

AN ABSTRACT OF THE THESIS OF

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Title: GEOGRAPHIC VARIATION IN JUVENILE GROWTH CHARAC-  
TERISTICS OF DOUGLAS-FIR (PSEUDOTSUGA MENZIESII  
(MIRB. ) FRANCO) FROM THE COASTAL RANGES OF  
CALIFORNIA

Abstract approved: \_\_\_\_\_

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K. K. Ching

A sample of 181 wind pollinated families, representative of the range of environmental conditions occupied by Douglas-fir in northern California, was used as a basis for studying variation in early height growth, phenology, and seed characteristics.

Seedlings were raised at Corvallis, Oregon, in a nursery trial designed to evaluate response to varying levels of moisture stress. Variation in cold hardiness was also assessed following a period of abnormally low winter temperatures.

It was demonstrated that seedlings from the coastal fog-belt region set buds later; grew taller; were less cold hardy; and had less capacity to go dormant in response to moisture stress than did samples from the inner ranges. Coastal samples were also characterized by

smaller seeds; slower germination; and seedlings with fewer cotyledons and shorter hypocotyls.

Lesser variation patterns associated with source elevation and latitude were apparent.

For characteristics related to the annual cycle of growth and dormancy, regional differences were greater in relation to family variation than they were for seed related factors. The adaptive significance of this is considered.

Regression analyses are presented relating seed weight, and epicotyl length at the end of the first growing season, to source climate and location; the models are then used to compare results of the present study with previously published data.

Finally, implications of the study for Douglas-fir seed movement within California, and to exotic planting sites, are discussed, and a procedure for seedlot origin verification suggested.

Geographic Variation in Juvenile Growth Characteristics  
of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)  
from the Coastal Ranges of California

by

Anthony Roderick Griffin

A THESIS

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Typed by Mary Jo Stratton for Anthony Roderick Griffin

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## TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION	1
Objection and Scope of the Study	3
II. DESCRIPTION OF THE STUDY AREA	4
III. LITERATURE REVIEW	7
Geological History	7
Vegetation History	8
Douglas-fir in Present Vegetation Association	12
California Tree Seed Zones	15
Climate of Northern California	18
Variation of Climate with Elevation	20
Adaptive Variation in Douglas-fir	22
Seed Characteristics	24
Growth and Phenology	25
Resistance to Frost, Winter Cold, and Drought	28
IV. SAMPLING AND EXPERIMENTAL PROCEDURES	33
Sampling	33
Seed Processing	35
Nursery Phase	36
Experimental Design and Establishment	36
Cultural Procedures	39
Assessment Techniques	41
Seed Characteristics	41
Phenology	42
Growth	43
Response to Stress Regimes	44
Cold Damage	44
V. RESULTS	47
Response to Stress Treatment	47
Analysis of Geographic Variation in Seed, Growth and Phenology	53

	<u>Page</u>
Inter-correlations of Seed and Seedling Characteristics	58
Regional Differences	60
Differences between Major Locations	61
Differences between Minor Locations	63
Regression on Location and Climate	66
Choice of Location Indices	69
Choice of Climatic Variables	74
Variation in Cold Hardiness	80
Relation of Hardiness and Date of Budset	84
Variation of Hardiness with Elevation	85
VI. DISCUSSION AND CONCLUSIONS	87
Response to Stress Regimes	87
Population Structure and the Adaptive Nature of the Observed Variation Patterns	88
The Breeding Unit in Douglas-fir	89
Adaptation to Spatial Environmental Heterogeneity--Theoretical Considerations	91
Nature of the Observed Variation Pattern	93
Adaptation of Factors Related to the Seasonal Growth Cycle	93
Adaptation of Seed-Related Characteristics	99
Conclusions	101
General Validity of the Seed Weight and Epicotyl Length Variation Models	102
Seed Weight	102
Epicotyl Length	108
Implications for Seed Movement	111
Definition of Seed Zones	111
Use of Californian Douglas-fir as an Exotic	113
Use of Juvenile Characteristics in Seed Source Identification	115
VII. SUMMARY	119
BIBLIOGRAPHY	124
APPENDIX	133

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
I	Source Data for Major Location Collections.	6
II	Effect of Stress Regimes on the Shoot Dry Weight and Epicotyl Length of Seedlings Used for PMS Determination.	50
III	Effect of Stress Regimes on Phenology and Height Growth--Analysis of Variance Summaries and Table of Means.	52
IV	Analysis of Variance Summaries and Estimates of Components of Variance for Ten Seed and Seedling Characteristics.	53
V	Regional and Major Location Means for Ten Seed and Seedling Characteristics.	57
VI	Correlation Matrix for Ten Seed and Seedling Characteristics.	59
VII	Analysis of Minor Location Effects and Correlation with Elevation within Major Locations, for Characters Showing Significant Variation at this Level in Combined Analysis.	64
VIII	Major Location Mean Residuals for the Epicotyl Length on Location Model, as a Percentage of Observed Length.	73
IX	Mean Adjusted Climatic Variables for Major Locations.	76
X	Correlation of Adjusted and Unadjusted Climatic Variables with Seed Weight and Epicotyl Length.	77
XI	Correlation Among Adjusted Climatic Variables.	77
XII	Percentage of Plants Showing Cold Damage Symptoms, by Date of Budset and Major Location Classes.	82

<u>Table</u>		<u>Page</u>
XIII	Chi-squared Values for Tests of Homogeneity of Cold Damage Data.	83
XIV	Comparison of Seed Weight Determined from 1956 and 1968 Collections, with Predictions from Models Based on 1968 and 1971 Data.	105
XV	Early Height Growth of Douglas-fir Seedlings of California origin when Raised in New Zealand, and Predicted Epicotyl Length of the Same Sources Based on Growth at Corvallis, Oregon.	109

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Northern California showing limits of the study area and major sampling locations.	5
2	Vegetation of northwestern California (after Daubenmire, 1969).	14
3	Physiographic and climatic regions of northern California as defined by the California Tree Seed Zone Map, and location of sub-region and zone boundaries within the study area.	17
4	A styroblock, showing layout of three six-seedling plots and two control seedlings within a section.	38
5	Rewatering levels for seedlings grown under three stress regimes.	48
6	Increase of shoot dry weight of control seedlings with time, by stress regimes (families and replicates combined).	49
7	Variation of epicotyl length with elevation by latitudinal transects and major locations.	65
8	Variation of epicotyl length with source elevation for a) combined coastal locations and b) inner range locations.	67
9	Variation of epicotyl length with source elevation for all locations combined.	70
10	Variation of epicotyl length with source distance from the ocean, all locations combined.	70
11	Percentage of seedlings showing cold damage symptoms by elevation classes within major locations.	86

<u>Figure</u>		<u>Page</u>
12	Variation of seed weight with distance from the ocean, by individual parent tree.	100
13	Variation of epicotyl length with distance from the ocean, by individual family means.	100
14	Correlation of predicted epicotyl length with a) one-year and b) two-year height growth in New Zealand.	110

## LIST OF APPENDIX TABLES

<u>Table</u>		<u>Page</u>
I	Location Data and Family Character Means (untransformed).	133
II	Supplemental Information, and Sample Calculations for Analysis of Variance of Seed and Seedling Characteristics	143
III	Meteorological Data Summary for Stations Representative of Major Locations.	151
IV	Meteorological Data Summary for Subsidiary Location Stations, and Those Used in Preliminary Climatic Analysis.	152
V	Correlation Matrix for Climate/Location Data, 18 Stations within the Study Area.	153

GEOGRAPHIC VARIATION IN JUVENILE GROWTH  
CHARACTERISTICS OF DOUGLAS-FIR  
(PSEUDOTSUGA MENZIESII (MIRB. )  
FRANCO) FROM THE COASTAL  
RANGES OF CALIFORNIA

I. INTRODUCTION

Coastal Douglas-fir (Pseudotsuga menziesii (Mirb. ) Franco var. menziesii) is a component of many forest types throughout its range from British Columbia to central California, and there is ample evidence of resulting adaptive variation in characters such as growth rate and hardness.

The species is very important for reforestation in western North America and as an exotic in many parts of the world. Therefore definition of geographic variation patterns, as a basis for introductions and specification of seed zones, is a major task facing tree improvement workers.

To date, the majority of Douglas-fir provenance studies have been carried out in Europe where, from climatic considerations, emphasis has been placed on Washington and British Columbia (B. C.) sources. In the western United States major trials such as that initiated in 1912 by the U. S. Forest Service (Munger and Morris, 1936; Silen, 1964), or that of Ching and Bever (1960), have also concentrated on more northerly sources from Oregon, Washington, and B. C. The

only study where sampling was concentrated in southern Oregon and northern California was that conducted in New Zealand by Sweet (1965). The recent seed collection expeditions sponsored by I. U. F. R. O. (Barner, 1966) did include a number of samples from that area, but unfortunately low-elevation coastal (fog-belt) sites in California were not well represented. Sweet's data indicated that seedlings from the latter region grew faster under New Zealand conditions than did those from more inland locations and higher latitudes. This observation provided the incentive for the present study, since more detailed definition of the species' variation pattern would facilitate the choice of sources for future provenance trials.

In contrast to the region to the north of the Columbia River, which was periodically glaciated during the Pleistocene epoch, the Klamath Mountain Province of southern Oregon and northern California has probably been continuously occupied by vegetation since the early Tertiary (Whittaker, 1960). Pseudotsuga fossils have been found in Pliocene deposits in Humboldt County (Dorf, 1933), so it appears that Douglas-fir or a closely related species has been present in the region for at least some ten million years.

The location of the Klamath Mountains and California Coast Range results in a steep climatic gradient inland from the Pacific Ocean (Engelbrecht, 1955). Douglas-fir is therefore found growing under a wide range of moisture and temperature conditions within

comparatively short distances. Apart from the practical considerations, both of the above factors make northern California a very suitable area for the study of adaptive variation in an essentially continuous plant population.

### Objective and Scope of the Study

The major objective was to define the pattern of variation in some seed, early growth, and phenology characteristics exhibited by Douglas-fir from northern California. The study was based on a wind-pollinated seed collection made in 1971 and a nursery trial grown at Corvallis, Oregon, in 1972-73.

Seedlings were raised under three different watering regimes to determine whether adaptation had occurred in response to the great range of moisture stress conditions to which the species is exposed. The abnormally cold weather in December 1972 also provided data demonstrating variation in cold hardiness.

Data for two characteristics of practical importance (seed weight and height growth) were analyzed to determine relationships with seed source location and climate, thus allowing tentative conclusions regarding the movement of seed within the region and to exotic planting sites.

Finally the general validity of the results was tested by comparison with those of published studies and the potential for developing early confirmatory tests of seedlot origin discussed.

## II. DESCRIPTION OF THE STUDY AREA

The area chosen for study is defined by the Pacific Ocean to the west, the Sacramento Valley to the east, in the north by the California-Oregon border (Latitude  $42^{\circ}\text{N}$ ), and the south by Monterey Bay (Latitude  $37^{\circ}\text{N}$ ) (Figure 1). It encompasses a north-south distance of 350 miles, is approximately 90 miles wide in the north, and tapers to a narrow coastal strip in the south.

In a north and northeasterly direction the boundary is arbitrary in that Douglas-fir distribution continues uninterrupted into the mountains of southern Oregon and the northern Sierra Nevada. In other directions it is delineated by the species range.

Isolated populations of Douglas-fir do occur on more southerly sites (Griffin, 1964), and several of these, including the most southerly one near Lompoc ( $34^{\circ}30'\text{N}$ ), were sampled. However, with the exception of one tree near Little Sur ( $36^{\circ}20'\text{N}$ ) no viable seed was obtained from these isolated stands. The population to the north of Santa Cruz may certainly be taken as the most southerly from which commercial quantities of seed could be obtained, and may therefore be considered as the effective southern limit of the range.

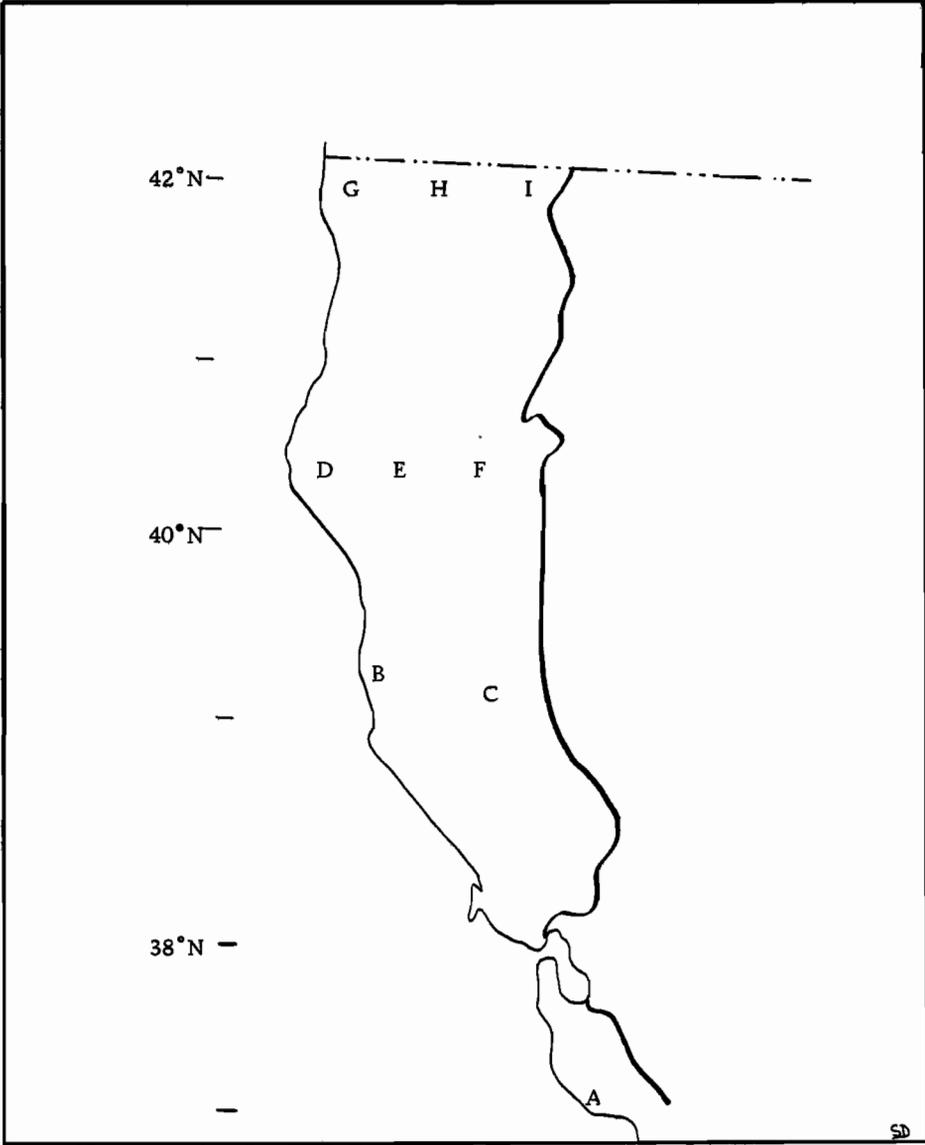


Figure 1. Northern California showing limits of the study area and major sampling locations.

