)		
	A	B(A)	E
LEAF ANATOMY	31.84	51.47	16.69
LEAF MORPHOLOGY	20.93	56.73	22.43
TWIG MORPHOLOGY	24.61	67.16	8.24
CONE MORPHOLOGY	36.44	23.28	29.03
TOTAL	28.01	-	71.97
$\bar{x}$ VEGETATIVE	25.79	58.45	15.76

---

this decreased polarity, the component correlations were
significantly correlated with those given in Table 23, implying
that fundamentally new sources of variation have not been added.
The amount of variation attributed to taxa in Table 25 is only 3
percent less than that given in Table 23.

Figure 18 further corroborates that new sources of

variation have not been added. However, compared with
Figure 16, the differences between the hypothesized taxa have
been obscured. On inspecting the component scores for different
trees it was observed that the samples of P. engelmannii from
the Cascade Mountains and Selkirks are co-incident. Similarly
co-incident were the samples of P. sitchensis from southern
Oregon and the study area.

The apportionment of variation indicated that there was
substantially more intra-taxonomic variation than
inter-taxonomic variation. Further (Table 23), only five
variables (NEEDEP, ABXANG, CENCYABX, ADXSTOM, PULVPUB) had an
inter-taxonomic variability that exceeded intra-taxonomic. All
reproductive variables had an intra-taxonomic variability that
exceeded the inter-taxonomic variability. Figure 18 for the
separate variable suites further substantiates the impression of
poorly separated taxa reported above in Table 22.

3.2.2 P. engelmannii, P. sitchensis, and P. glauca.

As with the analysis in Table 25, the polarity of the data
decreased, component correlations remained virtually unchanged,
and the inter-taxonomic variation was less than intra-taxonomic
variation (Table 26). The addition of more individuals
decreased the differences between taxa by 8 percent compared to
Table 24. Like Table 25, the removal of the hypothesized effect
of populations increased the inter-individual variability.
Inter-population variation, such as it was (i.e. approximately
25% of the inter-individual variation), was obscured by

Figure 18. Ordinations of first two components of PCAs of separate
    variable suites for all standards and putatives of P. engelmannii and
    P. sitchensis. Scores based on PCAs given in Table 45, Appendix III.
    Glyphs as in Figure 16.

LEAF ANATOMY

LEAF MORPHOLOGY

CONE MORPHOLOGY

TWIG MORPHOLOGY

TOTAL

(4858%)

(40 50 %)

(36 9/ %)
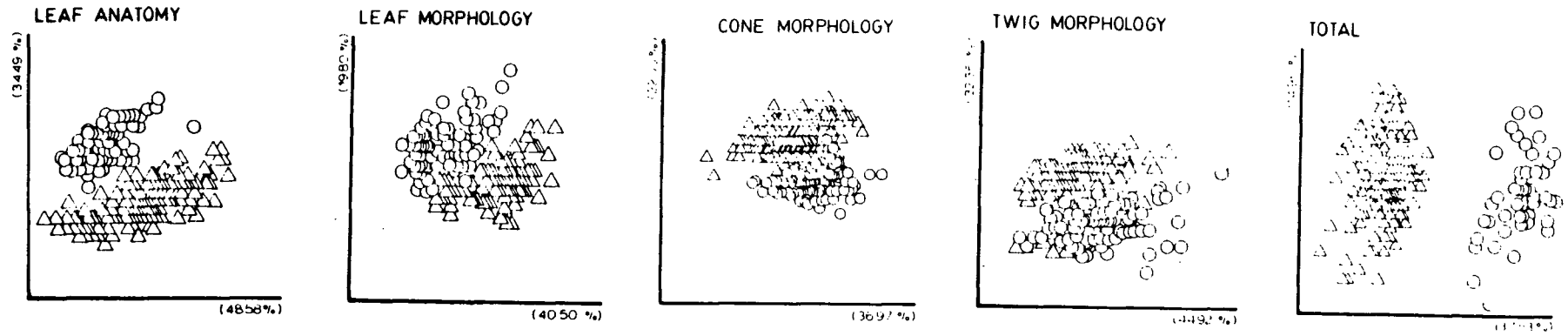
Table 26. Multivariate apportionment of variation for separate variable suites due to differences between taxa and individuals of standard and putative P. engelmannii. P. glauca. and P. sitchensis. Abbreviation of PCAs and ANOVAs given in Table 46. Appendix III. Symbols given in MODEL 3. Ordinations of resultant component scores given in Figure 19.

		%SS (mva)	
VARIABLE SUITE	A	B(A)	E
LEAF ANATOMY	32.10	51.03	16.90
LEAF MORPHOLOGY	21.50	54.32	22.53
TWIG MORPHOLOGY	25.00	66.48	8.52
CONE MORPHOLOGY	13.73	65.72	20.55
TOTAL	30.88	-	69.12
x̄ VEGETATIVE	26.20	57.28	16.52

inter-individual variation. Figure 19 further corroborates this impression of poorly separated taxa. The ordination based on all 36 variables further emphasized the polarity of P. glauca within the variation of P. engelmannii .

3.3 Artificial hybrids in the context of populations of standards.

The amount of variation accounted for by the separate PCAs (Table 40, Appendix III = Table 27) are similar to those given in Table 23. The ordinations (Fig. 20) suggested little in the way of intermediacy for these known hybrids, even though there was a tendency for the two taxa to occupy opposite poles of the ordination. Particularly important was the observation that the maternal "P. engelmannii" for the New Brunswick hybrids was closer to P. sitchensis than were its progeny based on the separate variable suites. Examination of the variance of component scores for individual trees did not indicate that, as a group, the hybrids were any more variable than the standards.

Figure 19. Ordinations of first two components of PCAs of separate
   variable suites for all inidividual standards and putatives of
   P. engelmannii, P. glauca, and P. sitchensis. Scores based on PCAs
   given in Table 46, Appendix III. Glyphs as in Figure 17.

LEAF ANATOMY

LEAF MORPHOLOGY

CONE MORPHOLOGY

TWIG MORPHOLOGY

TOTAL
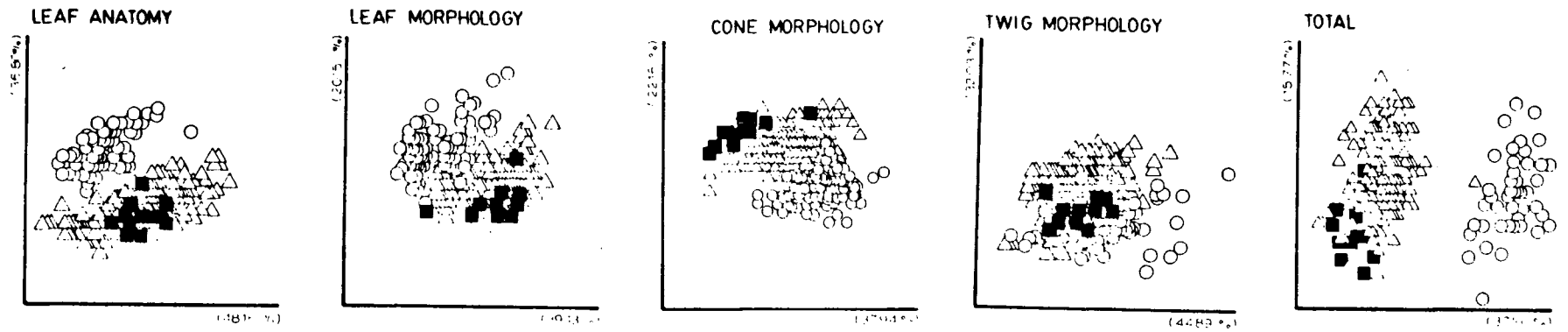
Figure 20. Ordinations of first two components of PCAs of separate
variable suites for sampled populations of standards and artifical
hybrids. Scores based on PCAs given in Table 47, Appendix III.
Glyphs as in Figure 16. Filled triangle - maternal P. engelmannii
for New Brunswick hybrids. Half-filled glyphs - artifical hybrids:
upper half filled - New Brunswick hybrids; lower half filled - Red
Rock hybrids.

LEAF ANATOMY   LEAF MORPHOLOGY   TWIG MORPHOLOGY   VEGETATIVE

(4418%)   (3902%)   (49%)
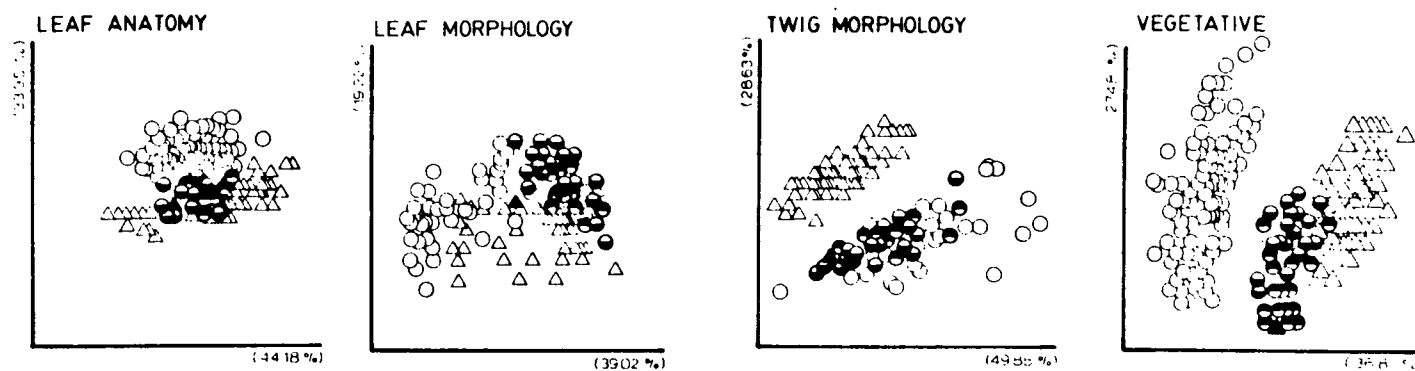
The ordination of the PCA based on all 21 vegetative variables (Fig. 20) corroborates the impression that the artificial hybrids are more like the maternal taxon than the paternal taxon. The polarity of the hybrids on the second component suggests a similarity to the disposition of P. glauca standards in Figures 16 and 18.

3.4 Artificial and putative hybrids.

ANOVAs of PCAs of just the artificial and putative hybrids (Table 28) suggested that there were small but significant differences between the two groups. Most of the variation is

Table 28. Multivariate apportionment of variation for separate variable suites due to differences between artifical and putative hybrids of P. engelmannii and P. sitchensis. Abbreviation of PCAs and ANOVAs given in Table 48, Appendix III. Symbols given in MODEL 3. Ordinations of resultant component scores given in Figure 21.

| | | %SS (mva) | |
VARIABLE SUITE	A	B(A)	E
LEAF ANATOMY	3.67	76.28	20.05
LEAF MORPHOLOGY	14.06	70.17	15.77
TWIG MORPHOLOGY	1.15	90.09	8.76
VEGETATIVE	8.82	-	91.18

between individual trees and the amount of intra-individual variation remains similar to that presented in Tables 23 and 24.

Figure 21 indicates a virtual overlap of the variation of the two groups, an impression corroborated by the high inter-individual variation (Table 28). The putative hybrids

constitute a significantly more heterogenous group of individuals than the artificial hybrids.

As evidenced by the amount of variation accounted for the first few components of these PCAs, the polarity in these data are not as pronounced as those in Table 27 (= Table 40, Appendix III). However, the component-correlations were radically different suggesting that previously undescribed patterns of variation were being described. None of the individual variables had a variation between the two types of hybrids that exceeded the variation within a group of hybrids. The largest source of variation was between trees.

3.5 Individual standards, putatives, and "hybrids".

Adding the hypothesized hybrids to the samples of standards and putatives of the two taxa (Table 29) decreased only slightly the polarity of the data compared to Table 23 and 24, and did not alter component correlations. To iterate, the variables most responsible for the polarization of the pattern of variation of the individual variable suites are: NEEDEP, PHLEND, XYLEND, ADXSTOM, RESCYNO, TIPWID, and SCALEN. If only inter-individual variation is considered, the variables responsible for polarization are: NEEDEP, ABXANG, CENCYABX, BRACTLEN, and BRACTAP. Figure 22 indicates that what separation appears to exist between the two taxa, is virtually obscured when the "hybrids" were also examined. The co-incidence of the vectors of variables that best describe the hypothesized taxonomic polarity or actual polarity of the data are at an

Figure 21. Ordination of first two components of PCAs of separate
variable suites for individual artificial hybrids and putative
hybrids. Scores based on PCAs given in Table 48, Appendix III.
Half-filled glyphs - artificial hybrids. Open circles - putative
hybrids. Glyphs represent means of individual trees.

LEAF ANATOMY

LEAF MORPHOLOGY

TWIG MORPHOLOGY

VEGETATIVE
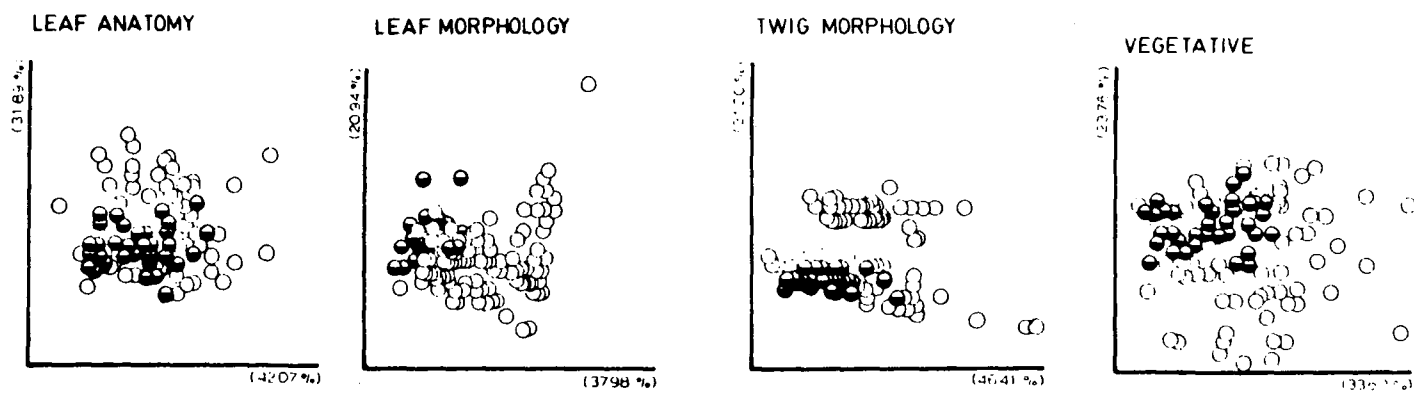
Table 29. Multivariate apportionment of variation for separate variable
suites due to either differences between taxa or individuals of
P. engelmannii, P. sitchensis, or their putative hybrid.
Abbreviation of PCAs and ANOVAs in Table 49, Appendix III. %SS (mva)
for taxa based on only standards and putatives of the two taxa.
Ordinations of resultant component scores given in Figures 22 and 23.

	%SS (mva)			
	TAXA		INDIVIDUAL	
VARIABLE SUITE	A	E	A	E
LEAF ANATOMY	35.70	64.30	83.00	17.00
LEAF MORPHOLOGY	25.37	75.63	78.92	21.08
TWIG MORPHOLOGY	22.20	77.80	93.90	6.10
CONE MORPHOLOGY	17.95	82.05	66.11	33.89
TOTAL	28.07	71.99		
			x̄ 80.48	19.52
x̄ VEGETATIVE	27.76	72.24	85.27	14.93

angle of about 22° to each other. This would suggest partial
co-incidence of hypothesis and data.

Without considering taxonomic circumscription, the
differences between individuals was emphasized. Based on these
values, the relative differences between taxa accounts for less
than half of the variation between individuals.

Analytically, ignoring intra-individual variation and using
all 36 variables does little to alter the impression of a
continuum of morphological and anatomical variation. Further,
the relation of the putative hybrids suggest intermediacy rather
than confusion with P. engelmannii or P. sitchensis as indicated
in Figure 20 for the artificial hybrids. Owing to the proximity
and overlap of the point swarms of standards, no populations
could be identified that contained examples of both hypothesized
parental taxa and hybrids. Individual putative hybrid
populations were no more variable than some of the individual
populations of standards, although as a group they were

Figure 22. Ordinations of first two components of PCAs of separate
    variable suites for all individuals of P. engelmannii, P. sitchensis,
    and "hybrids". Scores based on PCA's given in Table 49,
    Appendix III. Glyphs represent means of individual trees as in
    Figure 16. Half-filled glyphs represent "hybrids". Not all
    individual trees could be plotted.

LEAF ANATOMY

LEAF MORPHOLOGY

CONE MORPHOLOGY

TWIG MORPHOLOGY

TOTAL
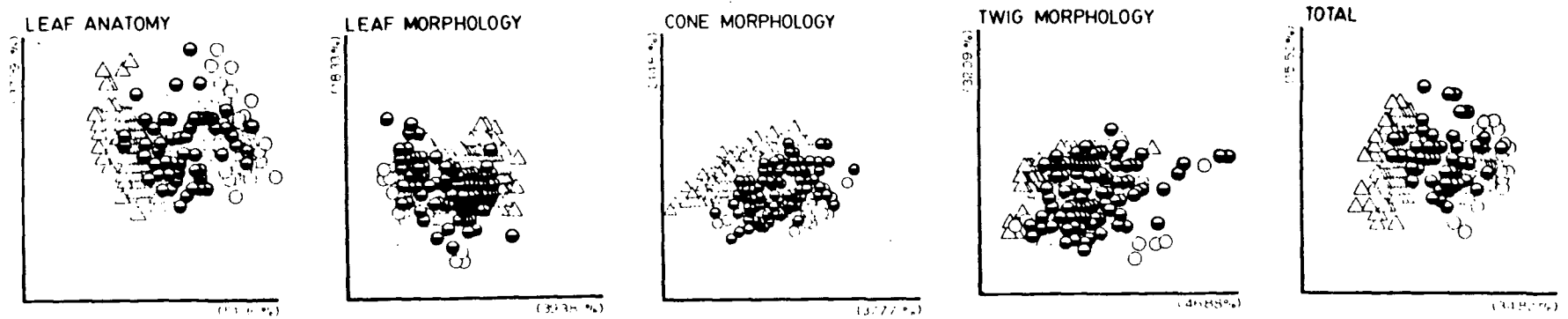
significantly larger.

4. Discussion.

The morphological and anatomical variation of _Picea_ sampled
in southwestern British Columbia suggest that there exists a
continuum of variation rather than a discrete pattern of
trans-individual variation such as that suggested by the two
hypothesized taxa. The results further the conclusion that
P. glauca and _P. engelmannii_ represent little more than
nomenclatural exaggerations of prominent populational or
intra-populational morphological features. The variables that
support the taxonomic polarity between _P. engelmannii_ and
P. sitchensis are, with the exception of the previously
unreported leaf anatomy variables, the same as have been used by
others – yet they are not the only variables that determine the
polarity of the data.

The difference in conclusions regarding the appropriateness
of the hypothesized taxa is attributable to the method of
analysis (no ipsative measures, no ratio variables), the
inclusion of intra-individual sources of variation against which
inter-individual sources of variation could be compared, and
large number of samples from areas not sampled previously. It
is instructive to compare these results with those of Gordon
(1976) dealing with the "_P. mariana_ – _P. rubens_" complex and
the results of Parker and McLachlan (1978) dealing with the
relation of _P. glauca_ to _P. mariana_. Clearly the relation shown

here between P. sitchensis and P. engelmannii is not as
discrete as that reported for P. mariana and P. rubens, nor
P. glauca, and P. mariana. However, neither is it as convoluted
as the relation shown here between P. glauca and P. engelmannii
(see also La Roi and Dugle 1968), nor P. engelmannii and
P. pungens (Mitton and Andalora 1981). Regardless of the
nomenclatural considerations, the results presented here suggest
that P. sitchensis should not be excluded from investigations of
the P. glauca complex.

4.1 Intra-population variation.

The largest source of inter-individual variation was
attributed to variation between individual trees within a
population. This corroborates the findings made by other
researchers working with Picea, as well as the majority of other
conifers. Similar results are reported for morphological and
anatomical variables, as well as for growth and yield variables,
isoenzymes and other chemicals, and physiological variables.
These results are based on naturally occurring materials as well
as nursery grown provenances, progeny, and family trials. Some
researchers have proposed that this high within-population
variation is related to the successional status of the species
(Rehfeldt and Lester 1969), however the large variability
consistently shown for many species irrespective of their
successional status (Guires 1984) suggests that this
hypothesized relation may be erroneous.

There is no independent information consistantly avaialble

in this study that would permit the systematic exploration concerning the source of this intra-individual variation. Research into this aspect of variation of conifers generally has not been addressed (Adams 1981). Where such studies have been undertaken or hypotheses advanced the proposed explanations have most frequently been tendered with respect to natural selection by the environment (Shaw and Allard 1981; Linhart, et al. 1981a,b; Ehrlich and Raven 1969; Mitton, et al. 1977; Grant and Mitton 1976, 1977; Hamrick 1976) in agreement with the well known microgeographic and edaphic variation shown in herbs. Mitton (1983) tendered other explanations based on the presumed ancient nature of the conifer lineage, large population sizes, longevity of the trees, and the associated high fecundity over such a long life span. Rehfeldt (1979a) has tendered explanations based on phenotypic plasticity. Stern (1972) suggested that the lack of selection and frequent mutation were explanations for the high within population variation

The demonstration of family structure in forest stands (Linhart, et al. 1981a,b; Rehfeldt 1978, 1983; Coles and Fowler 1976; Mitton, et al. 1977; Shaw and Allard 1981) and yearly vagrancies of breeding structure (King and Dancik 1984) as well as the demonstrated inefficiency of extrinsic sources of variation to account for within-population variation (Maze 1984) suggests that reproduction alone may be the principal variation-generating and ordering process in naturally occurring stands. Additionally, Rowe's (1961) comments and those of others (Falkenhagen 1977; King 1979; Burgar 1964; Bjornstad 1981) concerning environmental preconditioning (including

maternal effects) also should be considered in such
explanations.

These observations on inter-individual variation and
speculations concerning the large size of this component suggest
that the major evolutionary and ecological processes may be
occurring at an extremely local scale. Further, these results
suggest that reproduction and dispersal may be the primary
factors by which evolutionary novelties ultimately become
emergent from an ancestral taxon. If natural selection mediated
population differentiation is to be accepted as the causal
mechanism in evolution, these results and those of many others
would appear to contradict this hypothesis (see also Mitton
1983) for conifers. Natural selection may well be operative,
but its effects and operative scale would appear to be
conditional upon the specific lineage evolving (Rehfeldt 1984b).

4.2 Natural hybridization.

The results from the comparison of controlled hybrids and
standards suggest that the hybrids are difficult to recognize as
intermediates both in respect to form and variability. This may
be the result of pronounced maternal effects. These results are
at variance with other multivariate analyses of controlled
hybrids where such large maternal effects have not been as
pronounced. The polar disposition of the artificial hybrids and
the available maternal parent could also suggest a more
P. glauca -like maternal parent rather than P. engelmannii.
Indeed, based on the information provided for the origin of at

least the maternal parent of the New Brunswick hybridization (Tree 70418, Appendix II), this is a likely explanation. This situation is not as obvious for the Red Rock hybridization as the maternal parents were from a variety of comparatively high elevation origins. Other explanations for the appearance of the artificial hybrids are possible, but are primarily experimental (e.g. inadequate isolation during pollination[1]). Regardless of the hypothesized effects of maternal parent or exprimental error, the poor distinction between the two hypothesized taxa would suggest that, at best, it would be difficult to identify a hybrid. Further, the appearance of the artificial hybrids falls easily within the range of variability of the two species without suggesting new patterns of variation or increased variability. If expermental causes can be ruled out, then results presented here for the hybrids suggest that P. glauca shares the same relation to P. engelmannii and P. sitchensis as the hybrid P. engelmannii x P. sitchensis. This contradicts Roche's (1969) suggestions that P. engelmannii appears intermediate between P. sitchensis and P. glauca ; however, Roche's data were based on only cone morphology.

The relation of the putative hybrids to the artificial hybrids remains enigmatic with respect to the data presented so far. The higher heterogeneity of the putative hybrids

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[1] This explanation is not adequate for the Red Rock material as the maternal parents were pollinated in mid-winter in Vernon, where there were no other trees present that were contributing pollen. pers. comm., Guyla Kiss, British Columbia Ministry of Forests, Vernon.

(Fig. 20, 21) could reflect: the contribution of a greater number of parent trees than the artificial hybrids; greater environmental variability among the putative hybrids than the common garden conditions of the artificial hybrids; the consequence of introgressive hybridization; or, an inappropriate assignment of individual trees as putative hybrids based on a group of variables that were only partially co-incident with the patterns of variation shown here.

Owing to the appearance of the artificial hybrids it is suggested that the putative hybrids in southwestern British Columbia are not the result of, at least, contemporaneous hybridization between two taxa. This does not rule out historical hybridization or subsequent introgression or selection as explanations for the observed variation. Until further explorations of the pattern of variation encountered here are conducted, tendering explanations based on either introgressive hybridization or differentiation within a single polymorphic taxon must remain enigmatic. Regardless of the outcome of such research it is important to note that the relationship of P. engelmannii to P. glauca appears fundamentally different from that with P. sitchensis - this alone requires further elaboration.

4.3 Intra-individual variation in an inter-individual context.

The results presented emphasize the importance in
systematic studies of considering and quantifying
intra-individual variation. These results indicate that the
difficulty inherent in the identification of individual trees to
one of the a priori taxa on the basis of single characters and
single values results from dealing with tendencies rather than
actualities. In this context, it is worth pointing out that for
every statistic of location (i.e. a mean) there is a statistic
of spread (i.e. a standard deviation). If it can be
demonstrated that the variability among variable values is
entirely experimental in nature, then the spread or variability
of observations can be ignored. If the variability results, in
part, from causes independent of experimental error, then this
spread can be ignored only at the expense of misrepresenting the
nature of the situation being described. A statistic of
location is only as meaningful as the accompanying statistic of
spread and the sample size upon which both are based. As was
demonstrated in Chapter II, intra-individual morphological and
anatomical variation, whatever its cause, occurs and is not
random and thus should not be ignored.

The conclusions reached here suggest that in southwestern
British Columbia further research aimed at explanations of
variation need not consider previously hypothesized taxonomic
circumscription. Thus, investigations of say, population
differentiation, could be applied over the complete range of
variation illustrated here without having to consider the

"taxon" to which the population may be assigned. Explanations
for population variation thus could be addressed, say in the
context of geographic variation investigated by others concerned
with differentiation between marginal and central populations
(Tigerstedt 1973; Soulé 1973; Yeh and Layton 1979). Regardless
of how the problem is approached, the results presented here
suggest a more complex situation concerning <u>Picea</u> in western
North America than previously considered.

V. INTER-INDIVIDUAL VARIATION: RELATIONSHIPS OF PATTERNS OF VARIATION.

1. Introduction.

Having demonstrated in Chapter IV that there exists in southwestern British Columbia a complex clinal pattern of morphological and anatomical variation between P. engelmannii and P. sitchensis, explanations are required to interpret this pattern of variation irrespective of hypothesized circumscribing taxa. Indeed, the clinal pattern of variation suggests that the imposition of taxonomic circumscription is unwarranted in proposing explanations for variation.

Two general hypotheses can be offered to explain patterns of variation. These can be tendered as the result of either correlating morphological and anatomical variation with intrinsic and/ or extrinsic variation or apportioning variation to these sources of variation. Strong correlations more strongly suggest of possible causes than poor correlates. Larger sources of variation more strongly indicate possible causes than do smaller sources of variation. These hypotheses are often tendered as if they were mutually exclusive or that only the extrinsic explanations are acceptable. A priori dispositions toward extrinsic or intrinsic explanations is inappropriate.

Extrinsic explanations are offered more frequently than are intrinsic. Such explanations result from correlating patterns of phenotypic variation with the environment from which the

samples are taken. Discontinuities in geographic distribution are expected to be accompanied by discontinuities in pheotypic variation. In spite of the emphasis on extrinsic explanations, (i.e. extrinsic correlates reflect selection pressures, Thorpe 1976) there is a continuum of both extrinsic and intrinsic factors that is hypothesized to affect the observed phenotypic variation. This continuum can be divided into several scales: broad geographic environmental variation, such as climate, associated with longitude, latitude, and elevation; local climatic and topo-edaphic variation; and, within individual variation. Explanations based on the correlations between the external environment and inter-individual variation are formulated under arguments of natural selection. Intra-individual variation that is correlated with the environment is referred to under "phenotypic plasticity". In general, species that are widely distributed are expected to show correlation between phenotype and geography. Large individual plants are expected to show correlation between phenotype of organs and position in the plant with respect to the surrounding environment.

Intrinsic explanations are based on correlations of the pattern of morphological and anatomical variation with ancestor-descendant relations of various ages or ontogeny. As with extrinsic correlates, there is a continuum of intrinsic variation that can be divided into intervals of variable duration with respect to the life of the organism: long-term relations amongst individuals reflecting distant ancestors; parent-offspring relations; and, intra-individual variation

between separate organs or characters. Inter-individual explanations are formulated under phylogenetics and genetics, whereas intra-individual variation explanations are formulated with respect to development.

Explanations of inter-individual variation, regardless of their extrinsic or intrinsic nature, are evolutionary in nature. Explanations of intra-individual variation are ontogenetic.

There is an approximate one-to-one relation between the geographic scales of variation and the historical scales of variation. Ancestral relations are reflected in broad geographic variation. Similarly, local environmental variation is complexed with parent-offspring relations in that more widely separated individuals are assumed to be more distantly related than are indiividuals that are closer to each other. In studies, such as those reported here, that are based on a limited intra-individual sampling under naturally occurring situations, it is impossible to effectively discriminate or apportion variation into extrinsic or intrinsic. However, it is possible to apportion variation into these various scales of variation. For example, apportionment of variation into inter-individual versus intra-individual sources of variation and subsequent correlations with these scales of variation serves as a means of addressing the apportionment of variation.

Such an apportionment of variation serves as a first approximation for further research conducted under common garden conditions with controlled mating aimed at isolating the specific intrinsic and extrinsic factors operative at a scale

that accounts for the largest source of variation in the data.
Indeed, an investigation of the apportionment of naturally
occurring variation is essential to the initiation of a
biologically sound silvicultural or tree improvement programme.
Such programmes should be guided by the natural variation of the
organism being studied rather than by theoretical or economic
predisposition to a particular scale of variation for a
generalized organism.

An important aspect to consider with respect to the
inter-individual variation is the inter-relationship of various
variables and groups of variables. The demonstration of
inter-relationships between groups of variables are important
for more than just analytic purposes (Small, et al. 1982). Such
inter-relationships suggest developmental inter-dependence
between diverse groups of variables (Morishima and Oka 1968).
Falkenhagen (1974) points out that an organism grows and
survives only if adequate relations between organs, structures,
and physiology are maintained. Such intercorrelations also
carry evolutionary implications (Maze 1983); Variable
inter-correlations also carry important genetic inferences under
the rubric of "linkage disequilibrium" (Mitton, et al. 1980).
Such attention to the inter-relationships between groups of
variables aid in understanding the developmental nature of the
variables and the evolutionary status of the taxon being
examined. As well, they provide an alternate view of
morphological variation: variation is not necessarily adaptive,
simply the result of morphological dependency.

In addition to providing explanations for observed patterns
of variation, there is also a need to relate the observed
variation to that reported in the literature. Comparison with
studies based on naturally occurring trees is straightforward;
however, comparisons with the results based on common garden
situations is not as direct. Comparison of patterns of
variation based on trees from a common garden to the naturally
occurring pattern would faciliate such a comparison.

2. Materials and methods.

2.1 Materials.

Except for the artificial hybrids and the standards of
P. glauca, all the trees sampled and used in the previous
chapters were used in correlating with the various scales of
variation. Owing to limitations of the number of provenances
grown in the nursery, comparison between naturally occurring and
nursery grown trees could be made only for standards of
P. sitchensis. Similarly, as the nursery grown trees were still
immature, comparisons with naturally grown trees could be made
using only vegetative variables.