Table I. Source Data for Major Location Collections.

Major Location		Average Location Indices				Distance from Ocean (mi.)	Elevation (ft)	Elevation Range Sampled (ft)	No. Minor Locations	Total No. Families
		Latitude (N)		Longitude (W)						
		o	'	o	'					
Gasquet	(G)	41	47	124	00	7	1847	3500	10	19
Happy Camp	(H)	41	52	123	28	36	2437	3450	15	34
Mt. Ashland	(I)	41	56	122	47	74	3238	3200	11	26
Humboldt Redwood State Park	(D)	40	14	124	00	16	1490	2900	12	22
Forest Glen	(E)	40	23	123	23	42	3532	2250	8	14
Harrison Gulch	(F)	40	20	123	00	58	3567	1750	4	9
Jackson State Forest	(B)	39	32	123	36	11	1250	2450	10	19
Bear Creek (Mendocino National Forest)	(C)	39	17	122	50	50	3290	2250	6	11
Santa Cruz	(A)	37	08	122	11	5	1292	2650	9	27

### III. LITERATURE REVIEW

#### Geological History

The study area contains two distinct, though contiguous, mountain regions--the Klamath Mountains and the California Coast Range. Although the Klamaths are geographically part of the coastal chain, they differ from both the Oregon and California Coast Ranges in age, geologic character and complexity, height, and east-west extent (Whittaker, 1960). Their limits may be defined by the extensive outcropping of younger rocks in the surrounding mountains (McKee, 1972). To the north are Lower Tertiary marine strata of the Oregon Coast Range, with non-marine volcanic rocks of that period to the east, and Cretaceous marine beds forming the California Coast Ranges to the south. The latter strata, lying across the north end of the Sacramento Valley, flank the Klamaths for 50 miles southwest from Redding; from there the contact with the Coast Range follows the South Fork Mountain fault, which lies to the west of the Trinity River, in a northwest direction to the coast near the California-Oregon border.

The Klamath region is geologically complex, with metamorphosed Paleozoic sediments overlaid in some areas by Mesozoic sedimentary and volcanic strata (Fenneman, 1931). Following Mesozoic submergence the region was uplifted at the end of the Cretaceous Period. It has therefore existed, at least as low mountains, for some 60 million

years--in contrast to the more recently emerged Coast Ranges, where the oldest rocks are metamorphosed sediments of Jurassic age, and the remainder largely Cretaceous and Tertiary sandstones (Fenneman, 1931).

The two regions are distinguishable physiographically as well as geologically. The Klamaths are considered to be a dissected peneplain, with erosion beginning after the late Mesozoic uplift, though direct evidence is scanty since no Tertiary rocks are present. The Coast Ranges were severely deformed in the late Miocene, and at the end of the Pliocene. Towards the middle Pleistocene they subsided to 1,000 to 2,000 feet, later rising to form marine terraces along the coast. In general it appears that the present Coast Range topography dates from the close of the Tertiary or early Quaternary--some two million years ago.

#### Vegetation History

The climate of northern California was warm and humid during the Oligocene, a flora from Weaverville being described as subtropical (Wolfe, 1969). Conifer species were unimportant.

In the early Miocene a predominantly broad-leaved deciduous forest covered the Pacific Northwest, with an increasing conifer component in the north. Wolfe (1969) listed Pseudotsuga as being present in the fossil floras of Oregon by the early Miocene, although

the oldest Californian fossil record of the genus dates from the Pliocene epoch (Dorf, 1933).

As an aid to understanding the possible evolutionary history of Douglas-fir in the study area, the regional vegetational history since the Miocene will be discussed--although it should be remembered that the Klamath region has been continuously occupied by vegetation since at least the early Tertiary (Whittaker, 1960), and that the fossil record is quite inadequate to determine the period at which the genus was first present.

Pseudotsuga is part of the Arcto-Tertiary Geoflora, which was considered to be holo-arctic in distribution at higher latitudes during the early Tertiary (Axelrod in Munz and Keck, 1965). Recent work in Alaska (Wolfe, 1969) has cast doubt on the validity of this theory; however, since composition rather than origin per se is important in this discussion, it is simpler to maintain the term Arcto-Tertiary to denote the temperate forest of mixed hardwoods and conifers.

From consideration of the literature, Axelrod (in Munz and Keck, 1965) concluded that the West American Element of the Arcto-Tertiary began to invade the Sierra Nevada from the north during the late Miocene. Then with increasing aridity the flora was gradually confined to the moister upland sites and the humid coast sector. Sequoia forest, which had occurred at Ashland in the eastern Siskiyou Mountains in Oligocene times, was probably restricted to its present coastal location.

by the middle Pliocene (Whittaker, 1961). The later Pliocene saw a rapid differentiation of communities when more diverse climates developed in response to the uplift of the Sierra Nevada and Coast Ranges.

Pseudotsuga fossils bearing a close anatomical resemblance to P. menziesii were found in the Lower and Middle Pliocene Wildcat Formation in Humboldt County; in the Middle Pliocene Sonoma Formation east of Santa Rosa, and in Merced sandstones of the same age in the San Francisco Bay area (Dorf, 1933).

In all probability it has been present in the Klamath Mountains for a longer period still, since the latter acted as a refugium for Miocene plant populations destroyed in other areas by glaciation, submergence, climatic desiccation, or lava flows (Whittaker, 1960).

Species variation between older Pliocene floras is much greater from north to south in the interior than on the coast slopes of Oregon and California (Chaney, 1944)--an observation which is consistent with the modern vegetation. Assuming that Pseudotsuga was a component of both forests as it is now, current differential selection pressures may have been in operation since the Pliocene.

The increasing importance of Pseudotsuga since the Miocene has been noted by Wolfe (1969). He concluded that the primary difference between the late Miocene and the modern conifer forest of the Northwest is that Pseudotsuga did not play as significant a part in the vegetation

as today. On the basis of pollen deposits, he suggested that dominance of the genus in the present forest was attained during the middle or late Pleistocene. This is suggestive of adaptive evolution within the gene pool of the species, and it is interesting to note that Axelrod (1957) speculated that the time since the end of the Tertiary has been one of rapid evolution of plant species. He suggested that fluctuating glacial and pluvial climates intensified hybridization, since spatial relations of populations must have been continually changing. As an example, Babcock and Stebbins (1938) studied the genus Crepis in northern California and concluded that onset of the Pleistocene glacial climate was a great impetus for formation of apomictic species, since it produced moister conditions throughout the region and allowed previously isolated forms to come together and hybridize. All forms now found in the Coast Ranges are closely related to apomictic forms in the Klamath Mountains, are probably young in evolutionary terms, and attained their present distribution in the late Pleistocene.

It is known (Munz and Keck, 1965) that, during Pleistocene glacial periods, Sequoia sempervirens migrated some 200 miles south of its present distribution. Such latitudinal movements would have been reversed during inter-glacial periods, and there would have been a secondary direction of migration between low and high elevations. Since Pseudotsuga was a component of both the drier Sierran section of the Arcto-Tertiary flora and the coastal forest, it is likely

that the gene pool contained sufficient variability to accommodate such climatic fluctuation. In contrast to the Redwood, which has rather narrow physiological tolerances and fluctuated in distribution over time, the Douglas-fir could have responded to environmental changes by in situ adaptive changes in gene frequency. In support of this hypothesis it may be noted that, although the most southerly coastal occurrence of extensive stands is co-incident with the Redwood in the Santa Cruz area, the most southerly outlying population occurs about 170 miles to the south near Lompoc (Griffin, 1964). This is 100 miles south of the present limit of Redwood in southern Monterey County (Fowells, 1965).

#### Douglas-fir in Present Vegetation Associations

Munz and Keck (1965) provided a classification of the Californian flora consisting of a hierarchical system of plant communities within vegetation types within biotic provinces. According to their scheme, the study area contains portions of the Oregonian and Californian provinces.

Of the eight Coniferous Forest Type (V)<sup>1</sup> communities present, Douglas-fir occurs in the following:

- (10)<sup>1</sup> North Coastal Coniferous Forest
- (12) Redwood Forest
- (13) Douglas-fir Forest
- (14) Yellow Pine Forest

---

<sup>1</sup>Numbering system from Munz and Keck (1965, p. 13).

Of the remaining communities--(11) Closed Cone Pine Forest, (15) Red Fir Forest, (16) Lodgepole Forest, (17) Subalpine Forest--only the Red Fir Forest occupies any significant area. Douglas-fir is also a major component of the Mixed Evergreen Forest Type (VI). This widespread distribution has led to its use as a reference species for ecological studies in the Siskiyou Mountains (Cleary and Waring, 1969).

A broader classification of vegetation in the region is discussed by Daubenmire (1969). Excluding small areas of subalpine forest at the highest elevations, the vegetation falls into two major types. Along the coast is a cool, moist forest dominated by Redwood, while inland from the fog-belt is "forest characteristic of moderately dry climates," with Douglas-fir as the major climax dominant (Figure 2). A distinctive feature of this Douglas-fir belt, as opposed to its more northerly counterparts, is the abundance of evergreen sclerophyllous shrubs in the undergrowth.

The boundary of the coastal forest is shown to extend inland in a northeasterly direction through the Siskiyou Mountains. The vegetation of this area has been studied by Waring (1969), and a rather precise floristic boundary established on the basis of indicator species such as Picea breweriana and Quercus sadleriana. It was shown that the Eastern Siskiyou (included in Daubenmire's Douglas-fir province), had a substantially greater summer diurnal temperature fluctuation than

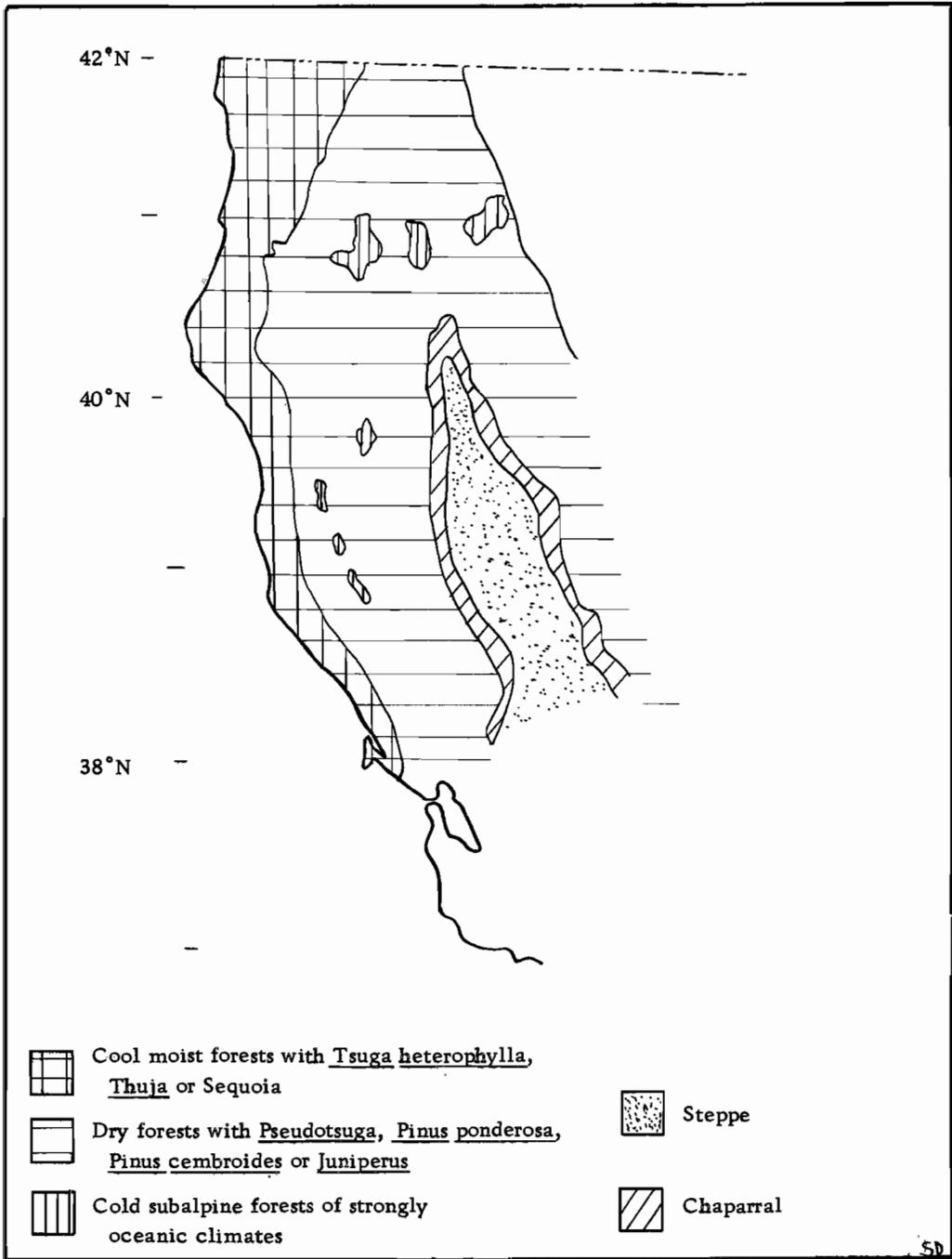


Figure 2. Vegetation of northwestern California (after Daubenmire, 1969).

did the Western Siskiyou which occupy the inner margin of the coast forest according to Figure 2.

Although treatment at this level is crude in terms of describing actual variation in vegetation types, these classifications nevertheless emphasize the regional relationship between climate and vegetation, allow comparison with conditions in previous eras, and provide a logical framework within which bio-systematic studies of widespread species such as Douglas-fir may be planned.

### California Tree Seed Zones

The Seed Policy Committee of the United States Department of Agriculture (McCall, 1939) recognized the need for delineating tree seed collection zones and produced a statement including the general recommendation that, whenever available, local seed from natural stands should be used, unless seed from another area had been specifically demonstrated as superior. To quote:

Local seed means seed from an area subject to similar climatic influences, and may usually be considered as that collected within 100 miles of the planting site and differing from it by less than 100 ft. in elevation.

The process of applying these general principles to Californian forests was begun by Fowells (1946). Forest type and site were used as a basis for the definition of 13 seed collection zones--four lying within the present study area. The coastal fog-belt was divided into

northern Redwood and southern Redwood zones, with the boundary at Cape Mendocino, on the grounds that the northern zone was more productive and had a greater variety of associated minor tree species than did the southern (including the Santa Cruz area) where Douglas-fir was the principal minor species. To the east of the fog-belt a coast range Douglas-fir zone was designated, and the remainder of the inner range coniferous forest was included in a north coast pine zone.

Roy (1963) sub-divided these broad major zones in northwestern California into local zones approximately 50 miles in latitude and 500-foot elevational sub-zones within each, and Schubert (1966) produced a map extending the system to the remaining major zones within the state. The only major change from Fowell's map was the separation of the Santa Cruz Mountains from the southern Redwood zone, presumably because of geographic isolation from the rest of the zone to the north on San Francisco Bay.

The current definitive recommendations were produced by the Forest Tree Seed Committee of the Society of American Foresters (Buck et al., 1970). The major seed collection zones of the previous maps were combined to form six Physiographic and Climatic regions (Figure 3). The North Coast Redwood region (series 090) combined the northern and southern Redwood zones (once again including the Santa Cruz Mountains) and was then divided into seven seed collection zones, each covering about 50 miles in latitude. The coast range

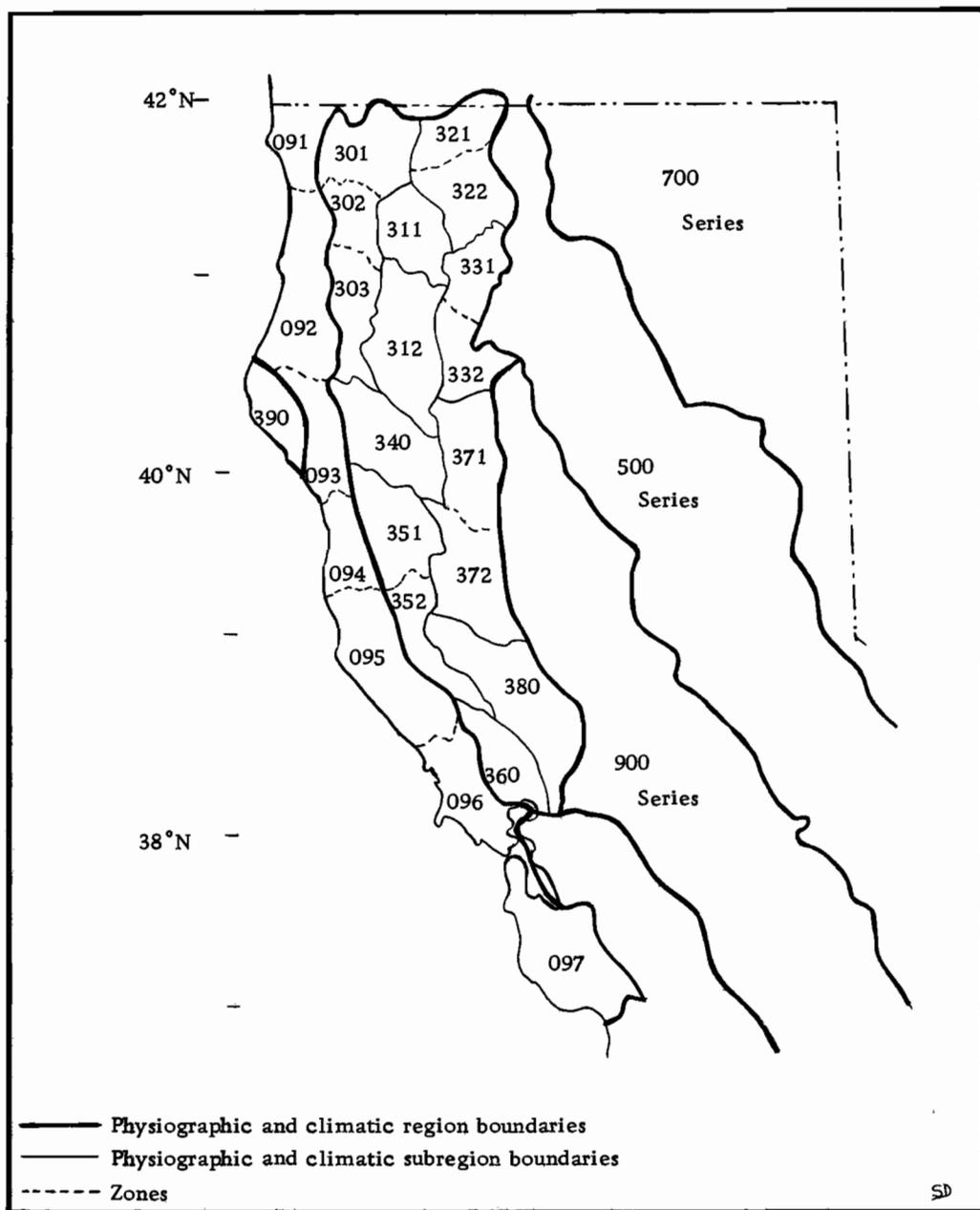


Figure 3. Physiographic and climatic regions of northern California as defined by the California Tree Seed Zone Map (Buck *et al.*, 1970), and location of subregion and zone boundaries within the study area.

Douglas-fir and north coast pine formed the North Coast Interior region, an adjustment which recognized that there is no distinct climatic or physiographic boundary between the former zones.

Within the region, nine sub-regions and 17 seed collection zones were designated.

Division into physiographic and climatic regions is appropriate since, if intra-specific differentiation has occurred at all, it is likely to be apparent within species subjected to such grossly different environmental conditions. At the present state of knowledge, however, subdivision of regions has greater utility for administrative than for biological reasons. The map provides a means of coding seed origin records which may be used for assessing the biological significance of current zone boundaries when growth data become available.

### Climate of Northern California

To a very great extent the climate of the region is determined by topography. In most parts of the world latitude is the major determinant of temperature, but in California isotherms have a north-south trend following the topographic contours (Sprague, 1941). As a result there is a strong east-west climatic gradient inland from the Pacific Ocean. The immediate coastal area has a true marine climate marked by moderate temperatures with small daily and annual range, and infrequent frosts. The outer coast ranges effectively shut off this

marine influence, resulting in a more continental climate in the inner ranges and the Sacramento Valley.

Average precipitation is also influenced by topography, being much heavier on the southern and western than on the northern and eastern slopes. In general it increases from south to north; however, nearly all the rainfall occurs during the winter months, with growing-season precipitation extremely limited throughout the area. This pattern is due to the development of a high pressure area over the North Pacific, which reaches maximum intensity in the late summer and diminishes until about February (McEwen, 1924). This causes the transfer of moist air towards the coast in winter, and the reverse in summer.

Visher (1954) contrasted the climate conditions of the coastal strip with those prevailing a short distance inland. The sharpest contrasts are between temperature extremes, with normal annual highest temperatures  $15^{\circ}\text{F}$  higher 100 miles or less inland than on the coast. Differences are even greater in winter, with normal annual minima some  $25^{\circ}\text{F}$  lower to the east of the coast ranges than on the coast. This is due to the exposure of the inner ranges and valleys to cold air masses from the northeast. The July noon humidity of the coastal zone is much greater than that of the inner ranges and valleys with approximate figures of 80% and 50% respectively. The coast has

sunshine about two-thirds of the possible time in summer compared to 90% further inland.

The biological significance of these differences, due largely to coastal fog, may be inferred from the associated changes in vegetation. The distribution of the fog-belt is closely correlated with that of the Coast Redwood (Waring and Major, 1964). Fog reduces air temperature and increases humidity, thereby reducing transpiration, and may also provide a source of moisture for the plant. Shreve (1927b) reported that August soil moisture content was nearly twice as high at Carmel than at ten miles inland, on a comparable soil. Soil moisture actually increased from August to September at Carmel, due to fog condensation on vegetation. Stone (1957) has demonstrated that artificial mist spray can increase survival of various conifer species under depleted soil moisture conditions.

In conclusion the following quotation from Kendrew (1953) appropriately emphasizes the great climatic diversity within the region: ". . . the difference between the coast and interior (Sacramento Valley) is as large as that between Scotland and north Africa. "

#### Variation of Climate with Elevation

A common difficulty when trying to relate properties of forest communities to climate is that Weather Bureau recording stations are frequently situated in valleys near centers of habitation, while the forests are growing at relatively higher elevation.

On an average world-wide basis mean annual temperature decreases  $3^{\circ}\text{F}$  per 1000 - ft. elevation rise (Kendrew, 1953). In the Pacific coastal regions, however, climate is determined by degree of exposure to oceanic influences, rather than by elevation per se. Shreve (1927b) measured summer temperature along an east-west transect through Carmel (Monterey County), and found a greater difference in daily maxima between Carmel and a site at 300 ft. 10 miles inland than between the latter and a 5000-ft. sampling point. In a related study (Shreve, 1927a) in the same area, altitude was placed behind topographic site, slope, and distance from the ocean, as determinants of vegetation type.

Baker (1944) divided the western U. S. A. into 28 areas and considered changes of climate with elevation within each. Two of these (Area 5 - Klamath Mountains and Inner Coast Ranges of California, and Area 6 - Outer Northern Coast Ranges of California) cover the study area. For Area 5, graphs were presented showing rates of change for each 1000-ft. elevational rise, for aspects of temperature and growing season length. None were suggested for Area 6, since weather stations at different elevations were not available. However, the over-riding influence of the coastal fog was stressed, and for the contiguous area 7--southward from the Russian River--it was observed that mean temperature increased somewhat with elevation.

A further factor reducing the correlation of climate and elevation in the Pacific coast region is the influence of the North Pacific High (Manley, 1945), since anti-cyclonic weather and clear skies are associated with a low lapse rate. Clark (1937) noted that certain zonal indicator plant species in the Yolla Bolly Range occur up to 1000 ft. higher than on the east side of the Sacramento Valley, because the steep slopes of the mountains do not cause the air to cool as effectively as do the long west slopes of the Sierras.

Sweet (1965) adjusted growing season length by 30 days for each 1000 ft. of deviation between seed collection site and the nearest weather station. Dates of the last spring and first fall frosts were adjusted by + and - 15 days per 1000 ft. respectively, and mean temperature of the coldest month by  $-3^{\circ}\text{F}$  per 1000 ft. These constants may be applicable for the inner coast ranges and Klamath Mountains but do not seem justified for fog-belt locations.

#### Adaptive Variation in Douglas-fir

The existence of adaptive intraspecific variability is well established. Burley (1965) reviewed the concepts of clinal and ecotypic variation as they have been found to apply to tree species.

Allen and Owen (1972) described the developmental aspects of the seasonal growth cycle in Douglas-fir. All individuals go through the same sequence of events each year, in response to changes in

environmental stimuli such as photoperiod, temperature, and available moisture. However, the time at which developmental events (phenology) occur may differ greatly. This is because the seasonal climatic cycle is largely responsible for changes in operational environmental factors, and this varies with location. As an example, it is known that cold hardiness is inversely proportional to growth rate (Levitt, 1966), therefore, to avoid recurrent injury an individual must be actively growing only between the normal dates of last spring and first fall frost.

The correlative approach, attempting to relate climatic data to observed plant responses, has the disadvantage that there is no explanation of mechanisms involved, and usually no tie to data supplied by physiological studies (Waring and Major, 1964). In studies of genetic variation, however, we are dealing with patterns that evolved in response to past environmental conditions--and these can only be assessed indirectly. The approach is useful with the understanding that each climatic parameter is itself only an index of the operational environmental factors to which the plant reacts. The same reservation is biologically applicable to discussion of variation in terms of geography.

This review will concentrate on studies of more southerly sources of the coastal Douglas-fir. For a more comprehensive treatment of British Columbian provenances and the Rocky Mountain variety see Haddock et al. (1967) and Wright et al. (1972).

Only two reported studies (Ching and Bever, 1960; Sweet, 1965) sampled both latitudinal and longitudinal variation in coastal Douglas-fir, and neither attempted to define ecotypic boundaries or clinal discontinuities. However, from the synthesis of published results certain general variation patterns are apparent.

### Seed Characteristics

Birot (1972) determined seed weight for samples from California through British Columbia, and found a cline of decreasing size with increasing latitude. Sziklai (1969) measured seed length on samples from the same collection, and observed a similar pattern. Superimposed on this gradient, at least within the southern Oregon/California region, is an increase in the seed weight with altitude. Independent collections (Ching and Bever, 1960; Sweet, 1965) confirmed the latter observation, though it must be remembered that these relationships are based on data from a wide range of environments, and are valid only on a region-wide scale. In a more localized study Sorensen (1967) sampled at intervals along an east-west transect through Corvallis, and reported no difference in seed weight between Lacombe (900 ft. - West Cascade foothills) and Santiam Pass (4400 ft. - Cascades). For a 3500-ft. transect in southern Oregon, Hermann and Lavender (1967) found that seed weight decreased from low to medium elevation, and then increased slightly again for the highest samples.

Allen (1961) presented data suggesting that at 10°C, after 40 days cold stratification, seed from the Cascades germinated faster than that from low-elevation, more coastal sources, although he warned that this characteristic may be altered by non-genetic factors. The result agreed with Owen (1957) who found that seed from high elevation in southern Oregon germinated faster than a low-elevation Polk County source.

The adaptive significance of seed size and germination characteristics is difficult to demonstrate, because of parallel variation in other growth and hardiness factors. However, it has been shown that in Trifolium sp. cotyledon area was related to seed weight, and in turn to growth rate of emerged seedlings (Harper et al., 1970). Since soil moisture can be an important factor in survival of Douglas-fir germinants in the field (Owen, 1953) the ability to germinate and make fast growth would presumably be of selective advantage on xeric sites.

### Growth and Phenology

Generalizations about geographic variation in growth patterns may be misleading in that they fail to take into account genotype x planting environment interaction. Thus, in the 1912 Heredity Study a Benton County, Oregon source grew well on its own site and poorly elsewhere, and the same was true of a high-elevation Santiam, Oregon source (Isaac, 1949). Variation in adaptability of seed sources

over a range of plantation elevations and latitudes was also reported by Rowe and Ching (1973). Lofting (1952) speculated that sources found to have wide adaptability in Europe (e. g., Darrington, Louella) originated in areas where site conditions were heterogeneous.

Although height growth rate is usually taken as an estimate of productivity in tree improvement studies, evidence from the 50-year assessment of the 1912 Heredity Study (Silen, 1966) emphasizes the importance of survival in determining stand volume production over a rotation.

With the above reservations in mind, a geographic pattern of growth potential under favorable conditions is apparent from the literature. At a given latitude, low-elevation and coastal sources are faster growing than those from more extreme environments further inland (Irgens-Moller, 1958, 1967; Owen, 1957; Sorensen, 1967). For the Pacific coast region as a whole there is a significant negative correlation of two-year height and source elevation (Sweet, 1965). Ching and Bever (1960) found no clear relationship of growth to elevation or latitude in the nursery stage, though at age nine the six fastest growing sources all came from coastal locations, and the two slowest from the Oregon Cascades (Rowe and Ching, 1973). Southern Oregon seedlings from low elevation grew faster in the nursery than those from high elevation, and for a given elevation north aspect seedlings

faster than those from more xeric southern aspects (Hermann and Lavender, 1967).

Latitudinal variation is not so pronounced, though Sweet (1965) reported a significant negative correlation of growth and source latitude, for his regional collection. Orr-Ewing (1966) showed that when trees from Lake Cowichan, Vancouver Island, were crossed with pollen from Oregon and California, growth of the resulting seedlings was faster than when both parents were local.