The lack of information pertaining to correlates for
intra-individual variation (i.e. exact position within the tree
and requisite replication within positions) necessitated that
averages of variables per tree be used. Such averaging removes
about 20 percent of the total variation. This averaging
simplifies analysis considerably but any correlates pertain only

to the inter-individual portion of the total variation of the data. This assumes that there is no interaction between inter-individual variation and intra-individual variation.

Although populations of <u>Picea</u> do occur (Table 7) this level of organization cannot be addressed directly as a large number of trees, especially on the coast, did not occur in populations. Where trees do occur in populations, the population sizes available are extremely variable making analysis difficult. This does not mean that the contribution of population differentiation to the pattern of morphological and anatomical variation is rejected, merely that the nature of the study and the samples available does not permit such an analysis, or at least an analysis which will yield reproducible results. For example, the regular occurrence of defined populations in the interior may well constitute an important difference between the extremes of the morphological continuum identified in this study. Table 23 suggests that apportioning 25 percent of the total inter-individual variation to inter-population variation is worth remembering when considering the results to be presented in this chapter.

2.2 Analyses.

In examining the relationships of patterns of variation to broad geographic variation, the results from the PCAs in Table 29 and Figure 22 were plotted separately against latitude, longitude, and elevation to assess the general form of the hypothesized relation.

Using means of each of the original variables per tree, a
multiple linear regression of the form:

(MODEL 4.)

y = elevation + longitude + latitude + e.

was performed and residual and predicted values were calculated
for each tree for each variable. Such a regression considers
all trees equally, regardless of populational disposition. The
residual and predicted values were subjected to separate PCAs
for each variable suite and the components of these PCAs were
examined by the ANOVA model:

(MODEL 5.)

y = A + e.

were A is the effect of the hypothesized taxa. Although the
PCAs upon which this ANOVA was based used all the available
trees, only the scores for the standards and putatives of the
taxa were used in the ANOVA. Such an analysis has been used in
examining subspecific variation in <u>Pseudotsuga menziesii</u> (Chen,
<u>et al</u>. 1984).

Based on such an analysis of residual and predicted values,
if the hypothesized taxa are indeed morphologically and
anatomically discrete then removing the effects of allopatry of
taxa and climatic variation associated with longitude, latitude,
and elevation should not affect the apportionment of variation
resulting from recognition of taxa. This approach effectively
standardizes the geographical and historical differentiation of

populations. Substantial re-arrangement of the apportionment of variation resulting from recognition of taxa and the pattern of variation as a result of removing the effects of geography would suggest that the taxa are more geographically than morphologically discrete. Such a conclusion would suggest that individuals are more genetically similar than geographic separation alone might suggest.

In examining the relationship between patterns of morphological and anatomical variation with local geographic environmental variation PCAs were performed on each separate variable suite for each of the 16 arbitrarily erected geographic areas (Table 7, Fig. 6). Average component scores were calculated for each tree for each PCA and the scores from each PCA correlated separately against elevation and relative moisture availability. Elevation has been suggested previously by Roche (1969) and others (Falkenhagen 1974, 1978; La Roi and Dugle 1968; Horton 1959; Ogilvie and von Rudloff 1968) as being the major determinant of local geographic variation. Singh and Owens (1981) and Harrison and Owens (1983) have concluded that elevation may affect the time of initiation of morphogenesis and other aspects of morphogenesis in P. engelmannii. As well, a multiple linear regression of mean component scores against moisture and elevation was performed. It should be emphasized that these geographic areas simply group together samples in a given geographic area and attempt to illustrate the local morphological and environmental variation that might be encountered in such an area. Although treated independently of the broad patterns of geographic variation, this is an analytic

convenience rather than a tested assumption. Testing for the interaction of the various scales of pattern would require more extensive localized sampling than were available here.

Comparing naturally and nursery grown P. sitchensis was made by performing separate PCAs on each group for each variable suite, averaging component scores for each tree, and then regressing the scores separately against latitude and longitude. The nursery grown materials represented P. sitchensis from throughout its range (Fig. 4B). As with the separate geographic areas, the mean scores were submitted to multiple linear regression against longitude and latitude. Using only naturally occurring standards of P. sitchensis was necessary to restrict the possible effects of elevation.

If the external environment, or at least the scale of environment associated with geography, is an important aspect of morphological variation then the correlation with the environment should be stronger for the naturally grown trees than the nursery grown trees. The observation of a large intra-population variation (Table 23) suggests that the converse may be expected; i.e. the naturally grown trees would be expected to be less strongly correlated with geography than the nursery grown trees as a consequence of the greater local edaphic variation and, potentially, larger number of parents contributing to the trees collected at any one site.

To examine the inter-relationships among the patterns of variation of separate suites of variables, average component scores for each tree in the separate PCAs were calculated. This

averaging assumes that intra-tree variation of reproductive and
vegetative variables are independent. Such independence is
suggested in Figures 12 and 13. Departures from independence of
vegetative and reproductive variables based on inter-individual
variation suggests that evolution in this lineage has resulted
in the emergence of developmental interdependence. The
appearance of such interdependence suggests either parallel
selection for reproductive and vegetative traits, or simply the
consequences of evolution being a variation generating process
(Wiley and Brooks 1982; Maze 1983).

Owing to the sampling constraints given in Chapter II,
there are several suites of variables. These variable suites
are not all expected to be independent. Based on the common
derivation of some the suites of variables, it would be
predicted that some suites of variables would be expected to be
more highly inter-correlated than others. That is, they would
show a similar development. As a consequence, suites of
variables that are spatially adjacent or developmentally
sequential would be expected to be more closely inter-correlated
than those on more removed parts or derived from different
apices (Morishima and Oka 1968; Scagel and Maze 1983). For the
different suites of vegetative variables measured here it would
be predicted that the twig morphology suite should be the least
inter-related, followed then by the leaf morphology and leaf
anatomy. This sequence is predicted on the basis of the work of
Owens (1968) dealing with the development of Douglas-fir needles
and that of Owens and Molder (1976a) and Harrison and Owens
(1983) dealing with development of the shoots of P. sitchensis

and <u>P. engelmannii</u>.

In all analyses, the identification of all individuals was retained in order to permit comparison with the results presented in earlier chapters. The retention of these identifications also aids the interpretation of the results based more on the convention of recognizing the two taxa rather than supporting the continued recognition of separate taxa in southwestern British Columbia.

3. Results.

3.1 Geographic variation.

3.1.1 Natural variation.

Table 29 and Figure 22 illustrate the relation between all the trees. Figure 23 depicts the scatters of the scores from these PCAs against latitude, longitude, and elevation. The significant r² values included in the figure are generally small. Over all variables, longitude and elevation account for the largest source of inter-individual variation. Latitudinal variation was much smaller. There was little in the way of a non-linear trend in the geographic variation of morphological and anatomical variation. The putative hybrids were intermediate appearing with respect to longitude and elevation - emphasizing the continuity between coast and interior as well as high and low elevation. It should be noted that there appeared to be an elevational discontinuity of about 200m between the

Figure 23. Ordinations of means of first components from PCA of separate variable suites for standards, putatives, and "hybrids" against elevation, latitude, and longitude. Scores based on PCAs given in Table 49, Appendix III. Glyphs as in Figure 22. First component that from PCAs in Figure 22. *, r^2 values significant @ p $\leq$ 0.01.

CONE MORPHOLOGY

$r^2 = 0.182$ * $r^2 = 0.123$ * $r^2 = 0.232$ *

LEAF ANATOMY

$r^2 = 0.532$ * $r^2 = 0.149$ * $r^2 = 0.528$ *

LEAF MORPHOLOGY

$r^2 = 0.326$ * $r^2 = 0.007$ $r^2 = 0.327$ *

TWIG MORPHOLOGY

$r^2 = 0.093$ * $r^2 = 0.008$ $r^2 = 0.074$ *

TOTAL

$r^2 = 0.577$ * $r^2 = 0.158$ * $r^2 = 0.573$ *
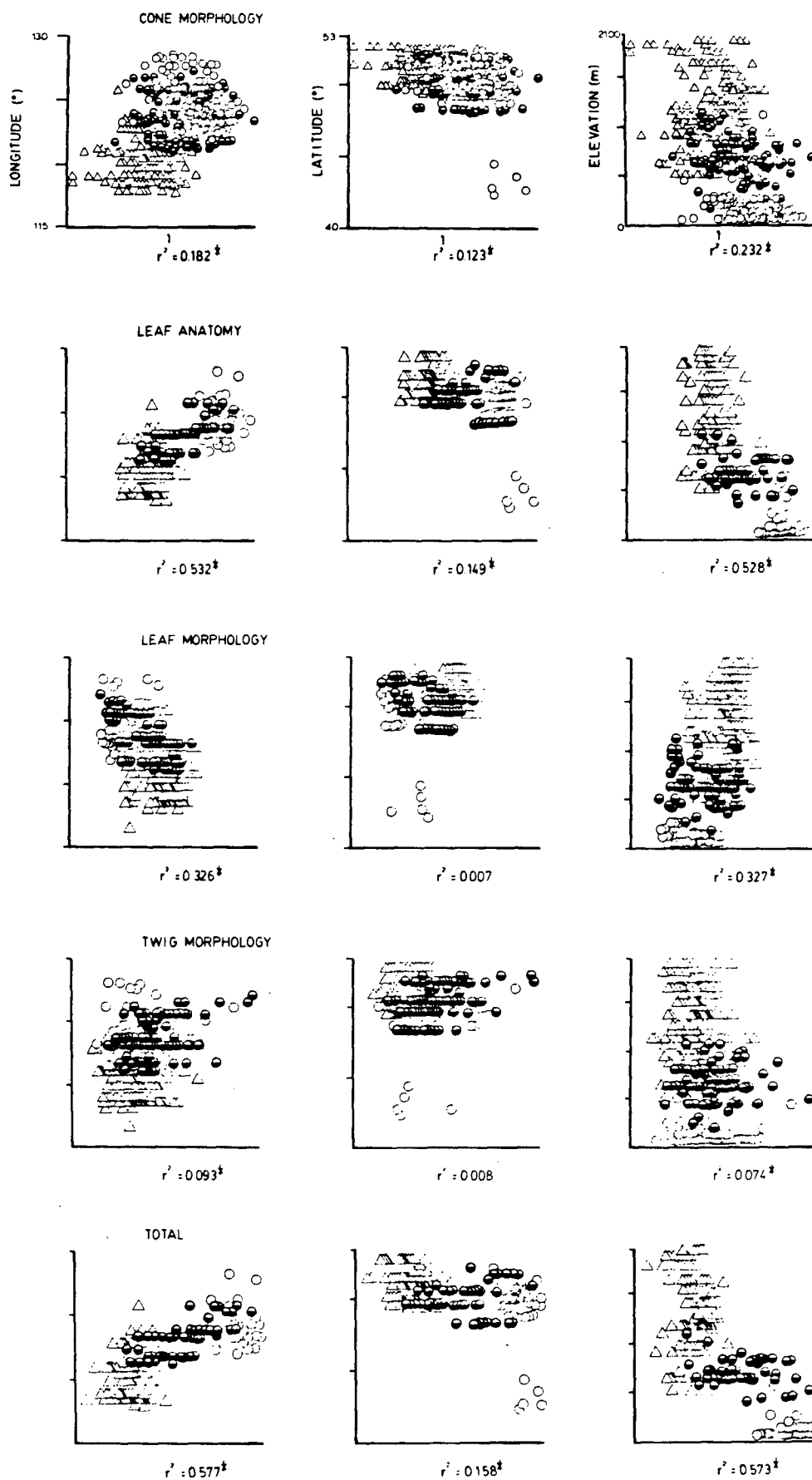
representatives of <u>P. sitchensis</u> and the putative hybrids and

<u>P. engelmannii</u> from 300 to 500m ASL. Figure 23 emphasizes the

co-incidence of Cascade and Selkirk Mountain <u>P. engelmannii</u> as

well as the Oregon and British Columbia <u>P. sitchensis</u>. It is

worthwhile noting that the <u>P. engelmannii</u> populations are 400 km

apart spanning 3° longitude and 2° latitude. The distances

separating the <u>P. sitchensis</u> are even larger: 500 to 1000 km

over 10 to 15° latitude.

Table 30 gives the r^2 values associated with each variable

for the multiple linear regresion given in MODEL 4. As a group,

Table 30. r^2 values for individual variables from multiple linear
regression given in MODEL 4. r^2 values expressed as a total of
inter-individual variation. Predicted and residual values calculated
on the basis of the regressions. *. r^2 values significant @ p $\le$
0.01.

VARIABLES	r^2	VARIABLES	r^2
NEEDWID	5.29*	NEEDLEN	4.64*
NEEDEP	47.68*	ADXSTOM	44.41*
ABXANG	35.40*	ABXSTOM	33.46*
ADXANG	20.89*	RESCYNO	23.92*
CENCYWID	9.12*	RESCYLOC	23.73*
CENCYLAT	10.32*	RESCYLEN	1.98
CENCYABX	60.01*	$\bar{x}$ 22.02	
CENCYADX	36.99*		
ENDONUM	16.56*	CONLEN	21.04*
PHLEND	28.73*	CONWID	20.90*
XYLEND	21.66*	SCALEN	13.71*
$\bar{x}$ 26.60		SCALWID	34.22*
		SCALTAP	9.44*
		WINGWID	16.74*
PULVLEN	21.25*	WINGTAP	6.66*
TIPWID	16.66*	FREESCAL	15.60*
TIPDEP	1.65	BRACTLEN	54.46*
PULVPUB	52.45*	BRACTWID	18.92*
$\bar{x}$ 23.00		BRACTAP	53.27*
		$\bar{x}$ 22.60	

TOTAL $\bar{x}$ 23.56

leaf anatomy variables are the most strongly associated with

geography. On the average, vegetative variables are only

slightly more correlated with the geography than are the reproductive. The variables which are the most strongly correlated (i.e. $r^2 \geq 50\%$) with the geographic variables are: NEEDEP, CENCYABX, PULVPUB, BRACTLEN, AND BRACTAP. Nearly all variables were related significantly to the geographic variables. Over all variables, the average r^2 for this multiple linear regression is 24 percent of the total inter-individual variation.

Table 31 gives the results of the PCAs based on the residual and predicted values from the multiple linear regressions given in MODEL 4. The amount of variation accounted

Table 31. Multivariate apportionment of variation for separate variable suites based on predicted and residual values from multiple linear regression (MODEL 4). Original values based on PCAs and ANOVAs given in Table 29. Abbreviation of PCAs and ANOVAs given in Table 49 and 50, Appendix III. Ordinations of resultant component scores given in Figures 22, 23, and 24.

VARIABLE SUITE	ORIGINAL	%SS$_A$ (mva) PREDICTED	RESIDUAL
LEAF ANATOMY	35.70	71.59	5.22
LEAF MORPHOLOGY	25.37	59.26	2.69
TWIG MORPHOLOGY	22.20	63.40	1.45
CONE MORPHOLOGY	24.98	53.22	1.44
TOTAL	27.06	61.87	2.70
$\bar{x}$ VEGETATIVE	27.76	64.75	3.12

for by the PCAs and the component correlations should be compared with those given in Table 29. The PCAs based on the predicted values were the most polar. Figure 24 illustrates the relation among the trees based on the residual and predicted values, these should be compared with those in Figure 22. It should be emphasized the PCA based on predicted scores from the

multiple linear regressions only accounts for 24 percent of the
total variation in the data.

ANOVAs of component scores (Tables 29 and 31) indicate that
removing the effect of geography by regression also removes a
large portion of the inter-taxonomic variation; the ordination
based on residuals (Fig. 24) emphasizes this lack of taxonomic
polarity. As important as the demonstration of the decline in
variation caused by recognition of hypothesized taxa results
from the analysis of residual values, is the demonstration of
the increased variation caused by taxon recognition resulting
from the analysis of predicted values. The ordinations of
predicted values also emphasize the intermediate appearance of
the putative hybrids.

Based on the predicted values from the regression, only 8
variables (NEEDWID, NEEDLEN, TIPDEP, CONWID, SCALEN, SCALTAP,
FREESCAL, and LOCOWID) displayed an inter-taxonomic variation
that exceeded inter-taxonomic variation. Those variables with
the largest r^2 values (Table 30) generally had the largest $\%SS_A$
(uva) attributed to taxon recognition (Table 31) based on
predicted values. The largest $\%SS_A$(uva) as a result of taxon
recognition for variables in Table 29 are those with the largest
$\%SS_A$(uva) attributed to taxa in Table 31 for residual values.
The polarity of the data based on predicted values emphasizes
BRACTLEN, BRACTAP, ABXANG, ADXSTOM, CENCYABX, NEEDEP, and
CENCYADX. By contrast the polarity of the data based on
residual values emphasizes TIPDEP, TIPWID, CENCYWID, and SCALEN.

Table 32 presents the correlation between the PCAs based on

Figure 24. Ordinations of first two components from PCAs of separate
variable suites for standards, putatives, and "hybrids" using
calculated predicted and residual values from multiple linear
regression in MODEL 4. Glyphs as in Figure 22. Scores based on PCAs
given in Table 50, Appendix III.

LEAF ANATOMY
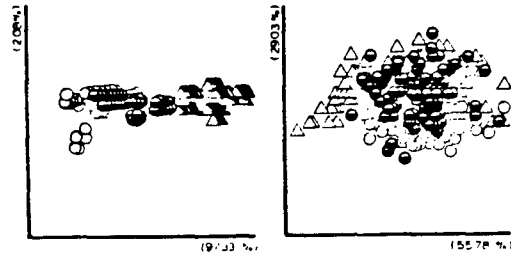
LEAF MORPHOLOGY

CONE COLLECTION
predicted   residual
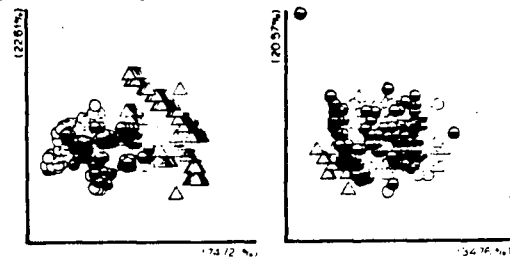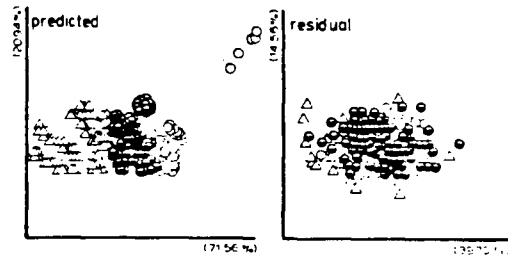
TWIG MORPHOLOGY
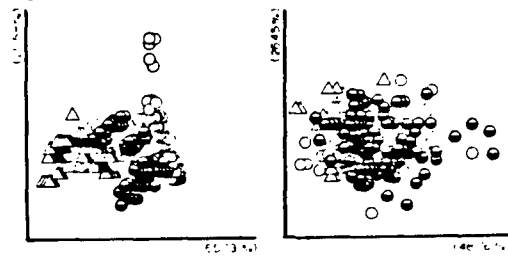
TOTAL
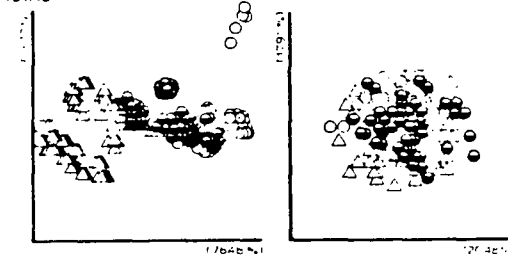
original, predicted, and residual values (Table 29 and 31) for

each variable suite.   In general, the original data are most

Table 32. Correlations among PCAs of original, predicted, and residual
values. *, correlations significant @ p ≤ 0.01. PCAs of predicted
and residual variation from Table 30. PCAs of for original,
predicted, and residual values given in Table 49 and 50,
Appendix III. - correlation missing as eigenvalue less than 1.0 for
the component in question.

		PREDICTED			RESIDUAL		
		I	II	III	I	II	III
ORIGINAL							
CONE							
	I	.554*	.112	-.005	.821*	.111	-.018
	II	-.449*	.292*	.159*	.400*	-.669*	-.009
	III	.049	-.018	-.296*	.002	-.107	.939
LEAF ANATOMY							
	I	.808*	.095	-	-.367*	-.512*	-
	II	-	-	-	.882*	-.328	-
TWIG MORPHOLOGY							
	I	.317*	-.121	-	.912*	.194	-
	II	-.659*	-.081	-	.361*	-.653*	-
LEAF MORPHOLOGY							
	I	.627*	.045	-	.738*	.177*	.034
	II	.454*	-.003	-	-.547*	.267*	-.316*
	III	.158*	.229*	-	-.236*	.026	.915*
TOTAL							
	I	.843*	-.058	-.028	.039	.990*	-.064
	II	.137	.069	.142	.531*	.018	-.010
	III	-.335*	-.021	-.154	.036	.043	.969*

strongly correlated with the results of the analysis of the

residual data.   By definition the predicted and residual scores

are uncorrelated.

Table 33 presents the inter-correlations among the analyses

of the various variable suites.   Figure 25 depicts the angular

co-incidence of the vectors of the various variable suites

plotted into the first two components from the PCA given in

Table 33.   Intercorrelations of variable suite analyses based on PCAs of
  results of regression analysis.   PCAs given in Table 49 and Table 50.
  Appendix III.   Inter-correlations based on scores from first
  component.   *, correlation signficant @ p ≤ 0.01.

```
                              ORIGINAL
TOTAL                .---
REPRODUCTIVE         .764*    .---
LEAF ANATOMY        -.921*   -.561*    .---
TWIG MORPHOLOGY      .238*    .293*   -.018      .---
LEAF MORPHOLOGY     -.745*   -.485*    .636*   -.251*     .---

                      T        R        A        P         L


                              PREDICTED
TOTAL                .---
REPRODUCTIVE         .970*    .---
LEAF ANATOMY        -.999*   -.959*    .---
TWIG MORPHOLOGY      .979*    .902*   -.987*     .---
LEAF MORPHOLOGY     -.964*   -.875*    .973*   -.997*     .---

                      T        R        A        P         L


                              RESIDUAL
TOTAL                .---
REPRODUCTIVE         .679*    .---
LEAF ANATOMY         .729*    .065*    .---
TWIG MORPHOLOGY      .730*    .199*    .685*     .---
LEAF MORPHOLOGY     -.213*   -.163    -.126    -.149      .---

                      T        R        A        P         L
```

Tables 29 and 31 and Figure 22 and 24.   Based on original or
residual variable values the pattern of variation of samples
based on leaf anatomy most closely approximates the total
pattern from all 36 variables.   Twig morphology is the least
correlated variable suite with the total pattern of variation.
Leaf anatomy and leaf morphology variable suites are the most
inter-correlated.   Based on original values, the average
inter-correlation between vegetative and reproductive suites of
variables is about 21 percent.   Predictably, all patterns based
on predicted variation are highly correlated.

A contrast to these patterns of variable suite

Figure 25. Average vectors of separate variable suites plotted into co-ordinates of first two axes from PCAs of all individual trees based on original and predicted and residual values from multiple regression. PCAs given in Tables 49 and 50, Appendix III. Components illustrated previously in Figures 22 and 24. C - cone morphology; T - twig morphology; A - leaf anatomy; M - leaf morphology.
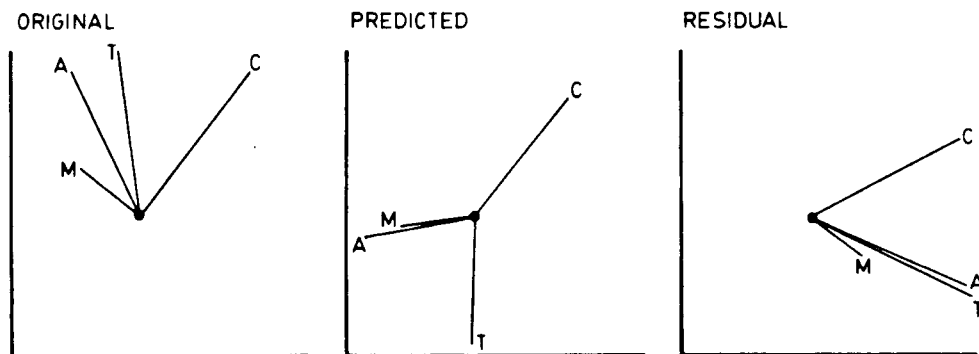
intercorrelations is seen in the patterns of variable suite intercorrelations based on residual patterns of variation from the regression on geography. Residual patterns of variable suite intercorrelations are generally less inter-correlated than are those based on original values. Vegetative and reproductive suites of variables are correlated by an average r^2 of about 2 percent, suggesting independence.

Figure 25 corroborates the differences between vegetative and reproductive variable suites. PCAs of predicted and original values emphasize the disparity between twig morphology and the other vegetative variable suites.

3.1.2 Nursery and natural variation.

Table 34 gives the results of the separate PCAs of naturally occurring and nursery grown trees of P. sitchensis. Correlations of eigenvector-values indicated that the patterns of variation from these PCAs were highly correlated yet the relationships between samples to the geographic scale are different. Over all variables, natural and nursery PCAs have

Table 34. Multivariate relationship of variation for separate variable suites for nursery and naturally grown materials to geographic variation. Abbreviation of PCAs and regressions in Table 51, Appendix III. r^2 values given for multiple linear regression against longitude and latitude. r^2 values expressed as a percentage of the total inter-individual variation. Ordinations of resultant component scores given in Figure 26.

| | r^2 (mva) | |
VARIABLE SUITE	NURSERY	NATURAL
LEAF ANATOMY	4.58	25.56
LEAF MORPHOLOGY	8.10	18.52
TWIG MORPHOLOGY	10.94	25.52
VEGETATIVE	7.87	23.20

similar polarities. Figure 26 gives ordinations of the first components of these PCAs against longitude and latitude. The morphology and anatomy of the nursery grown trees was more strongly correlated with the geographic location than were the naturally occurring trees. Although the collections from the nursery were more latitudinally extensive, the naturally collected materials did not display the same pronounced relationship with geography for even those areas where the two collections overlap. There is apparently no latitudinal discontinuity in morphological or anatomical variation in either

Figure 26. Ordinations of means of components scores for individual
trees from PCAs of separate variable suites of naturally and nursery
grown trees plotted and regressed separately against longitude and
latitude. r² values expressed as a percentage of the total
inter-individual variation. *, r² values significant @ p ≤ 0.01.
First component from PCAs in Table 34.
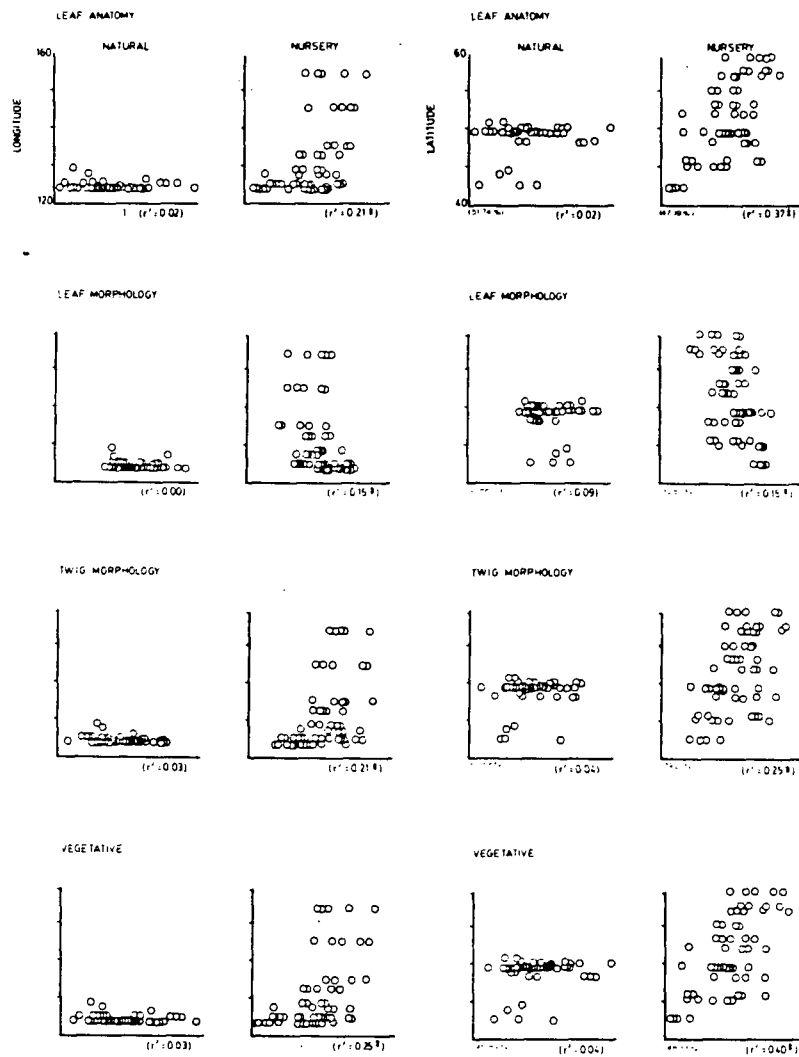
natural or nursery materials.

3.2 Local geographic variation.

Table 35 gives the results of the PCAs of separate variable suites for the 16 separate geographic areas. Also given in

Table 35. Multivariate relationship of variation for separate variable suites for separate geographic areas related to environment. Abbreviation of PCAs and regressions in Table 52, Appendix III. r^2 values given for multiple linear regression against elevation and moisture. Those geographic areas without r^2 values could not be analyzed due to an inadequate sample size. r^2 values expressed as a percentage of the total inter-individual variation. Ordinations of resultant component scores given in Figure 27.

r^2 (mva)

GEOGRAPHIC AREA	LEAF ANATOMY	LEAF MORPHOLOGY	TWIG MORPHOLOGY	CONE MORPHOLOGY	$\bar{x}$ VEGETATIVE	$\bar{x}$ TOTAL
1	11.27	44.12	29.93	19.63	28.44	26.24
2	32.17	18.27	10.37	13.02	20.77	18.46
3	-	-	-	18.41	-	-
4	-	-	-	33.02	-	-
5	-	-	-	24.84	-	-
6	34.97	29.69	20.69	51.58	28.45	34.25
7	-	-	-	7.38	-	-
8	32.25	35.95	32.00	36.16	33.40	34.09
9	-	-	-	33.88	-	-
10	25.64	14.86	14.93	37.29	18.48	23.18
11	24.47	20.73	24.11	13.54	23.10	20.71
12	9.02	16.10	5.09	14.31	10.07	11.13
13	17.12	32.55	14.01	17.54	21.23	20.31
14	14.59	14.04	19.44	14.69	16.02	15.69
15	36.16	19.20	36.44	37.18	30.06	32.25
16	25.01	43.40	54.20	42.03	40.87	41.16
$\bar{x}$	23.88	26.26	23.75	25.41	24.64	24.83

Table 35 are the r^2 values of the means of component scores for each geographic area with separate regressions on elevation and moisture. As well, multiple regressions using elevation and moisture are expressed as an r^2 (mva). Only the first components are given as these had the highest correlations with elevation or relative moisture.

The PCAs of the separate geographic areas indicates little relationship between the pattern of local morphological and anatomical variation and local environmental variation. Where these r^2 values are significant (e.g. Knight Inlet, Table 35: 6), they are generally small. Relative moisture is only significantly correlated with twig morphology for MICA (Table 35: 16) and cone morphology at TOBA (Table 35: 4). Elevation is particularly correlated with patterns of variation based on leaf morphology. Over all variables and all geographic areas the average r^2 value for elevation is about 13 percent and that for relative moisture is about 11 percent. These values are half the size of the average r^2 value for the broader scale geographic variation (Fig. 23). Over all variables and geographic areas the average r^2 value for the multiple linear regression of elevation and moisture is about 25 percent of the total inter-individual variation. In general, cone morphology is only slightly more strongly related to these environmental variables than are the vegetative variables. The three broad physiographic areas (Fig. 6) all had approximatly the same correlation with the local environment.