Most of the above studies report a negative correlation between date of terminal budset and height growth, but this does not hold for budburst. The latter characteristic seems to be related more to local than regional environmental factors. Munger and Morris (1936) found that ranking of provenances remained constant over successive years, and that sources could be grouped according to spring temperature conditions. First to burst were those from low-elevation plains and wide valleys, followed by high-elevation sources, and lastly those from foothill valleys where cold air drainage produced frosty nights after warm days. In accordance with this hypothesis seedlings from Corvallis, Oregon burst buds earlier than those from Burnt Woods in the Coast Range (Irgens-Moller, 1966; Sorensen, 1967). In the latter study and that of Sweet (1965), there was little relationship between average date of budburst and source climate. This may merely reflect

inadequacy in available climatic data, or it may indicate action of some as yet unresolved selection pressures.

Resistance to Frost, Winter  
Cold, and Drought

Susceptibility to spring frost damage may be accurately assessed from consideration of budburst dates, since there is no evidence for inter-provenance variation in resistance at the same developmental stage (Munger and Morris, 1936). Phenology may be less satisfactory, however, as an index of fall frost resistance. For Oregon and Washington Coast Range sources, October frost damage was more severe, at an identical stage of budset, for the most southerly sources (Campbell and Sorensen, 1973). Susceptibility of the latter sources was also increased by their tendency to set buds at a later date. Of climatic correlations investigated by Sweet (1965) the strongest was between height growth and mean temperature of the coldest month ( $r = +0.79$ )--evidence of the adaptive importance of growth cessation and hardening as a preparation for winter.

Latitudinal variation in cold hardiness has been observed. All seedlings of a low-elevation coastal California source (Jackson S. F., Mendocino County) were killed by exposure to  $-11^{\circ}\text{C}$  at Haney, British Columbia (Haddock et al., 1967), in contrast to lesser damage to more northerly coastal sources, and none to those from interior British

Columbia. Lines (1970) precluded the use of southern Oregon and Californian sources of Douglas-fir in Scotland because of susceptibility to winter damage. In a trial in Pennsylvania, coastal provenances did not show a marked latitudinal variation pattern, but highest elevation ones were least susceptible to injury (Gerhold, 1967). Plantations of high-elevation origin were also more resistant than adjacent low-elevation trees when subjected to a freeze on Mount Hood in 1938 (Isaac, 1949).

These observations from field trials are complimented by controlled-environment data. Owen (1957) exposed young seedlings to 0°F for 40-minute periods and scored mortality. Of the Oregon sources tested, high-elevation (Jackson and Douglas Counties) were rated as highly resistant, low-elevation (Douglas County) intermediate, and a low-elevation coastal source (Polk County) very susceptible to injury.

Finally it may be noted that even native stands of Douglas-fir may be damaged by winter cold (Childs, 1961; Duffield, 1966). Daubenmire (1957) surveyed damage from the 1955 freeze in Washington and Idaho and concluded that coastal ecotypes sustained a greater degree of injury than did those growing to the east of the Cascades.

On the basis of field evidence there is less variation in drought resistance. Possibly this is because drought has its greatest effect on survival at the establishment stage, whereas the chance of cold

damage occurs annually throughout the lifespan. Alternatively, because moisture stress is dependent upon interaction between plant and micro-site factors, genetic differences may have been obscured by large residual variation. Rowe and Ching (1973) report that a provenance plantation near Medford, Oregon was severely damaged by drought, but apparently survival was not related to provenance.

Most controlled-environment and nursery tests of response to moisture stress have either used survival as a response criterion, or else investigated specific physiological processes. Lavender et al. (1968) did determine, however, that a stress regime involving rewatering when soil moisture tension reached 15 atmospheres hastened budset and reduced dry matter production for three seed sources tested.

Heiner and Lavender (1972) raised 1+0 transplants from xeric sites in southern Oregon and a mesic northwest Oregon location in a lysimeter at Corvallis, Oregon. After the soil had dried naturally through the summer, the latter source showed only 16% survival, compared with up to 70% for the others. Differential survival was also evident when seedlings from the west end of the Columbia Gorge (60 in. annual precipitation) were grown under dry conditions and compared with a sample from the eastern end (20 in. ppt.) (Isaac, 1949). The dry-site seedlings had relatively smaller crowns and better-developed root systems--an observation confirmed by Owen

(1957), Lavender and Overton (1972), and Hermann and Lavender (1967).

Ferrell and Woodard (1966) and Pharis and Ferrell (1966) showed inter-source variation in glasshouse survival tests designed to assess drought avoidance and hardiness. Although the primary contrast was between the coastal and interior varieties of the species, it is significant that seedlings from Corvallis and Rogue River, Oregon responded more like the inland sources than did those from mesic coastal locations. Inter-source drought avoidance characteristics (root ramification and/or transpiration control) were generally better developed than those for hardiness (ability to withstand a dry internal environment). Mesic sources also have a higher rate of transpiration and respiration than xeric ones (Zavitkovski and Ferrell, 1968, 1970).

According to Waring (1969), Douglas-fir cambial growth ceases above a minimum plant moisture stress (PMS) of 18 atmospheres, and death results above 45 atmospheres. On sites in the Siskiyou Mountains moisture stress causes growth cessation only in late summer (Cleary and Waring, 1969), but growth appears to be reduced at much lower stress levels. Zahner (1968) concluded that tree growth responds more to environmental water stress than to any other normal perennial factor in the forest, and Griffith (1960) found that soil moisture content accounted for 69% of the variation in basal area increment among 70-year-old Douglas-fir stands at Haney, B. C. On

drier sites a greater proportion of the annual growth occurred early in the season. These data were collected in an area which is by no means among the drier sites occupied by the species, since annual rainfall is 91 in., with 10 in. falling in the summer months. If there is interprovenance variation in the ability to express growth potential in the face of summer drought conditions, there are important implications for plantation productivity.

From the above literature synthesis it appears that there is a trend of reduced growth and increasing drought and cold tolerance as one proceeds inland from the coast, and to a lesser extent from south to north--a trend paralleled by increasing extremity of climate. It is known that factors which slow or stop growth induce hardiness, the most important being decrease of temperature below a critical level, and shortening of photoperiod beyond a critical length (Alden and Hermann, 1971). On the basis of this physiological generalization, the observed variation pattern in coastal Douglas-fir fits well with the hypothesis of regional adaptation to climatic conditions.

#### IV. SAMPLING AND EXPERIMENTAL PROCEDURES

##### Sampling

Burley (1965) has aptly stated that "probably the most acceptable concept of variation in forest trees is that climate has a continuous variation pattern, and tree growth is related to climate." The sampling plan was designed in light of the above premise, and with knowledge of the climatic variation pattern in the study area.

A necessary initial decision was that regarding allocation of sample points within and between stands. The I. U. F. R. O. recommendations for standardization of provenance tests (Lines, 1967) suggested that seed should be obtained from at least ten, and preferably 25 to 50, dominant or co-dominant trees located at random, or along a transect. In Slash pine, Squillace (1966) found that within-stand variation could not be adequately sampled by five-tree collections, and even with a 20-tree sampling scheme Jack pine varied more within than between stands for a number of morphological characteristics (Schoenike, 1963). To quote Larson (1956) regarding Douglas-fir: "everywhere one is bound to be impressed by the great individual variation of this tree species. . . ."

It was therefore concluded that in this study accurate estimates of variation within particular stands could not be obtained without sacrificing the primary objective of describing variation throughout the whole area.

Assuming a continuous variation pattern, data are amenable to multiple regression analysis, with location indices or climatic observations as independent variables. The sampling pattern was designed to cover the range of study area locations in terms of latitude, elevation, and distance from the ocean, and thereby minimize interpolation and extrapolation.

Since the steepest environmental gradients run east-west, with a lesser latitudinal gradient, it was decided that samples should be collected at four latitudes, more or less evenly spaced throughout the region, and at intervals along an east-west transect at each latitude. This resulted in designation of nine major locations, each located in the general vicinity of a weather station, and accessible by road (Figure 1). The distribution of 3-3-2-1 major locations at latitudes from north to south reflects the greater environmental range of the species in the northern part of the study area. Within each major location, sampling of the complete elevational range of Douglas-fir was attempted. The plan was derived without specific reference to the California Tree Seed Zone map (Figure 3), to reduce a priori assumptions about variation patterns.

Ideally cones were collected from two trees not less than 200 ft. apart, at elevational intervals of 250 ft. Each collection point at a particular elevation is referred to as a minor location. Deviations from this ideal, in terms of number of trees per minor location, and

elevational intervals, occurred at all major locations because of the distribution of suitable cone-bearing individuals. In all an average of 2.1 trees were sampled at each of the 85 minor locations.

In addition to major location collections (Table I), cones were collected from several isolated populations to the south of the study area and from intermediate points within it. Finally, to allow comparison with more northerly provenances, seed was obtained from five locations in Oregon, two in Washington, and four in British Columbia. Complete sampling data are presented in Appendix Table I.

Cones were collected from roadside trees using a pruning pole, or less frequently by climbing. The latter practice was avoided where possible for safety reasons. No attempt was made to restrict collection to trees of particular age or crown class, but patently diseased or suppressed individuals were avoided. The procedure may have introduced a negative selection for form, since branchy, wide-crowned trees were more accessible; however, there is no reason to think that this will have affected the seedling characteristics studied.

### Seed Processing

Cone collection was carried out over a period of four weeks in August 1971. Since most cones were still green when picked, a modification of the method suggested by Silen (1958) was used to complete the ripening process artificially. Cones were wrapped in

damp, unground sphagnum moss, placed in brown paper bags, and stored in boxes for transportation back to Corvallis. The bags were then stored in a cool basement until early October when cones were removed and spread out to dry. A combination of resin, peat, and mould had glued up many scales, necessitating hand extraction of the seed. Each seedlot was dewinged by hand-rubbing and cleaned using an air column. A cutting test where two successive five seed samples each contained at least four full seeds was used as a measure of adequate cleaning. This standard was adopted since many seedlots were in short supply, and wastage of any viable seed was undesirable. All lots were hand-counted and weighed, and mean seed weight was calculated. These weights are probably underestimates in some cases, due to the inclusion of unfilled seed.

### Nursery Phase

#### Experimental Design and Establishment

The nursery trial was laid out in a split-plot design with two replications. Main-plot treatments were watering regimes at three levels, with 212 individual families as sub-plots. These comprised 181 samples from the major locations, plus an additional 19 from California, 7 from Oregon, 2 from Washington, and 3 from British Columbia (Appendix Table I).

Two-inch styroblocks (Figure 4) were used as containers, since preliminary studies had shown that control of moisture regime in conventional nursery beds was difficult. The containers had the added advantage that they were moveable, and individual seedlings could be permanently identified for recurrent measurement. A disadvantage was that only eight cubic inches of soil were available to each seedling.

There was space in each container for 12 sub-plots; therefore 18 blocks were required for each main-plot. After being filled with a screened forest topsoil that had previously been mixed with a coarse sand in a 3:1 ratio, the blocks were laid out in six groups of 18 on glasshouse benches. Families were allocated at random to sub-plots within each group, together with space for eight control seedlings per block. These controls were subsequently used for determination of plant moisture stress (PMS). To allow for possible variation in response to a given moisture regime, half the controls in each block were from a low-elevation coastal family (No. 10), and the remainder from a high-elevation inner range site (No. 213).

Following moist stratification for four weeks at  $2^{\circ}\text{C}$ , each seedlot was germinated in a Petri dish under an 8-hour light period at  $27^{\circ}\text{C}$ , alternating with a dark period of 16 hours at  $18^{\circ}\text{C}$ . Germinants were pricked out into the containers when radicles were approximately 1 cm long. This procedure ensured that each sub-plot initially

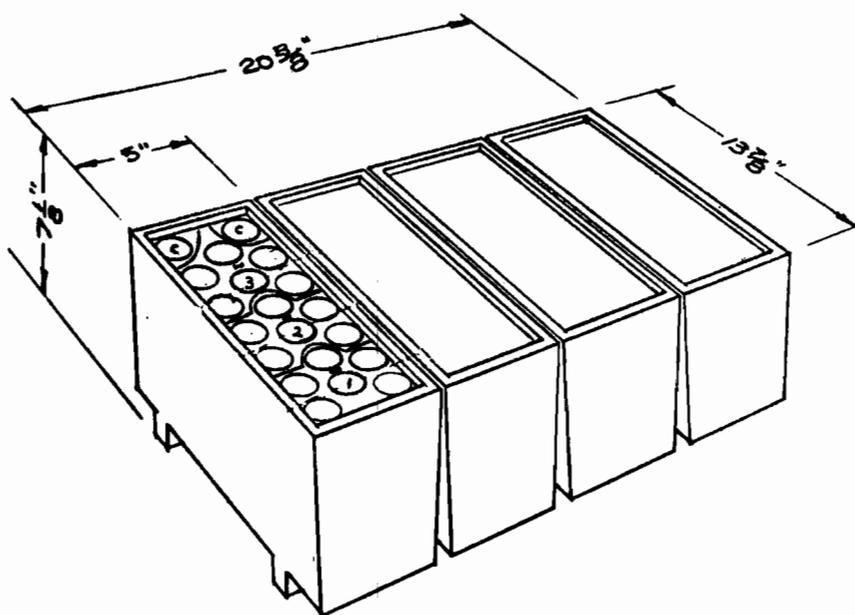


Figure 4. A styroblock, showing layout of three six-seedling plots and two control seedlings within a section.

contained six healthy seedlings, so minimizing the effects of viability differences between seedlots. Immediately after planting, seedlings were watered with a Captan solution to protect against damping-off fungi.

### Cultural Procedures

Seedlings were grown in the glasshouse under a 70°F temperature regime for five weeks. They were then moved to the nursery under shade, and kept well watered for a further three weeks to allow adjustment to the changed environment. At that time (early June) a watering regime was assigned to each of the six main-plots, and differential stress treatment commenced.

Preliminary tests showed that water could most evenly be applied over a main-plot with a hand-held trigger-type hose nozzle. To minimize within-plot variation in application the same nozzle was used throughout the trial, and the investigator personally carried out the operation. As a further precaution against edge effects, blocks were re-randomized within main-plots at two to three-week intervals.

Stress regimes were designed to determine growth responses rather than survival ability. Minimum PMS values of 30, 60, and 90 pounds per square inch (p. s. i.) were assigned as the respective base rewatering levels of Low (L), Moderate (M), and High (H) stress

treatments. These are realistic growing season stresses for Douglas-fir planting sites in Oregon (Cleary, 1971). According to laboratory data derived by Cleary (1971) each level is low enough to permit maximum photosynthesis in the early morning. However, since daily maximum stress values do restrict photosynthesis, growth responses were anticipated under the hypothesis that cumulative production of photosynthate would be affected by experimentally induced variation in the daily duration of conditions when water relations were favorable for photosynthesis.

Minimum PMS was monitored with a pressure bomb (Waring, and Cleary, 1967), measurements being made on a sample of two seedlings from each control family within each main-plot, at intervals dictated by time elapsed since last watering and by weather conditions. On average each main-plot was sampled every five days. If the mean PMS of the four seedlings per main-plot was greater than the specified base rewatering level, water was applied. At first an attempt was made to maintain stress levels constant over time, but this proved to be impracticable with the system available. Therefore each application consisted of enough water to resaturate the soil in the blocks. Whenever rain appeared imminent the M and H main-plots were protected with removable plastic screens. The differential watering regimes were continued until mid-September, by which time nearly all seedlings had set bud.