Based on the amount of variation extracted by the these PCAs and their component correlations, there were varying degrees of variation in each of the separate areas. In spite of this variability some variables (i.e. SCALEN, CENCYWID, TIPWID, TIPDEP) account consistently for the major pattern of variation in each area. These were the same variables that polarized the data based on residuals from multiple linear regression on elevation, longitude, and latitude (MODEL 4; Table 35). There

was no single variable that accounted consistently for the major

pattern of local geographic variation of leaf morphology.

Similarly there was no single area that proved to be

consistently more variable than any other geographic areas

(i.e. MICA (Table 35: 16) is only the most variable location for

leaf morphology). Likewise, no single area was consistently

more strongly correlated with the local environment than any

other area.

Figure 27 gives ordinations of the first two components

from these PCAs. The uniform scale of these ordinations allows

the variation of the separate geographic areas to be compared

with respect to position and variation. There is a tendancy,

over all geographic areas, for the representatives of

P. engelmannii and P. sitchensis to occupy opposing poles of the

ordinations, however in any single geographic area there is no

discrete separation of the two taxa. In those geographic areas

where there were standards of both taxa and their putative

hybrids (Table 35: CHILLI (8), HOWHIS (2), KNIGHT (6)), there

was little polarity in the pattern of variation that reflected

the presence of two taxa.

Averaging and summarizing the apportionment of variation

presented in Tables 29, 30, 35 and assuming that the identified

scales of variation were independent, produces the apportionment

of variation presented in Figure 28. Regardless that the

assumption of independence is admittedly a liberal

interpretation, the variation within an individual tree was

porportional to or larger than the two hypothesized scales of

Figure 27. Ordinations of first two components from PCAs of separate
geographic areas and separate variable suites. Scores based on PCAs
given in Table 52, Appendix III. Glyphs as in Figure 22. Solid
glyphs - standards; empty glyphs - putatives. Glyphs represent means
of individual trees.

LEAF ANATOMY
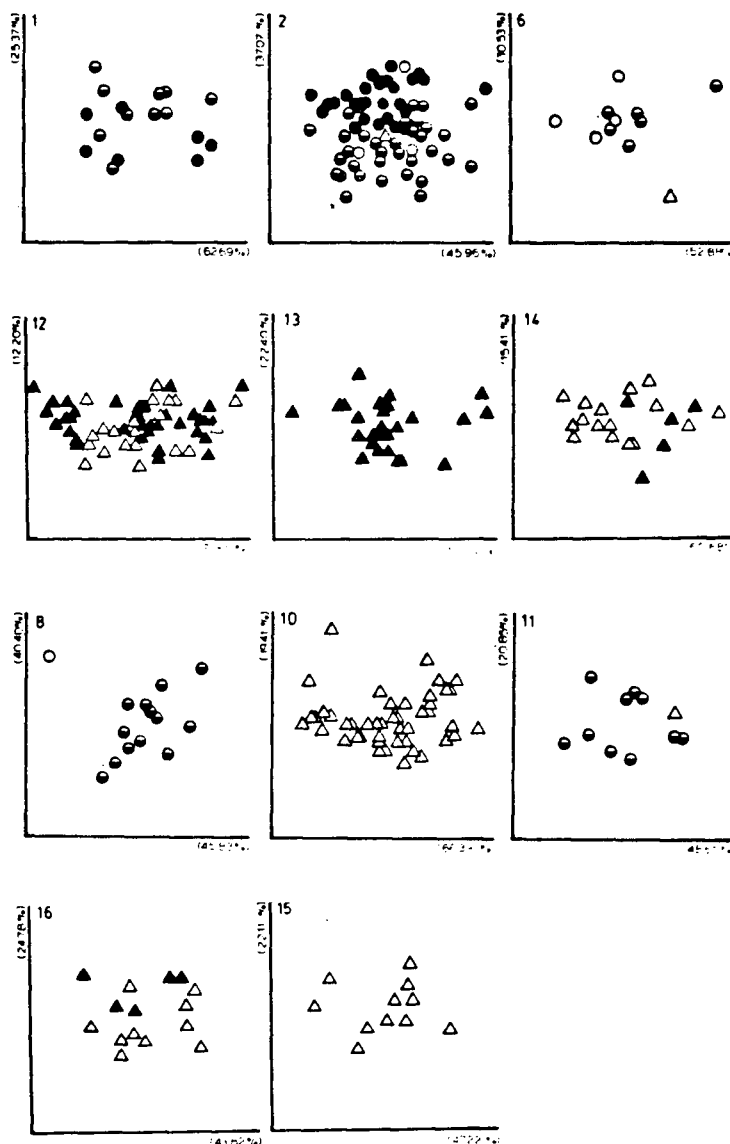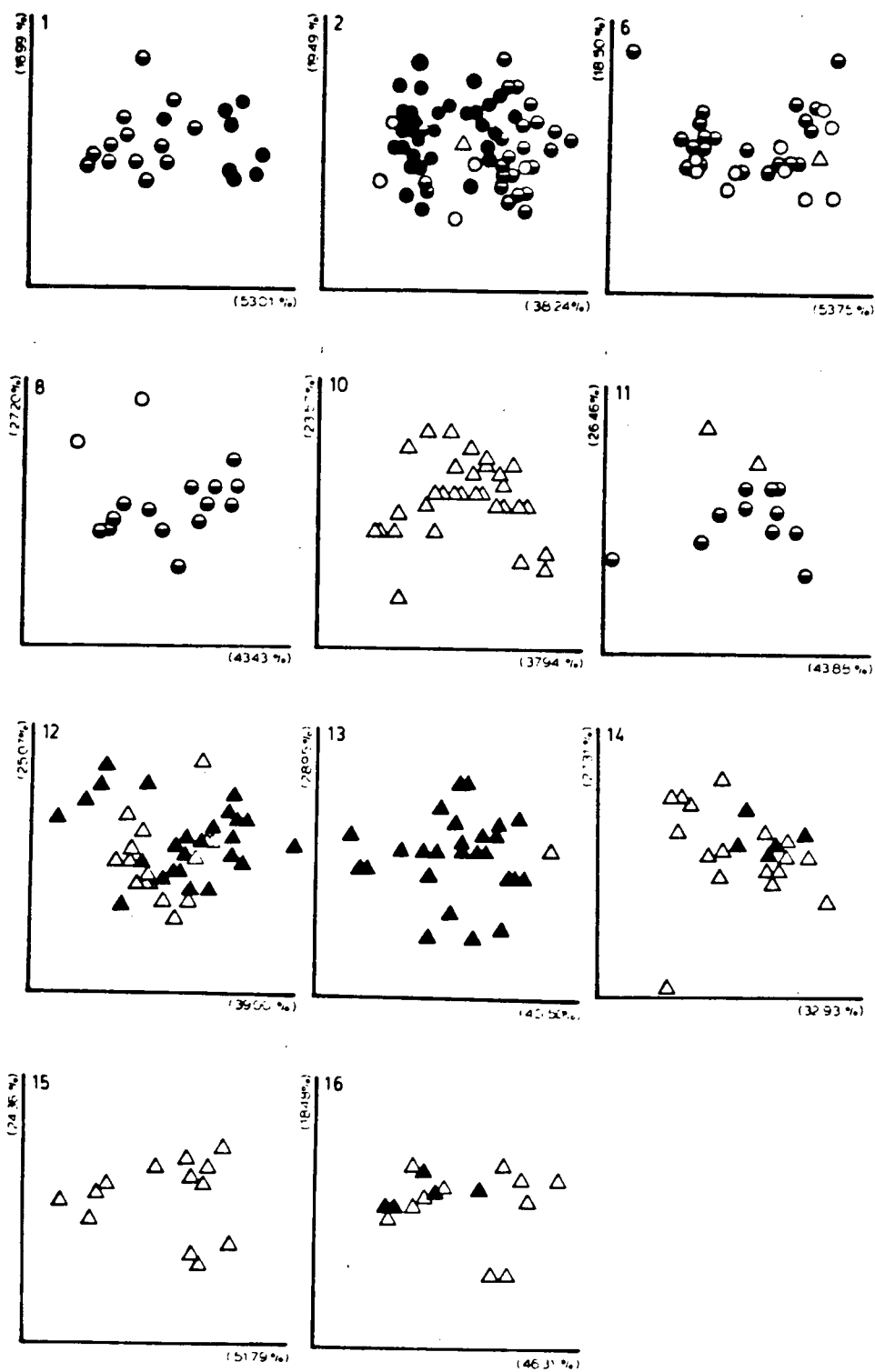
LEAF MORPHOLOGY

TWIG MORPHOLOGY
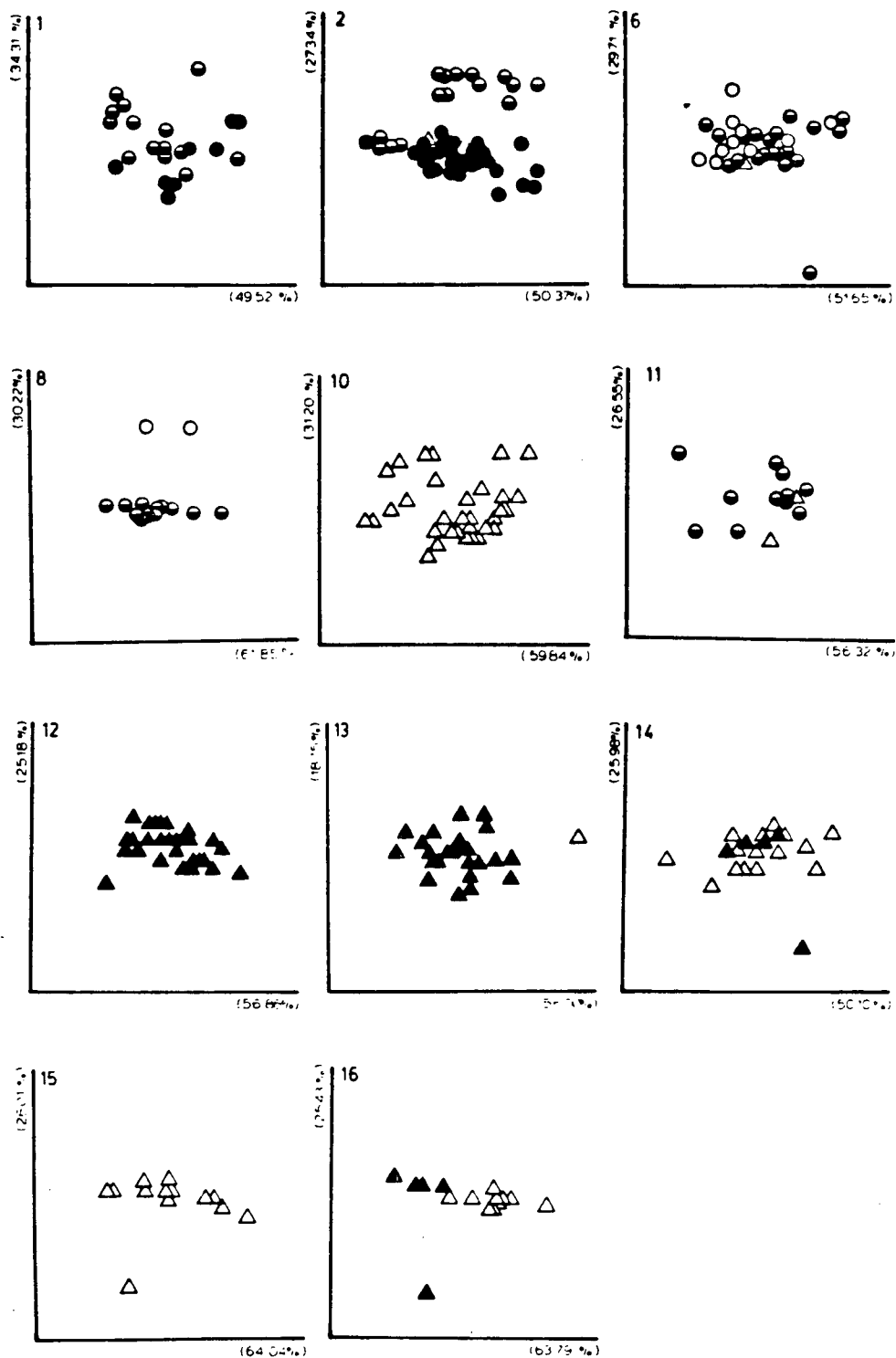
CONE COLLECTION
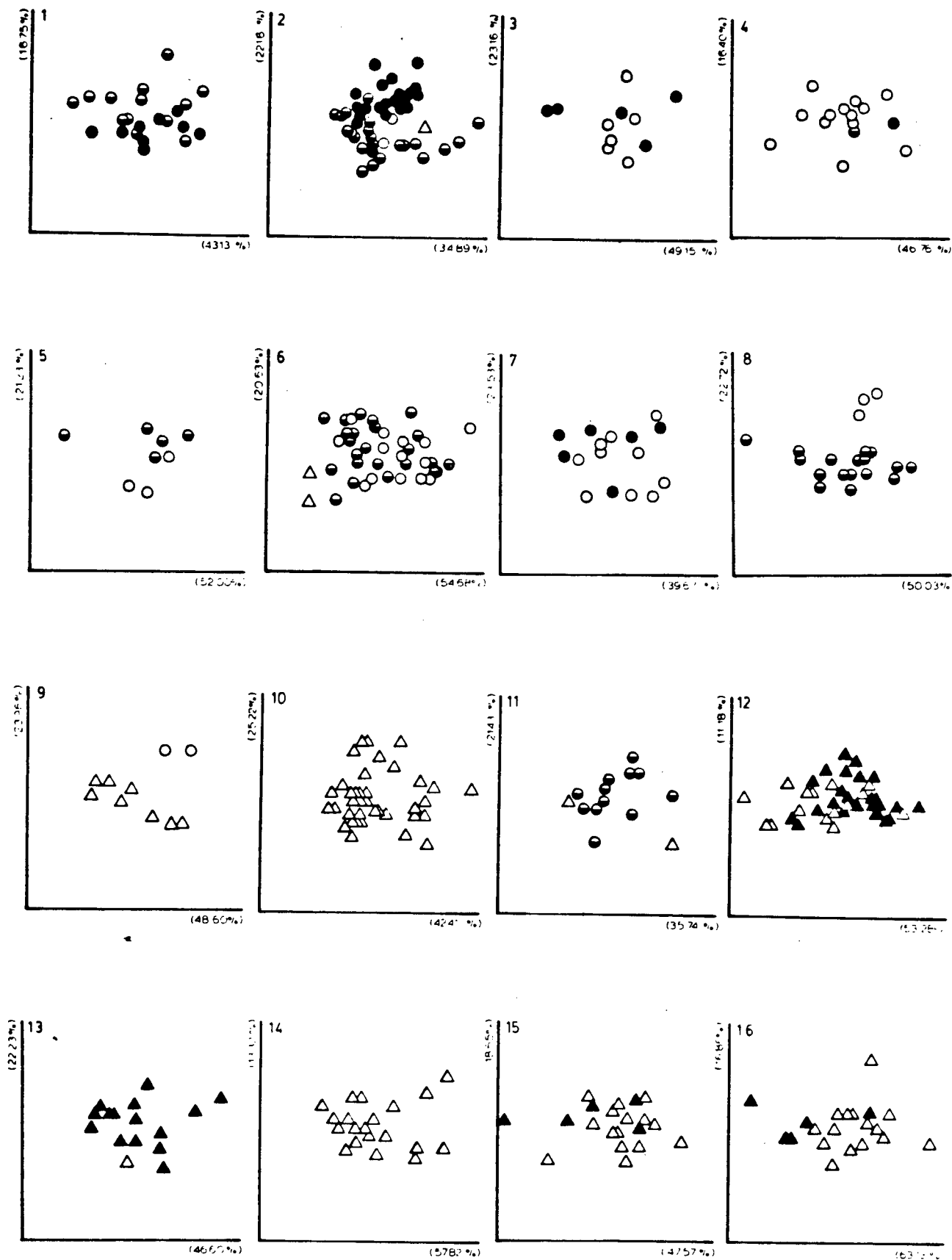
Figure 28. Partioning of sources of variation for naturally occurring
   Picea in study area. Stipled border of pie indicates
   intra-individual variation corresponding to stipled area in
   Figure 15.
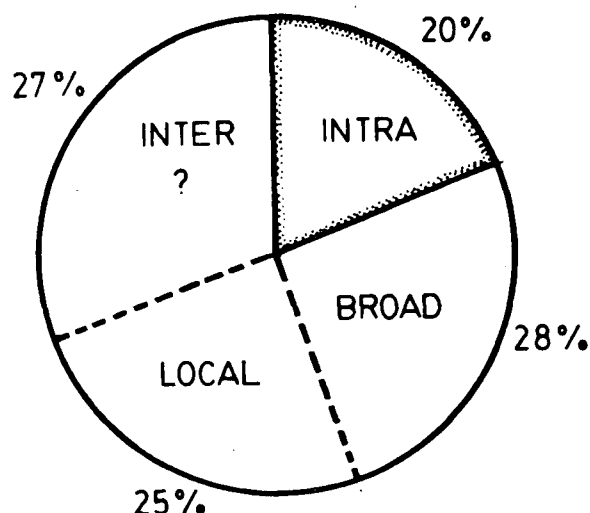
inter-individual variation.   There was still an unaccounted for

27 percent of the total variation that resulted from unspecified

inter-individual variation.   It should also be noted that the

hypothesized twenty-five percent of the variation in the data

attributable to populations is spread over the hypothesized

sources of inter-individual variation.

4.   Discussion.

   The results presented here indicate that the continuum of

morphological variation exhibited by P. sitchensis and

P. engelmannii in southwestern British Columbia is not strongly

related either to broad or to local scales of environmental

variation.   In this regard it is analogous to the weak regional

and local variation shown for P. abies (Andersson 1965).   These

hypothesized sources of inter-individual variation are only

slightly larger than intra-individual variation. Longitude and elevation are the major correlates over the broad geographic range, whilst elevation and moisture availability are approximately equally correlated with local geographic variability. The demonstrated co-incidence of widely separate groups of individuals agrees with the report for other conifers (Kung and Wright 1972; Parker, et al. 1981) and suggests that there is something more fundamental to evolution and population differentiation than simply isolation from gene flow (Ehrlich and Raven 1969). The demonstrated lack of taxonomic pattern in local geographic areas suggests that this continuum is representative of a single large polymorphic taxon and is suggestive of possible local topo-edaphic effects hypothesized by others (Burley 1966b; Falkenhagen 1974).

4.1 Inferences from environmental and geographic correlations.

The lack of a strong inter-relationship between morphological and anatomical variation and the hypothesized scales of variation could be experimental or actually reflect aspects about the biology of the organisms. If the explanation for the poor correlation is experimental then the cause would have to lie with the types of variables measured and/ or the error associated with such measurements. Maze (1984) provides further discussion with respect to the nature of such experimental based explanations. If measurement error can be ruled out, then all that can be presumed is that smaller environmental and genealogical scales of variation may be more

important than the scales investigated here. Suffice it to say, the lack of a phenotypic difference does not perclude the existence of habitat dependent selection on the basis of physiological traits.

This second biological explanation, may gain some support on the basis of the demonstrated stronger correlation between broad geographic variation for the nursery grown materials than the naturally collected material. This observation suggests that the variation in the naturally collected material could reflect extremely local environmental and genetic variation, specifically, the immediate environment of the tree sampled and the tree's immediate parentage. This conclusion would appear to substantiate the old adage that local trees are best adapted to the environment of their origin, although they are not necessarily the best economic investment at their site of origin (Silen 1982). Conversely, the smaller correlation of the naturally occurring trees could simply be the consequence of differences in ages of the trees (Maze, et al. 1981).

The demonstration that the major broad geographic pattern is related to elevation and longitude contradicts much previous research. Previous research has favoured elevational and latitudinal variation with the exception of Dietrichson's (1971) work. Whether the trend presented here represents the result of post-glacial migration, secondary longitudinal migration following primary latitudinal migration, or the selective influenece of climate is difficult to ascertain. The important point remains that a large degree of inter-individual variation,

whatever its explanation, appears to have occurred at an extremely local scale. Perhaps this simply indiciates that given certain minimal physiological requirements, a great deal of variation can be expressed (Falkenhagen 1974).

The difference in patterns of variation between nursery and naturally grown materials is especially worthy of comment. Indeed, based on nursery grown materials, one would be tempted to provide explanations for the especially strong relationship between geography and morphology of P. sitchensis. However, the naturally grown material suggests that there may be other relationships that may be more significant in explaining morphological and anatomical variation. Basing evolutionary explanations upon these nursery grown materials may misrepresent the actual variation. Establishing a tree breeding programme or making silvicultural recommendations on the basis of the same materials could lead to disastrous consequences in a plantation. Additionally, the demonstration of the apparent homogeneity of nursery grown materials suggests that caution should be exercised in growing reforestation materials in the nursery.

Previous research in Picea that has suggested strong interrelationships with latitude and, at a local scale, elevation, needs to be carefully reviewed in the light of the results reported here. Under certain local environmental and genealogical conditions elevation may well be an important factor, however it is just as likely to not be of consequence compared to other factors or where different geneologies are present. Similar conclusions are presented by other researchers

for other conifers (Parker, et al. 1983; Fowler and Mullin 1977; Teich and Holst 1974). Similarly, in some portions of the range, latitude may be an important factor; however, the assumed effect might be much smaller than that of longitude and elevation.

Such observations question the adequacy of tendering evolutionary explanations or silvicultural prescriptions based entirely on common garden experiments. Further questions arise based on the observation of changing patterns of variation for the same provenances in separate nurseries (O'Driscoll 1976b; Ching and Sziklai 1978b; Campbell and Sorenson 1978) or test environments (Smith 1976; Mergen, et al. 1974; Bjornstad 1981). Similar questions concerning the adequacy and applicability of the results of common garden experiments have been raised by Falkenhagen (1972, 1979, 1982). Under common garden conditions the homogeneity of the edaphic environment, parentage, seed quality, and inadvertant selection during nursery growth may lead to erroneous conclusions or representation of conditions occurring outside the nursery. The results presented here suggest that conclusions based on nursery grown materials should be compared to those reported for naturally occurring materials. Secondly, nursery grown materials should be compared under a variety of different experimental environments and more attributes about the geneology and parental environment should be noted so that more precise explanations can be made concerning the observed patterns of variation. A logical consequence of such considerations is the need for a comparison of parents and resultant progeny for the same morphological and

anatomical variables. Few studies of conifers have been conducted in such a manner because of the longevity of the trees and a predisposition towards growth and yield variables rather than morphological and anatomical variables (see however Ruby 1967).

The results of the analysis based on predicted values from regression of geography corroborates the impression of discontinuity between the two hypothesized taxa more on the basis of geography than any fundamental morphological or anatomical differences. In Figure 23, apparent elevational discontinuity indicated between the two hypothesized taxa may simply be a consequence of the inability to sample in the appropriate environment at that elevation or recent historical disturbance of the occurrence of _Picea_ in the study area. The appearance of scattered, single veterans of _Picea_ in the study area at high elevations and in isolated drainages suggests that _Picea_ may have been more widely distributed in the past than at present. Such observations would argue for attributing the elevational discontinuity to recent historical circumstances. Further support for this explanation could come from examining harvest records from these intervening elevations to determine the extent that such a discontinuity could be attributed to recent logging.

The observation of scattered veterans, scattered sparse populations along the coast mainland, and the more frequent occurrence of _Picea_ in older Quaternary sequences could also be taken as evidence for the more widespread occurrence of _Picea_ in

the past, thus having led to hybridization of the two hypothesized taxa during immediate post-glacial times and subsequent introgression. The primary successional nature of Picea in the coastal areas and higher elevations along with the low frequency of natural disturbance of these forests today would appear to be diametrically opposed factors that would preclude the widespread occurrence of Picea. Other naturally occurring factors that might be responsible for the apparent discontinuity could be insect or pathogen infestation, or simply the lack of suitable habitats at these elevations owing to the physiography or associated vegetation (Stern and Roche 1974). Investigations of Picea at elevations that bound this discontinuity may reveal other explanations than those offered here. Such observations heighten the perception of the spatio-temporal nature of the occurrence of hybrids (Clifford 1961).

4.2 Inferences from variable suite inter-correlations.

Inter-correlations of vegetative and reproductive suites of variables were slighly larger than those reported by Maze (1983) for four species of Abies. Additionally, all variable suites are almost equally correlated with local and regional geographic variation. The interdependence is much larger than that shown for any single lineage of Abies. Further it reflects Taylor's (1959) claim that cone and needle variables are, as a group, independent. Removing the hypothesized effect of geographic location of the trees indicated that the two suites of variables were virtually independent. Contrary to the results reported by

Maze (1983), these results suggest that developmental inter-dependence appears to have accompanied geographic migration and evolution of _Picea_ in southwestern British Columbia and that there has not been a marked re-arrangement of variable inter-correlations over the evolution and migration in this area. The differences between the results reported for _Abies_ (Maze 1983) and those reported here for _Picea_ could simply reflect inherent differences in the degree of morphological and anatomical differentiation that can occur within this lineage prior to closure (Wiley and Brooks 1982). This suggests that a greater degree of intra-taxonomic differentiation can occur in _Picea_ before closure than in _Abies_. Conversely, it could indicate that _Picea_ in southwestern British Columbia is simply more diverse at present than any of the species of _Abies_ that Maze (1983) examined. Examining the patterns of variable suite inter-correlations in other species may help to understand the significance of the degree of within-lineage co-incidence of variable suites. Additionally, controlled crosses would establish the validity of Taylor's (1959) hypothesis concerning the independent inheritance of variables distinguishing the two taxa as opposed to the variables polarizing the data.

The demonstration of low inter-correlations between twig morphology and all other suites of variables hints at fundamental developmental differences between these variables and the other variables. Examining the work of Cannell, _et al_. (1976) suggests that an explanation may be found in that the twig morphology variables are primarily variables of indeterminate elongation rather than more complex, determinate

structures assessed by the other vegetative variables. The hypothesis concerning the developmental similarity of spatially adjacent and developmentally sequential variable suites is apparently upheld, in that the leaf morphology and anatomy suites are the most highly correlated.

In examining the correlation matrices upon which the various PCAs were performed, it was noted that bract morphology variables were more highly inter-correlated than they were to the cone scale variables. This observation agrees with the hypothesis of the spatio-temporal nature of developmental interdependence. Following the observations of Owens and others (Owens and Molder 1976b, 1977; Harrison and Owens 1983) the bracts are initiated and develop prior to the cone scales. The bract morphology variables would thus be predicted to be more strongly inter-correlated than with cone scale morphology.

The observation that cone scale morphology does not as strongly differentiate among individuals as do vegetative variables (Table 2, Fig. 22) requires some explanation. In Picea, vegetative and reproductive apices are initially similar, however with the advent of induction they become markedly different. Once an apex has been induced, the continued differentiation of reproductive structures is subject to a delicate balance between vegetative and reproductive developmental paths. Evidence for this balance is derived from observations of a continuum of needles to bracts at the base of cones and proliferated bracts at the apices of cones (Owens 1980). Other teratological observations on cone scale

morphology have been reported by Guedes and Dupey (1974) as well as observed for a number of collections in the present study and serve to support this impression. This sensitivity to perturbation could be the result of the longer duration of the development of reproductive variables than vegetative variables (Stebbins 1950). As the developmental differences between reproductive and vegetative variables would be expected to be large, the susceptibility of development to perturbation between these two extremes would probably be greater than the perturbation necessary to alter the development of reproductive morphologies.

This attention to the developmental basis of variable inter-relations carries suggestions with respect to our understanding of the patterns of variation in Picea of southwestern British Columbia. The variables that are responsible for polarizing the data (Table 29) come from a variety of different variable suites and are determined at various stages and are the result of various durations during the morphogenesis of these structures. The polarity in the data, although reflecting some of the presumed more terminal and indeterminate variables, is not determined entirely by such terminal additions to the developmental sequence. Thus the polarity of the data can be viewed as reflecting the consequence of complex variable inter-relations over the entire course of development and not just simple growth and terminal elaboration of developmental patterns.

Harrison and Owens (1983) indicate that the developmental

differences of reproductive morphology between P. sitchensis and P. engelmannii are more of the timing and duration of morphogenetic events. The same has been indicated for different provenances of P. sitchensis (Pollard, et al. 1975, 1976; Cannell and Willet 1975). It can be concluded that there are small fundamental differences in the patterns of reproductive morphogenesis. Such observations would seem to be reflected in the first component of PCAs based on cone scale morphology where the component correlations are all the same sign and are more similar in magnitude than are vegetative variables.

Such observations and speculations emphasize the need to examine the sequential appearance of morphological differences between individuals of different species. Such analyses would prove useful in understanding the degree to which morphogenesis is shared by individuals of different species and suggest the degree of similarity in developmental pathways underlying the phenotypic pattern.

4.3 Hybridization or differentiation in a polymorphic taxon?

The role of hybridization in evolution has always been disputed (Anderson 1949; Böcher 1967; Heiser 1973; Parson and Kirkpatrick 1972; Schueler and Rising 1975). In Picea, much of the diversity in the boreal species is attributed to hybridization (Wright 1955; Bobrov 1972, 1973; Schmidt-Vogt 1977). The alternate to any hypothesis of hybridization is some form of differentiation in a single polymorphic taxon. Distinguishing between these two hypotheses in the present study

is dependent, ultimately, on information pertaining to the
discreteness of the two parental taxa prior to the post glacial
migration in the study area. None of the inferences drawn from
contemporary criteria for hypothesizing hybridity forms a
rigorous and unequivocal test of these hypotheses (Gottlieb
1972). The pattern of variation reported here for _Picea_
emphasizes the inadequacy of such tests. The ambiguity in
explaining the variation in _Picea_ in southwestern British
Columbia as a consequence of hybridization centers around the
poor separation of the hypothesized taxa regardless of the
presence or absence of putative hybrids.

The primary criterion concerning hybridization is
morphological intermediacy in several variables in areas
intermediate geographically and/ or edaphically between the two
hypothesized parental taxa (Stebbins and Major 1965) or on the
periphery of the range of the two species (Little and Pauley
1958). However, as the results presented here indicate, such
intermediacy is not displayed by the putative hybrids even
though they occur in intermediate geographic areas and edaphic
conditions. Intermediacy of the controlled hybrids can be
used to support or refute the hypothesis of hybridity.
Supporting hybridity would be arguments concerning the artifact
of maternal or environmental effects (Benson, _et_ _al_. 1967).
Alternatively, even if the results were attributed to maternal
or environmental effects, they are larger than differences
between hypothesized taxa thus suggesting rejection of the
taxonomic hypothesis and reducing hybridization to an
inter-racial occurrence rather than inter-specific.

Further tests of the consequence of maternal and
environmental effects should be conducted in a diallel cross
involving parents from provenances from the extremes of
variation seen here. Important contrasts in such a test would
be the reciprocity of maternal effects, the pattern of
intra-provenance versus inter-provenance crosses, and
consistancy in such results over several test environments.
Such a test also could examine the co-incidence of breeding and
morphological relationships.

Secondary criteria concerning the adequacy of the
hypothesis of hybridization are not as unequivocal nor testable
as the demonstration of intermediacy. First, as none of the
trees in areas of suspected hybridization could be unequivocally
identified as representing either hypothesized parental taxon,
hybridization would appear to be more historical than
contemporaneous. That the two taxa are not entirely
morphologically or anatomically discrete even though they are
geographically discrete further suggests that hybridization was
an historical event followed by subsequent introgression. The
observed fertility of putative hybrids further implicates
introgression. The significance of the observed geographic
discontinuity with respect to the issue of hybridization and
introgression has been detailed above.

That, as a group, the variability of the putative hybrid
populations was larger than the variability of populations of
the standards of the hypothesized parental taxa suggest

hybridization and subsequent introgression. However, this inference is contradicted by the observation that individual populations of putative hybrids are no more variable than individual populations of standards, an observation that corroborates one of Roche's (1969) observations. Additionally, the variation in areas in which hybrids occur are not more strongly correlated with environmental variation than in areas of hypothesized parental taxa. Further, intra-individual variability in putative hybrids is not any larger than any individuals of the putative parental taxa.