In order to obtain vigorous growth in the containers frequent application of aqueous fertilizer is recommended (Matthews, 1971). However fertilizing was ruled out in this experiment because of the danger of unspecifiable interaction with watering regimes. Therefore growth was dependent upon nutrients available in the soil mixture, and was markedly less than that normally expected in open-root beds.

To reduce the chance of freezing damage from the movement of cold air under and around the containers, each main-plot was surrounded by Sawdust in October 1972. A layer of this material was also spread over the surface between seedlings.

In February 1973, the drainage holes in the bottom of the containers were enlarged, and the latter set into prepared beds of screened forest soil. This procedure allowed the seedlings to grow in an essentially open-rooted condition in the second growing season, without undergoing transplanting shock which could have affected flushing. The original experimental design was maintained.

### Assessment Techniques

#### Seed Characteristics

Seed weight determination has been described on p. 36. To assess germination rate approximately 100 seeds from each stratified

seedlot were germinated under the same conditions as those for the nursery trial (p. 37). Germination was first noted on the third day, and a count of germinants was made at two-day intervals thereafter. Any seedlings with a radicle length in excess of 2 mm was classified as a germinant. For this purpose no distinction was made between those which continued healthy development, and those which, as in some seedlots, succumbed to post-germination fungal or bacterial attack. Counts were terminated at the end of 21 days, and the cumulative number of germinants at each count expressed as a percentage of the total. Percentage germinated after seven days was used as a measure of rate in subsequent analysis.

### Phenology

Budset assessment was initiated at the commencement of stress treatment, and continued at intervals through the remainder of the growing season. If the shoot apex was visible between the terminal needles, a seedling was recorded as having a set bud. Many seedlings made two or more growth flushes, and buds were classified as burst if one or more needles had ruptured the budscales. At the end of the growing season the date at which each seedling had set its final bud was determined from records, and the mean date for each subplot calculated, and expressed as the number of days elapsed since the mean establishment date (April 12th).

All seedlings were assessed for bud burst during the spring of the second growing season. Observations were made at two to three day intervals from March 16th 1973, when the first seedling flushed, and, as before, needle emergence through the ruptured budscales was the criterion adopted. Data were recorded for both terminal and lateral buds, but only the former was subsequently used, since a number of seedlings did not have well developed laterals, and where both were present, dates tended to be closely correlated.

Flushing date was recorded as the number of days from March 16th, and sub-plot means were calculated. Because of cold damage to the Low stress main-plots, only data from the Moderate and High regime plots were used in computing family means. Seedlings which had suffered fall frost, winter cold, or other terminal bud damage, were not included in the assessment.

### Growth

When germinants were pricked out, initial differences in size were apparent. Total height at the end of the growing season therefore contained a component due to hypocotyl length (cotyledon height), the remainder representing shoot growth (epicotyl length).

Total height from the container surface to the base of the terminal bud was measured to the nearest mm, together with the height of the cotyledons. Epicotyl length was then obtained by

subtraction, and plot means computed. The number of cotyledons was also counted on three sub-plots of each family, and the resulting 18 observations averaged to express the character on a family basis.

### Response to Stress Regimes

It would have been desirable to use dry matter production as a measure of response to the watering treatments, but this destructive method was ruled out by the desirability of making subsequent observations on the live seedlings. Sub-plots were too small to allow a subsampling approach. It was, however, possible to demonstrate the effect on shoot dry weight over the test period from control seedling data, since each of the latter was oven dried and its weight and epicotyl length recorded.

It was apparent that stress regimes had an effect on both date of budset and epicotyl length. From consideration of the data it was decided that the difference between mean date of budset under Low and Moderate stress (bud sensitivity), and the difference in epicotyl length between these two levels expressed as a percentage of the Low stress epicotyl length (height sensitivity), were the best methods of quantifying family response to moisture stress.

### Cold Damage

The trial was unexpectedly exposed to a period of abnormally

cold weather in December 1972 with a minimum temperature of  $-7^{\circ}\text{F}$ . Fortunately snowfall was sufficient to cover most seedlings and protect them from damage; however, parts of both Low stress main-plots were exposed, and needle discoloration and death were apparent on some seedlings within two weeks.

Since the exact extent of the exposed area was not noted while snow cover persisted, and damage was obviously not uniform over the whole of either main-plot, the following criteria were adopted in deciding whether a particular sub-plot should be assessed. The three sub-plots within each container section were inspected, and assessed only if the section, together with at least one adjacent to it, contained two or more damaged seedlings. A section with one or no damaged seedlings was not assessed unless it was completely surrounded by assessable sections. The method was biased against sections containing three of the more hardy families; however, this was considered preferable to the possibility of including families that had in fact been under snow cover.

A further possible source of variation--that the taller seedlings were more exposed than the shorter ones--was discounted because adjacent seedlings of different origin were damaged to different levels in the crown.

Each seedling within assessable sub-plots was scored on a scale of 0 (no damage) to 4 (all needles dead). In all, 119 of the 212

families in the trial were assessed for winter cold damage, and 47 of the 119 were exposed in both main-plots.

## V. RESULTS

### Response to Stress Treatment

Plant Moisture Stress for each main-plot treatment level is shown in Figure 5. Levels fluctuated throughout the growing season, and the prescribed base levels of 90, 60, and 30 p. s. i. resulted in final mean rewatering stresses of 120, 82, and 46 p. s. i. for the High, Moderate and Low regimes, respectively.

Increases in shoot dry weight and epicotyl length with time for the control sample seedlings are given in Figure 6 and Table II. Dry weight of these seedlings under High stress was significantly less than that for the Moderate treatment, and the latter in turn less than for those grown under Low stress. Epicotyl length proved to be a less precise index of response in that the H and M seedlings were not significantly different, though both were significantly shorter than the L seedlings.

A split-plot analysis of variance was calculated on the sub-plot data for date of budset and epicotyl length. Somewhat unexpectedly it was noted that watering regime also affected the date of budburst in the spring of the second growing season. Therefore a similar analysis was performed on budburst data from the 126 families for which data from all main-plots were available.

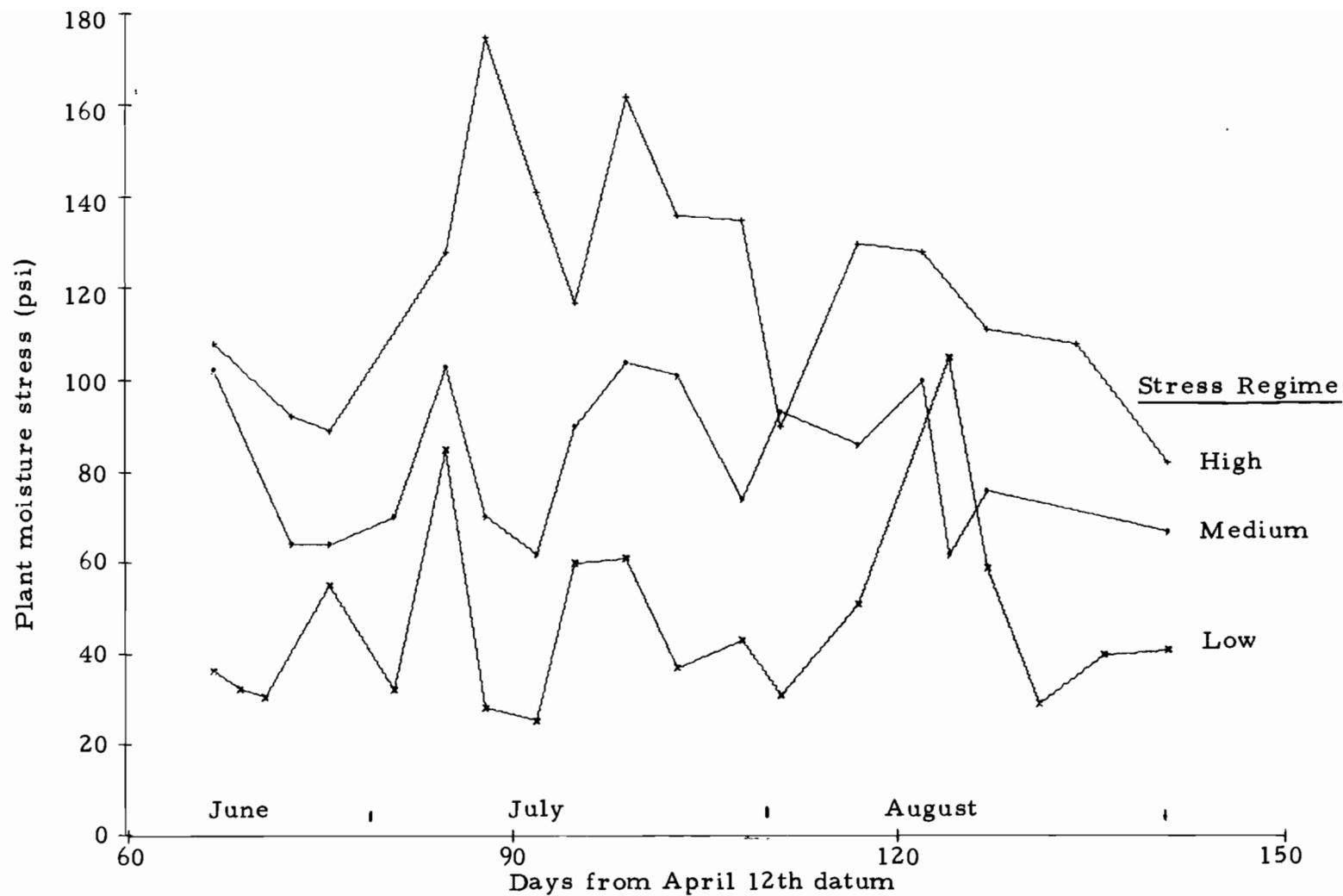


Figure 5. Rewatering levels for seedlings grown under three stress regimes. Each curve represents the mean of two replications.

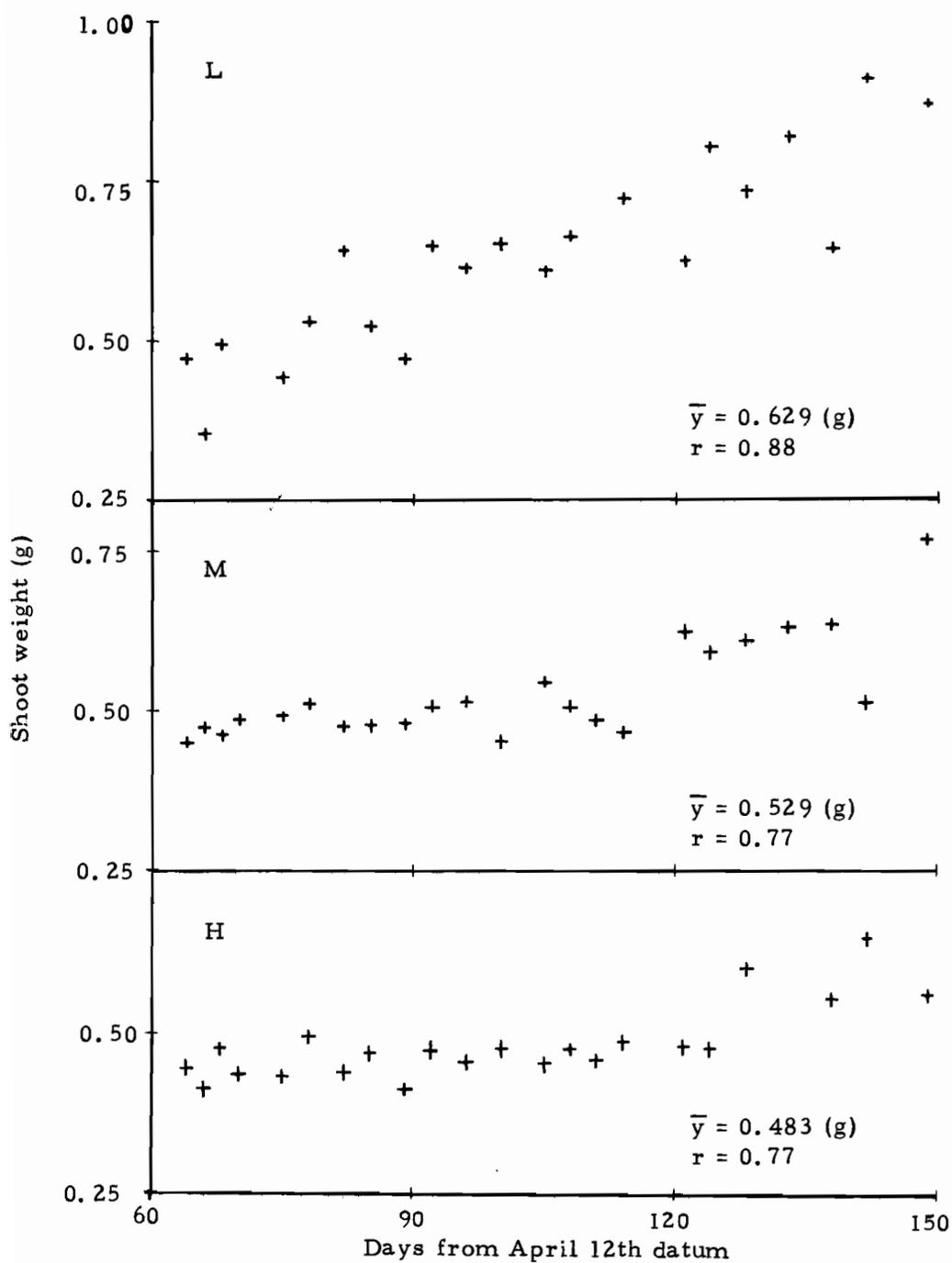


Figure 6. Increase of shoot dry weight of control seedlings with time, by stress regimes (families and replicates combined).

Table II. Effect of Stress Regimes on the Shoot Dry Weight and Epicotyl Length of Seedlings Used for PMS Determination.

Stress Regime	Family	Seasonal Mean Dry Weight (g)	Seasonal Mean Epicotyl Length (cm)
Low (L)	10	0.632	2.88
	213	0.627	2.19
	Combined	0.629	2.54
Moderate (M)	10	0.526	2.35
	213	0.529	1.78
	Combined	0.528	2.07
High (H)	10	0.489	2.26
	213	0.471	1.72
	Combined	0.483	2.01
Paired t-values for contrasts of			
Combined Means:	L v H	5.74 <sup>***</sup>	5.05 <sup>***</sup>
	L v M	3.78 <sup>***</sup>	4.37 <sup>***</sup>
	M v H	2.83 <sup>*</sup>	1.12 n. s.

Significance levels:     \* 5%  
                               \*\* 1%  
                               \*\*\* 0.5%

Apart from Table III, this convention is followed throughout the text.

For days to budset the watering regime effect was significant at 5%, and at 10% for epicotyl length and budburst. Family effects were highly significant (Table III). Rather than attempting the laborious task of further partitioning the family-x-water regime sum of squares from these analyses, new variables for bud sensitivity and height sensitivity (p. 44) were generated from the table of family means, and these subjected to single factor analysis of variance to determine the extent of geographic variation in the response to stress regimes.

It may be seen (Table III) that Moderate stress advanced the date of budset by ten days compared with the Low stress treatment, but High stress did not result in a similar change in budsetting date. The only tentative explanation that can be offered is that the formation of a terminal bud, itself a growth process, was retarded by the severity of the High stress level, whereas the Moderate level produced the stimulus for bud formation and also allowed sufficient photosynthesis and growth for development to be realized. In support of this hypothesis, High stress control seedlings showed no increase in top dry weight until the end of the growing season (Figure 6) when atmospheric stress conditions would have been more moderate, whereas there was a slight continuous increase under Moderate stress conditions. Also, when mean epicotyl length over all families is compared, that for High stress (1.39 cm) is slightly less than that for

Table III. Effect of Stress Regimes on Phenology and Height Growth--Analysis of Variance Summaries and Table of Means.

Source of Variation	d. f.	Days to Budset		Epicotyl Length		Days to Budburst		
		M. S.	F	M. S.	F	d. f.	M. S.	F
Water Regime (W)	2	12474	11.24**	7.600	7.31*	2	2149	8.65*
Error	3	1110		1.040		3	248	
	-					-		
	5					5		
Families	211	3712	5.99***	0.397	17.31***	125	79	5.73***
F x W	422	671	1.08	0.024	1.05	250	12	0.85
Error	<u>633</u>	620		0.023		<u>375</u>	14	
Total	1271					755		

<u>Stress Regime</u>	<u>Days to Budset</u>	<u>Epicotyl Length (cm)</u>	<u>Days to Budburst</u>
High	123.8a <sup>+</sup>	1.39a	25.5a
Moderate	114.9b	1.42a	26.1a
Low	124.8a	2.01b	30.9b

<sup>+</sup> Means with a subscript letter in common do not differ at 5% level ( LSD ).

Significance levels for F-tests:

(This table only)

\* -- 10%  
 \*\* -- 5%  
 \*\*\* -- 0.5%

Moderate stress (1.42 cm). Therefore the additional period without terminal buds did not result in additional extension growth, though over the whole experiment there was a close correlation between epicotyl length and date of budset ( $r = 0.93$ ) (Table VI).

Watering regime also acted in some manner to precondition seedlings and affect the date of budburst. Compared with the other two levels, the seedlings grown under Low stress burst buds 5.1 days later (Table III). The family-x-water regime interaction was not statistically significant.

#### Analysis of Geographic Variation in Seed, Growth and Phenology

Family means were calculated for each character, and in each case the resulting 181 observations were subjected to analysis of variance. The sampling design was nested (families-in-minor-in-major-locations), with unequal class sizes (Appendix Table II). Since preliminary analysis showed that, for the majority of variables, the major contrast was between the four fog-belt locations (A, B, D, G) and five from the inner ranges (C, E, F, H, I), classification into these regions was added as a further level in the analysis. The latter was conducted under the assumptions of a mixed model, region effects being fixed, and the remaining levels random:

$$X_{ijkl} = \mu + \alpha_i + B_{ij} + C_{ijk} + \epsilon_{ijkl} \quad i = 1, 2 \quad j = 1 \dots n_i$$

$$\sum \alpha_i = 0; B = N(0, \sigma_B); C = N(0, \sigma_C); \epsilon = N(0, \sigma) \quad k = 1 \dots n_{ij}$$

Prior to analysis the mean and variance of each character were calculated for each major location sample, and their correlations computed. If the assumption of independence of these parameters appeared to be seriously violated, various transformations were performed, and the correlation re-evaluated (Appendix Table II). Seed weight, epicotyl length, and total height were analyzed following square root transformation, while the natural logarithm was appropriate in the case of bud sensitivity. For the latter variable it was also necessary to add a constant term to each observation to eliminate negative values. After analysis contrasts were calculated on transformed means and these then back-transformed for presentation. All other variables were analyzed using untransformed data.

The merits of alternative tests for multiple mean comparisons were discussed by Gill (1973), and from his conclusions it was decided that Scheffé's test (Snedecor and Cochran, 1967) was the most appropriate for this study, in view of the unequal sample sizes. The test is conservative, protecting Type I error probability more satisfactorily than other commonly used tests. Region and major location means are given in Table V, and complete family means and sample sizes in Appendix Table II.

Table IV summarizes the analysis of variance estimates for each character. Inequality of sample sizes invalidated the usual F-test based directly on appropriate mean squares; therefore Satterthwaite's

Table IV. Analysis of Variance Summaries and Estimates of Components of Variance for Ten Seed and Seedling Characteristics.

Source of Variation	d. f.	$\sqrt{\quad}$ Seed Weight			Germination % at 7 days			Cotyledon No.		
		MS	F	S <sup>2</sup> +	MS	F	S <sup>2</sup>	MS	F	S <sup>2</sup>
Regions	1	8.73	9.95*	0.09	13361	7.53*	129.4	8.01	9.53*	0.08
Major-in-Regions	7	0.74	4.42***	0.03	1501	2.86*	52.2	0.71	3.37***	0.027
Minor-in-Major	76	0.15	1.25	0.014	476	1.38	62.3	0.19	1.36	0.024
Families	<u>96</u> 180	0.12		0.12	345		345.0	0.14		0.14
		Cotyledon Height			Bud Sensitivity (log X + 27)			Height Sensitivity		
Regions	1	2.730	19.86***	0.029	4.906	23.6***	0.052	13849	31.0***	148.6
Major-in-Regions	7	0.127	1.80	0.003	0.046	0.31	0	378	0.92	0
Minor-in-Major	76	0.064	2.13***	0.016	0.198	1.18	0.014	403	1.27	40.5
Families	<u>96</u> 180	0.03		0.03	0.168		0.168	318		318

(Continued on next page)

Table IV. (Continued)

Source of Variation		Days to Budset			Days to Budburst		
		MS	F	S <sup>2+</sup>	MS	F	S <sup>2</sup>
Regions	1	87890	94.4***	962.6	340.0	1.40	1.07
Major-in-Regions	7	783	5.13***	33.2	206.0	15.56***	10.00
Minor-in-Major	76	136	1.64**	25.2	11.7	1.43*	1.67
Families	<u>96</u> 180	83		83	8.2		8.20
		$\sqrt{\quad}$ Epicotyl Length			$\sqrt{\quad}$ Total Height		
Regions	1	9.461	84.7***	0.1035	3.138	110.2***	0.034
Major-in-Regions	7	0.094	5.00***	0.0039	0.024	1.31	0.0003
Minor-in-Major	76	0.017	1.55*	0.0029	0.017	2.43***	0.005
Families	<u>96</u> 180	0.011		0.011	0.007		0.007

<sup>+</sup>For Regions this value estimates K<sup>2</sup>.

Table V. Regional and Major Location Means for Ten Seed and Seedling Characteristics.

Major Location	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
<u>Coastal</u>										
A	11.76abc <sup>+</sup>	30.3a	6.78a	1.28a	145.6a	23.9b	4.2a	18.2ab	2.33a	3.62a
B	10.37ab	40.7ab	6.81ab	1.27a	143.9a	31.6a	5.5a	19.4ab	2.49a	3.76a
D	12.46abcd	45.3abc	7.27bc	1.42ab	133.9a	25.4b	3.0a	26.2ab	1.94b	3.36b
G	9.61a	49.3abc	6.86ab	1.27a	145.5a	33.1a	2.1a	13.2a	2.43a	3.71a
Region Mean	11.51	40.5	6.93	1.31	142.3	27.9	3.7	19.4	2.28	3.60
<u>Inner Range</u>										
C	12.74abcd	46.5abc	7.39c	1.39ab	102.7bc	27.5ab	13.4a	37.1ab	1.25c	2.63cd
E	13.91bcd	71.0c	7.10abc	1.57b	104.3b	25.2b	20.5a	42.1b	1.17c	2.74c
F	17.98d	66.6c	7.55c	1.69b	93.1bc	26.3b	14.7a	41.7b	1.00c	2.70cd
H	13.62cd	52.1bc	7.32c	1.54b	102.0bc	24.5b	14.7a	35.7ab	1.17c	2.71c
I	14.82d	59.5bc	7.43c	1.61b	89.7c	24.8b	16.8a	34.0ab	0.98c	2.59d
Region Mean	14.28	57.7	7.35	1.56	98.2	25.2	15.7	36.9	1.11	2.67
Region Contrast (F-test)	*	*	*	***	***	n. s.	***	***	***	***
Grand Mean	12.72	49.4	7.15	1.44	119.4	26.5	9.4	28.5	1.62	3.10

<sup>+</sup> For each characteristic, means with a letter in common do not differ significantly at the 5% level (Scheffé Test).

approximate test procedure (Ostle, 1963) was used to form synthetic Mean Squares. Ratios of the latter approximately follow the F distribution, and were the basis for the values given in Table IV.

Computation procedure for the approximate F-tests and derivation of the components of variance are shown in Appendix Table II.

#### Inter-correlations of Seed and Seedling Characteristics

The correlation matrix for all characters is given in Table VI. Calculations were made on a family mean, rather than on an individual seed or plant basis, over all 181 families.

Of the 45 coefficients, 39 were statistically significant at the 1% level. Many of these relationships were expected because of inter-dependencies of measurement methods; e. g., height sensitivity and epicotyl length. Others, of biological importance, are:

- 1) Seed weight, cotyledon number and cotyledon height, which may be considered as functions of embryo size, all showed moderate positive correlation. The relationship with the other seed-related character (germination rate) was also significant for seed weight and height, but not cotyledon number.

- 2) The amount of epicotyl growth was strongly and positively correlated with date of budset ( $r = 0.93$ ), but flushing date was not closely related to either of these characters.

Table VI. Correlation Matrix for Ten Seed and Seedling Characteristics.

	Seed Weight	Germination Rate	Cotyledon No.	Cotyledon Height	Budset	Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length
Germination Rate	.25								
Cotyledon No.	.56	.18							
Cotyledon Height	.68	.46	.44						
Budset	-.53	-.41	-.51	-.51					
Budburst	-.30	-.07	-.14	-.27	.36				
Bud Sensitivity	.21	.22	.08	.21	-.39	-.17			
Height Sensitivity	.23	.21	.08	.26	-.41	-.24	.62		
Epicotyl Length	-.46	-.36	-.47	-.47	.93	.42	-.45	-.44	
Total Height	-.23	-.21	-.34	-.11	.83	.37	-.42	-.39	.93

Critical  $r$  (0.01, 179 d. f.) =  $\pm 0.19$

3) The inter-relationship of total height, cotyledon height, and epicotyl length has implications regarding the most appropriate estimator of growth potential of young seedlings.

Cotyledon height is positively correlated with seed weight ( $r = 0.68$ ) but has no apparent correlation with total height ( $r = -0.11$ ), suggesting that initial size effects do not affect total height at the end of the first growing season, however, this conclusion is erroneous. The low correlation is due to a negative relationship between epicotyl length and cotyledon height ( $r = -0.47$ ). Thus samples from the inner ranges had larger seeds and cotyledon heights, but made less epicotyl extension growth than those from the coast. The relatively greater proportion of inland family total height attributable to cotyledon height is reflected in an intra-regional correlation of  $r = 0.68$  for these characters, compared with  $r = 0.26$  for the coastal families.

It is clear that epicotyl length, rather than total height should be used as an index of growth in this study. The height component due to initial size effects will, of course, remain fixed and become less important with each successive year's growth.

### Regional Differences

All characters except date of budburst differed significantly between regions (Table V). Compared with inner-range samples, coastal seeds were lighter and germinated more slowly; coastal

seedlings had fewer cotyledons and shorter hypocotyls, but greater total height and epicotyl length; grew for a longer period before setting buds, and showed less bud and height sensitivity.

Regional contrasts were greater for growth characteristics than for those related to seed. Thus fixed regional effects for seed weight, cotyledon number, and cotyledon height were numerically comparable with their respective estimated family variance components (Table IV), while for epicotyl length, total height, and date of budset they differed by a factor of ten or more.

For the remaining characters (germination rate, bud and height sensitivity), family variance was greater than the regional effect, although the latter was always greater than variance between major locations in regions, or minor-in-major locations. Each of these characters is a rather arbitrary index of an aspect of metabolic activity, and much of the family variance may be ascribable to this fact.

#### Difference between Major Locations

According to the approximate F-tests (Table IV), six characters showed significant major-location within-region variation, but the Scheffé test procedure was not always sensitive enough to demonstrate this in terms of individual pairwise contrasts (Table V).

Compared with other coastal locations the seedlings from the Humboldt Redwood State Park (D) were distinguished by heavier seed, a larger number of cotyledons, earlier budset, and less height growth. The buds also burst earlier than those from adjacent samples to the north (Gasquet - G), or south (Jackson S. F. - B), but did not differ significantly from the most southerly coastal source (Santa Cruz - A) for this character. In each of the above characters, D seedlings tended to resemble the inner range samples, though there is no doubt of their general affinity with the other coastal samples.

No pairwise contrasts were significant within the inner range group, though when the two most easterly locations (Harrison Gulch - F, and Mount Ashland - I) were compared with the other three (Bear Creek - C, Forest Glen - E and Happy Camp - H), they exhibited heavier seed, set buds earlier, and had shorter epicotyls.

The major-location variance estimate for date of budburst was greater than the regional effect by a factor of ten. In all other cases the latter estimate had a higher numerical value. Compared with minor location estimates, those for major locations were greater for seed weight and budburst; of the same order for germination rate, cotyledon number, bud and height sensitivity, date of budset, and epicotyl length; and smaller for cotyledon and total height. In no case was the major location variance greater than the family component.

### Differences between Minor Locations

For those characters which showed significant minor-within-major variation, data from each major location were separately re-analyzed by minor locations. To determine whether such variation as existed could be ascribed to elevation of collection site, correlations of phenology and epicotyl length with elevation was also calculated.

Only five of the characters showed a significant minor-within-major effect (Table VII), and for none of these was the variation distributed over major locations in a manner which provided strong evidence for a consistent pattern of localized adaptation.

For days to budset, minor location variation was significant at one coastal location (A), and the two most easterly inner range samples (F and I). The correlation coefficients indicate that this was due to a negative relationship with elevation. Budburst date varied between minor locations only at D, and in this case the correlation with elevation was not significant.

Total height did vary significantly within four major locations, but when growth was expressed as epicotyl length significant variation remained only at the inner range locations E and I. In spite of the general lack of statistical significance, growth within all locations except D was negatively correlated with source elevation, as may be seen from Figure 7.

Table VII. Analysis of Minor Location Effects and Correlation with Elevation within Major Locations, for Characters Showing Significant Variation at this Level in Combined Analysis (Table IV).