More population-specific collecting would be required in order to explore the implications of accepting hybridization and subsequent introgression as an accurate explanation for the pattern of variation in Picea. Specifically, such a sampling would involve comparing extensive populations at the extremes of the continuum along with hypothesized introgressed populations. In addition to addressing edaphic variation in such populations sampling would have to address the age structure. Regeneration in nature should also be compared to families of progeny grown under more controlled experimental conditions. The intra-individual sampling would have to be considerably larger than that used for the present study.

Admittedly, the evidence necessary to substantiate any hypothesis of hybridity is not particularly convincing for the situation described here. Several other results suggest that the hypothesis of hybridity be examined critically concerning the pattern of partial co-incidence of the hypothesized

taxonomic polarity and actual polarity of the data. The closest co-incidence of the two aspects of the data is evident only for the largest geographic scales of sampling. Hypothesized taxonomic polarity is virtually absent in examining local scales of variation. This contrasts markedly with the local variation shown by Parker, et al. (1979) for two species of Abies. Additionally, regardless of the scale of sampling the data appeared to conform to multivariate normality rather than departing, as might otherwise have been predicted for situations involving lineages as divergent as species. These results suggest either the a priori taxonomic hypothesis is not appropriate, or that the results of hybridization and introgression have taken on divergent patterns of variation in different areas. Such divergence would suggest that post-glacial migration in Picea in southwestern British Columbia was accompanied by an inter-action of the dispersal and reproduction with a spatio-temporal mosaic of lineages and environment.

Addressing the issue of divergent patterns of variation and introgressive hybridization would engender expanding the sampling strategy outlined above to several areas of suspected hybridity and juxtaposed areas of standards. Three such areas would be: the lower reaches of the Kleena Kleene River Valley; Green Lake and Alta Lake; and the southern end of the Chilliwack Valley. Data would also have to be collected to tender explanations for differing variation between all populations. Particularly important would be possible explanations for von Rudloff's (1975) observations concerning differential population

variation for the two extremes shown here.

Expanding intra-individual sampling in such intensive studies would address directly the issue concerning the differential nature of variable inter-correlations of hybrids compared to hypothesized parental species (Adams 1982; Ashton 1981; Flake, et al. 1978; Scagel and Maze 1984).

VI.   UNIFYING DISCUSSION.

The results presented here broadly circumscribe patterns of morphological and anatomical variation reflected in the data collected from _Picea_ in southwestern British Columbia. The interpretation of these patterns adds information to our understanding of the variation of _Picea_ in western North America. These interpretations provide both corroboration and refutation of the various assumptions and conclusions of previous research. Additionally, the interpretations for some of the results remain enigmatic with respect to various alternate hypotheses. However, these conclusions, in themselves, suggest new directions for research and experimentation that may assist in solving currently unanswerable questions. The conclusions also identify subjects and areas for more specific studies. The ambiguous nature of some of these conclusions is a reflection of not just the subject of the study in the geographic area, but also the limits of conventional systematic studies based on naturally occurring material.

In addition to contributing specific information about _Picea_ in southwestern British Columbia, the results also reflect on the taxonomy of _Picea_ of western North America and beyond. On a more theoretical level, the interpretations suggest important consequences in understanding the ecology and genetic variability of conifers. Conceptually, the results and interpretations provide important new directions for further

research aimed at integrating aspects of developmental and evolutionary biology. Intra- and inter-individual variation appears far more complex and intrinsically constrained than otherwise suggested.

1. The nature of _Picea_ in southwestern British Columbia.

The morphological and anatomical variation of _Picea_ in southwestern British Columbia suggests the existence of a single, large polymorphic taxon. However this conclusion is not unequivocal, two (perhaps three) taxa (_P. sitchensis_, _P. engelmannii_, and _P. glauca_) could be hybridized and introgressed. The major variation in the data was demonstrated to be only partially co-incident with the hypothesized taxonomic polarity. Indeed, it is possible to recognize the hypothesized taxa only arbitrarily and then only at the extremes over a broad geographic area.

These conclusions question the validity of recognizing _P. sitchensis_ and _P. engelmannii_ as discrete taxa in this area. This conclusion is not simply another manifestation of Anderson's anecdote (Stebbins 1972) concerning the statistician's inability to distinguish between individual apples and oranges. The analytic approach insures that if there is any trans-individual source of variation it will emerge. Further, if the hypothesized taxa are to be accepted and recognized then it should be remembered that they account for less variation in the data than do trees within a single population. The operational and taxonomic consequence of

accepting such comparatively large variation within a population compared to between taxa is obvious.

Regardless of the enigmatic nature of these results and any possible taxonomic circumscription, there exists a complex clinal morphological and anatomical gradient. This gradient of biological variation can be partially explained only by reference to regional and local scales of variation. Explanations for this observed pattern could be selective, however historical (genealogical and dispersal) and developmental explanations cannot be denied a priori. The immediate parentage, stand origin, nature of the maternal parent, and the immediate environment of the individual tree may all contribute to the appearance of an individual tree and the observed variability among trees.

At a broad geographic level, the higher correlation with longitude and elevation represents a major difference compared with previous research. This reflects not only differences in the intensity and areas sampled, but also the underlying assumptions of the research. With respect to the previously reported discontinuities in both P. sitchensis (Falkenhagen 1974, Daubenmire 1968, Illingworth 1976) and P. engelamannii (Daubenmire 1968), the results presented here suggest that such interpretations result from a combination of the consequences of various degrees of averaging or excluding samples (Lewis and Lines 1976) during analysis imposed on an insufficient sampling intensity and other sampling artifacts. Reliance on nursery grown materials may also have contributed to these erroneous

conclusions.

At a regional and local scale, the results presented here should be compared to other situations and specific collections should be undertaken to address these issues of scales of variation. Specifically, the results should be compared to the complex situation of morphological variation described for more northerly areas (i.e. Skeena River). Such a comparison might answer some of the questions concerning hybridization versus polymorphism brought up in this study and provide resolution of the complexity of the situation in these northerly areas.

Further collections in the southern Interior of British Columbia, especially the leeward side of the Cascades, should be made to further circumscribe the nature of variation in these areas, particularly at low elevations. Especially important would be collections aimed at addressing the nature and explanations of population variation. A particularly useful sampling design would be elevational transects with replicate populations sampled at each elevational station over a variety of environments.

More detailed collections are also required on southern and western Vancouver Island. Such collections would be necessary to address the issue of hypothesized differentiation and variability of insular populations from mainland populations of Picea (Daubenmire 1968; Falkenhagen 1977; Burley 1965a; Illingworth 1976).

The demonstration of variable local inter-correlations with

the environment serves to emphasize the extremely local nature of morphological and anatomical variation. Secondly, these results emphasize the need to consider more than just a single hypothesized source of variation in proposing explanations for local variation in spite of any theoretical disposition toward a single source.

Specific collections need to be made at the level of the population in an attempt to better understand the nature and dynamics of variation in a population. Such intensive collections should be made at the obvious extremes of the morphological continuum shown here as well as incorporating populations of high variation (i.e. Chilliwack Lake, Alta and Green Lakes, Knight Inlet, Olympic Peninsula). Such collections would require larger within-individual sampling than was possible here and would have to address inter-generation variation.

2. Reflections on the taxonomy of Picea.

The conclusions presented here refute the assumed validity of discreteness of P. sitchensis in another portion of its range. Yet inspection of Roche's (1969) results as well as research of others would suggest that this assumption should have been rejected long ago. The results presented here, although ambiguous with respect to the taxonomic circumscription of Picea in southwestern British Columbia, cleary refute the validity of this assumption for the study area.

The demonstrated comparatively large intra-individual

variation (Fig. 28) suggests that the interpretations of previous research be questioned. Especially questionable should be the paleo-botanical, -ecological, and -climatological interpretations dependent on evidence based upon the specific identification of species of _Picea_. These observations place the understanding of present and past variation of _Picea_ into question and challenge the liberal taxonomy that has been applied to _Picea_. The analytic acknowledgement of intra-individual variation may carry important ramifications with respect to any monographic treatment of _Picea_. This will be especially important with respect to understanding the systematic relation among the plethora of allopatric species of _Picea_ recognized in Asia (Schmidt-Vogt 1977; Bobrov 1971; Wright 1955).

In resolving the taxonomic issues there are several aspects which need to be addressed prior to radical nomenclatural amalgamation. First, the relation within the _P. glauca_ complex must be examined. Starting with _P. sitchensis_ and _P. engelmannii_, the relationship of the two taxa in areas of clear allopatry (i.e. southern Washington, Oregon, northern California - Fowells 1965) must be examined to determine whether the broad overlap shown here is a local phenomenon restricted to areas glaciated during the Quaternary. Porsild (cited by Garman 1957) regards the more southerly _P. engelmannii_ as being a distinct subspecies from that investigated here. Important in this regard would be a comparison of Cascade and Rocky Mtn. _P. engelmannii_. Further, the available sample size of _P. glauca_ must be expanded as the present results suggest that taxonomic

variation may only become analytically emergent with large
sample sizes over large geographic areas. Inclusion of such
materials would thus provide comparison with larger studies of
others (Wilkinson, et al. 1971; La Roi and Dugle 1968; Roche
1969) and aid in understanding the relation of P. glauca to that
shown here for P. engelmannii and P. sitchensis.

Secondly, the relation of this more northerly portion of
the P. glauca complex needs to be compared to the southerly
species: P. pungens and P. mexicana. As with the relation among
hypothesized taxa of the northerly P. glauca complex, the
relation of P. pungens and P. mexicana needs to be considered in
the broader context of "Glaucoides". In particular,
discriminant analyses produced by others with respect to this
southern complex (Taylor, et al. 1975; Taylor and Patterson
1980; Mitton and Andalora 1981) need to be re-structured in such
a manner that the a priori hypothesis of different taxa is not
forced upon the data.

Thirdly, on a circumboreal note, the remarks of Husitch
(1953) regarding the hypothesized conspecific status of the
P. abies and P. glauca complexes may be worth considering.
Lindquist's (1948) study would provide a convenient example for
comparison. Indeed, the conclusions of Lindquist (1948) with
respect to P. abies complex and the results presented here are
remarkably co-incident: a polymorphic taxon exhibiting regional
extremes; and three major forms - coastal, continental, montane.
Pravdin, et al.'s (1976) recent demonstration of β-chromosome
compliment in P. obovata, considered in the context of recent

karyological work on P. sitchensis and P. glauca (Moir and Fox 1977), provides further incentive to consider such comparisons. Especially interesting in this regard may be the materials of P. banksii (Hills and Ogilvie 1970) and their relationship to extant individuals. The extent of the materials of P. banksii would appear to be sufficient to allow for interpretations that would not be as limited by sample size as might be for interpretations based on other macrofossils.

The relationships between the various hypothesized taxa of the P. glauca complex are not the only taxonomic issues where clarification is required. The relation to P. mariana is also important to consider. First the controversy over the putative parentage of P. lutzii needs to be examined in this regard: P. sitchensis x P. glauca (Little 1953) versus the proposed P. sitchensis x P. mariana (Hultén 1968). This hypothesized relation between P. glauca complex and P. mariana may not be as esoteric as the eastern North American literature has presumed (Little and Pauley 1958; Parker and McLachlan 1978). Indeed, Morgenstern (1969a,b; 1978) does not even discuss possible relations between the two taxa in his range wide study of P. mariana. However, Fowler's studies (1983; Fowler, et al. 1980, 1982) of artifical hybrids lends credence to Kiss's (1976) and Krajina, et al.'s (1982) observations made in northern British Columbia concerning the widespread occurrence of hybrids between the two species. Roche's (1969) data also tend to corroborate the impression of a closer relation between the two species in northeastern British Columbia. Fowler's (1983) report that crosses between P. glauca and P. mariana in the

range of sympatry of the two fail, whereas wider crosses are more successfull is a particularly provocative observation worthy of more critical attention.

In short, understanding the systematics of Picea appears to call for attention to several sources of variation not frequently entertained in such studies. Specifically, intra-individual variation and large geographic scale inter-individual variation. Such sources of variation must be addressed if statements regarding the apparent lack of morphological differentiation accompanying conifer species evolution compared to Angiosperm evolution (Wright 1955; Mitton and Andalora 1981; Mitton 1983) are to be challenged. Indeed, statements indicating a lack of genetic and morphological differentiation between allopatric and sympatric species of Picea suggest that species definition problems in Picea may be an artifact of human weighting of geography over biology.

With the patterns of variation established here among individual trees, it would seem relevant to examine the applicability of the assumed co-incidence of "biological" and "morphological" species concepts in Picea. More specifically, are those trees that are indicated as being morphologically and anatomically similar, more capable of inter-breeding and producing viable offspring than those which are less similar? This type of comparison need not be conducted on the material collected for this study but could be addressed readily in some of the clonal seed orchards for Picea developed by the British Columbia Ministry of Forests where a wide variety of parents are

available. Such a comparison would address directly Wright's (1955) provocative comment suggesting that speciation in Picea has been primarily a result of geographic isolation rather than the evolution of morphological and breeding differences.

3. Sources of variation in population studies of conifers.

The largest inter-individual source of variation in this study was demonstrated to be between individuals within a population. Being the greatest source of variation suggests that this may be an evolutionarily important source of variation. This is in direct contradiction to the traditional emphasis on inter-population variation and the assumption that intra-population variation is random (Stern 1964). Further, the relative size of this source of variation is proportional to that reported in many other studies of conifer species (Guires 1984; Zobel and Talbert 1984). Regardless of whether material was naturally occurring or nursery grown and irrespective of the experimental design (provenance, family, progeny), the largest source of variation was attributed to individual trees. This pattern has been observed for morphological and anatomical variables, isoenzymes and other chemicals, growth and yield variables, and physiological variables. It is manifest with respect to single variables as well as multivariate situations.

As this hypothesized source of variation is often the residual term from an ANOVA or regression, there is usually no independent information available that might be used to serve as a possible explanation. The essential question concerning this

source of variation is whether it is simply the consequence of sexual reproduction or if there are patterns that can be attributed to other sources (i.e. maternal effects, natural selection, mating system, stand structure, vagrancies of pollination). Conventionally, this variation has been assumed to be random (Stern 1964) and its sole purpose has been to serve as a convenient denominator in an ANOVA.

Similarly, in the present study there was no information available that could be used to account for this high inter-individual variation. However, the analytic acknowledgement of inter-individual variation does provide a clearer picture of the true magnitude of this source of inter-individual variation. Further, the demonstration of local and regional correlates appears to corroborate the impression that this inter-individual variation may reflect very local conditions.

Provided that ample information is systematically collected on parents, parental environment, and position in the maternal parent that seedlings came from, a progeny trial could be used to further our understanding of the nature of intra-population variation. Picea would seem to represent a particularly good subject in this regard because of the abundance of cones produced.

The prevailing evidence indicates that even under carefully controlled and genotyped clonal and family seed orchards, the assumption of randomness is not valid (El-Kassaby, et al. 1984). Conventional provenance and progeny trials have reported some of

the highest residual sources of variation. The underlying
assumption, which may be inviable (King and Dancik 1984), has
been that offspring from one tree represent true half-sibs. In
explaining such large residual sources of variation, experiments
have been designed that focus on the relationship with the
environment or natural selection.

Other investigations have attempted to quantify the genetic
structure of stands (Linhart, et al. 1981a, b; Coles and Fowler
1976; Rehfeldt 1978, 1983; Mitton, et al. 1977). The result of
these investigations has been the predictable demonstration of
family structure within stands and consequent large departures
from panmictic equilibrium as a result of the presence of
consanguineous matings and selfing. Additionally, linkage
disequilibrium has been shown to occur over very small distances
(Mitton, et al. 1980; Rehfeldt 1979b). Such large within stand
variation observed in conifers is hypothesized to be a result of
their mating system and gene flow (Hamrick 1983; Mitton 1983).
The temporal distribution in other conifer species of viable
pollen cones and receptive female strobili combined with
vagrancies associated with wind pollination (Fowler 1965a, b, c;
Sorensen and Franklin 1977; King and Dancik 1984) complicate the
issue further.

Horton (1959) indicates different naturally occurring stand
densities of the P. glauca and P. engelmannii complex in the
Rocky Mountains, and suggests that stand history and composition
may be important in understanding the morphological variation.
Such a condition may well prove worthy of attention in the

present study owing to the markedly different stand densities
found at the extremes of the continuum shown here between
P. sitchensis (reviewed in Phelps 1973) and P. engelmannii
(reviewed in Klinka, et al. 1982).

Having presented a picture of the relation between patterns
of morphological and anatomical variation of Picea with various
scales of environmental variation it would be informative to
determine whether other conifer species growing in the same area
display parallel variation. The demonstration of such parallel
patterns of variation in evolutionarily distinct taxa could be
cited as evidence for a similar impact of natural selection
(Kung and Wright 1972). As well, the prescription of
silvicultural options and seed transfer rules might be that much
easier. Particularly interesting may be comparison to other
species, besides trees, exhibiting the same unusual increasing
elevational distribution with latitude as that demonstrated by
P. sitchensis.

4.   Ontogeny and phylogeny - the interface.

The single largest difference between the conceptual basis
of this study and other morphometric studies of Picea relates to
the rationale for incorporating intra-individual variation into
analysis and, consequently, developmental variation into
explanations. Not only does this carry pragmatic connotations
(i.e. identifying individual trees; statistical accuracy in
describing the variables for a tree), it also emphasizes the
developmental basis of systematic and evolutionary inferences

drawn from such data (see also Thorpe 1976) and the similarity
of the processes (i.e. change of variable inter-relations with
time). Morphological variation between individuals or between
taxa is also developmental variation. To be pre-disposed
towards only inter-individual variation admits either that there
is no intra-individual developmental variation, chooses to
ignore the developmental basis of inter-individual variation, or
considers intra-individual variation to reflect only size
differences (Thorpe 1976). The incorporation of
intra-individual variation preserves the developmental nature of
inter-individual variation.

Picea is a perennial organism. It must face a continual
yearly variation that may manifest itself in numerous
physiological, morphological, and anatomical alterations and
interactions. Such alterations and interactions may result in
differential fecundity or growth within a stand. This
differential between trees may be altered from one year to the
next as a consequence of cumulative changes in the individual
and the vagrancies of the environment. Differential survival in
nature may occur; however, distinguishing this from the unique
nature of reproductive events stratified in the canopy of the
maternal parent and subjected to the randomness of dispersal
would be difficult to ascertain.

With respect to the degree of intra-individual variation
shown here, studies of intra-individual variation in other
species of intra-individual variation for the same variables
would be worthwhile. Particularly important for comparative

purposes would be information concerning the degree of
intra-individual variation in species hypothesized to be
genetically depauperate, such as Pinus resinosa (Fowler
1965a,b,c; Fowler and Morris 1977)[1] and Pinus torreyana (Ledig
and Conkle 1983). As Table 3 indicates, such reports of
intra-individual variation are infrequent. Such studies would
address the relationship between the degree of inter-individual
and intra-individual variation over a wide variety of degrees of
genetic variation in many species. To date, such inter-specific
studies have not been conducted.

Attention to developmental variation may suggest that
intrinsic sources of variation may be as adequate as any
hypothesized extrinsic source in accounting for inter-individual
variation. Foremost among these would seem to be environmental
pre-conditioning (Rowe 1961) which, in its broadest sense, would
include maternal effects.

In Picea, with the female strobili scattered throughout the
upper third of the canopy and occurring on various orders of
branches, attention to such sources of variation cannot be
considered esoteric. It becomes even more of a tangible source
of variation when one considers the variability of ovules within
strobili, the temporal variation within a single canopy of ovule
maturation, and the temporal variability within the pollen pool
of the stand.

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[1] Fowler (1964) measured intra-individual variation of needle
morphology for Pinus resinosa, however the results were not
reported.

Few studies have considered any aspect of such intrinsic sources of variation. Perry (1976) calls attention to the maternal effects on height growth in _Pinus_ for the first four to eight years of growth. Similar data are provided for height growth of _P. sitchensis_ (Ching and Sziklai 1978b) as well as other species (Ching and Sziklai 1978a). Fowler's work on _Pinus resinosa_ (Fowler 1965a,b,c; Fowler and Morris 1977) and Mattson's (1979) are exemplary in directing attention to some of the aspects of spatial and temporal variation in breeding that can occur.

Attention to quantification of development in different individuals, populations, and species may offer insight into relationships between epiphenotypes not evident on the basis of mature structures. Such attention to the change of intra-individual variable inter-correlation in the context of changing inter-individual variable inter-correlations addresses directly the common process of evolution and ontogeny - changing variable inter-correlations with time. Comparison of the intra- and inter-individual variability of the variables measured here under different environments would also prove useful. Also important in this regard would be the relative variability of vegetative _versus_ reproductive variables.[1] Particularly important would be a comparison of the development of variables

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[1] The trees collected by Roche (1969) would be valuable in this regard as they are now of reproductive age (K. Illingworth, Ministry of Forests, Victoria, pers. comm.).

that have low intra-individual variation to those with high
intra-individual variation. Such comparisons may suggest
fundamental differences capable of providing an explanation for
the Kluge-Kerfoot phenomenon (Kluge and Kerfoot 1973; Rohlf,
et al. 1983; Pierce and Mitton 1979; Sokal 1976).

In conclusion, the panacea of explanations for patterns of
morphological variation may not necessarily be found in broad
environmental/ ancestral correlates. Rather contemporaneous
environment of the seedling, immediate parentage, and
relationship to the architectural complexity of the parent may
offer equally plausible explanations. Regardless, a diverse
number and kind of phenomena are hypothesized to effect the
expression and pattern of variability in conifers.

VII.   EPILOGUE: IMPLICATIONS AND APPLICATIONS FOR FORESTRY.

Forestry utilizes and manipulates patterns of natural variation. In manipulating patterns of variation an effort is made to enhance natural change. This manipulation can be accommodated directly in the short-term by silvicultural and utilization practises. Genetic manipulation through tree improvement constitutes a long-term silvicultural-dependent strategy (Zobel and Talbert 1984).

To manipulate patterns of variation presupposes knowledge of the actual variation that one is attempting to alter. Patterns of variation are identified as being of two sources: within- and between-individual trees (Powell 1980). Explanations for these patterns are intrinsic and extrinsic to the tree. Thus manipulation is intrinsic or extrinsic. The essential question concerning manipulation for forestry asks where and at what scale intrinsic and/ or extrinsic alterations to trees will maximize and provide a continued profit from a given area over a given length of time.

In this study, patterns of variation have been described and explanations offered. Assuming that the introductory remarks are an accurate reflection of the goals and objectives of forestry, then these results may have an impact on forestry. The results reflect on the present practises of silviculture, tree improvement, and utilization. More specifically, they reflect on _Picea_ forestry in southwestern British Columbia and further abroad.

1. Implications for tree improvement and silviculture.

Having made a decision concerning the scale of manipulation necessary to maximize profit from forestry, decisions are required concerning the best long-term strategy. The essential source of contention regarding these decisions concern the projected gain of productivity from either a silviculture and utilization programme compared to a tree improvement programme. Complicating this decision are matters concerning investment, profit margin, product utilization, and market (Bennett 1981).

Productivity can be defined in a number of ways but just what is altered depends upon the species concerned and the projected utilization and economic return for that species. The fundamental economic coinage has been wood quantity: height, volume, stems. Zobel (1963) and others (Denne 1976a, b) have pointed to wood quality as another important consideration in estimating productivity.

Implicit in this definition and alteration of productivity is that trees survive to a harvestable age. Without trees one does not have forestry. Such matters as frost tolerance and pathogen resistance may limit productivity and also need to be considered in forestry manipulation.

Many of the issues concerning forestry manipulation come into play with the harvest of naturally occurring forests and subsequent decisions concerning reforestation (Libby, et al. 1969). Silviculture has focused on species selection, site specific alteration and planting, subsequent pre-commercial

thinning, pruning and fertilizing, and commercial thinnings.
Utilization has focused upon composite products and reducing
dependency upon species-specific products and old growth grades.
Tree improvement forces additional concerns such as nursery
stock, seed source, and hypothesized gain. The essential demand
of tree improvement is that good seed be made available now -
not 60 years from now (Carlisle and Teich 1976). All of these
concerns are generally expressed in deriving a harvesting and
post-harvesting strategy, however they do not generally impact
on the scale of harvest (Brown and Moran 1981). The observed
high local variation of conifer species suggests that these
concerns be addressed when considering the scale of harvest. To
assume that silviculture and tree improvement alone can produce
a forest on any scale ignores the high local variation of
conifers and the impact of this variability with respect to
stand management (Adams 1981).

Genetic variation is a pre-requisite for any tree
improvement programme. Without any genetic variation for a
given variable (i.e. a monomorphic or univariate variable) there
is no reason for any selective practise. Forestry manipulation
of such a genetically invariate variable is entirely dependent
on silvicultural and utilization decisions. The presence and
organization of genetic variation is the fundamental resource of
tree improvement programmes. Except in the case of identical
twins, each individual is genetically unique. Some individuals
will be more similar to others on the basis of specific
variables as a simple consequence of the random events during
reproduction. This similarity among individuals may extend over

various geographic scales. The goal of tree improvememnt programmes is to detect that scale at which the most genetic variation exists for the variable of interest and to select desirable variations from the range of variation available at that scale. In the present study of <u>Picea</u>, as well as many other coniferous species, the largest scale of variation is within a population.

The basis of such selection are economic variables. However, as is often the case, these variables are not independent of other variables (Grant 1971; Falconer 1981). Owing to the multivariate nature of the biological system, selection on the basis of a single trait inadvertantly imposes selection on other variables. In this context it is worth pointing out that physiological and growth variables that serve as the basis for selection often are genetically complicated (Falkenhagen 1974). It is this multivariate nature of selection that is the reason for the common observation that local sources are best suited to local sites even though they may not be the most economically profitable for that site (Silen 1982).

Recent concerns have been expressed regarding the multivariate nature of selection for tree breeding programmes. Denne (1976a, b) has remarked about the need to examine the inter-correlations between quantitative variables that were the basis for selection and qualitative variables inadvertantly selected. Cannell (1974) and Rehfeldt (1983) have called attention to the role of multiple trait selection in tree improvement programmes, particularly the incorporation of

multiple trait segregates into a tree improvement programme
(Rehfeldt 1984a). Stonecypher (1969) provides an overview of
this area. Complicating the entire issue of selection is the
identification of the product that is to be selected for (Larson
1984).

Such multiple trait selection programmes attempt to insure
that the selection of individuals on the basis of yield
variables will not result in the inadvertant selection of, say,
frost intolerance. Essentially such programmes examine the
co-incidence between selection practises and naturally occurring
variation. Such practises are multivariate in nature and
respect the multivariate nature of the biological system being
investigated. Implicit in these programmes is the continual
survey, recurrent selection, and incorporation of new materials
into a tree breeding programme.

In making recommendations and incorporating materials into
tree improvement programmes, a variety of common garden tests
are used. These tests emphasize aspects of inter-individual
variation of various geographic and genealogical scales:
provenance, family, progeny. Traditionally (Adams 1981)
materials in these experiments are only from widely separated
areas. Intra-individual variation is addressed only in clonal
tests. These tests should be replicated under several different
environments (Falkenhagen 1979) owing to the
environment-specific effects of a given common garden. It
should be pointed out that such analyses of spacing trials are
generally lacking, although they fall under the rubric of

"different environments". Analyses of various variables in such tests indicates that the largest source of hypothesized variation is between trees in the residual source, however explanations are not forthcoming (Adams 1981). Experiments aimed at understanding something about this largest source of variation are infrequent. Such consistently large residual variation suggests either a common biological situation among many conifer species is not being addressed or that the experiments upon which tree improvement is based suffers from a common experimental flaw. These results suggest that the genotype-environment interactions may indeed occur but at a finer scale than previously accepted in these experiments. As genotype-environment interactions confound selection practises (Mergen, et al. 1974), such fine scale variation may be difficult to accommodate in a selection programme.

Another limitation of these experiments has been that they have been based on common garden studies of seedlings or very young trees. In North America, experiments based on trees of rotation age with known family structure have not been available (Silen 1982). First these studies on seedlings may inadequately reflect the conditions of the mature tree (Callaham and Liddicoet 1961). Where correlations between variables of mature and immature trees have been calculated, the relation is generally small (Libby, et al. 1969). Secondly, the demonstration of large maternal effects in some variables suggest that ignorance concerning parentage, especially in provenance trials, is inadequate for tendering explanations about observed patterns of inter-individual variation. Thirdly,

inadvertant selection and ameleoration during growth in a
nursery may represent inaccurately the conditions of the parents
or that of the plantation into which the seedlings will
ultimately be placed.

Such considerations question the assumed efficacy of the
traditional selection procedures (Morgenstern 1980) in a forest
tree improvement programme. This questioning concerns both the
long term and short term projected gains and the ability to meet
demands. It would seem that after 200 years of applied
genecology in forestry (Langlet 1972) that such questions would
be entertained (see also Lester 1982).

2. Implications for _Picea_ forestry.

Species of _Picea_ constitute the largest commercial tree
species in British Columbia and the boreal region.
P. sitchensis is a major reforestation and aforestation species
species in western Europe. In respect to the economic
importance of _Picea_, the results presented above for
southwestern British Columbia should be considered carefully as
they may provide an understanding for the local management of
naturally occurring _Picea_ in southwest British Columbia and
faciliate incorporation into current silvicultural and tree
improvement programmes. Further, they may provide insight into
the care and maintenance of plantations of _P. sitchensis_ in
western Europe.

The results are suggestive of new sources of variation
previously unreported for the genus. These new sources should

be more fully evaluated (Klinka, et al. 1982) for their silvicultural potential and utilization. With respect to aforestation and reforestation interests in P. sitchensis, present provenance studies (i.e. I.U.F.R.O.) should be expanded to include more inland sources of P. sitchensis and adjacent representatives of P. glauca and P. engelmannii. Such information would be of interest in Europe (Dietrichson 1971) as well as in Canada (Khalil 1976; Rauter 1976). Such elaborated provenance studies could increase information concerning utilization of different provenances. As well, incorporation of such additional materials into a breeding programme for seed production might yield enhanced vigor or other qualities from inter-provenance hybridization (Orr-Ewing 1966; Rehfledt 1977; Ying 1978; Nilsson 1963; Morgenstern 1974) or inter-specific hybridization (Lester 1974). Such utilization could prove to be a valuable adjunct to the experimental designs already in existence.

Owing to the local scarcity of naturally occurring Picea in some regions of the study area and other areas of its native range as a result of logging and leader weevil infestation (Pissodes sitchensis), incorporation of veterans and small isolated populations in a clonal orchard could provide seed for these areas where Picea is not generally considered as a silvicultural option owing to the lack of a local seed source or the potential for poor seedling quality resulting selfing and inbreeding (Franklin 1970; Samuel, et al. 1972). The present high elevation spruce grafting project at Chilliwack Lake[1] represents such a clonal situation

into which scions from such veterans could be placed. Breeding such materials in a clonal orchard could avoid the hypothesized poor seedling quality expected from naturally collected seed resulting from selfing.

Owing to the desirability of primary successional tree species as elements of a silvicultural programme and the nature of its wood, Picea represents an under-utilized forest resource on this part of the coast. The demonstration here of clinal variation suggests the possibility of broader application, especially onto drier sites where P. sitchensis is not normally found. However, the cost of such an undertaking needs to be carefully weighed in relation to the expected profit and alternate species and silvicultural options for a given site. The demonstration of trends is necessary but not sufficient to recommend the broader application of Picea in the coastal forestry without testing. Tests, such as those of Armit (1969), should be carefully monitored and interpretations based on the wider relations shown here. Tests of the assumed efficacy of the results of selection should also be devised (i.e. parallel selection of non plus-tree trees, multiple test environments, and maternal effects).