Character	All	Major Location <sup>†</sup>								
		A	B	D	G	C	E	F	H	I
Days to Budset r	**	** -.42*	-.16	.41	-.40	-.31	-.25	*** -.66*	-.22	-.46*
Days to Budburst r	*	-.41*	-.40	* .28	.27	.39	.62*	-.47	.04	.23
Epicotyl Length r	*	-.38	-.12	.24	-.49*	-.57	* -.46	-.60	-.18	*** -.61**
Total Height	***				*	*			*	***
Cotyledon Height	***								***	

<sup>†</sup>Blank entries denote non-significance at the 5% level by F-test.

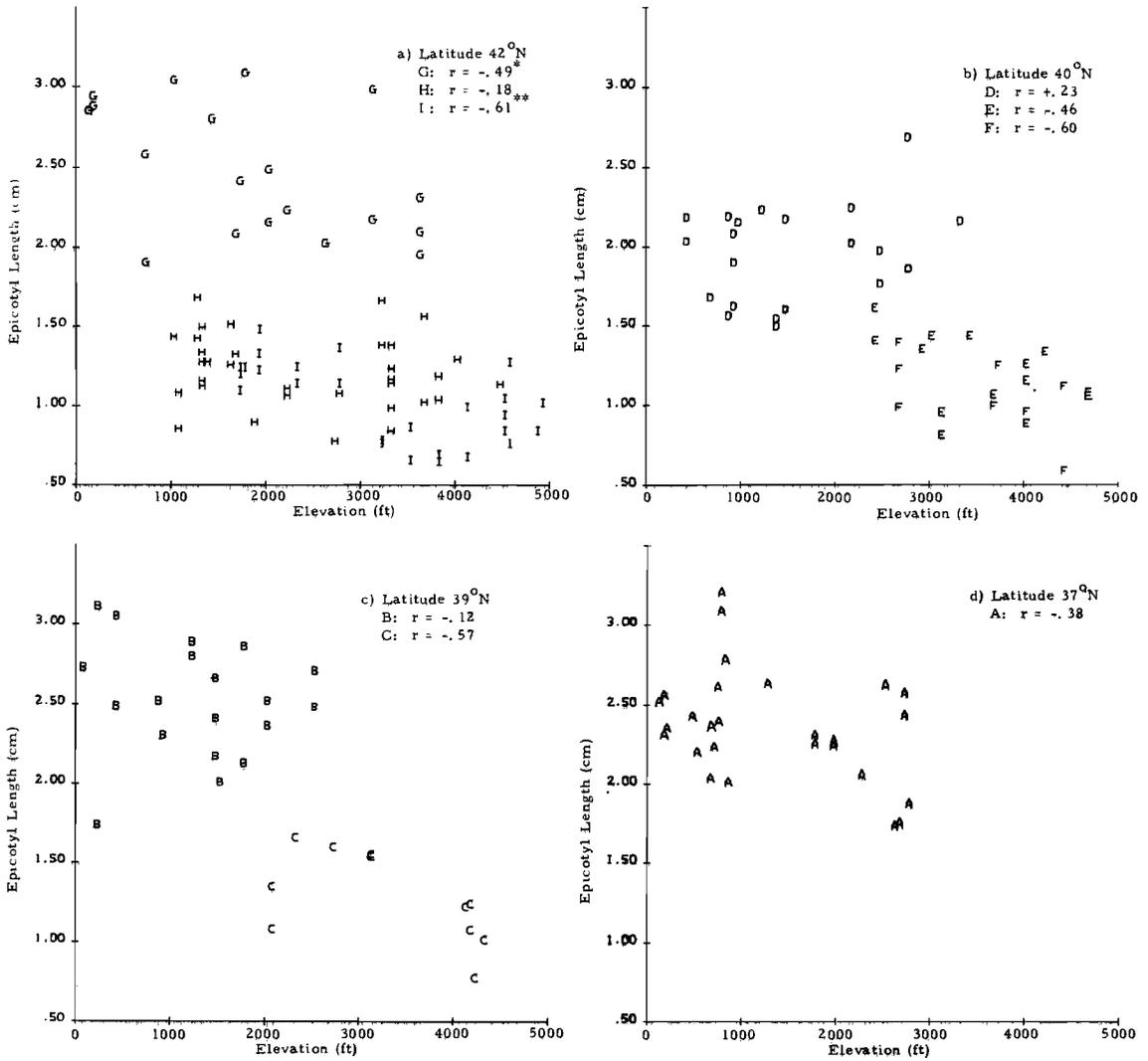


Figure 7 (a-d). Variation of epicotyl length with elevation by latitudinal transects and major locations. Each point represents a family mean.

Of the coastal locations, only Gasquet (G), which covered the greatest elevation range, showed a significant reduction in growth for the higher minor locations. When all coastal observations were pooled the relationship was non-significant; there was, however, a significant negative correlation ( $r = -0.42$ ) for the combined inner range group (Figure 8). In the case of the most northern inner range locations (H and I), a curvilinear pattern of variation was apparent, with seedlings from intermediate elevations (2500-3500 ft) being slower growing than those from higher or lower sites. The other three inner range locations all showed non-significant but probably real growth reduction with increasing elevation.

It is apparent (Figure 7) that growth adaptation is dependent upon environmental factors independent of elevation per se, since seedlings from a given elevation in the coastal group grew taller than those from the same elevation and latitude further inland.

For all characters the minor-within-major location variation was small in relation to total variability. The tendency for a higher frequency of significance within inner range locations may reflect greater site heterogeneity within the latter.

#### Regression on Location and Climate

Analysis of variance has been used to compare variability at different sampling levels in the Douglas-fir population, and to

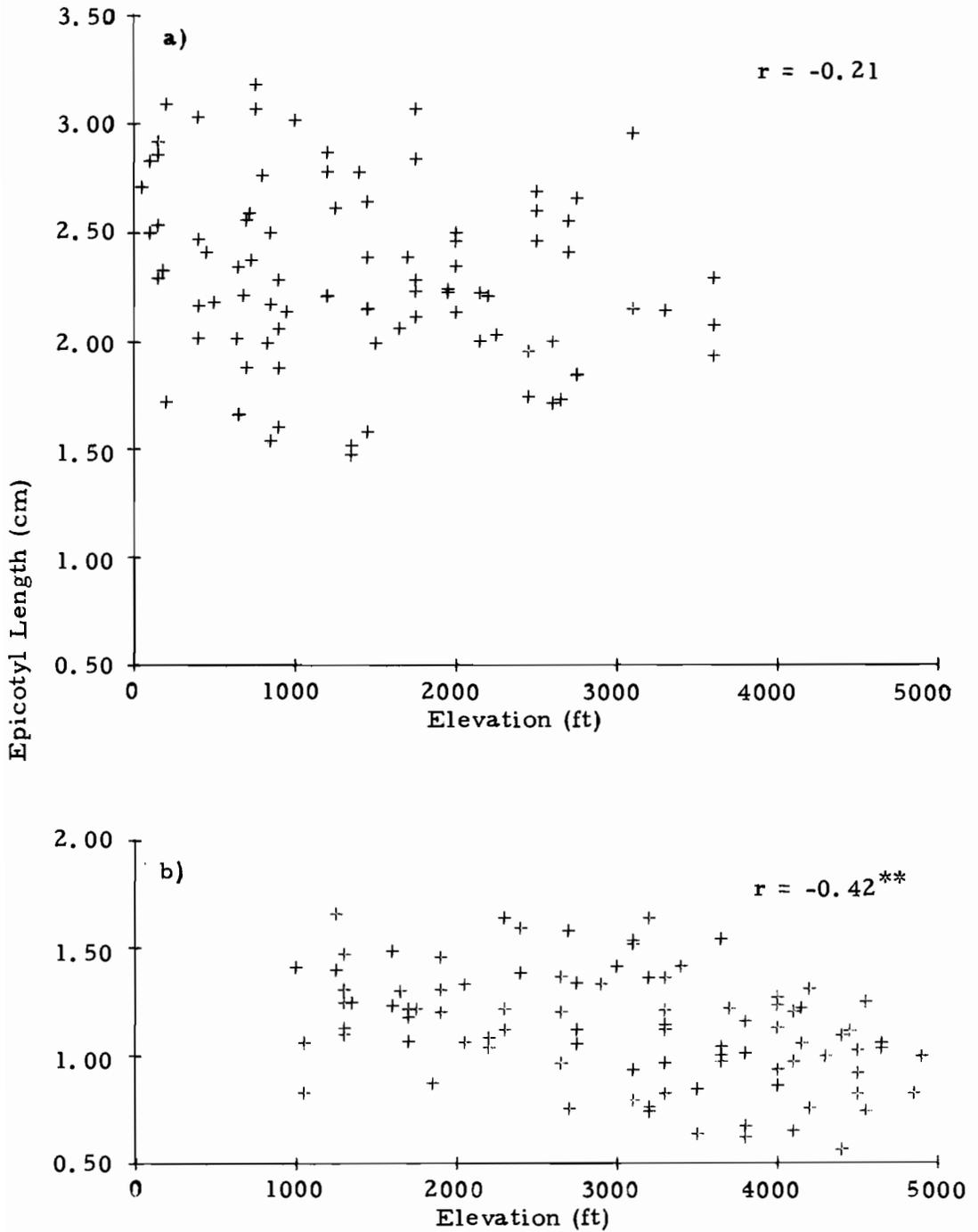


Figure 8. Variation of epicotyl length with source elevation for a) combined coastal locations, and b) inner range locations.

describe characteristics of seedlings from particular locations. However, in drawing evolutionary conclusions, specifying seed zones, and matching potential exotic planting sites, it is the relationship of the observed pattern of variation to geographic and climatic gradients that is important. Under an assumption of continuous variation, seed weight and epicotyl length were subjected to multiple regression analysis, first with location indices, and then with climatic observations, as independent variables.

Seed weight was selected for this analysis because it is correlated with cotyledon number and height, and to a lesser extent with germination rate (Table VI) and so may be taken as an expression of possibly adaptive initial size differences. The character also has been previously treated in the literature, allowing comparison with the results of independent collections. Finally, knowledge of variation in seed characteristics may be useful in verifying the reported origin of commercial seedlots--an important consideration in countries where the species is planted as an exotic.

Epicotyl length is an integral measure of adaptive variation in the annual cycle of growth, and an index of potential productivity; therefore, full knowledge of its variation pattern is of great practical importance.

## Choice of Location Indices

Latitude, longitude, and elevation have most frequently been used as location indices in studies where correlation or regression methods have been used to describe patterns of geographic variation.

Latitude is an index of daylength and frequently of temperature and so has biological significance, though north-south environmental variation in the study area is not great.

Longitude measures "continentality" in western North America, but since the coastline does not run due north-south, distance from the ocean is a more logical measure of this aspect of the environment.

With other factors held constant, environment may change with elevation as discussed on p. 20, but in northern California there are steep gradients unrelated to elevation per se. There is an apparent correlation of growth with elevation (Figure 9), even though the sampling scheme was designed to include high-elevation coastal locations and valley bottoms further inland, but this may be ascribed to the fact that average elevation increases as one goes inland. The relationship is, therefore, really a less precise expression of variation with distance from the ocean (Figure 10).

The regression accounted for 47.5% of the minor location variation in seed weight, while for epicotyl length the corresponding value was 87.7%. For each model, and those related to climate

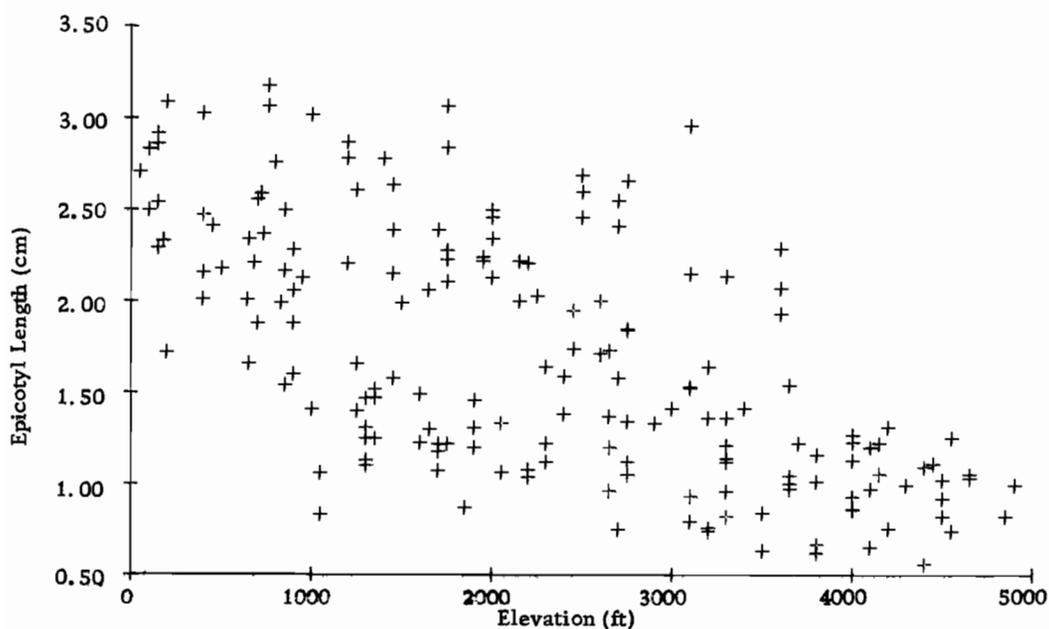


Figure 9. Variation of epicotyl length with source elevation, all locations combined.

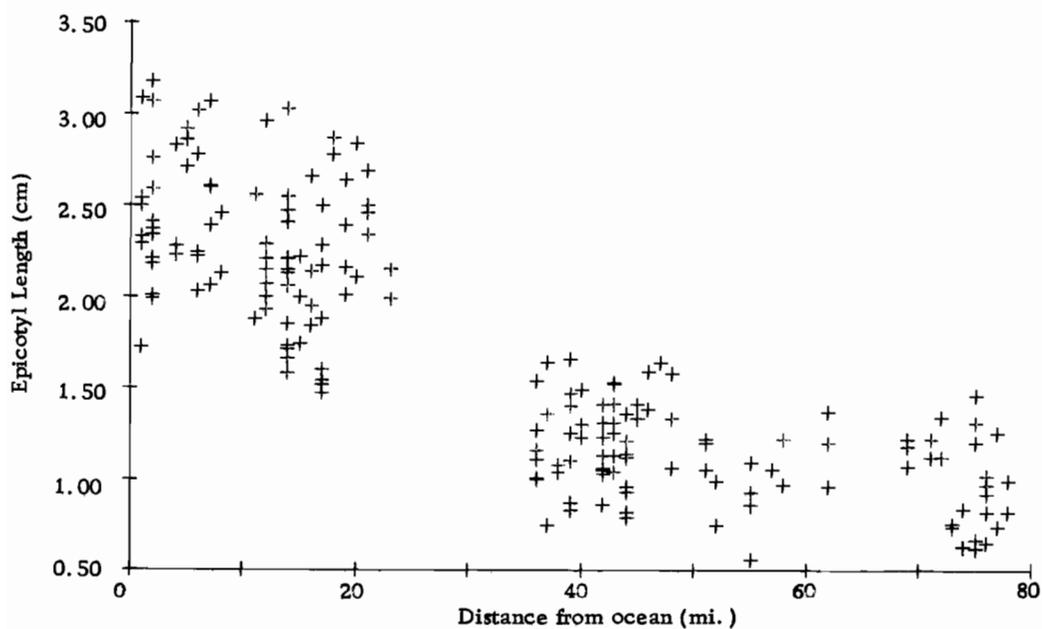


Figure 10. Variation of epicotyl length with source distance from the ocean, all locations combined.