An immediate concern with respect to the results presented here is how well the pattern of morphological and anatomical variation corresponds with the various physiological and economic traits by which individuals have been selected. Such a

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[1] Ulf Bitterlick; British Columbia Ministry of Forests

comparison is critical to understanding whether the prevailing selection practises are currently co-incident with any prevailing pattern of natural variation shown here.

Secondly, the relationship of the scattered veterans and small populations may provide important information concerning the understanding of the polymorphic variation demonstrated. Such materials are likely to prove to be multiple trait segregates from the major trend of variation and may be potentially useful in a breeding programme (Rehfeldt 1984a).

An important aspect to recognize in any selection programme is the high variability within populations and the possible consequences of environmental preconditioning. _Picea_ in southwestern British Columbia is no exception and this variability should be acknowledged. Such results suggest that selection and designation of seed zones is liable to require very specific local sampling and testing prior to tendering recommendations concerning the utilization of _Picea_. The work of Rehfeldt (1978; 1979a,b; 1983; 1984a, b) is particularly instructive with respect to addressing intra- and inter-population variation and incorporating these results into a tree improvement programme. For _Picea_, these recommendations will probably be fairly site and region specific owing to the high variation encountered at this scale.

3. Suggestions for independent studies and collections.

The taxonomic circumscription of the situation in southwestern British Columbia, from a forestry perspective, is a non sequitor. It makes no difference what taxon a tree belongs to provided that the continuum of variation is recognized and that the extremely local nature of variation is addressed in planning for the utilization of Picea.

In spite of the ambiguity of the present results with respect to the taxonomic circumscription by P. sitchensis or P. engelmannii, there is a need to relate the results presented here to the entrenched segregation of the two taxa by foresters. That certain places in the morphological and anatomical continuum described here have been accorded specific status and given nomenclatural recognition may serve as a convenient marker along this scale of variation - just as inches may be a more convenient marker than cm.

The retention of the hypothesized taxonomic circumscription in the results should aid in the interpretation. Additionlly, the univariate results reported in Appendix III for individual variables may aid in designing independent studies. Table 36 provides a summary of the redundancy and contribution to the total dispersion of samples (see Orlóci 1973, 1975, 1978; Green 1972; Beshir 1975) which could aid in selecting variables for an independent study.

Table 36 suggests that in an assessment of an independent collection based on PCA only three variables need be considered:

Table 36.   Ranking of variables on a dispersion criterion and redundancy
       analysis.   Based on mean variable values for individual trees.

	%SS	%Redundancy
NEEDWID	12.47	99.45
NEEDEP	0.03	98.83
ABXANG	0.35	88.12
ADXANG	0.84	79.37
CENCYWID	0.28	95.02
CENCYLAT	0.02	99.35
CENCYABX	29.86	96.89
CENCYADX	0.45	95.51
ENDONUM	3.10	80.10
PHLEND	0.48	87.17
XYLEND	0.68	87.05
NEEDLEN	1.85	48.35
ADXSTOM	0.52	83.60
ABXSTOM	0.96	69.08
RESCYNO	1.20	66.26
RESCYLOC	1.68	50.56
RESCYLEN	4.40	56.87
PULVLEN	4.49	59.65
TIPWID	0.36	87.18
TIPDEP	1.85	81.99
PULVPUB	0.96	73.64
CONLEN	0.24	91.86
CONWID	0.46	86.31
SCALEN	13.14	86.38
SCALWID	0.27	91.74
SCALTAP	1.91	92.02
WINGWID	3.57	90.23
WINGTAP	1.48	75.44
FREESCAL	0.20	92.88
BRACTLEN	1.12	91.75
BRACTWID	1.64	56.60
BRACTAP	0.24	92.21
SHCOLEN	2.44	77.39
SHCOWID	1.23	76.89
LOCOLEN	1.17	87.21
LOCOWID	4.08	74.83

NEEDWID, CENCYABX, and SCALEN.   These three variables account

for 56 percent of the total dispersion in the data available for

this study.   Table 36 indicates only one variable, NEEDLEN, had

a specific variance that exceeded its common or shared variance

with the other 35 variables.   Most of the variables have a

redundancy of over 80 percent, suggesting a highly

inter-correlated group of variables.   Twelve variables have a

redundancy of less than 80 percent: ADXANG, RESCYNO, RESCYLEN,

RESCYLOC, PULVLEN, PULVPUB, WINGTAP, and the variables describing cone collection. This would suggest that virtually any single variable could be used in a multiple regression against some indepedent variable. In CCA, the twelve variables with the lowest redundancies would be preferable as this would reduce the amount of intra-set redundancy which may limit performing a CCA (Gittins 1979).

In order to facilitate the comparison of the results presented here with any subsequent independent collection, the coefficients and variable values necessary for assigning an independently collected tree to the results presented here are given in Table 37. Table 37 includes coefficients based on several different PCAS. The PCAs differ in the number of variables used and reflect the differing measuring and collecting technques available to potential users. Ideally, one would want to collect as much information as possible, however where this is not possible the co-incidence of the results of these separate PCAs is given in Table 38 and the ordinations based on these analyses are given in Figure 29.

To use the coefficients given in Table 37 an algorithm based on a similar one given in Chatfield and Collins (1981) is provided. It should be remembered that the input values to the algorithm are means of individual trees based on intra-individual samples. Sample sizes used should be in accordance with those listed in Table 10. Actual measurements and measuring should correspond as closely as possible to those given in Appendix I.

Table 37. Coefficients (a_i) for variables used in various PCAs. TOTAL - all variables; CONES - all cone variables; BEST - variables accounting for the largest sums of squares (Table 36); VEG - all vegetative variables; LEAF ANAT. - all leaf anatomy; LEAF MOR - available vegetative morphology. All values based on means for individual trees. Abbreviations given in algorithm in text.

| VARIABLES | MEAN | SD | RANGE | TOTAL | CONES | ANALYSES (a_i) BEST | VEG | LEAF MOR. | LEAF ANAT. |
	($\bar{x}_g$)	(sd_g)		(p=36)	(p=11)	(p=3)	(p=21)	(p=5)	(p=11)
NEEDWID	0.817	0.203	0.268 - 1.37	.087		.636	-.109		.118
NEEDEP	0.674	0.132	0.384 - 0.98	-.248			.327		.399
ABXANG	107.20	25.95	37.00 - 165.4	.230			-.283		-.135
ADXANG	62.00	21.97	20.00 - 116.4	.180			-.217		-.065
CENCYWID	0.148	0.03	0.061 - 0.232	-.143			.196		.357
CENCYLAT	0.254	0.071	0.088 - 0.441	.125			-.156		.058
CENCYABX	0.161	0.044	0.076 - 0.254	-.254		-.722	.332		.335
CENCYADX	0.220	0.041	0.124 - 0.324	-.227			.288		.352
ENDONUM	17.60	2.82	11.40 - 27.8	-.165			.243		.360
PHLEND	0.042	0.012	0.015 - 0.079	-.201			.274		.394
XYLEND	0.030	0.010	0.006 - 0.060	-.191			.269		.389
NEEDLEN	19.30	4.09	9.40 - 31.8	-.012			.035	.011	
ADXSTOM	10.80	3.75	4.20 - 29.2	.212			-.237	-.559	
ABXSTOM	4.00	1.85	0 - 11.6	-.201			.255	.416	
RESCYNO	1.50	1.22	0 - 5.8	-.141			.123	.374	
RESCYLOC	2.1	2.55	0 - 11.80	-.172			.200		
RESCYLEN	1.7	2.04	0 - 15.58	-.064			-.040		
PULVLEN	5.60	2.00	2.30 - 13.2	.087			-.108		
TIPWID	0.86	0.19	0.50 - 1.9	.090			-.094		
TIPDEP	0.66	0.09	0.40 - 1.0	-.056			.081		
PULVPUB	0.46	0.49	0 - 1	-.219			.293	.612	
CONLEN	51.90	8.70	28.40 - 84.80	.194	.320				
CONWID	15.50	1.96	11.20 - 22.20	.154	.293				
SCALEN	14.60	1.67	9.50 - 19.4	.106	.309	.273			
SCALWID	8.60	1.22	5.60 - 12.07	-.128	.007				
SCALTAP	6.90	0.95	4.50 - 10.0	.042	.226				
WINGWID	6.90	0.77	4.60 - 9.1	-.076	.056				
WINGTAP	3.30	0.38	2.10 - 4.3	.121	.260				
FREESCAL	4.40	0.91	1.90 - 7.5	.062	.229				
BRACTLEN	7.20	1.45	3.70 - 11.0	.247	.301				
BRACTWID	2.50	0.35	1.50 - 3.5	.176	.264				
BRACTAP	3.50	1.15	1.40 - 6.6	.247	.279				
SHCOLEN	39.80	7.89	22.00 - 69.00	.182	.289				
SHCOWID	14.00	2.51	8.00 - 25.00	.158	.259				
LOCOLEN	61.90	10.73	31.00 - 96.00	.202	.295				
LOCOWID	16.30	2.25	10.00 - 26.00	.128	.257				

Table 38. Correlation amongst PCAs given in Table 37. *, correlation
significant @ p ≤ 0.01.

```
TOTAL           .---
CONES           .764*     .---
"BEST"          .858*     .649*    .---
VEGETATIVE     -.939*    -.514*   -.782*    .---
AVAILABLE
  VEGETATIVE   -.912*    -.533*   -.998*   .924*    .---
LEAF
  ANATOMY      -.822*    -.421*   -.531*   .924*    .763*    .---

                 T          C        B       V        AV       LA
```

Trees with individual variable values exceeding the range given

in Appendix I or means exceeding the range shown in Table 37

cannot have reliable scores calculated. The algorithm is:

1) Measure p variables as in Appendix I giving a vector $\underline{x}_j$,

   where:

   $$\underline{x}_j = [\ x_1,\ldots,\ x_i,\ldots,\ x_p].$$

2) Average all $\underline{x}_j$ for a tree based on sample size in Table 10,

   yielding a vector:

   $$\underline{x}_m = [\ \overline{x}_1,\ldots,\ \overline{x}_i,\ldots,\ \overline{x}_p].$$

3) Calculate z-scores, z_i, in vector $\underline{z}_m$ by:

   $$z_i = (\overline{x}_i - \overline{x}_{gi})/ sd_{gi}.$$

   where $\overline{x}_{gi}$ and sd_{gi} are given in Table 37; and:

   $$\underline{z}_m = [\ z_1,\ldots,\ z_i,\ldots,\ z_p].$$

4) Calculate component scores, c_m, by:

$$c_m = \sum_{i=1}^{i=P} (z_{im} \times a_{gi}).$$

where a_{gi} given in Table 37.

5) Compare c_m to appropriate scale.

In addition to being used to refer independent collections to a hypothesized taxon, Figure 29 also provides reference to particular biogeoclimatic zones. One could have used seed collection zones (Bower 1982) or for that matter any other political or administrative boundary. As the biogeoclimatic framework is based on associated forest trees and inferred climate and environment it serves as an ecological basis upon which intensive forest management is being conducted. Further, being ecologically based it takes into account elevational variation of vegetation and environment and is thus independent of more political and administrative boundaries. Owing to the extent of sampling, smaller geographic and ecological classifications seemed inappropriate. It is hoped that the simplicity of the algorithm and auxiliary information will prove to be motivating and informative.

Figure 29. Ordination of means, standard deviations, and ranges of
first component scores for a priori identifications and
biogeoclimatic zones. Scores based on coefficients in Table 37.
First components given in Figures 22 and 23 correspond to the
components for TOTAL, CONES, and LEAF ANATOMY here. Note that all
values based on means for individual trees.
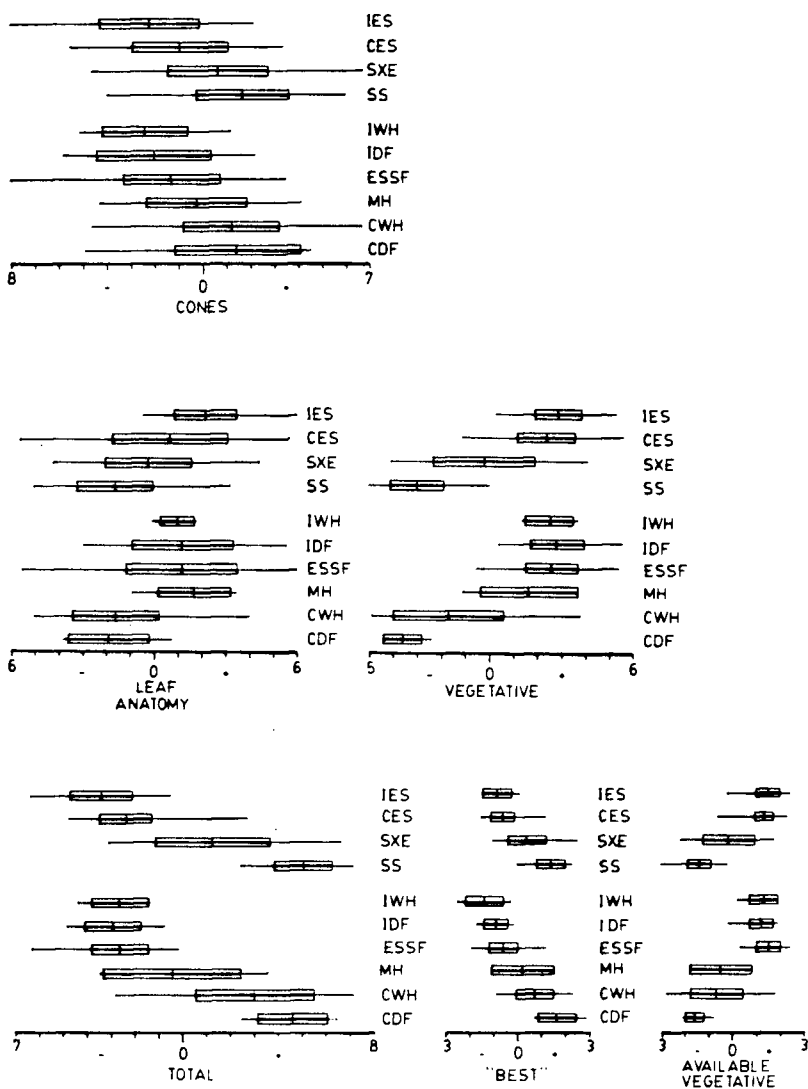
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Appendix I. Description of variables and variable suites.
    Measurement accuracy, range, standard deviation, and mean
    given parenthetically. Range, standard deviation, and mean
    given for all samples in the study area. All measurements
    made directly from objects or projected images rather than
    photographs (Roche 1969; Garman 1957).

VARIABLE SUITE: cone collections.

    Cones were collected from around the base of individual
trees. In order to be sampled there had to be at least five
cones collected from the individual tree. In the laboratory only
those cones were used that belonged to the most recent cone
crop. Prior to measuring, the longest cone (LOCO...) and
shortest cone (SHCO...) were selected and boiled. All
measurements were made on wet cones with a flexible plastic
ruler incremented in mm.

1. LOCOLEN - length of the longest cone in collection. Measured
    by placing long axis of the cone parallel to the ruler and
    recording length from tip of apical-most scale to base of
    basal-most scale.
    (+/- 0.5mm; range: 31 - 96; mean: 61.9; standard deviation:
    10.7).

2. LOCOWID - maximum width of the longest cone in collection.
    Measured by placing long axis of the cone perpendicular to
    the ruler and recording the width at the widest portion.
    (+/- 0.5mm; range: 10 - 26; mean: 16.3; standard deviation:
    2.25).

3. SHOCOLEN - length of the shortest cone in collection. Same as
    LOCOLEN but measured on smallest cone in collection.
    (+/- 0.5mm; range: 22 - 69; mean: 39.8; standard deviation:
    7.89).

4. SHOCOWID - maximum width of the shortest cone in collection.
    Same as LOCOWID but measured on smallest cone in
    collection.
    (+/- 0.5mm; range: 8 - 25; mean: 14.0; standard deviation:
    2.51).

VARIABLE SUITE: cone, cone scale, and bract morphology.

    Following selection of cones that belonged to most recent
cone crop, 5 cones were selected at random. These cones were
boiled until the scales became appressed and the cones sank
(Taylor 1959). Measurements on whole cones were conducted while
cones were still wet and in a manner similar to that above for
the cone collection suite. Following measurement of whole cones,

cones were cut in half and the first five whole scales and attached bracts immediatly above this cut were removed and placed in a plant press to remove scale curvature (Daubenmire 1968). Selection of scales from this medial position avoids the intra-cone variation described by Garman (1957; see also Meagher 1976). Following drying these scales and attached bracts were measured with either a flexible plastic ruler incremented in mm, or an ocular micrometer in the eye-peice of a dissecting microscope at 9.5x magnification.

1. CONLEN - length of cone. Same as SHCOLEN and LOCOLEN but measured on each cone to be dissected.
   (+/- 0.5mm; range: 20 -95; mean: 51.3; standard deviation: 10.9).

2. CONWID - Same as CHCOWID and LOCOWID but measured on each cone to be dissected.
   (+/- 0.5mm; range: 8 - 31; mean: 15.8; standard deviation: 2.6).

3. SCALEN - maximum length of cone scale. Measured by placing long axis of the scale parallel to the ruler and recording length from base to the tip. If scale is bifid then measurement made to the tip of the longer prong. Measured while observing outer surface of the scale.
   (+/- 0.5mm; range: 8 - 24; mean: 14.8; standard deviation: 2.2).

4. SCALWID - maximum width of cone scale. Measured perpendicular to the long axis of the scale for maximum width. If scale not symmetrical then measurement made to consider absolute maximum width. Measurement made while observing inner surface of the scale.
   (+/- 0.05mm; range: 4.9 - 13.9; mean: 8.6; standard deviation: 1.4).

5. SCALTAP - scale taper. Measured parallel to the long axis of the scale from the maximum width to the tip of the scale. If the scale is asymmetric for maximum width, then the point of reference is taken as the average position between the two widths. Measurements made observing inner surface of the scale.
   (+/- 0.05mm; range: 0.5 - 12.5; mean: 6.9; standard deviation: 1.3).

6. WINGWID - maximum width of seed wing impressions. Measured perpendicular to the long axis of the scale at the widest portion of the wings. If wing impression asymmetric for maximum width, then the point of reference is taken as the average position between the two widths.
   (+/- 0.05mm; range: 2.9 - 10.1; mean: 6.8; standard deviation: 1.0).

7. WINGTAP - taper of seed wing impression. The distance
    parallel to the long axis of the scale between the tip of
    the seed wing impression and the widest portion of the wing
    impression.
    (+/- 0.05mm; range: 1.2 - 6.2; mean: 3.3; standard
    deviation: 0.6).

8. FREESCAL - freescale length above seed wing impression. The
    distance from the tip of the seed wing impression to the
    tip of the scale. Measured parallel to the long axis of the
    scale.
    (+/- 0.05mm; range: 0.9 - 8.6; mean: 4.6; standard
    deviation: 1.2).

9. BRACTLEN - maximum bract length. The distance from the tip of
    the bract to the base of the bract, the point at which the
    bract fuses with the scale.
    (+/- 0.05mm; range: 1.9 - 12.5; mean: 7.1; standard
    deviation: 1.5).

10. BRACTWID - maximum bract width. Measured perpendicular to
    the long axis of the bract at the widest portion of the
    bract. If bract is asymmetric measure as for SCALWID.
    (+/- 0.05mm; range: 1.0 - 4.4; mean: 2.5; standard
    deviation: 0.4).

11. BRACTAP - bract taper. Measured parallel to the long axis of
    the bract and similar to SCALTAP.
    (+/- 0.05mm; range: 0.85 - 8.0; mean: 3.5; standard
    deviation: 1.2).

VARIABLE SUITE: leaf anatomy.

   Needles were stripped from the middle portion of a two year
old increment and allowed to dry. Needles were rehydrated in
boiling water, passed through an tert-butyl alchol series, then
imbedded in Paraplast. Prior to orientation in wax blocks, five
needles were selected and cut in half. 20 m sections were made
with a rotary microtone, and stained in safrannin and fast green
schedules (Johansen 1940). Sectioning was started at the cut end
of the basal half of the needle and proceeded distally. Owing to
the highly sclerified hypodermis, 20 m sections were preferred
as this thickness avoided the shattering and distortion found in
thinner sections. A repeatability study indicated that with the
preparative techniques used here that 20 m was the thinnest
sectioning that could be measured without introducing
substantial error in measurement due to this shattering and
distortion.

   Measurements made directly from the projection head of a
Zeiss Ultraphott II photomicroscope with a flexible plastic
ruler. NEEDWID, NEEDEP, ABXANG, ADXANG observed at 100x
magnification; CENCYWID, CENCYLAT, CENCYABX, CENCYADX, ENDONUm
observed at 330x magnification; PHLEND, XYLEND observed at 1000x
magnification.

1. NEEDWID - <u>needle width</u>. Maximum width of the needle without respect to the curvature of the leaf. Measured parallel to the vascular cambium of the central cylinder.
(+/- 0.005mm; range: 0.22 - 1.69; mean: 0.87; standard deviation: 0.24).

2. NEEDEP - <u>needle depth</u>. Maximum depth of the needle without respect to the curvature of the leaf. Measured perpendicular to NEEWID and parallel to the central ray of the phloem.
(+/- 0.005mm; range: 0.11 - 1.11; mean: 0.67; standard deviation: 0.14).

3. ABXANG - <u>angle of abaxial surface of needle</u>. Measured for the central portion of the leaf and, depending upon the shape of the transition between the central portion of the leaf and margins, may extend on to the margins of the leaf
(+/- 5°; range: 20 - 175; mean: 112.7; standard deviation: 29.5).

4. ADXANG - <u>angle of adaxial surface of needle</u>. The same as for ABXANG but on the opposite surface of the leaf.
(+/- 5°; range: 15 - 160; mean: 67.4; standard deviation: 28.4).

5. CENCYWID - <u>maximum width of central cylinder</u>. Measured from the outer surface of the endodermis to the outer surface of the endodermis parallel to the vascular cambium of the central cylinder.
(+/- 0.0025mm; range: 0.054 - 0.279; mean: 0.15; standard deviation: 0.033).

6. CENCYLAT - <u>maximum distance from central cylinder to needle margin</u>. The largest distance from the outer surface of the endodermis to the margin of the leaf parallel to the vascular cambium of the central cylinder.
(+/- 0.0025mm; range: 0.081 - 0.57; mean: 0.273; standard deviation: 0.083).

7. CENCYABX - <u>distance from central cylinder to abaxial surface of needle</u>. Distance from the outer surface of the endodermis to the abaxial surface of the leaf. Measured parallel to the central ray of the phloem.
(+/- 0.0025mm; range: 0.054 - 0.282; mean: 0.155; standard deviation: 0.047).

8. CENCYADX - <u>distance from central cylinder to adaxial surface of needle</u>. Same as for CENCYABX but on opposite side of the central cylinder.
(+/- 0.0025mm; range: 0.042 - 0.369; mean: 0.217; standard deviation: 0.046).

9. ENDONUM - <u>number of endodermal cells</u>. Number of endodermal
    cells constituting the endodermis in cross-section.
    (+/- # ; range: 10 - 40; mean: 17.8; standard deviation:
    3.3).

10. PHLEND - <u>distance from outer periphery of phloem to inner</u>
    <u>surface of endodermis</u>. Distance from the phloem to the
    inside of the endodermis, measured parallel to the central
    ray of the phloem.
    (+/- 0.0005mm; range: 0.012 - 0.092; mean: 0.043; standard
    deviation: 0.013).

11. XYLEND - <u>distance from outer periphery of xylem to inner</u>
    <u>surface of endodermis</u>. Same as for PHLEND but for xylem
    pole of vascular bundle.
    (+/- 0.0005mm; range: 0.003 - 0.082; mean: 0.030; standard
    deviation: 0.012).

VARIABLE SUITE: leaf morphology.

Needles were stripped from the middle portion of a two year
old increment. Needles examined when dry except where the
needles were highly curved and twisted. If needles were
contorted then they were soaked for half and hour in warm water
to facilitate manipulation during measurement. Measurements made
with a flexible plastic ruler incremented in mm and an ocular
micrometer in the eye-peice of a dissecting microscope at 9.5x
magnification.

Measurements made on the resin cysts were made by holding
the needle up to a bright light source and rotating the needle
till it was oriented in such a manner that the resin cyst
refracts the incident light. When correctly oriented, the resin
cyst will appear to "glow". The extent of the resin cyst was
delimited by scribing the surface of the leaf with a razor
blade.

1. NEEDLEN - <u>needle length</u>. Measured from the tip of leaf to the
    base when the needle pressed flat and straight.
    (+/- 0.5mm; range: 7 - 39; mean: 18.6; standard deviation:
    4.7).

2. ADXSTOM - <u>maximum number of stomatal rows on the adaxial</u>
    <u>surface of the needle</u>. Measured as the maximum number of
    stomatal rows across the adaxial surface of the leaf at any
    one spot.
    (+/- # ; range: 2 - 31; mean: 11.0; standard deviation:
    4.0).

3. ABXSTOM - <u>maximum number of stomatal rows on the abaxial</u>
    <u>surface of the needle</u>. Same as for ADXSTOM but on opposite
    surface.
    (+/- # ; range: 0 - 19; mean: 3.9; standard deviation:
    2.1).

4. RESCYNO - <u>number of resin cysts in the needle</u>. Total number
   of resin cysts in the leaf.
   (+/- # ; range: 0 - 7; mean: 1.5; standard deviation: 1.3).

5. RESCYLOC - <u>average distance from needle base to base of resin</u>
   <u>cyst</u>. The distance from the base of the leaf to the base of
   the resin cysts. All resin cysts measured in the leaf then
   averaged for that leaf.
   (+/- 0.05mm; range: 0 - 21.3 mean: 2.84; standard
   deviation: 3.30).

6. RESCYLEN - <u>average length of resin cyst in the needle</u>. The
   distance from the base to the tip of the individual resin
   cyst. All resin cysts measured then averaged for that leaf.
   (+/- 0.05mm; range: 0 - 17.2; mean: 2.03; standard
   deviation: 2.16).

VARIABLE SUITE: twig morphology.

   Five sequential pulvini (de Laubenfels 1953; = leaf
cushion, Dalgas 1973) selected in the middle portion of a two
year old increment. Pulvini adjacent to or abutting buds or
lateral branchlets were not measured.

   Measurements made with an ocular micrometer in the
eye-piece of a dissecting microscope.

   PULVLEN measured at 9.5x magnification, all other variables
measured or observed at 33x magnification.

1. PULVLEN - <u>length of pulvinus</u>. Distance from the base to the
   tip of the pulvinus along the surface of the stem. Owing to
   curvature of the stem the twig may have to be rotated to
   finish the measurement. The tip of the pulvinus may be
   obscured by the sterigmata.
   (+/- 0.05mm; range: 1.7 - 13.9; mean: 5.4; standard
   deviation: 2.0).

2. TIPWID - <u>width of sterigmata tip</u>. Measured on the face of the
   sterigmata where the leaf abscisized parallel to the width
   of the pulvinus
   (+/- 0.025mm; range: 0.43 - 1.8; mean: 0.82; standard
   deviation: 0.17).

3. TIPDEP - <u>breadth of sterigmat tip</u>. Same as for TIPWID but
   perpendicular to width of the pulvinus.
   (+/- 0.025mm; range: 0.34 - 0.99; mean: 0.62; standard
   deviation: 0.09).

4. PULVPUB - <u>pulvinus pubescence</u>. Recorded regardless of
    density, position, or glandulosity. Generally if pubescence
    present, hairs will be found along the lateral margins of
    the sterigmata or in the furrows of the pulvinus. More
    densely pubescent twig will have hairs across the surface
    of the sterigmata and the pulvini. If pubescence present,
    invariably some hairs will be glandular.
    (presence/absence; range: 0 - 1; mean: 0.41; standard
    deviation: 0.49).

VARIABLE SUITE: twig anatomy.

    Preparation of twigs for sectioning and staining followed
that outlined for needle anatomy. None of the measurements were
made in the vicinity of a leaf trace.

    Like leaf anatomy, all measurements made directly from the
projection head of a Zeiss Ultraphott II photomicroscope with a
flexible plastic ruler. All variables measured at 100x
magnification.

1. PITHDIA - <u>maximum diameter of pith</u>. Maximum width of the pith
    measured through the center of the pith.
    (+/- 0.005mm; range: 0.08 - 1.12; mean: 0.43; standard
    deviation: 0.20).

2. CORTHIK - <u>maximum thickness of cortex</u>.
    (+/- 0.005mm; range: 0.06 - 0.52; mean: 0.192; standard
    deviation: 0.69).

3. PERITHIK - <u>maximum thickness of periderm</u>. Measured through
    the pulvinus, not through the sterigmata.
    (+/- 0.005mm; range: 0.05 - 0.43; mean: 0.190; standard
    deviation: 0.71).

4. VBTHIK - <u>maximum thickness of vascular bundle</u>.
    (+/- 0.005mm; range: 0.09 - 0.78; mean: 0.263; standard
    deviation: 0.118).

Appendix II. Location and disposition of individual trees and populations of trees. Locations given for Chilliwack R. Nursery saplings that of the parents. Locations given for Red Rock Nursery saplings that of the maternal parents. TREE - sample number. ID - identification: SSS - P. sitchensis standard; SSP - P. sitchensis putative; SXE - "hybrid"; ESP - P. engelmannii putative; ESS - P. engelmannii standard; IESP - P. engelmannii putative, Monashee Mtns.; IESS - P. engelmannii standard, Monashee Mtns.; WSS - P. glauca standard; NBSEX - New Brunswick controlled hybrid; RRSXE - Red Rock controlled hybrid; SSSS - south coastal P. sitchensis standard. ELEV - elevation (mASL). LONG - longitude(°). LAT - latitude(°) BGCZ - Biogeoclimatic zone (Table VI): CDF coastal douglas-fir zone; CWH - coastal western hemlock zone; MH - mountain hemlock zone; ESSF - engelmann spruce subalpine fir zone; IDF - interior douglas-fir zone; IWH - interior western hemlock zone. MOIST - relative moisture availability (Table V): XERIC; SXERIC - subxeric; SMESIC - submesic; MESIC; SHYGR - subhygric; HYGRIC. GEOG - geographic areas (Fig. 6, Table VIII): 1 - SVANCI; 2 - HOWHIS; 3 - LOFRAV; 4 - TOBA; 5 - BUTE; 6 - KNIGHT; 7 - NVANCI; 8 - CHILLI; 9 - HOPLYT; 10 - PEMBRA; 11 - HOPMAN; 12 - MANPRI; 13 - OKAN; 14 - MTREV; 15 - ROGPAS; 16 - MICA. SUITES - variable suites for each tree: C - cone; L - leaf anatomy; P - twig morphology; N - leaf morphology.

TREE	ID.	ELEV	LONG	LAT	BGCZ	MOIST	GEOG	SUITES	LOCATION
						SINGLE TREES			
1	SXE	690	122.92	50.17	CWH	HYGRIC	2	CLPN	Green L., N of Whistler.
2	SXE	700	122.92	50.17	CWH	SHYGR	2	CLPN	Mons Wye, N of Whistler.
3	SXE	710	123.00	50.08	CWH	XERIC	2	CLPN	Alta L. E side, Whislter.
4	SXE	700	122.99	50.08	CWH	SHYGR	2	CLPN	Whistler townsite.
6	SXE	350	123.00	49.92	CWH	MESIC	2	CLPN	Garibaldi Station, S of Whislter.
7	SSP	50	123.25	49.83	CWH	SHYGR	2	CLPN	Squamish R. at Cheekeye.
8	SXE	320	123.00	49.75	CWH	SHYGR	2	C	Jct. Raffuse C. and Mamquam R.
9	SSP	10	123.17	49.67	CWH	SHYGR	2	C	Squamish, Dike Rd.
11	SSS	40	123.25	49.25	CWH	SHYGR	3	C	UBC Endowment lands.
12	SSS	5	123.06	49.17	CWH	SHYGR	3	CLPN	Steveston, Richmond.
13	SSS	20	122.83	49.25	CWH	MESIC	3	C	E. end Burrard In., Ioco.
14	SSP	50	122.59	49.25	CWH	SHYGR	3	CLPN	Jct. N. Alouette and Alouette R.
15	SSP	200	122.33	49.17	CWH	SHYGR	3	C	Silverdale C., NW of Mission.
16	SSP	85	122.00	49.08	CWH	HYGRIC	8	CLPN	Vedder R., N of Cultus L.
17	SSP	50	121.75	49.25	CWH	SHYGR	8	C	Harrison L.
18	SSP	70	121.75	49.17	CWH	SHYGR	9	CLPN	Bridal Falls, E of Hope.
19	SSP	60	121.59	49.33	CWH	SHYGR	9	CLPN	Ruby C., W of Hope.
20	SXE	1100	121.75	49.08	MH	SMESIC	8	CLPN	Borden C., Mt. McGuire, Chilliwack V.
21	SXE	1100	121.75	49.08	MH	HYGRIC	8	CLPN	Borden C., Mt. McGuire, Chilliwack V.
22	SXE	1200	121.75	49.08	MH	SHYGR	8	C	Borden C., Mt. McGuire, Chilliwack V.
23	SXE	1080	121.50	49.00	CWH	SHYGR	8	CLPN	Nesakwatch C., Chilliwack V.
24	SXE	700	121.50	49.00	CWH	SHYGR	8	C	Nesakwatch C., Chilliwack V.
25	SXE	890	121.50	49.00	CWH	SHYGR	8	CLPN	Centre C., Chilliwack V.
32	SXE	810	121.33	49.00	CWH	SHYGR	8	CLPN	Depot C., Chilliwack V.
33	SXE	910	121.54	49.75	CWH	SMESIC	8	C	Foley C., Chilliwack V.
34	ESP	1200	121.25	49.08	MH	SHYGR	11	CLPN	Maselpanik C., lower Skagit V.
35	ESP	1190	121.25	49.00	CWH	SHYGR	11	C	Maselpanik C., lower Skagit V.
36	SXE	0600	121.25	49.08	CWH	SHYGR	11	CLPN	Maselpanik C., lower Skagit V.
37	SXE	0530	121.06	49.00	IDF	SHYGR	11	CLPN	Skagit R., Ross L. Rd.
38	SXE	570	121.17	49.08	IDF	MESIC	11	CLPN	Skagit R., Ross L. Rd.
39	SXE	640	121.33	49.17	CWH	SHYGR	11	CLPN	Skagit R., Ross L. Rd.
40	SXE	770	121.25	49.25	CWH	HYGRIC	11	C PN	Sumalo R., Hwy. 3.
41	SXE	700	121.25	49.25	CWH	HYGRIC	11	CLPN	West Gate, Manning Pk.
42	SXE	730	121.17	49.17	CWH	SHYGR	11	LPN	Sumalo R., Hwy. 3.
43	SXE	650	121.06	49.17	CWH	SHYGR	11	CLPN	Sumalo R., Hwy. 3.

44	SXE	670	121.06	49.17	CWH	SHYGR	11	C	Sumalo R., Hwy. 3.
45	SXE	670	121.06	49.17	CWH	SHYGR	11	CLPN	Sumalo R., Hwy. 3.
46	ESP	1210	121.83	49.08	CWH	SHYGR	11	C	Skagit R., Hwy. 3.
47	SXE	860	121.17	49.17	CWH	SHYGR	11	LPN	Skagit R., Hwy. 3.
48	SXE	860	121.00	49.17	CWH	SHYGR	11	C	Skagit R., Hwy. 3.
49	SXE	770	120.92	49.08	CWH	SHYGR	11	CLPN	Skagit R., Hwy. 3.
50	SXE	770	120.92	49.08	CWH	SHYGR	11	C	Skagit R., Hwy. 3.
51	ESP	1100	120.83	49.08	ESSF	SHYGR	12	C	Skagit R., Hwy. 3.
52	ESS	1260	120.83	49.00	ESSF	SHYGR	12	CLPN	Manning Pk. Lodge.
53	ESS	1250	120.75	49.00	ESSF	SMESIC	12	CLPN	Manning Pk. Lodge.
56	ESP	1060	121.25	49.17	CWH	SHYGR	12	C	Sumalo R., Hwy. 3.
57	ESP	770	121.06	49.50	CWH	SHYGR	9	C	Coquahalla R., NE of Hope.
58	ESP	1120	121.50	49.58	CWH	SHYGR	9	C	Inkwathia L., W of Yale.
59	ESP	1365	121.25	49.67	MH	SHYGR	9	C	E. Anderson R., E of Boston Bar.
60	ESP	680	121.25	49.67	IDF	SMESIC	9	C	Anderson R., E of Boston Bar.
61	ESP	980	121.59	49.75	CWH	SHYGR	9	C	Scuzzy C., W of Boston Bar.
62	ESP	930	121.59	49.75	CWH	MESIC	9	C	Scuzzy C., W of Boston Bar.
63	ESP	1140	121.92	50.17	IDF	SHYGR	9	C	Kwoiek C., Boston Bar.
64	ESP	1050	121.83	50.17	IDF	SHYGR	9	C	Kwoiek C., Boston Bar.
65	SSS	50	127.25	50.58	CWH	HYGRIC	7	C	Beaver L., E of Port Alice.
66	SSS	50	127.25	50.58	CWH	HYGRIC	7	C	Beaver L., E of Port Alice.
67	SSS	50	127.33	50.58	CWH	HYGRIC	7	C	Rupert In., S of Port Hardy.
68	SSS	50	127.33	50.58	CWH	HYGRIC	7	LPN	Rupert In., S of Port Hardy.
202	SSS	30	124.30	50.50	CWH	SHYGR	4	C	Klite R., Toba In.
203	SSP	610	124.20	50.70	CWH	SHYGR	4	CLPN	Montrose C., Toba In.
204	SSS	488	124.20	50.50	CWH	SHYGR	4	C	Little Toba R., Toba In.
205	SSS	25	127.60	50.70	CWH	SHYGR	7	CLPN	Quatse R., Port Hardy.
206	SSP	500	125.66	51.55	CWH	MESIC	6	CLPN	Jct. Remote C. and Klinaklini R., Knight In.
207	SSP	85	125.60	51.20	CWH	SMESIC	6	C	Devereaux L., Knight In.
208	SSP	160	126.40	51.10	CWH	SHYGR	6	C	Atwaykellesse C., Wakeman Sd., Kingcome In.
210	SSP	400	126.20	50.30	CWH	HYGRIC	7	CLPN	Eve R., N of Kelsey Bay.
211	ESP	1000	123.20	50.10	MH	SMESIC	2	CLPN	Brew Mtn., SW of Brandywine Falls.
213	SSP	150	126.70	50.00	CWH	SHYGR	7	C	Woss L., S of Port McNeil.
214	SSP	630	126.10	50.75	CWH	MESIC	6	CLPN	Thompson Sd., Knight In.
215	SSP	5	124.50	50.50	CWH	SHYGR	4	C	Tuhuming R., Toba In.
216	SSP	5	127.60	50.70	CWH	MESIC	7	C	Bear Cove, Port Hardy.
217	SSP	610	124.20	50.60	CWH	SHYGR	4	C	Filer C., Toba In.
218	ESS	937	120.60	49.20	ESSF	SHYGR	12	CLPN	Similkameen Falls, Manning Pk.
219	ESS	1013	120.70	49.10	ESSF	SHYGR	12	CLPN	E. Gate Manning Pk.
220	SSP	85	125.60	51.20	CWH	SMESIC	6	CLPN	Devereaux L., Knight In.
221	SSS	1	125.90	49.10	CWH	SHYGR	-	CLPN	Long Beach, S of Tofino.
301	ESP	1036	120.50	50.00	IDF	MESIC	12	CLPN	Corbett L., S of Merritt.
303	ESP	700	120.50	49.60	IDF	HYGRIC	12	CLPN	Summers C., N of Princeton.
501	SSP	120	127.30	50.30	CWH	HYGRIC	7	C	Victoria L., S of Port Alice.
502	SSP	120	127.40	50.35	CWH	HYGRIC	7	C	Victoria L., S of Port Alice.
503	SSP	110	126.90	50.50	CWH	SMESIC	7	C PN	Kokish R., S of Beaver Cove.
504	ESP	1000	121.00	49.23	MH	SXERIC	11	PN	Skagit R., Manning Pk. Hwy. 3.
505	SSP	180	127.25	50.35	CWH	MESIC	7	C	Victoria L., S of Port Alice.
506	SXE	400	125.60	50.10	CWH	SMESIC	6	C	N.Stafford R., Knight In.
510	SXE	400	125.60	50.10	CWH	HYGRIC	6	C	N.Stafford R., Khight In.
511	SXE	370	125.60	50.80	CWH	HYGRIC	6	C	Bolivar C., Knight In.
512	SSS	70	127.30	50.70	CWH	HYGRIC	7	C	Rupert In., S. of Port Hardy.
513	SXE	150	125.40	50.90	CWH	HYGRIC	6	C	Stafford R., Knight In.
514	SSS	130	127.35	50.05	CWH	SMESIC	-	C	Kyuquot Penn., W of Zebalos.
515	SSP	110	127.50	50.60	CWH	HYGRIC	7	C	Port Alice.
516	SSP	190	127.20	50.40	CWH	HYGRIC	7	C	Benson L., SE of Port Alice.

517	SSP	229	125.60	51.35	CWH	SHYGR	6	C	Hoodoo C., Knight In.
518	SSP	229	125.60	51.35	CWH	SHYGR	6	C	Hoodoo C., Knight In.
519	SSP	1219	125.60	51.15	CWH	HYGRIC	6	C PN	Knight In. Camp.
521	ESP	1189	119.92	49.50	ESSF	MESIC	13	C PN	Apex Mtn. Pk., W of Penticton.
522	ESP	1311	122.40	50.40	ESSF	MESIC	10	C PN	Joffre C., E of Pemberton.
523	SSP	5	124.90	50.90	CWH	SHYGR	5	C PN	Waddington Harbour, Bute In.
524	SSP	20	124.90	51.00	CWH	SHYGR	5	C PN	Homathko R., Bute In.
525	SSP	152	124.90	51.10	CWH	SHYGR	5	C PN	Jelwakwa C., Bute In.
526	SSP	244	122.00	49.00	CDF	MESIC	8	C PN	Columbia V., S of Cultus L.
527	SSS	5	123.60	49.40	CDF	SHYGR	2	CLPN	Roberts C., Sechelt Penn.
528	SSS	10	123.60	49.40	CDF	SHYGR	2	C	Roberts C., Sechelt Penn.
529	ESP	1020	122.60	50.60	ESSF	SMESIC	10	PN	Anderson L., N of D'Arcy.
530	IESP	792	120.17	50.75	IDF	SMESIC	-	C PN	Paul L., N of Kamloops.
531	IESP	1189	118.58	52.17	ESSF	SMESIC	16	C	Fred Laing Ridge, E of Mica Dam.
532	SSP	5	124.90	50.90	CWH	SHYGR	4	C PN	Cumsack C., Toba In.
533	SSP	76	124.10	50.50	CWH	SHYGR	4	C PN	Toba R., Toba In.
534	SXE	540	124.70	50.85	CWH	SMESIC	5	C PN	Elliot C., Bute In.
535	SXE	457	124.25	50.80	CWH	SHYGR	4	C PN	Filer C., Toba In.
536	SSP	20	124.30	50.50	CWH	SHYGR	4	C PN	Toba R., Toba In.
537	SXE	575	125.60	51.15	CWH	SMESIC	6	C PN	Klinaklini R., Knight In.
538	SSP	20	125.60	50.60	CWH	MESIC	6	C PN	Klinaklini R., Knight In.
539	SSP	20	125.60	51.15	CWH	HYGRIC	6	PN	Knight In. Camp.
540	SSP	135	125.60	51.20	CWH	SHYGR	6	C	Dice C., Knight In.
541	SXE	1100	125.60	51.20	MH	MESIC	6	C PN	Devereaux Ridge, Knight In.
542	SSP	85	125.60	51.20	CWH	SMESIC	6	C PN	Klinaklini R., Knight In.
543	SSP	85	125.60	51.20	CWH	SMESIC	6	C	Klinaklini R., Knight In.
544	SXE	152	125.60	51.20	CWH	MESIC	6	C PN	Dice C., Knight In.
545	SXE	960	125.60	51.20	MH	MESIC	6	C	Devereaux Ridge, Knight In.
546	SSSS	20	124.40	42.25	-	SHYGR	-	CLPN	Pistol R., Oregon.
547	SSSS	20	124.10	41.80	-	SHYGR	-	CLPN	Crescent City, California.
548	SSSS	20	124.00	44.00	-	SHYGR	-	CLPN	Florence, Oregon.
549	SSSS	100	124.30	43.10	-	SHYGR	-	CLPN	Bandon, Oregon.
550	SSSS	20	124.20	42.00	-	SHYGR	-	CLPN	Brookings, Oregon.
551	SSS	120	126.80	49.70	CWH	SHYGR	-	C	Nootka Is., W of Gold River.
552	SXE	850	125.60	51.40	MH	SHYGR	6	C PN	Dorothy C., Knight In.
553	SXE	600	125.60	51.20	CWH	SHYGR	6	C PN	Dice C., Knight In.
554	SXE	700	125.60	51.25	MH	SHYGR	6	CLPN	Icy C., Knight In.
555	SXE	1050	125.60	51.35	MH	SHYGR	6	C PN	Hoodoo C., Knight In.
556	SXE	975	125.55	51.25	MH	MESIC	6	C PN	Klinaklini R., Knight In.
557	ESS	1494	119.50	49.66	ESSF	SHYGR	13	CLPN	Greyback Mtn. Rd., Okanagon Plateau.
558	SSS	5	122.80	49.00	CDF	SHYGR	3	CLPN	Whiterock.
559	SSS	5	122.80	49.00	CDF	SHYGR	3	CLPN	Whiterock.
560	SXE	1036	126.55	51.55	MH	MESIC	6	C PN	Machmell R., E of Owikeno L.
561	SXE	1189	126.55	51.55	MH	MESIC	6	C PN	Machmell R., E of Owikeno L.
562	SXE	914	126.55	51.55	MH	MESIC	6	C PN	Machmell R., E of Owikeno L.
563	SXE	975	126.55	51.55	MH	MESIC	6	C PN	Machmell R., E of Owikeno L.
564	SXE	762	125.60	51.20	MH	MESIC	6	C PN	Dice C., Knight In.
565	SXE	991	125.60	51.20	MH	MESIC	6	C PN	Dice C., Knight In.
566	SXE	213	126.10	51.10	CWH	SHYGR	6	C PN	Atlatzi R., Kingcome In.
567	SXE	457	126.90	51.20	CWH	HYGRIC	6	C PN	Wump C., Alison Sd., Belize In.
568	SSP	40	126.00	50.90	CWH	MESIC	6	C PN	Klukwite R., Thompson Sd., Knight In.
569	SSP	427	125.80	50.90	CWH	XERIC	6	C PN	Anuhati R., Knight In.
570	SSP	440	125.80	50.80	CWH	MESIC	6	C PN	Naena Pt., Knight In.
571	SSS	50	123.70	48.30	CDF	HYGRIC	1	C PN	Sooke.
572	ESP	1981	122.90	50.20	MH	XERIC	2	LPN	Wedge Ridge, N of Whistler.
70301	WSS	100	76.25	45.00	-	-	-	CLPN	Pakenham, Ont.

TREE	ID.	ELEV	LONG	LAT	BGCZ	MOIST	GEOG	SUITES	LOCATION
						POPULATIONS			
60101	SSS	5	123.20	49.50	CWH	SHYGR	2	CLPN	Porteau Beach, S of Squamish.
02								CLPN	
03								C	
04								CLPN	
05								CLPN	
06								CLPN	
07								LPN	
08								LPN	
09								LPN	
10								LPN	
11								LPN	
12								LPN	
13								LPN	
14								LPN	
15								LPN	
16								LPN	
60201	SSS	5	123.25	49.58	CWH	HYGRIC	2	CLPN	Fury C., S of Squamish.
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
06								CLPN	
07								C	
08								C	
09								C	
10								C PN	
60301	SXE	430	123.00	49.92	CWH	MESIC	2	CLPN	Garibaldi Station, S of Whistler.
02								LPN	
03								LPN	
04								LPN	
05								LPN	
06								LPN	
07								LPN	
08								LPN	
09								LPN	
10								LPN	
60401	SXE	637	123.00	50.10	CWH	SHYGR	2	LPN	Alta L., W side, Whistler.
02								C PN	
03								LPN	
04								CLPN	
05								CLPN	
06								CLPN	
07								CLPN	
60501	SXE	600	122.90	50.20	CWH	HYGRIC	2	CL N	Green R., N of Whistler.
02								CLPN	
03								C	
60601	SXE	637	123.00	50.10	CWH	HYGRIC	2	CL	S end Green L., Whistler.
02								CLPN	
03								CLPN	
04								C	

05								C	
06								CL	
07								LPN	
08								LPN	
09								LPN	
10								LPN	
11								LPN	
12								PN	
13								PN	
14								LPN	
15								PN	
16								LPN	
60701	ESS	1450	120.83	49.05	ESSF	MESIC	12	C	Strawberry Flats, S of Manning Pk. Lodge.
02								C	
03								C	
04								C	
05								CLPN	
06								CLPN	
07								C	
08								CLPN	
09								CLPN	
10								CLPN	
11								L	
12								L	
13								L	
14								L	
15								L	
16								L	
17								L	
18								L	
19								L	
20								L	
21								CLPN	
60801	ESS	2012	120.80	49.10	ESSF	SMESIC	12	CLPN	Blackwell Mtn., Manning Pk.
02								CLPN	
03								CL N	
04								CLPN	
05								CLPN	
06								CLPN	
07								CLPN	
60901	ESS	1300	120.80	49.10	ESSF	MESIC	12	LPN	Blackwell Mtn. Rd., N of Manning Pk. Lodge.
02								LP	
03								LPN	
04								CLPN	
05								CLPN	
61001	ESS	1250	120.50	49.00	ESSF	MESIC	12	CLPN	Manning Pk. Lodge, sanistation.
02								CLP	
03								CLPN	
04								CLPN	
05								CLPN	
06								CLPN	
07								CLPN	
61101	SXE	650	121.42	49.00	CWH	SHYGR	8	CLPN	Sapper Pk., S end Chilliwack L.
02								CLPN	
03								LPN	
04								LPN	

05								LPN	
06								CLPN	
07								C	
08								C	
09								CLPN	
10								CLPN	
11								C	
12								C	
13								C PN	
61201	ESS	1737	119.52	49.16	ESSF	MESIC	13	LPN	Greyback Mtn., Okanagon Plateau.
02								LPN	
03								LPN	
04								CL N	
05								CLPN	
06								CLPN	
07								LPN	
08								CLPN	
09								LPN	
10								L N	
61301	ESS	1585	119.50	49.66	ESSF	MESIC	13	CLPN	Greyback Mtn., Okanagon Plateau.
02								LPN	
03								LPN	
04								LPN	
05								PN	
06								CLPN	
07								LPN	
08								CLPN	
09								CLPN	
10								LPN	
11								CLPN	
61401	ESS	1920	119.92	49.50	ESSF	SHYGR	13	CLPN	Apex Mtn. Pk., W of Penticton.
02								CLPN	
03								CLPN	
04								CLP	
05								CLPN	
61501	ESP	1219	122.50	50.30	ESSF	SMESIC	10	CLPN	Joffre C., E of Pemberton.
02								CLPN	
03								CLPN	
04								L	
05								L	
06								L	
07								LPN	
08								LPN	
09								LPN	
10								LPN	
11								PN	
12								L	
13								L	
61601	ESP	1219	122.30	50.40	ESSF	HYGRIC	10	CLPN	E end Duffy L., E of Pemberton.
02								CLPN	
03								CLPN	
04								C	
05								CLPN	
06								CLPN	
61701	ESP	1219	122.40	50.30	ESSF	SHYGR	10	CLPN	W end Duffy L., E of Pemberton.
02								CLPN	

03								CLPN	
04								CLPN	
05								CLPN	
06								CLPN	
07								LP	
08								L	
09								L	
10								L	
11								LPN	
12								L	
13								L	
14								P	
15								L	
16								LPN	
17								L	
18								L	
21								L	
22								L	
61801	ESP	914	122.50	50.30	ESSF	SMESIC	10	C	Joffre C., E of Pemberton.
02								C	
03								C	
61901	ESP	884	120.60	49.35	ICF	MESIC	12	CLPN	Yellow Pine Eco. Res., W of Princeton.
02								CLPN	
03								CLPN	
62001	ESP	640	120.40	49.40	IDF	SXERIC	12	CLPN	Similkameen R., E of Princeton.
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
07								L N	
08								LP	
09								LP	
10								LP	
11								LP	
12								LP	
13								LP	
14								L	
15								L	
62101	ESP	610	120.00	49.17	IDF	SMESIC	12	CLPN	Ashnola R., S of Keremeos.
02								LPN	
03								CLPN	
04								CLPN	
05								CLPN	
06								CLPN	
62201	SSP	533	122.20	49.10	CWH	SHYGR	3	C	Sumas Mtn., S of Mission.
02								CLPN	
03								C	
04								C	
62301	ESP	1000	122.60	50.40	ESSF	MESIC	10	C P	Eight Mi. C., Joffre C., E of Pemberton.
02								C	
03								CLPN	
62401	ESP	990	123.30	50.80	IDF	MESIC	10	CLPN	McParlin C., Carpenter L., N of Gold Bridge.
02								CLPN	
03								CLPN	
62501	ESP	1200	122.80	50.40	ESSF	MESIC	10	CLPN	Owl C., Birkenhead R., N of Pemberton.
02								CLPN	

62601	ESP	1150	122.90	50.70	ESSF	MESIC	10	C	Hurley C., Bralorne.
02								CLP	
03								C	
62701	ESP	671	122.70	50.50	IDF	SHYGR	10	C	Birkenhead L., N of Pemberton.
02								C	
03								C	
62801	SXE	610	122.90	49.70	CWH	SHYGR	2	C	Mamquam R., E of Squamish.
02								C	
03								C	
04								C	
05								C	
62901	SXE	305	125.70	51.30	CWH	HYGRIC	6	LPN	Deveraux C., Knight In.
02								C	
63001	SSP	60	125.70	50.90	CWH	MESIC	6	LPN	Ahnuhatti R., Knight In.
02								CLPN	
63101	ESP	1067	125.30	51.80	MH	SMESIC	6	CLPN	Colwall C., E. Klinaklini R.
02								CLPN	
63201	SXE	610	125.70	51.30	CWH	SHYGR	6	CLPN	Canyon L., Knight In.
02								CLPN	
63301	SXE	610	125.50	51.80	CWH	SMESIC	6	CLPN	Jobin C., E. Klinaklini R.
02								CLPN	
63401	SSP	76	124.20	50.50	CWH	SHYGR	4	CLPN	Toba R., Toba In.
02								CLPN	
63501	SXE	715	124.60	50.70	CWH	MESIC	6	CLPN	Orford R., Knight In.
02								C	
63601	SXE	435	125.10	51.10	CWH	SMESIC	5	CLPN	Brew C., Bute In.
02								CLPN	
63701	SXE	470	125.20	50.50	CWH	SXERIC	5	CLPN	Bear R., Bute In.
02								C	
63801	SSP	180	124.20	50.40	CWH	SHYGR	4	CLPN	Little Toba R., Toba In.
02								CLPN	
63901	SSP	215	124.60	50.50	CWH	MESIC	4	C	Brem R., Toba In.
02								C	
03								LPN	
64001	IESP	884	120.50	50.90	IDF	MESIC	–	CLPN	McQueen L., N of Kamloops.
02								CLPN	
03								CLPN	
64101	IESP	1250	117.66	51.17	ESSF	MESIC	15	C	Rogers' Pass.
02								C	
03								C	
04								C	
05								C	
64201	IESP	1128	117.66	51.17	ESSF	MESIC	15	CLPN	Rogers' Pass.
02								C PN	
03								CLPN	
64301	IESP	975	117.75	51.01	ESSF	SXERIC	15	CLPN	Rogers' Pass.
02								CLPN	
03								CLPN	
64401	IESP	975	117.75	51.01	ESSF	SXERIC	15	LPN	Rogers' Pass.
02								LPN	
03								LPN	
64501	IESP	457	118.00	51.00	IWH	HYGRIC	15	C	Rogers' Pass.
02								CLPN	
03								C	
04								PN	
05								C	

Code	Type	Elev	Long	Lat	Zone	Subzone	No	Class	Location
06								C	
07								C	
08								CLPN	
09								C	
10								CLPN	
64601	IESS	1981	118.58	52.17	ESSF	SXERIC	16	CLPN	Fred Laing Ridge, E of Mica Dam.
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
64701	IESP	1768	118.58	52.17	ESSF	SMESIC	16	CLPN	Fred Laing Ridge, E of Mica Dam.
02								CLPN	
03								C	
64801	IESP	1737	118.58	52.17	ESSF	MESIC	16	CLPN	Fred Laing Ridge, E of Mica Dam.
02								CLPN	
64901	IESP	1554	118.58	52.17	ESSF	MESIC	16	C	Fred Laing Ridge, E of Mica Dam.
02								LPN	
65001	IESP	1341	118.58	52.17	ESSF	SHYGR	16	LPN	Fred Laing Ridge, E of Mica Dam.
02								C	
65101	IESP	1097	118.58	52.17	ESSF	SHYGR	16	C	Fred Laing Ridge, E of Mica Dam.
02								CLPN	
03								CLPN	
65201	IESP	914	118.58	52.17	ESSF	SHYGR	16	CLPN	Fred Laing Ridge, E of Mica Dam.
02								CLPN	
03								C PN	
65301	IESS	1920	118.17	51.00	ESSF	SXERIC	14	CLPN	Mt. Revelstoke.
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
65401	IESP	1768	118.17	51.00	ESSF	MESIC	14	CLPN	Mt. Revelstoke.
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
65501	IESP	1646	118.17	51.00	ESSF	MESIC	14	CLPN	Mt. Revelstoke.
02								CLPN	
03								CLPN	
65601	IESP	1494	118.17	51.00	ESSF	HYGRIC	14	LPN	Mt. Revelstoke.
02								LPN	
03								LPN	
04								LPN	
05								LPN	
65701	IESP	1494	118.17	51.00	ESSF	SHYGR	14	CLPN	Mt. Revelstoke.
02								CLPN	
03								CLPN	
65801	IESP	1341	118.17	51.00	ESSF	MESIC	14	C	Mt. Revelstoke.
02								C	
03								C	
65901	IESP	1097	118.17	51.00	ESSF	MESIC	14	C	Mt. Revelstoke.
02								C	
03								C	
66001	IESP	610	118.17	51.00	IWH	SXERIC	14	CLPN	Mt. Revelstoke.
03								LPN	
04								C	
66101	SSP	150	128.20	50.70	CWH	SHYGR	7	CLPN	Stranby R., N of Holberg.

02								C PN	
66201	SSP	201	127.80	50.70	CWH	SHYGR	7	LPN	Nahwitti L., W of Port Hardy.
02								C	
03								C	
04								C	
05								C	
06								C	
66301	SSS	10	122.60	48.20	CDF	MESIC	1	C	Fort Casey, Whidbey Is., Washington.
02								CLPN	
03								CLPN	
66401	SXE	823	123.30	48.00	CWH	HYGRIC	1	CLPN	Pat's Prairie,S of Sequim, Washington.
02								CLPN	
03								C	
04								CLPN	
05								CLPN	
06								C	
07								CLPN	
08								CLPN	
09								CLPN	
10								C PN	
11								CLPN	
12								C PN	
13								CLPN	
14								LPN	
15								CLPN	
66501	SSS	10	124.05	48.40	CDF	HYGRIC	1	CLPN	River Jordan, N of Sooke.
02								CLPN	
66601	SSS	10	123.70	48.30	CDF	HYGRIC	1	CLPN	Sooke
02								CLPN	
03								CLPN	
66701	SSS	20	123.20	49.70	CWH	SHYGR	2	C	Squamish Industrial Pk.
02								LPN	
03								LPN	
04								LPN	
05								LPN	
06								LPN	
07								LPN	
08								LPN	
09								CLPN	
10								LPN	
70101	WSS	220	76.00	45.55	–	–	–	CLPN	Gatineau Pk., Quebec
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
70201	WSS	80	75.50	45.30	–	–	–	CLPN	Gatineau Pk., Quebec
02								CLPN	
03								CLPN	
04								CLPN	
05								CLPN	
06								CLPN	
70401	NBSXE	–	–	–	–	–	–	LPN	New Brunswick hybrids.
02								LPN	
03								LPN	
04								LPN	
05								LPN	

06							LPN	
07							LPN	
08							LPN	
09							LPN	
10							LPN	
11							LPN	
12							LPN	
13							LPN	
14							LPN	
15							LPN	
16							LPN	
17							LPN	
18		860	119.25	56.00			LPN	Maternal "ES" of NBSXE
70501	RRSXE	1700	115.80	49.50	ESSF	-	LPN	Red Rock hybrid, Cranbrook.
70601	RRSXE	1700	115.80	49.50	ESSF	-	LPN	Red Rock hybrid, Cranbrook.
02							LPN	
03							LPN	
04							LPN	
70701	RRSXE	1800	115.30	49.50	ESSF	-	LPN	Red Rock hybrid, Bull R. E of Cranbrook.
02							LPN	
03							LPN	
04							LPN	
70801	RRSXE	1800	115.30	49.50	ESSF	-	LPN	Red Rock hybrid, Bull R. E of Cranbrook.
02							LPN	
03							LPN	
04							LPN	
05							LPN	
06							LPN	
07							LPN	
08							LPN	
09							LPN	
71101	SSS		155.00	57.00		-	LPN	Chilliwack Nurs. Kodiak Is., Alaska.
02							LPN	
03							LPN	
04							LPN	
05							LPN	
71201	SSS		145.00	60.00		-	LPN	Chilliwack Nurs. Cordova Bay, Alaska.
02							LPN	
03							LPN	
04							LPN	
05							LPN	
71301	SSS		134.00	58.00		-	LPN	Chilliwack Nurs. Juneau, Alaska.
02							LPN	
03							LPN	
04							LPN	
05							LPN	
71401	SSS		128.00	55.00		-	LPN	Chilliwack Nurs. Terrace, B.C.
02							LPN	
03							LPN	
04							LPN	
05							LPN	
71501	SSS		127.00	52.00		-	LPN	Chilliwack Nurs. Bella Coola, B.C.
02							LPN	
03							LPN	
04							LPN	
05							LPN	

71601	SSS	122.00	49.00		-	LPN	Chilliwack Nurs. Chilliwack, B.C.
02						LPN	
03						LPN	
04						LPN	
05						LPN	
06						LPN	
07						LPN	
08						LPN	
09						LPN	
10						LPN	
11						LPN	
71701	SSS	124.00	48.00		-	LPN	Chilliwack Nurs. Forks, Washington.
02						LPN	
03						LPN	
04						LPN	
05						LPN	
71801	SSS	123.80	45.25		-	LPN	Chilliwack Nurs. Hebo, Oregon.
02						LPN	
03						LPN	
04						LPN	
05						LPN	
71901	SSS	124.00	44.40		-	LPN	Chilliwack Nurs. Waldport, Oregon.
02						LPN	
03						LPN	
04						LPN	
05						LPN	
72001	SSS	122.00	42.00		-	LPN	Chilliwack Nurs. Klamath, Calif.
02						LPN	
03						LPN	
04						LPN	
05						LPN	
72101	SSS	132.00	53.00		-	LPN	Chilliwack Nurs. Queen Charlotte Is.
02						LPN	
03						LPN	
04						LPN	
05						LPN	

Appendix III. Complete tables of ANOVAs and PCAs abbreviated in body of text.

Table 39. PCAs of separate variable suites for whorl primary and secondary branches of P. sitchensis and ANOVAs of component scores and original variables comparing order of branching. Only those components with a $\lambda \geq 1.0$ given. * , component correlations (r) or F-values significant @ p $\leq$ 0.01. inv - variable invariate, excluded from analysis. Other symbols given in Table 12. Abbreviation given in Table 15. Component scores used in Figure 9.

		COMPONENTS (>1.0)		
		I	II	
LEAF ANATOMY (n=90)				
%var.		51.15	13.71	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	35.43*	0.78	18.37
B(A)	16	40.87*	40.63*	35.32
e	72	23.70	58.59	46.31
COMPONENT CORRELATIONS (r)				%SS$_A$(uva)
NEEDWID		.928*	.096	31.54*
NEEDEP		.899*	-.257	32.16*
ABXANG		-.255	.702*	0.09
ADXANG		.079	.562*	0.15
CENCYWID		.877*	.237	31.21*
CENCYLAT		.887*	.015	27.95*
CENCYABX		.646*	-.271*	9.10*
CENCYADX		.694*	-.440*	14.68*
ENDONUM		.568*	.340*	10.96*
PHLEND		.807*	.132	24.55*
XYLEND		.677*	.390	19.67*

LEAF MORPHOLOGY(n=100)				
%var.		49.76	18.81	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	11.37*	8.38*	7.67
B(A)	18	40.10*	24.70*	36.97
e	80	48.53	66.92	55.36
COMPONENT CORRELATIONS (r)				%SS$_A$(uva)
NEEDLEN		.601*	.073	5.31
ADXSTOM		.536*	.638*	14.91*
ABXSTOM		.451*	.695*	10.26*
RESCYNO		.901*	-.304*	7.54*
RESCYLOC		.785*	-.304*	0.20
RESCYLEN		.840*	-.222*	7.80*

TWIG MORPHOLOGY (n=100)				
%var.		58.21		
SOURCE	df	%SS		%SS (mva)
A	1	56.24*		33.42
B(A)	18	31.92*		44.95
e	80	11.83		21.65
COMPONENT CORRELATIONS (r)				%SS$_A$(uva)
PULVLEN		.387*		2.52*
TIPWID		.878*		50.76*
TIPDEP		.909*		46.98*
PULVPUB		inv.		0.00

Table 40. PCAs of separate variable suites of whorl branch
positions of mature and immature P.engelmannii and
P. sitchensis and ANOVAs of component scores and individual
variables comparing branch positions. Only those components
with λ ≥ 1.0 given. *, component correlations (r) or
F-values significant @ p ≤ 0.01. Other symbols given in
Table 12. Abbreviation given in Table 17. Component scores
used in Figure 10.

		COMPONENTS (>1.0)		
		I	II	
LEAF ANATOMY (n=373)				
%var.		59.73	20.25	
SOURCE	df	%SS	%SS	%SS (mva)
A	7	71.88*	41.49*	55.53
B(A)	56	17.96*	39.94*	22.90
e	309	10.16	18.57	21.57
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID		.653*	.694*	30.22*
NEEDEP		.958*	-.148*	73.08*
ABXANG		-.458*	.677*	51.73*
ADXANG		-.115	.687*	32.64*
CENCYWID		.916*	.141*	57.65*
CENCYLAT		.498*	.781*	29.58*
CENCYABX		.854*	-.354*	68.97*
CENCYADX		.815*	-.225*	57.15*
ENDONUM		.900*	-.076	73.99*
PHLEND		.934*	.097	68.30*
XYLEND		.922*	.025	67.56*

LEAF MORPHOLOGY(n=370)				
%var.		44.45	23.30	
SOURCE	df	%SS	%SS	%SS (mva)
A	7	62.32*	48.58*	44.96
B(A)	56	17.06*	23.23*	23.90
e	306	20.62	28.19	31.14
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDLEN		.603*	.412*	33.52*
ADXSTOM		.522*	.688*	73.64*
ABXSTOM		-.229*	.664*	22.93*
RESCYNO		.910*	-.221*	63.90*
RESCYLOC		.617*	-.510*	13.04*
RESCYLEN		.877*	.0685	62.74*

TWIG MORPHOLOGY (n=368)				
%var.		48.30	29.21	
SOURCE	df	%SS	%SS	%SS (mva)
A	7	30.99*	79.78*	46.23
B(A)	56	55.48*	15.42*	46.59
e	304	13.53	4.80	7.18
COMPONENT CORRELATIONS (r)				%SSA(uva)
PULVLEN		.465*	.602*	40.91*
TIPWID		.930*	.015	26.26*
TIPDEP		.918*	-.233*	24.81*
PULVPUB		-.092*	.867*	92.93*

CONE MORPHOLOGY (n=416)				
%var.		52.08	17.08	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	43.11*	28.46*	27.64
B(A)	11	10.49*	12.59*	11.91
C(AB)	91	41.05*	40.11*	42.97
e	312	5.34	18.84	17.49
COMPONENT CORRELATIONS (r)				%SSA(uva)
CONLEN		.876*	.128*	28.66*
CONWID		.043	.519*	4.74*
SCALEN		.939*	-.056*	46.37*
SCALWID		.902*	.024	27.47*
SCALTAP		.869*	-.156*	42.79*
WINGWID		.872*	.190*	16.82*
WINGTAP		.768*	.115	14.89*
FREESCAL		.862*	-.256*	47.78*
BRACTLEN		.263*	.800*	3.68*
BRACTWID		.288*	.538*	0.10
BRACTAP		-.512*	.721*	70.76*

Table 41. PCAs of separate variable suites of whorl branch positions of individual trees of
P. engelmannii and P. sitchensis and %SS (mva) for each individual tree. Only first components given.
*, component correlations (r)and F-values significant ⊕ p ≤ 0.01. Other symbols given in Table 12.
Abbreviation given in Table 20. Component scores usedin Figures 12 and 13.

TREE:	Is T1	T2	T3	T4	T5	T6	Ms T7	Me T8
WHORLS OR POSITIONS	(11)	(6)	(6)	(11)	(6)	(6)	(10)	(8)
POSITIONS WITH CONES	-	-	-	-	-	-	(4)	(5)
LEAF MORPHOLOGY (n=)	(55)	(30)	(30)	(55)	(30)	(30)	(60)	(80)
%var.	38.29	37.53	37.81	35.22	53.71	38.90	54.52	47.50
%SS (mva)								
A	43.01	41.89	42.93	42.92	72.89	52.47	82.79	27.30
e	56.99	58.11	57.07	57.08	27.11	47.53	17.21	72.70
COMPONENT CORRELATIONS (r)								
NEEDLEN	.395*	.097	.742*	.391*	.821*	.594*	.774*	.396*
ABXSTOM	-.099	.263	.485*	-.026	.297	.173	.426*	.052*
ADXSTOM	-.199	.110	-.034	-.148	-.599*	-.029	.083	-.241
RESCYNO	.836*	.822*	.608*	.820*	.879*	.742*	.869*	.919*
RESCYLOC	.658*	.811*	.723*	.781*	.756*	.851*	.851*	.944*
RESCYLEN	.770*	.360	.678*	.576*	.872*	.804*	.862*	.900*
TWIG MORPHOLOGY (n=)	(55)	(30)	(30)	(55)	(30)	(30)	(60)	(79)
%var.	59.97			77.32			63.29	59.24
%SS (mva)								
A	94.25	-	-	96.55	-	-	74.84	30.90
e	5.75	-	-	3.45	-	-	25.16	69.10
COMPONENT CORRELATIONS (r)								
PULVLEN	.070	-	-	.741*	-	-	.223	-.126
TIPWID	.995*	-	-	-.670*	-	-	-.974*	.996*
TIPDEP	.066	-	-	.038	-	-	.030	.053
PULVPUB	inv.	-	-	inv.	-	-	inv.	inv.
LEAF ANATOMY (n=)	(55)	(31)	(32)	(55)	(30)	(30)	(60)	(80)
%var.	58.49	54.32	60.89	64.85	43.15	30.74	59.48	48.39
%SS (mva)								
A	67.89	53.39	60.72	67.82	53.21	35.16	59.05	29.90
e	32.11	46.61	39.28	32.20	46.79	64.84	40.95	70.10
COMPONENT CORRELATIONS (r)								
NEEDWID	.970*	.945*	.927*	.968*	.912*	.695*	.876*	.920*
NEEDEP	.856*	.881*	.936*	.929*	.895*	.880*	.914*	.626*
ABXANG	.640*	.348	.420	.599*	-.419	.216	-.475*	.370*
ADXANG	.434*	.286	.309	.316	-.336	-.426*	.115	.176*
CENCYWID	.533*	.906*	.938*	.964*	.801*	.547*	.930*	.966*
CENCYLAT	.961*	.897*	.867*	.948*	.837*	.743*	.856*	.882*
CENCYABX	.387*	.592*	.520*	.551*	.782*	.318*	.744*	.210
CENCYADX	.693*	.780*	.759*	.768*	.317	.803*	.615*	.222
ENDONUM	.790*	.496*	.786*	.774*	.194	-.025	.755*	.717*
PHLEND	.920*	.828*	.905*	.920*	.261	.373	.925*	.905*
XYLEND	.925*	.769*	.881*	.843*	.816*	.403	.865*	.884*
CONE MORPHOLOGY (n=)							(96)	(320)
%var.							51.89	48.44
%SS (mva)								
A							24.85	8.92
B(A)							62.72	63.87
e							12.42	27.21
COMPONENT CORRELATIONS (r)								
CONLEN							.789*	.845*
CONWID							.590*	.230*
SCALEN							.848*	.908*
SCALWID							.868*	.846*
SCALTAP							.640*	.790*
WINGWID							.896*	.857*
WINGTAP							.646*	.731*
FREESCAL							.434*	.786*
BRACTLEN							.834*	.558*
BRACTWID							.500*	.442*
BRACTAP							.708*	.075

Table 42. PCAs of separate variable suites of intra-individual
variation in the context of inter-individual variation and
%SS (mva). Only first component given. *, component
correlations significant @ p ≤ 0.01. Only %SS (mva) given.
WO - without any sources of intra-individual variation
besides intra-increment; 1°/2° - with primary and secondary
orders of branches and branches within order; POS. - with
inter-positional variation. IND. - one way ANOVA assessing
inter-individual variation. TAXA - one way ANOVA assessing
inter-specific variation. df - degrees of freedom WO. Other
symbols given in Table 12. Abbreviation given in Table 22.
Component scores used in Figure 14.

	WO	1°/2°	POS.
LEAF ANATOMY (n=)	(601)	(691)	(740)
%var.	51.35	49.76	53.58
SOURCE: IND. df=120		%SS (mva)	
A	87.72	86.96	79.89
e	12.82	13.04	20.11
SOURCE: TAXA df=1		%SS (mva)	
A	31.87	36.49	30.27
e	68.13	63.51	69.27
COMPONENT CORRELATIONS (r)			
NEEDWID	.497*	.178*	.647*
NEEDEP	.903*	.954*	.871*
ABXANG	-.220*	-.456*	-.083
ADXANG	-.067	-.323*	.073
CENCYWID	.908*	.811*	.947*
CENCYLAT	.353*	.027	.531*
CENCYABX	.746*	.846*	.647*
CENCYADX	.780*	.852*	.752*
ENDONUM	.837*	.715*	.879*
PHLEND	.935*	.907*	.946*
XYLEND	.919*	.886*	.935*

LEAF MORPHOLOGY(n=)	(570)	(670)	(710)
%var.	44.78	41.25	44.11
SOURCE:IND. df=108		%SS (mva)	
A	79.60	75.52	77.09
e	20.40	24.48	22.91
SOURCE:TAXA df=1		%SS (mva)	
A	26.58	21.80	23.00
e	73.42	78.20	77.00
COMPONENT CORRELATIONS (r)			
NEEDLEN	.075	.114*	.286*
ADXSTOM	-.555*	-.392*	-.384*
ABXSTOM	.552*	.532*	.450*
RESCYNO	.863*	.871*	.879*
RESCYLOC	.891*	.835*	.881*
RESCYLEN	.728*	.756*	.787*

TWIG MORPHOLOGY (n=)	(564)	(664)	(694)
%var.	52.79	50.92	47.97
SOURCE:IND. df=108		%SS (mva)	
A	93.68	90.63	87.41
e	6.32	9.37	12.59
SOURCE:TAXA df=101		%SS (mva)	
A	35.42	35.05	31.27
e	64.58	64.95	68.73
COMPONENT CORRELATIONS (r)			
PULVLEN	.718*	.659*	.712*
TIPWID	.909*	.911*	.911*
TIPDEP	.580*	.571*	.585*
PULVPUB	-.659*	-.670*	-.658*

CONE MORPHOLOGY (n=)	(1000)		(1416)
%var.	40.55		37.53
SOURCE:IND. df=100		%SS (mva)	
A	67.73		63.50
e	32.27		35.50
SOURCE:TAXA df=1		%SS (mva)	
A	19.02		17.87
e	80.98		82.13
COMPONENT CORRELATIONS (r)			
CONLEN	.688*		.702*
CONWID	.624*		.624*
SCALEN	.847*		.841*
SCALWID	.334*		.377*
SCALTAP	.695*		.664*
WINGWID	.449*		.425*
WINGTAP	.618*		.573*
FREESCAL	.659*		.557*
BRACTLEN	.720*		.680*
BRACTWID	.623*		.611*
BRACTAP	.600*		.547*

Table 43. ANOVAs and PCAs of separate variable suites for sampled populations of standards of P. engelmannii and P. sitchensis. Only components with $\lambda \geq 1.0$ given. *, component correlations and F-values significant @ $p \leq 0.01$. Other symbols given in text, MODEL 2. Abbreviation given in Table 23. Component scores used in Figure 16.

COMPONENTS (>1.0)

		I	II	

LEAF ANATOMY (n=536)

%var.		51.47	34.19	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	13.00*	66.69*	29.21
B(A)	13	35.99*	12.76*	24.49
C(AB)	92	44.40*	12.65*	33.61
e	429	6.60	7.90	12.69

COMPONENT CORRELATIONS (r)			%SSA(uva)
NEEDWID	.654*	.709*	17.63*
NEEDEP	.830*	-.524*	45.95*
ABXANG	.040	.894*	65.98*
ADXANG	.176*	.830*	27.90*
CENCYWID	.952*	.203*	2.07*
CENCYLAT	.538*	.776*	26.59*
CENCYABX	.602*	-.728*	69.10*
CENCYADX	.689*	-.552*	31.54*
ENDONUM	.865*	.111	5.37*
PHLEND	.935*	-.055	16.29*
XYLEND	.926*	-.052	12.29*

LEAF MORPHOLOGY(n=516)

%var.		45.49	20.63	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	54.51*	13.50*	29.09
B(A)	13	11.52*	21.44*	16.16
C(AB)	81	23.58*	44.76*	33.50
e	420	10.40	20.31	21.26

COMPONENT CORRELATIONS (r)			%SSA(uva)
NEEDLEN	-.038	.853*	2.85*
ADXSTOM	-.561*	.458*	62.96*
ABXSTOM	.576*	-.302*	32.72*
RESCYNO	.875*	.041	29.70*
RESCYLOC	.889*	.126*	37.93*
RESCYLEN	.724*	.436*	8.36*

TWIG MORPHOLOGY (n=495)

%var.		57.31	29.18	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	57.38*	28.54*	41.81
B(A)	13	8.70*	28.45*	16.74
C(AB)	81	32.07*	37.76*	36.84
e	399	1.85	6.25	4.62

COMPONENT CORRELATIONS (r)			%SSA(uva)
PULVLEN	.796*	-.362*	45.76*
TIPWID	.894*	.291*	29.95*
TIPDEP	.536*	.814*	0.08
PULVPUB	-.757*	.539*	91.46*

CONE MORPHOLOGY (n=412)

%var.		43.54	24.74	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	1.95*	76.55*	20.79
B(A)	11	51.30*	2.73*	27.70
C(AB)	29	17.48*	9.04*	20.35
e	370	29.27*	11.68	31.14

COMPONENT CORRELATIONS (r)			%SSA(uva)
CONLEN	.729*	-.406*	18.30*
CONWID	.708*	-.244*	9.87*
SCALEN	.853*	.238*	1.04*
SCALWID	.351*	.828*	39.56*
SCALTAP	.724*	.473*	6.69*
WINGWID	.460*	.699*	21.84*
WINGTAP	.666*	.096*	0.06
FREESCAL	.657*	.398*	3.94*
BRACTLEN	.716*	-.574*	52.08*
BRACTWID	.597*	-.372*	18.95*
BRACTAP	.620*	-.638*	56.40*

TOTAL VARIABLES (t=61)

%var.		39.93	17.07	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	87.60*	4.59	31.54
B(A)	13	6.85	51.96*	27.14
e	46	5.55	43.45	41.32

COMPONENT CORRELATIONS (r)			%SSA(uva)
NEEDWID	.209	.229	18.12
NEEDEP	-.889*	.358*	49.91
ABXANG	.831*	-.190	76.11
ADXANG	.396*	-.161	38.26
CENCYWID	-.537*	.476*	2.60
CENCYLAT	.322	.157	27.96
CENCYABX	-.913*	.282	74.36
CENCYADX	-.819*	.361*	38.77
ENDONUM	-.563*	.432*	6.98

PHLEND	-.762*	.324	19.07
XYLEND	-.729*	.445*	15.30
NEEDLEN	.212	.232	2.20
ADXSTOM	.765*	-.032	72.97
ABXSTOM	-.771*	.328*	47.86
RESCYNO	-.711*	-.123	33.62
RESCYLOC	-.742*	.158	21.29
RESCYLEN	-.474*	-.033	1.48
PULVLEN	.704*	.048	44.66
TIPWID	.455*	.291	31.94
TIPDEP	.009	.528*	0.03
PULVPUB	-.809*	.266	82.06
CONLEN	.801*	.409*	41.40
CONWID	.525*	.585*	17.05
SCALEN	.338*	.831*	0.04
SCALWID	-.400*	.671*	42.14
SCALTAP	.143	.773*	4.17
WINGWID	-.203	.680*	22.79
WINGTAP	.498*	.542*	4.03
FREESCAL	.113	.711*	2.18
BRACTLEN	.913*	.174	65.63
BRACTWID	.704*	.149	29.70
BRACTAP	.912*	.041	69.43
SHCOLEN	.811*	.378*	49.16
SHCOWID	.570*	.422*	24.72
LOCOLEN	.817*	.365*	46.43
LOCWID	.431*	.545*	10.99

Table 44. ANOVAs and PCAs of separate variable suites for sampled
populations of standards of P. engelmannii, P. glauca, and
P. sitchensis. Only components with λ ≥ 1.0 given. *, component
correlations and F-values significant @ p ≤ 0.01. Other symbols
given in text. MODEL 2. Abbreviation given in Table 24. Component
scores used in Figure 17.

		COMPONENTS (>1.0)		
		I	II	III
LEAF ANATOMY (n=850)				
%var.		51.26	36.04	
SOURCE	df	%SS	%SS	%SS (mva)
A	2	29.12*	56.96*	35.68
B(A)	18	33.78*	23.71*	27.39
C(AB)	106	25.59*	9.97*	20.75
e	723	11.51	9.35	16.18
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID		.473*	.847*	19.58*
NEEDEP		.902*	-.373*	54.04*
ABXANG		-.227*	.880*	68.85*
ADXANG		-.094	.873*	40.53*
CENCYWID		.916*	.333*	7.57*
CENCYLAT		.342*	.892*	29.50*
CENCYABX		.700*	-.639*	74.99*
CENCYADX		.801*	-.413*	42.08*
ENDONUM		.837*	.262*	11.51*
PHLEND		.944*	.074	25.34*
XYLEND		.929*	.104*	18.46*

LEAF MORPHOLOGY(n=581)				
%var.		43.63	21.04	
SOURCE	df	%SS	%SS	%SS (mva)
A	2	57.20*	13.98*	29.98
B(A)	15	10.38*	20.91*	13.90
C(AB)	90	22.34*	45.87*	32.68
e	473	10.08	19.24	21.78
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDLEN		-.147*	.826*	6.78*
ADXSTOM		-.594*	.444*	64.58*
ABXSTOM		.579*	-.243*	32.98*
RESCYNO		.864*	.097	29.03*
RESCYLOC		.863*	.103*	37.57*
RESCYLEN		.643*	.551*	8.91*

TWIG MORPHOLOGY (n=560)				
%var.		55.18	29.07	
SOURCE	df	%SS	%SS	%SS (mva)
A	2	50.51*	38.66*	41.70
B(A)	15	10.81*	23.37*	16.48
C(AB)	90	34.91*	32.26*	35.92
e	420	3.77	5.74	5.91
COMPONENT CORRELATIONS (r)				%SSA(uva)
PULVLEN		.779*	-.367*	44.94*
TIPWID		.891*	.277*	31.64*
TIPDEP		.595*	.759*	1.18*
PULVPUB		-.673*	.613*	89.05*

CONE MORPHOLOGY (n=820)					
%var.		46.94	22.94	10.01	
SOURCE	df	%SS	%SS		%SS (mva)
A	2	46.27*	38.87*	30.02	35.39
B(A)	15	26.14*	18.30*	10.26	19.39
C(AB)	64	12.50*	19.90*	29.57	18.64
e	738	14.78	22.94	30.15	26.02
COMPONENT CORRELATIONS (r)					%SSA(uva)
CONLEN		.790*	-.055	.350*	35.41*
CONWID		.803*	-.081	.037	36.19*
SCALEN		.822*	.364*	-.182*	5.62*
SCALWID		-.045	.933*	-.027	37.17*
SCALTAP		.765*	.369*	-.429*	24.08*
WINGWID		-.041	.914*	.230*	32.05*
WINGTAP		.425*	.525*	.442*	3.47*
FREESCAL		.757*	.054	-.617*	50.90*
BRACTLEN		.852*	-.278*	.215*	61.48*
BRACTWID		.697*	-.125*	.275*	30.62*
BRACTAP		.817*	-.409*	.103*	72.35*

TOTAL VARIABLES (t=72)				
%var.		39.07	18.55	
SOURCE	df	%SS	%SS	%SS (mva)
A	2	88.07*	36.39*	38.90
B(A)	14	6.57*	30.38*	24.15
e	55	5.37	33.23	36.95
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID		.403*	.670*	22.82
NEEDEP		-.818*	.496*	50.45
ABXANG		.852*	.103	77.39
ADXANG		.498*	.224	40.51
CENCYWID		-.332*	.847*	2.55
CENCYLAT		.494*	.586*	33.70
CENCYABX		-.882*	.337*	75.04
CENCYADX		-.746*	.435*	38.05
ENDONUM		-.360*	.751*	6.81

ABXSTOM	-.737*	.332*	44.16*
RESCYNO	-.491*	-.008	24.12*
RESCYLOC	-:629*	-.004	14.15*
RESCYLEN	-.268*	-.017	0.44
PULVLEN	.359*	.156	12.12*
TIPWID	.355*	.579*	20.27*
TIPDEP	-.188	.717*	.98
PULVPUB	-.823*	.175	55.42*
CONLEN	.708*	.464*	27.63*
CONWID	.608*	.353*	17.43*
SCALEN	.345*	.577*	1.54
SCALWID	-.484*	.497*	44.97*
SCALTAP	.070	.540*	0.79
WINGWID	-.292*	.476*	21.34*
WINGTAP	.402*	.436*	5.96*
FREESCAL	.154	.479*	0.00
BRACTLEN	.896*	.148	66.82*
BRACTWID	.644*	.282*	25.61*
BRACTAP	.905*	.076*	72.33*
SHCOLEN	.651*	.428*	25.97*
SHCOWID	.602*	.288*	19.82*
LOCOLEN	.756*	.388*	33.58*
LOCOWID	.516*	.290*	10.98*

Table 45. ANOVAs and PCAs of separate variable suites for sampled
individual standards and putatives of P. engelmannii and
P. sitchensis. Only components with $\bar{\lambda} \geq 1.0$ given. *, component
correlations or F-values significant @ p $\leq$ 0.01. Other symbols given
in text. MODEL 3. Abbreviation given in Table 25. Component scores
used in Figure 18.

		COMPONENTS (>1.0)			
		I	II	III	
LEAF ANATOMY (n=1520)					
%var.		48.58	39.49		
SOURCE	df	%SS	%SS		%SS (mva)
A	1	21.01*	58.88*		31.84
B(A)	254	67.83*	32.18*		51.47
e	1264	11.16	8.93		16.69
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
NEEDWID		.500*	.825*		18.65*
NEEDEP		.864*	-.434*		50.23*
ABXANG		-.131*	.886*		60.18*
ADXANG		-.009	.876*		40.48*
CENCYWID		.911*	.312*		3.64*
CENCYLAT		.370*	.870*		28.05*
CENCYABX		.657*	-.664*		69.24*
CENCYADX		.739*	-.496*		40.53*
ENDONUM		.848*	.205*		7.26*
PHLEND		.919*	.009		20.63*
XYLEND		.907*	.116*		11.30*

LEAF MORPHOLOGY(n=1490)					
%var.		40.05	19.80		
SOURCE	df	%SS	%SS		%SS (mva)
A	1	30.50*	33.97*		20.93
B(A)	244	52.66*	50.58*		56.73
e	1244	16.84	15.45		22.43
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
NEEDLEN		.252*	.685*		0.04
ADXSTOM		-.406*	.675*		64.97*
ABXSTOM		.431*	-.331*		25.10*
RESCYNO		.856*	-.071*		17.17*
RESCYLOC		.843*	.024		16.06*
RESCYLEN		.738*	.386*		1.71*

TWIG MORPHOLOGY (n=1513)					
%var.		44.92	32.36		
SOURCE	df	%SS	%SS		%SS (mva)
A	1	15.59*	43.92*		24.61
B(A)	251	74.58*	51.82*		67.16
e	1260	9.83	4.26		8.24
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
PULVLEN		.453*	-.558*		6.57*
TIPWID		.926*	.079*		20.38*
TIPDEP		.803*	.535*		0.92*
PULVPUB		-.299*	.976*		70.58*

CONE MORPHOLOGY (n=4002)					
%var.		36.97	22.00	14.97	
SOURCE	df	%SS	%SS	%SS	%SS (mva)
A	1	7.91*	47.17*	2.46*	36.44
B(A)	391	55.65*	29.56*	68.51*	23.28
e	3609	36.44.	23.28	29.03	29.03
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
CONLEN		.689*	-.155*	.401*	9.47*
CONWID		.582*	-.144*	.370*	6.68*
SCALEN		.839*	.218*	-.225*	0.01
SCALWID		.305*	.830*	.332*	11.70*
SCALTAP		.647*	.353*	-.595*	1.34*
WINGWID		.402*	.722*	-.469*	3.46*
WINGTAP		.638*	.198*	-.005	0.02
FREESCAL		.533*	.169*	-.748*	0.85*
BRACTLEN		.705*	-.595*	.055	31.22*
BRACTWID		.593*	-.244*	.228*	8.94*
BRACTAP		.580*	-.717*	.034*	48.64*

TOTAL VARIABLES (t=159)					
%var.		37.53	14.96		
SOURCE	df	%SS	%SS		%SS (mva)
A	1	88.89	1.02		28.01
e	157	11.11	98.98		71.99
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
NEEDWID		.296*	.514*		18.26*
NEEDEP		-.895*	.355*		53.57*
ABXANG		.847*	.036		70.59*
ADXANG		.657*	.036		49.56*
CENCYWID		-.562*	.585*		4.07*
CENCYLAT		.437*	.424*		28.90*
CENCYABX		-.918*	.236*		73.66*
CENCYADX		-.825*	.358*		44.18*
ENDONUM		-.652*	.473		11.31*
PHLEND		-.741*	.445*		23.35*
XYLEND		-.697*	.525*		15.21*
NEEDLEN		-.037	.309*		0.00
ADXSTOM		.778*	.137		69.35*

ABXSTOM	-.730*	.347*	44.84*
RESCYNO	-.496*	.020	24.13*
RESCYLOC	-.632*	.017	17.04*
RESCYLEN	-.220*	.070	0.45
PULVLEN	.340*	.096	12.16*
TIPWID	.382*	.620*	20.94*
TIPDEP	-.147*	.752*	1.15
PULVPUB	-.655*	.328*	57.23*
CONLEN	.730*	.393*	30.04*
CONWID	.647*	.330*	25.95*
SCALEN	.419*	.500*	9.81*
SCALWID	-.497*	.331*	46.45*
SCALTAP	.188	.500*	12.79*
WINGWID	-.346*	.204*	28.56*
WINGTAP	.356*	.214*	6.66*
FREESCAL	.289*	.491*	27.70*
BRACTLEN	.903*	.123	69.13*
BRACTWID	.671*	.245*	29.53*
BRACTAP	.910*	.095	75.16*
SHCOLEN	.667*	.340*	26.48*
SHCOWID	.635*	.252*	24.13*
LOCOLEN	.778*	.341*	35.75*
LOCOWID	.560*	.287*	18.75*

Table 46. ANOVAs and PCAs of separate variable suites for sampled individual standards and putatives of P. engelmannii, P. glauca, and P. sitchensis. Only components with λ ≥ 1.0 given. *, component correlations or F-values significant ⊕ p ≤ 0.01. Other symbols given in text. MODEL 3. Abbreviation given in Table 26. Component scores used in Figure 19.

| | | COMPONENTS (>1.0) | | |
		I	II	III
LEAF ANATOMY (n=1585)				
%var.		48.16	36.80	

SOURCE	df	%SS	%SS		%SS (mva)
A	2	20.84*	59.41*		32.10
B(A)	265	67.81*	31.52*		51.03
e	1317	11.35	9.07		16.90

COMPONENT CORRELATIONS (r)				%SS_A(uva)
NEEDWID	.493*	.823*		20.34*
NEEDEP	.860*	-.441*		50.12*
ABXANG	-.125*	.887*		60.53*
ADXANG	-.010	.875*		40.44*
CENCYWID	.910*	.313*		3.65*
CENCYLAT	.363*	.873*		29.99*
CENCYABX	.649*	-.672*		69.21*
CENCYADX	.735*	-.498*		39.95*
ENDONUM	.846*	.211*		7.20*
PHLEND	.917*	.015		20.46*
XYLEND	.906*	.110*		11.19*

| **LEAF MORPHOLOGY (n=1555)** | | | | |
| %var. | | 39.43 | 20.15 | |

SOURCE	df	%SS	%SS	%SS (mva)
A	2	32.06*	32.92*	21.50
B(A)	255	51.36*	51.58*	54.32
e	1297	16.57	15.50	22.53

COMPONENT CORRELATIONS (r)			%SS_A(uva)
NEEDLEN	.218*	.696*	0.65*
ADXSTOM	-.423*	.656*	65.26*
ABXSTOM	.438*	-.330*	25.83*
RESCYNO	.856*	-.053*	17.61*
RESCYLOC	.838*	.012*	17.59*
RESCYLEN	.716*	.428*	2.05*

| **TWIG MORPHOLOGY (n=1578)** | | | |
| %var. | | 44.89 | 32.03 | |

SOURCE	df	%SS	%SS	%SS (mva)
A	2	14.24*	45.82*	25.00
B(A)	262	75.38*	50.13*	66.48
e	1313	10.38	4.05	8.52

COMPONENT CORRELATIONS (r)			%SS_A(uva)
PULVLEN	.451*	-.562*	6.64*
TIPWID	.923*	.068*	21.35*
TIPDEP	.820*	.503*	1.26*
PULVPUB	-.263*	.841*	70.76*

| **CONE MORPHOLOGY (n=4142)** | | | | |
| %var. | | 37.94 | 22.16 | 14.37 |

SOURCE	df	%SS	%SS	%SS	%SS (mva)
A	2	17.85*	39.68*	16.74*	13.73
B(A)	403	51.04*	34.60*	55.66*	65.72
e	3736	31.11	25.72	27.60	20.55

COMPONENT CORRELATIONS (r)				%SS_A(uva)
CONLEN	.694*	.001	.436*	9.89*
CONWID	.613*	-.065*	.341*	8.66*
SCALEN	.834*	.245*	-.240*	1.07*
SCALWID	.167*	.907*	.175*	13.60*
SCALTAP	.667*	.259*	-.627*	3.43*
WINGWID	.231*	.857*	.349*	7.16*
WINGTAP	.566*	.338*	.028	1.31*
FREESCAL	.595*	-.009	-.733*	11.36*
BRACTLEN	.766*	-.479*	.181*	33.22*
BRACTWID	.624*	-.149*	.269*	9.67*
BRACTAP	.665*	-.620*	.167*	51.69*

| **TOTAL VARIABLES (t=170)** | | | | |
| %var. | | 37.16 | 15.77 | |

SOURCE	df	%SS	%SS	%SS (mva)
A	2	88.69*	14.41*	30.88
e	167	11.31	85.59	69.12

COMPONENT CORRELATIONS (r)			%SS_A(uva)
NEEDWID	.360*	.631*	19.85*
NEEDEP	-.872*	.406*	53.62*
ABXANG	.853*	.106	70.92*
ADXANG	.676*	.107	49.64*
CENCYWID	-.488*	.720*	4.04*
CENCYLAT	.489*	.532*	30.89*
CENCYABX	-.910*	.249*	73.85*
CENCYADX	-.798*	.396*	43.71*
ENDONUM	-.578*	.606*	11.17*
PHLEND	-.682*	.572*	23.22*
XYLEND	-.644*	.627*	15.17*
NEEDLEN	.002	.319*	1.03
ADXSTOM	.780*	.165	69.70*

PHLEND	-.592*	.702*	18.90
XYLEND	-.561*	.740*	15.10
NEEDLEN	.286	.207	6.49
ADXSTOM	.794*	.158	74.17
ABXSTOM	-.718*	.477*	48.40
RESCYNO	-.672*	.135	33.44
RESCYLOC	-.730*	.136	26.45
RESCYLEN	-.331*	.323	1.87
PULVLEN	.628*	-.121	43.89
TIPWID	.518*	.471*	33.72
TIPDEP	.095	.633*	0.79
PULVPUB	-.440	.527*	83.48
CONLEN	.837*	.246*	45.26
CONWID	.651*	.437*	43.27
SCALEN	.514*	.576*	21.88
SCALWID	-.455*	.187*	46.12
SCALTAP	.395*	.563*	37.52
WINGWID	-.364*	-.021	40.39
WINGTAP	.356*	-.043	6.02
FREESCAL	.423*	.603*	64.24
BRACTLEN	.926*	.097	72.48
BRACTWID	.749*	.085	40.34
BRACTAP	.910*	.116	80.47
SHCOLEN	.560*	.462*	48.19
SHCOWID	.623*	.218*	35.26
LOCOLEN	.721*	.360*	50.11
LOCOWID	.512*	.310*	34.44

Table 47. PCAs of separate variable suites for artificial hybrids and populations of standards of P. engelmannii and P. sitchensis. Only components with $\lambda \geq 1.0$ given. *, component correlations significant @ $p \leq 0.01$. Component scores usedin Figure 20.

| | COMPONENTS (>1.0) | |
	I	II
LEAF ANATOMY		
%var.	44.18	33.95
COMPONENT CORRELATIONS (r)		
NEEDWID	.515*	.804*
NEEDEP	.847*	-.459*
ABXANG	-.042	.912*
ADXANG	.056	.787*
CENCYWID	.903*	.304*
CENCYLAT	.412*	.841*
CENCYABX	.589*	.-.697*
CENCYADX	.676*	-.393*
ENDONUM	.753*	.041
PHLEND	.896*	.038
XYLEND	.846*	-.049
LEAF MORPHOLOGY(n=881)		
%var.	39.02	19.22
COMPONENT CORRELATIONS (r)		
NEEDLEN	-.059	-.874*
ADXSTOM	-.526*	.128*
ABXSTOM	.503*	-.439*
RESCYNO	.817*	.351*
RESCYLOC	.861*	-.177*
RESCYLEN	.631*	.162*
TWIG MORPHOLOGY (n=864)		
%var.	49.88	28.63
COMPONENT CORRELATIONS (r)		
PULVLEN	.647*	-.339*
TIPWID	.901*	.158*
TIPDEP	.709*	.654*
PULVPUB	-.508*	.760*
VEGETATIVE (t=183)		
%var.	36.80	27.48
COMPONENT CORRELATIONS (r)		
NEEDWID	-.383*	.846*
NEEDEP	.886*	.359*
ABXANG	-.851*	.305*
ADXANG	-.588*	.390*
CENCYWID	.374*	.870*
CENCYLAT	-.483*	.777*
CENCYABX	.946*	.104
CENCYADX	.739*	.288*
ENDONUM	.532*	.573*
PHLEND	.682*	.629*
XYLEND	.682*	.616*
NEEDLEN	-.077	.398*
ADXSTOM	-.707*	.601*
ABXSTOM	.689*	.377*
RESCYNO	.432*	-.152
RESCYLOC	.614*	-.100
RESCYLEN	-.133*	-.009
PULVLEN	-.534*	.382*
TIPWID	-.473*	.791*
TIPDEP	-.074*	.809*
PULVPUB	.790*	.050*

Table 48. ANOVAs and PCAs of separate variable suites for all
individuals of artificial hybrids and putative hybrids of
P. engelmannii and P. sitchensis. Only components with $\lambda \geq$
1.0 given. *, component correlations or F-values significant
@ p $\leq$ 0.01. Abbreviation given in Table 28. Component
scores used in Figure 21.

		COMPONENTS (>1.0)		
		I	II	
LEAF ANATOMY (n=557)				
%var.		42.07	31.89	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	5.99*	6.13*	3.67
B(A)	109	80.12*	67.45*	76.28
e	446	13.89	26.42	20.05
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID		.722*	.559*	4.43*
NEEDEP		.631*	-.732*	1.53*
ABXANG		.262*	.755*	4.35*
ADXANG		.351*	.680*	2.09*
CENCYWID		.924*	.099*	3.48*
CENCYLAT		.612*	.618*	2.63*
CENCYABX		.392*	-.759*	4.33*
CENCYADX		.401*	-.765*	9.90*
ENDONUM		.750*	.074	2.01*
PHLEND		.854*	-.120*	2.12*
XYLEND		.826*	-.239*	3.47*

LEAF MORPHOLOGY(n=684)				
%var.		37.98	20.94	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	10.05*	2.65*	14.06
B(A)	135	77.57*	77.30*	70.17
e	547	12.38	20.05	15.77
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDLEN		.176*	-.588*	15.34*
ADXSTOM		.517*	.596*	2.57*
ABXSTOM		.004	.700*	2.45*
RESCYNO		-.878*	.237*	40.23*
RESCYLOC		-.799*	.064	6.71*
RESCYLEN		-.754*	-.069	2.40*

TWIG MORPHOLOGY (n=675)				
%var.		46.41	31.00	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	11.13*	0.01	1.15
B(A)	134	88.59*	96.95*	90.09
e	539	0.28	3.05	8.76
COMPONENT CORRELATIONS (r)				%SSA(uva)
PULVLEN		.082	.246*	1.15
TIPWID		.921*	-.314*	5.43
TIPDEP		.970*	.043	7.75
PULVPUB		.245*	.929*	16.42

VEGETATIVE (t=109)				
%var.		33.60	23.76	
SOURCE	df	%SS	%SS	%SS (mva)
A	1	11.78*	5.78	8.82
e	107	88.22	94.30	91.18
COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID		.764*	-.494*	5.74
NEEDEP		.532*	.781*	1.60
ABXANG		.367*	-.767*	6.15*
ADXANG		.490*	-.660*	3.80
CENCYWID		.940*	-.017	8.21*
CENCYLAT		.664*	-.567*	4.72
CENCYABX		.318*	.813*	3.35
CENCYADX		.295*	.823*	5.41
ENDONUM		.808*	-.003	13.76*
PHLEND		.841*	.256*	3.06
XYLEND		.852*	.339*	3.20
NEEDLEN		.474*	.098	18.04*
ADXSTOM		.452*	-.590*	3.12
ABXSTOM		.421*	.581*	3.24
RESCYNO		-.412*	.350*	48.66*
RESCYLOC		-.062	.453*	11.39*
RESCYLEN		-.252*	.181	10.64*
PULVLEN		.160	.222	1.19
TIPWID		.796*	-.179*	5.49*
TIPDEP		.767*	.187	8.10*
PULVPUB		.356*	.316*	16.42*

Table 49. ANOVAS and PCAs of separate variable suites for all
individuals of P. engelmannii, P. sitchensis, and putative hybrids.
Only components with λ ≥ 1.0 given. *, component correlations or
F-values significant @ p ≤ 0.01. Only the first three components are
given for the PCA of all variables. Results for the ANOVA refer to
only those samples that were standards and putatives. Note %SSA
(uva) refers only to the %SSA TAXA. Abbreviation given in Table 29.
Component scores used in Figure 22 and 23.

		COMPONENTS (>1.0)			
		I	II	III	

LEAF ANATOMY (n=1903)

%var.		51.36	37.09		

SOURCE:TAXA	df	%SS	%SS		%SS (mva)
A	1	32.49*	49.85*		35.70
e	1518	67.51	50.15		64.30

SOURCE:IND.					
A	331	89.02*	90.70*		83.00
e	1571	10.98	9.30		17.00

COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDWID	.317*	.909*		18.26*
NEEDEP	.926*	-.301*		53.57*
ABXANG	-.272*	.908*		70.59*
ADXANG	-.109*	.882*		49.56*
CENCYWID	.853*	.459*		4.07*
CENCYLAT	.181*	.927*		28.90*
CENCYABX	.762*	-.559*		73.66*
CENCYADX	.802*	-.327*		44.18*
ENDONUM	.838*	.207*		11.31*
PHLEND	.927*	.144*		23.35*
XYLEND	.922*	.169*		15.21*

LEAF MORPHOLOGY(n=1994)

%var.		39.38	18.33	17.79	

SOURCE:TAXA	df	%SS	%SS	%SS	%SS (mva)
A	1	54.81*	27.22*	8.73*	25.37
e	1488	45.19	72.78	92.27	75.63

SOURCE:IND.					
A	345	83.56*	84.02*	75.67*	78.90
e	1648	16.44	15.98	24.33	21.08

COMPONENT CORRELATIONS (r)				%SSA(uva)
NEEDLEN	.056	-.525*	.829*	0.00
ADXSTOM	-.663*	-.139	-.159*	69.35*
ABXSTOM	.341*	.714*	.399*	44.16*
RESCYNO	.831*	.021	-.310*	24.12*
RESCYLOC	.819*	.046	.154*	14.15*
RESCYLEN	.666*	-.541*	-.235*	0.44

TWIG MORPHOLOGY (n=2008)

%var.		46.88	78.97		

SOURCE:TAXA	df	%SS	%SS		%SS (mva)
A	1	13.14*	49.08*		22.20
e	1512	86.86	50.92		77.80

SOURCE:IND.					
A	352	92.63*	97.25*		93.90
e	1655	7.37	2.75		6.10

COMPONENT CORRELATIONS (r)			%SSA(uva)
PULVLEN	.436*	.598*	12.12*
TIPWID	.940*	.073	20.27*
TIPDEP	.864*	.451*	0.98*
PULVPUB	-.233*	.848*	55.42*

CONE MORPHOLOGY (n=4257)

%var.		37.77	21.48	13.79	

SOURCE:TAXA	df	%SS	%SS	%SS	%SS (mva)
A	1	7.57*	65.17*	4.29*	17.95
e	3192	92.43	34.83	95.71	82.05

SOURCE:IND.					
A	385	67.36*	85.38*	71.81*	66.11
e	3871	32.64	14.62	28.19	33.89

COMPONENT CORRELATIONS (r)				%SSA(uva)
CONLEN	.687*	-.167*	.392*	13.15*
CONWID	.602*	-.108*	.311*	11.29*
SCALEN	.847*	.169*	-.217*	.10
SCALWID	.390*	.802*	.303*	28.48*
SCALTAP	.683*	.287*	-.583*	3.87*
WINGWID	.468*	.689*	.442*	11.35*
WINGTAP	.631*	.152*	.004	1.00*
FREESCAL	.577*	.129*	-.726*	1.82*
BRACTLEN	.648*	-.648*	.077*	49.75*
BRACTWID	.584*	-.261*	.240*	15.55*
BRACTAP	.522*	-.754*	.051*	61.06*

TOTAL VARIABLES (t=209)

%var.		34.82	15.50	13.13	

SOURCE:TAXA	df	%SS	%SS	%SS	%SS (mva)
A	1	88.58*	1.79	3.97	28.07
e	157	11.42	98.21	96.03	71.99

```
COMPONENT CORRELATIONS (r)                                %SS_A(uva)
          NEEDWID      .308*        .463*       -.766*     18.26*
          NEEDEP      -.877*        .396*        .006      53.57*
          ABXANG       .815*        .008        -.397*     70.59*
          ADXANG       .638*        .038        -.524*     49.56*
          CENCYWID    -.508*        .591*       -.526*      4.07*
          CENCYLAT     .441*        .369*       -.726*     28.90*
          CENCYABX    -.901*        .262*        .111      73.66*
          CENCYADX    -.803*        .388*        .110      44.18*
          ENDONUM     -.586*        .501*       -.367*     11.31*
          PHLEND      -.708*        .458*       -.374*     23.35*
          XYLEND      -.677*        .555*       -.248*     15.21*

          NEEDLEN     -.043         .420*        .178*      0.0
          ADXSTOM     -.749*        .131*       -.501*     69.35*
          ABXSTOM     -.713*        .378*       -.130      44.16*
          RESCYNO     -.500*       -.065        -.108      24.12*
          RESCYLOC    -.610*       -.008         .098      14.15*
          RESCYLEN    -.227*       -.070         .065       0.44

          PULVLEN      .307*        .234*        .073      12.12*
          TIPWID       .319*        .579*       -.589*     20.27*
          TIPDEP      -.198*        .690*       -.355*      0.98
          PULVPUB     -.777*        .196*        .230      55.42*

          CONLEN       .686*        .444*        .142      27.64*
          CONWID       .545*        .423*        .288*     17.43*
          SCALEN       .377*        .585*        .535*      1.54
          SCALWID     -.453*        .482*        .438*     44.96*
          SCALTAP      .147         .531*        .544*      0.79
          WINGWID     -.270*        .465*        .443*     21.34*
          WINGTAP      .427*        .415*        .406*      5.96*
          FREESCAL     .219*        .474*        .454*      0.00
          BRACTLEN     .873*        .158         .070      66.82*
          BRACTWID     .622*        .295*        .247*     25.61*
          BRACTAP      .876*        .101        -.043      72.33*
          SHCOLEN      .644*        .353*        .160      25.97*
          SHCOWID      .560*        .354*        .246*     19.82*
          LOCOLEN      .715*        .363*        .055      33.58*
          LOCOWID      .454*        .352*        .291*     10.98*
```

Table 50. ANOVAs and PCAs of separate variable suites for standards, putatives, and "hybrids" of *P. engelmannii* and *P. sitchensis* based on calculated predicted and residual variation from multiple linear regression with elevation, latitude, and longitude. Multiple linear regression given in MODEL 4 and detailed in Table 30. *, component correlations significant @ p ≤ 0.01. Only first components given. %SS$_A$(uva) refers to differences between hypothesized taxa. Abbreviation given in Table 31. Component scores used in Figure 24.

		PREDICTED I		RESIDUAL I	
LEAF ANATOMY (t=332)					
%var.		97.33		55.78	
SOURCE	df	%SS	%SS (mva)	%SS	%SS (mva)
A	1	75.60*	71.59	0.71	5.22
e	330	24.40	28.41	99.29	94.78
COMPONENT CORRELATIONS (r)			%SS (uva)		%SS$_A$(uva)
NEEDWID		-.213*	49.35*	.848*	9.17*
NEEDEP		.690*	77.10*	.508*	0.59
ABXANG		-.588*	74.57*	.387*	17.50*
ADXANG		-.456*	66.98*	.501*	12.12*
CENCYWID		.297*	75.53*	.918*	1.10
CENCYLAT		-.309*	60.41*	.755*	11.54*
CENCYABX		-.774*	76.81*	.238*	4.56*
CENCYADX		-.599*	74.67*	.399*	0.16
ENDONUM		.403*	76.04*	.786*	0.15
PHLEND		.534*	77.75*	.763*	0.06
XYLEND		.465*	78.06*	.800*	0.51
LEAF MORPHOLOGY(t=346)					
%var.		74.72		34.76	
SOURCE	df	%SS	%SS (mva)	%SS	%SS (mva)
A	1	76.91*	59.26	1.77	2.69
e	344	23.09	40.74	98.23	97.31
COMPONENT CORRELATIONS (r)			%SS (uva)		%SS$_A$(uva)
NEEDLEN		-.069	5.29*	.124	0.32
ADXSTOM		-.652*	76.91*	-.361*	12.11*
ABXSTOM		.560*	74.03*	-.264*	0.05
RESCYNO		.487*	76.93*	.661*	0.00
RESCYLOC		.471*	68.27*	.608*	1.34
RESCYLEN		.109	54.11*	.811*	2.99*
TWIG MORPHOLOGY (n=353)					
%var.		65.73		48.68	
SOURCE	df	%SS	%SS (mva)	%SS	%SS (mva)
A	1	77.22*	63.40	0.02	1.45
e	351	22.78	36.60	99.98	98.55
COMPONENT CORRELATIONS (r)			%SS (uva)		%SS$_A$(uva)
PULVLEN		.399*	57.13*	.271*	0.00
TIPWID		.334*	75.49*	.851*	3.73*
TIPDEP		-.069*	44.67*	.959*	0.00
PULVPUB		.709*	76.29*	.155*	2.07
CONE MORPHOLOGY (n=382)					
%var.		71.56		39.76	
SOURCE	df	%SS	%SS (mva)	%SS	%SS (mva)
A	1	70.12*	53.22	0.70	1.44
e	380	29.88	46.78	99.30	98.56
COMPONENT CORRELATIONS (r)			%SS (uva)		%SS$_A$(uva)
CONLEN		.442*	76.14*	.663*	0.90
CONWID		.399*	45.00*	.578*	1.07
SCALEN		.263*	13.88*	.773*	0.35
SCALWID		-.484*	69.03*	.424*	2.75*
SCALTAP		.048	5.60*	.683*	0.16
WINGWID		-.332*	63.68*	.483*	1.09
WINGTAP		.247*	54.32*	.645*	0.11
FREESCAL		.145*	0.07	.597*	0.10
BRACTLEN		.720*	74.33*	.412*	3.33*
BRACTWID		.432*	74.47*	.500*	0.85
BRACTAP		.630*	73.48*	.350*	6.60*
SHCOLEN		.435*	75.11*	.572*	0.42
SHCOWID		.401*	57.16*	.455*	0.99
LOCOLEN		.442*	77.58*	.578*	1.80
LOCOWID		.300*	38.44*	.528*	1.14
TOTAL VARIABLES (t=209)					
%var.		78.48		20.48	
SOURCE	df	%SS	%SS (mva)	%SS	%SS (mva)
A	1	75.23*	61.87	0.50	2.70
e	207	24.77	38.13	99.50	97.30
COMPONENT CORRELATIONS (r)					%SS$_A$(uva)
NEEDWID		.194*	<see above>	.508*	<see above>
NEEDEP		-.763*		.370*	
ABXANG		.672*		.047	
ADXANG		.535*		.076	
CENCYWID		-.416*		.601*	
CENCYLAT		.296*		.415*	
CENCYABX		-.809*		.227*	
CENCYADX		-.700*		.368*	
ENDONUM		-.491*		.501*	
PHLEND		-.653*		.449*	
XYLEND		-.579*		.545*	
NEEDLEN		-.009		.431*	

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ADXSTOM	.664*	.198*
ABXSTOM	-.676*	.357*
RESCYNO	-.502*	-.109
RESCYLOC	-.481*	-.046
RESCYLEN	-.178*	-.111
PULVLEN	.353*	.279*
TIPWID	.308*	.618*
TIPDEP	-.134	.691*
PULVPUB	-.696*	.139*
CONLEN	.523*	.489*
CONWID	.391*	.403*
SCALEN	.317*	.556*
SCALWID	-.456*	.431*
SCALTAP	.062	.468*
WINGWID	-.290*	.420*
WINGTAP	.280*	.384*
FREESCAL	.158	.421*
BRACTLEN	.755*	.196*
BRACTWID	.507*	.309*
BRACTAP	.733*	.143
SHCOLEN	.498*	.387*
SHCOWID	.426*	.347*
LOCOLEN	.557*	.411*
LOCOWID	.301*	.326*

Table 51. PCAs of separate variable suites of standards of
  P. sitchensis comparing naturally occurring trees and trees
  grown in the nursery. Only first components given. r²
  (multivariate given for multiple linear regression of
  morphology and anatomy with longitude and latitude. *,
  component correlations significant ℗ p ≤ 0.01. Abbreviation
  given in Table 34. Component scores used in Figure 26.

	COMPONENTS (>1.0)	
	I(natural)	I(nursery)
LEAF ANATOMY (n=)	(376)	(500)
%var.	51.74	47.39
r² (mva)	4.58	25.56
COMPONENT CORRELATIONS (r)		
NEEDWID	.910*	.866*
NEEDEP	.789*	.871*
ABXANG	-.051	.144*
ADXANG	.301*	.121*
CENCYWID	.930*	.910*
CENCYLAT	.869*	.818*
CENCYABX	.580*	.590*
CENCYADX	.499*	.661*
ENDONUM	.669*	.573*
PHLEND	.872*	.799*
XYLEND	.855*	.647*
LEAF MORPHOLOGY(n=)	(415)	(500)
%var.	41.88	30.85
r² (mva)	8.10	18.52
COMPONENT CORRELATIONS (r)		
NEEDLEN	.439*	-.644*
ADXSTOM	.452*	-.727*
ABXSTOM	.066	-.595*
RESCYNO	.873*	.606*
RESCYLOC	.784*	.430*
RESCYLEN	.857*	.011
TWIG MORPHOLOGY (n=)	(414)	(499)
%var.	62.58	79.21
r² (mva)	10.94	25.52
COMPONENT CORRELATIONS (r)		
PULVLEN	.205*	.801*
TIPWID	.958*	.914*
TIPDEP	.959*	.947*
PULVPUB	inv	inv
VEGETATIVE (t=)	(49)	(57)
%var.	45.84	48.33
r² (mva)	7.87	23.20
COMPONENT CORRELATIONS (r)		
NEEDWID	.933*	.815*
NEEDEP	.756*	.912*
ABXANG	.138	-.238
ADXANG	.401*	.049
CENCYWID	.949*	.926*
CENCYLAT	.887*	.777*
CENCYABX	.573*	.794*
CENCYADX	.471*	.733*
ENDONUM	.786*	.755*
PHLEND	.893*	.855*
XYLEND	.920*	.873*
NEEDLEN	.149	.539*
ADXSTOM	.763*	.838*
ABXSTOM	.769*	.566*
RESCYNO	-.241	-.089
RESCYLOC	.023	.026
RESCYLEN	-.098	-.309
PULVLEN	.292	.566*
TIPWID	.938*	.944*
TIPDEP	.901	.890*
PULVPUB	inv	inv

Table 52. PCAs of separate geographic areas for separate variable
suites. Geographic areas excluded from analysis due to insufficient
sample size. Only first components given. *, component correlations
(r) and r' values significant ⊕ p ≤ 0.01. Geographic areas given in
Table 8 and Figure 7. Environment r' are specific to the first
component from each analysis. Abbreviation given in Table 35.
Component scores used in Figure 27.

GEOGRAPHIC AREAS

VARIABLES
LEAF ANATOMY

(n=)	1 (90)	2 (430)	3	4	5	6 (60)	7	8 (70)
%	62.69	45.96				52.88		45.83

ENVIRONMENT r'
ELEVATION	1.51	3.31				16.48		27.99
MOISTURE	2.43	5.57				0.08		5.48
ELEV + MOIST r' (mva)	11.27	32.17				34.97		32.25

COMPONENT CORRELATIONS (r)
NEEDWID	.908*	.663*				.762*		-.006
NEEDEP	.776*	.736*				.839*		.943*
ABXANG	.335	.057				-.109		-.486*
ADXANG	.655*	.246				.210		-.045*
CENCYWID	.979*	.942*				.975*		.762*
CENCYLAT	.887*	.559*				.693*		-.303
CENCYABX	.679*	.497*				.506		.741*
CENCYADX	.471	.561*				.611		.793*
ENDONUM	.855*	.781*				.869*		.772*
PHLEND	.926*	.910*				.932*		.867*
XYLEND	.948*	.901*				.890*		.847*

(n=)	9	10 (240)	11 (55)	12 (330)	13 (205)	14 (101)	15 (55)	16 (70)
%		66.39	48.61	77.85	60.02	60.68	47.22	43.82

ENVIRONMENT r'
ELEVATION		1.19	15.05	2.53	0.31	19.98	17.06	0.27
MOISTURE		6.66	7.34	0.58	9.99	0.35	37.82	2.62
ELEV + MOIST r' (mva)		25.64	24.47	9.02	17.12	14.59	36.16	25.01

COMPONENT CORRELATIONS (r)
NEEDWID		.914*	.699*	.969*	.894*	.923*	.945*	.666*
NEEDEP		.860*	.846*	.926*	.882*	.826*	.659	.846*
ABXANG		.486*	.154*	.757*	.248	.369	.536	-.014
ADXANG		.672*	.279*	.756*	.376	.248	.444	.158*
CENCYWID		.964*	.891*	.972*	.971*	.957*	.962*	.749*
CENCYLAT		.833*	.501*	.935*	.843*	.872*	.913*	.613
CENCYABX		.676*	.779*	.724*	.587*	.807*	-.002	.561
CENCYADX		.678*	.354*	.777*	.691*	.856*	.558	.696*
ENDONUM		.913*	.878*	.910*	.781*	.593*	.706	.709*
PHLEND		.899*	.879*	.965*	.964*	.882*	.735	.753*
XYLEND		.926*	.896*	.956*	.899*	.867*	.516	.913*

LEAF MORPHOLOGY

(n=)	1 (105)	2 (456)	3	4	5	6 (165)	7	8 (80)
%	53.01	38.24				53.75		43.43

ENVIRONMENT r'
ELEVATION	70.39*	20.43				6.15		44.89*
MOISTURE	2.10	3.96				0.25		6.45
ELEV + MOIST r' (mva)	44.12	18.27				29.69		35.95

NEEDLEN	.302	-.119				.568*		-.274
ADXSTOM	.832*	-.455*				-.638*		-.591
ABXSTOM	.310	.309*				-.802*		.193
RESCYNO	-.858*	.909*				.810*		.809*
RESCYLOC	-.870*	.681*				.712*		.799*
RESCYLEN	-.899*	.829*				.829*		.922*

(n=)	9	10 (154)	11 (65)	12 (245)	13 (215)	14 (105)	15 (65)	16 (80)
%		37.94	43.88	39.00	40.50	32.93	51.79	46.31

ENVIRONMENT r'
ELEVATION		7.51	1.93	24.11*	0.98	8.18	8.18	34.34
MOISTURE		11.16	1.90	0.56	4.37	3.53	17.14	34.46
ELEV + MOIST r' (mva)		14.86	20.73	16.10	32.55	14.04	19.20	43.40

NEEDLEN		-.356	.517	.364	.502*	-.631*	.013	.809*
ADXSTOM		-.477*	-.739*	.705*	-.126	.555*	.859*	.731*
ABXSTOM		-.219	.592	.652*	.085	.800*	.588*	.764*
RESCYNO		.904*	.109	.655*	.862*	.743*	.758*	-.819*
RESCYLOC		.549*	.843*	.505*	.774*	-.133	.816*	.136
RESCYLEN		.869*	.864*	.775*	.902*	.179	.885*	-.421

TWIG MORPHOLOGY

(n=)	1 (105)	2 (450)	3	4	5	6 (163)	7	8 (80)
%	49.52	50.37				51.65		61.85

ENVIRONMENT r²

ELEVATION	22.00	0.98			20.07*	7.78
MOISTURE	1.73	3.13			0.02	0.59
ELEV + MOIST r² (mva)	29.93	10.37			20.69	32.00
PULVLEN	.453	.544*			-.423	.878*
TIPWID	.917*	.896*			.957*	.953*
TIPDEP	.878*	.932*			.958*	.892*
PULVPUB	-.406	.219			.230	.065*

	9	10	11	12	13	14	15	16
(n=)		(167)	(65)	(265)	(204)	(105)	(65)	(80)
%		59.84	56.32	56.86	56.00	50.10	64.04	63.79

ENVIRONMENT r²

ELEVATION		6.45	4.97	2.50	16.56	0.31	0.98	53.88*
MOISTURE		7.78	15.76	7.13	0.17	3.96	18.40	58.51*
ELEV + MOIST r² (mva)		14.93	24.11	5.09	14.01	19.44	36.44	54.24
PULVLEN		-.127	-.534	.446*	.785*	.546	.791*	.888*
TIPWID		.916*	.871*	.929*	.877*	.875*	.979*	.893*
TIPDEP		.960*	.881*	.919*	.925*	.930*	.948*	.949*
PULVPUB		.786*	.659	.606*	invar.	-.275	.281	.257

CONE MORPHOLOGY

	1	2	3	4	5	6	7	8
(n=)	(213)	(527)	(110)	(146)	(88)	(437)	(170)	(210)
%	43.13	34.89	49.15	46.76	52.00	54.68	39.67	50.03

ENVIRONMENT r²

	1	2	3	4	5	6	7	8
ELEVATION	0.62	0.24	0.20	11.76	0.50	21.07*	0.18	20.07*
MOISTURE	10.63	0.66	0.30	47.00*	2.10	4.20	0.00	2.53
ELEV + MOIST r² (mva)	19.63	13.02	18.41	33.02	24.84	51.58	7.38	36.16
CONLEN	.695*	.482*	.758*	.463	.759	.639*	.607*	.736*
CONWID	.573*	.551*	.565	.787*	.754	.729*	.085	.783*
SCALEN	.958*	.874*	.977*	.929*	.906*	.902*	.818*	.856*
SCALWID	.289	.663*	.223	.539	.878*	.518*	.505	.573*
SCALTAP	.776*	.741*	.706	.829*	.908*	.829*	.726*	.846*
WINGWID	.378	.697*	.213	.551	.878*	.558*	.477	.500
WINGTAP	.789*	.698*	.519	.726*	.657	.831*	.492	.779*
FREESCAL	.567*	.649*	.794*	.724*	.668*	.645*	.682*	.856*
BRACTLEN	.821*	.120	.930*	.761*	.655	.864*	.852*	.573*
BRACTWID	.298	.359	.742*	.335	.197	.676*	.528	.579*
BRACTAP	.691*	.110	.806*	.649*	.217	.829*	.773*	.565*

	9	10	11	12	13	14	15	16
(n=)	(100)	(362)	(148)	(464)	(469)	(220)	(200)	(197)
%	48.60	42.41	35.74	53.28	46.60	57.82	47.57	63.13

ENVIRONMENT r²

	9	10	11	12	13	14	15	16
ELEVATION	41.47	0.06	0.58	17.06*	11.56	1.72	7.18	3.76
MOISTURE	4.75	3.26	2.76	12.53	10.69	18.66	22.97	22.85
ELEV + MOIST r² (mva)	33.88	37.29	13.54	14.31	17.54	14.69	37.18	42.03
CONLEN	.760	.368	.556	.716*	.495	.791*	.302	.866*
CONWID	.745	.568*	.317	.544*	.762*	.801*	.559*	.881*
SCALEN	.759	.875*	.814*	.892*	.832*	.865*	.939*	.950*
SCALWID	.485	.558*	.676*	.787*	.631*	.729*	.886*	.823*
SCALTAP	.739	.909*	.872*	.833*	.859*	.851*	.905*	.917*
WINGWID	.742	.505*	.729*	.739*	.678*	.711*	.666*	.713*
WINGTAP	.550	.733*	.202	.695*	.629*	.712*	.591*	.787*
FREESCAL	.375	.861*	.767*	.773*	.618*	.692*	.749*	.817*
BRACTLEN	.879*	.479*	.371	.697*	.860*	.784*	.787*	.735*
BRACTWID	.662	.588*	.568	.576*	.357*	.599*	.272	.679*
BRACTAP	.807*	.441*	.143	.706*	.607*	.791*	.547	.446*