Seed Weight Regression on Location

Model (A): (see p. 104)

$$Y = 25.296 - 0.3866X_1 + 0.1798X_3 - 0.00000017X_2X_2 - 0.00092X_3X_3$$

where Y = Seed Weight (mg)

$X_1$  = Latitude ( $^{\circ}$ N)

$X_2$  = Elevation (ft)

$X_3$  Distance from the ocean (miles)

<u>Source of Variation</u>	<u>Analysis of Variance</u>			
	<u>d. f.</u>	<u>S. S.</u>	<u>M. S.</u>	<u>F</u>
Regression	4	648.53	162.12	21.5***
Residual	78	716.18	9.31	1.43*
Family	<u>96</u>	<u>623.38</u>	6.49	
Total	180	1988.09		
		$r = 0.689$	$r^2 = 0.475$	

t-Test of Coefficients:

<u>Variable</u>	<u>S. E. of Coefficient</u>	<u>t</u>
$X_1$	0.155	-2.50*
$X_3$	0.0036	5.03***
$X_2X_2$	0.000000041	-4.09***
$X_3X_3$	0.00042	-2.20*

Epicotyl Length Regression on Location

Model:

$$Y = -2.5224 + 0.1336X_1 - 0.000098X_2 + 0.614X_3 - 0.01614X_1X_3 - 0.00869X_3X_3 + 0.00022X_1X_3X_3$$

where  $Y$  = Epicotyl length (cm)       $X_1$  = Latitude ( $^{\circ}$ N)  
 $X_2$  = Elevation (ft)                       $X_3$  = Distance from ocean (miles)

<u>Source of Variation</u>	<u>Analysis of Variance</u>			
	<u>d. f.</u>	<u>S. S.</u>	<u>M. S.</u>	<u>F</u>
Regression	6	66.441	11.07	115.83***
Residual	78	9.277	0.1189	1.55*
Families	<u>96</u>	<u>7.361</u>	0.0767	
	180	83.079		
		$r = 0.937$	$r^2 = 0.877$	

## t-Tests of Coefficients:

<u>Variable</u>	<u>S. E. of Coefficient</u>	<u>t</u>
$X_1$	0.0274	4.87***
$X_2$	0.000024	-4.01***
$X_3$	0.1097	5.60***
$X_1X_3$	0.0027	-6.06***
$X_3X_3$	0.0019	-4.53***
$X_1X_3X_3$	0.000046	4.77***

(p. 78 and 79),  $r^2$  was calculated following removal of the sum of squares due to families.

For each characteristic, distance from the ocean was the single most important independent variable in the respective location models.

To test the adequacy of the epicotyl length model over the whole study area, predicted epicotyl length was calculated for each family, and the mean deviation of predicted and observed values for all families at each location expressed as a percentage of mean observed length (Table VIII).

The major defect is that values for location D (Humboldt Redwoods S. P.) are overestimated, with the reverse true for B (Jackson S. F.). Location D is only some 16 miles from the ocean, yet because of the barrier formed by Cape Mendocino, coastal air masses tend to reach it from the northwest via the Eel River valley, rather than directly. At B the topography rises gradually from the coast allowing exposure of west-facing slopes to direct ocean influence for some 20 miles inland, so most collection sites were probably more mesic than would be inferred from the distance index.

Table VIII. Major Location Mean Residuals for the Epicotyl Length on Location Model, as a Percentage of Observed Length.

---

G: + 2.8	H: +0.6	I: -0.3
D: -12.1	E: -4.7	F: +5.7
B: +10.2	C: +2.8	
A: - 0.8		

---

If percentage is + then observed values are greater than predicted, and vice versa.

### Choice of Climatic Variables

While geographic variation is of interest in specifying criteria for seed movement within the study area, the relationship of genetic and climatic patterns of variation are more pertinent when choosing provenances for introduction to other regions of the world, and when attempting to interpret the evolution of observed intra-specific variation.

To obtain information on climate within the study area, U. S. Weather Bureau data from 18 stations were assembled and correlated with latitude, elevation, and distance from the ocean (Appendix Table V). Normal dates of last spring and first fall temperatures below  $28^{\circ}\text{F}$  were used throughout the analysis, since this was considered to be more valid than  $32^{\circ}\text{F}$  in determining the period when actively growing plant tissue would be susceptible to injury. For simplicity these dates are referred to in the text as spring and fall frosts, and the intervening period as the frost-free period.

It was apparent that, as discussed on p. 19, annual temperature range increased with distance from the ocean, and frost-free period decreased; mean annual temperature was not correlated with elevation or distance, but decreased with increasing latitude; and growing season precipitation shows no strong pattern of variability.

Temperature and growing season data for the stations nearest to major locations were tabulated, and those corresponding to the five inner range locations adjusted for elevational differences between station and each minor location. For the reasons previously discussed (p. 21) unadjusted data were taken as the best available estimate of climate for all minor locations within each coastal major location.

Adjustments per 1000 ft. rise in elevation were as follows

(after Baker, 1944):

Mean temperature of the hottest month:	-1.7 <sup>o</sup> F
Mean temperature of the coldest month:	-2.5 <sup>o</sup> F
Date of last spring frost:	+19 days
Date of first fall frost:	- 9 days
Frost-free period:	-28 days

Mean adjusted major location data are shown in Table IX, and the unadjusted records in Appendix Table III.

Adjustment had little effect on the correlation of seed weight with climate, but it did improve the relationship of epicotyl length and the temperature variables (Table X). The lack of change on the relationship with dates of frost occurrence is probably because this aspect of climate is more closely related to local topography.

Correlations among the adjusted climatic variables are given in Table XI. Since the frost-free period is derived by subtraction from the normal dates of last spring and first fall frost, which in turn are

Table IX. Mean Adjusted Climatic Variables for Major Locations.

Location <sup>+</sup>	Day from Jan. 1st datum		Frost free period (days)	Temperature (°F)			
	Last spring frost	First fall frost		Mean annual temp.	Mean hottest month	Mean coldest month	Annual range of monthly means
G	10	360	350	52.6	58.2	46.4	11.8
H	105	316	211	52.7	70.8	43.8	27.0
I	106	326	220	49.4	66.2	34.8	31.4
D	7	355	348	54.9	61.5	47.7	13.8
E	148	277	130	48.7	66.4	32.5	33.9
F	129	286	157	52.8	73.0	34.0	39.0
B	36	333	297	53.4	60.3	46.7	13.6
C	160	267	106	51.7	68.6	37.5	31.1
A	31	344	313	56.6	63.8	47.7	16.1

<sup>+</sup> Locations grouped by latitude, and within each the most coastal location listed first.

Table X. Correlation of Adjusted and Unadjusted Climatic Variables with Seed Weight and Epicotyl Length.

	Seed Weight	Epicotyl Length
Last spring frost	.35 (.44) <sup>+</sup>	-.78 (-.77)
First fall frost	-.29 (-.37)	.62 (.63)
Frost free period	-.33 (.43)	.73 (.73)
Temperature (°F)		
Mean annual	-.09 (-.15)	.58 (.32)
Mean hottest month	.53 (.42)	-.68 (-.67)
Mean coldest month	-.36 (-.39)	.73 (.59)
Annual range	.52 (.50)	-.84 (-.83)

<sup>+</sup>Figures in parentheses are correlations with unadjusted data.

Table XI. Correlation Among Adjusted Climatic Variables.

	Last spring frost	First fall frost	Frost free period	Mean annual temp.	Mean temp. hottest month	Mean temp. coldest month
First fall frost	-.94					
Frost free period	-.99	.97				
Temp. (°F)						
Mean annual	-.66	.52	.62			
Mean hottest month	.71	-.65	-.70	-.07		
Mean coldest month	-.85	.76	.83	.83	-.42	
Annual range	.93	-.84	-.91	-.58	.80	-.88

### Seed Weight Regression on Climate

Model:

$$Y = -19.171 + 0.028166X_1 + 0.26883X_2 + 0.47392X_3$$

where Y = Seed weight (mg)

$X_1$  = Frost free period (days)

$X_2$  = Mean annual temp. ( $^{\circ}$ F)

$X_3$  = Annual mean monthly temp. range ( $^{\circ}$ F)

#### Analysis of Variance

<u>Source of Variation</u>	<u>d. f.</u>	<u>S. S.</u>	<u>M. S.</u>	<u>F</u>
Regression	3	821.47	273.82	40.8***
Residual	81	543.23	6.71	1.03
Families	<u>96</u>	<u>623.38</u>	6.49	
Total	180	1988.08		
	$r = 0.776$		$r^2 = 0.602$	

t-Tests of Coefficients:

<u>Variable</u>	<u>S. E. of Coefficient</u>	<u>t</u>
$X_1$	0.0058	4.88***
$X_2$	0.0860	3.12***
$X_3$	0.0516	9.18***

All three independent variables are significant, with temperature range alone accounting for 27% of the total variation.



dependent upon the seasonal temperature cycle, the high values of most coefficients are to be expected.

The Seed Weight Model is an improvement on that where location indices constituted the independent variables, in spite of the fact that there was greater precision in measurement of locations. This indicates non-linearity in the seed weight variation pattern. Weather data from a particular locality are able to reflect environmental modifications due to factors such as local topography in a way which is probably not possible without a complex extension of the location indexing approach.

The Epicotyl Length Model is comparable to that based on location in terms of the proportion of total variation accounted for. Growth is reduced with increasing temperature range, later spring frost, and a shortened frost-free period. As can be seen from Table IX, such a combined gradient is encountered when proceeding inland from the coast at any given latitude. Correlations of unadjusted climatic variables and distance from the ocean for 18 weather stations in the region are:  $r = 0.86$ ,  $-0.85$ , and  $0.94$  for date of last spring frost, frost-free period, and annual temperature range, respectively.

#### Variation in Cold Hardiness

Because of its unbalanced nature, no analysis of variance of

cold damage data was attempted. Observations from the two main plots were combined and the individual seedling regarded as the sampling unit. Observations were classified by major locations and date of budset (Table XII) and  $\chi^2$  used as a test statistic under the null hypothesis of equal damage frequencies over classes. Since the seedlings were planted in six-tree plots, rather than completely at random, any variance due to common environment would tend to over-emphasize the significance of inter-class differences, although there is no reason to think that this was an important source of variation.

The irregular intervals between budset dates in Table XII result from the dependence of frequencies on the number of growth flushes of individual seedlings. Some seedlings set buds at intervening dates, but not in sufficient numbers to meet the arbitrary minimum of 10 seedlings per class, and therefore were excluded from the analysis.

Each seedling was scored for severity of damage, and the mean percentage of damaged crown for seedlings bearing dead needles is shown for each major location. From preliminary analysis it was apparent that there was a close parallel between the number of seedlings with damage symptoms, and the severity of damage, therefore the latter data were not further analyzed.

Considering major location means over all set dates, the most obvious contrast was once again between regional groups. Within the coastal locations, differences were also significant, with a clinal

Table XII. Percentage of Plants Showing Cold Damage Symptoms, by Date of Budset and Major Location Classes<sup>a</sup>.

Location	Days to Budset (from April 12th)										All Dates	Degree of Damage <sup>b</sup> (%)	Mean Days to Budset	
	59		124		138		152		159					
	N	%	N	%	N	%	N	%	N	%				N
G			27	33	11	54	44	61			96	56	55	146
H	40	10	83	17	19	21	14	14			163	14	53	102
I	38	8	61	10							118	8	44	90
D			58	60	15	72	41	56	10	60	133	60	59	134
E	19	0	40	8							79	5	35	104
F	14	0	15	20							41	17	33	93
B			37	51	22	86	64	84	21	81	155	75	69	144
C	16	0	30	43							55	33	56	103
A			29	79	19	74	46	77	17	87	128	82	78	146
Combined	127	7	380	31	86	51	209	65	48	74				

<sup>a</sup>Classes with  $\geq 10$  seedlings only.

<sup>b</sup>Mean percentage of live crown of damaged seedlings carrying dead needles.

Table XIII. Chi-squared Values for Tests of Homogeneity of Cold Damage Data.

Type of Contrast	d. f.	$\chi^2$
<b>a) <u>Over All Budset Dates</u></b>		
Between Regions	1	309***
Within Coastal Region	3	24.9***
Within Inner-range Region	4	20.6***
<b>b) <u>Between Budset Dates within Individual Locations</u></b>		
G	2	5.86
H	3	8.50*
I	1	1.70
D	3	1.34
E	1	2.41
F	1	3.03
B	3	16.31***
C	1	9.66***
A	3	1.07
<b>c) <u>Over All Locations</u></b>		
Between Budset Dates	4	169***
Within Budset Dates		
59 days	4	4.77
124 days	8	84***
138 days	4	49***
152 days	3	42***
159 days	2	2.69

reduction in damage from 82% at the most southerly location (A) to 56% at (G) on the Oregon border. None of the few seedlings from the coast ranges of Oregon, Washington, and Vancouver Island showed any damage symptoms.

Comparing the inner range locations, the significant  $\chi^2$  value is largely due to the difference between the most southerly (C), and those further north. A combined sample of 69 seedlings from Boggs Mountain and Las Pasadas (Appendix Table I) contained 52% damaged seedlings, confirming the increased susceptibility of those from the southern inner ranges.

#### Relation of Hardiness and Date of Budset

Within locations there was a tendency for those seedlings which set buds early to suffer less damage--though this was only highly significant for Jackson S. F. (B) and Bear Creek (C). Over all locations the amount of damage was strongly related to date of budset (7% for those that set at 59 days, and 74% at 159 days). However this is due to inter-location differences in mean date of budset, rather than date per se, since comparison of damage to seedlings that set buds on a particular day, revealed a pattern of inter-location variation similar to that discussed for location means.

### Variation of Hardiness with Elevation

In order to determine possible within-major-location variation, data were grouped by 500 ft. elevation classes, except where small numbers made the use of larger classes necessary. Figure 11 illustrates this classification with histograms of percentage damaged seedlings per class, and the appropriate  $\chi^2$  values for testing homogeneity.

Within the coastal region high elevation seedlings were least damaged at D and G; no difference existed at B; and the significantly greater damage to high elevation seedlings at A is anomalous. However, in the latter case even the most resistant class exhibited 70% damage.

For major locations from the inner ranges the contrast of high and low elevation seedlings was greatest at the most southerly (C), where seedlings from below 3000 ft. showed damage levels equivalent to higher elevation coastal sources further north. However, those from above 4000 ft. behaved like more northerly inner range samples. At each of the other inner range locations the lowest elevation seedlings were more susceptible to injury, but because of low damage frequencies, sample sizes were not large enough to statistically confirm a probable real effect.

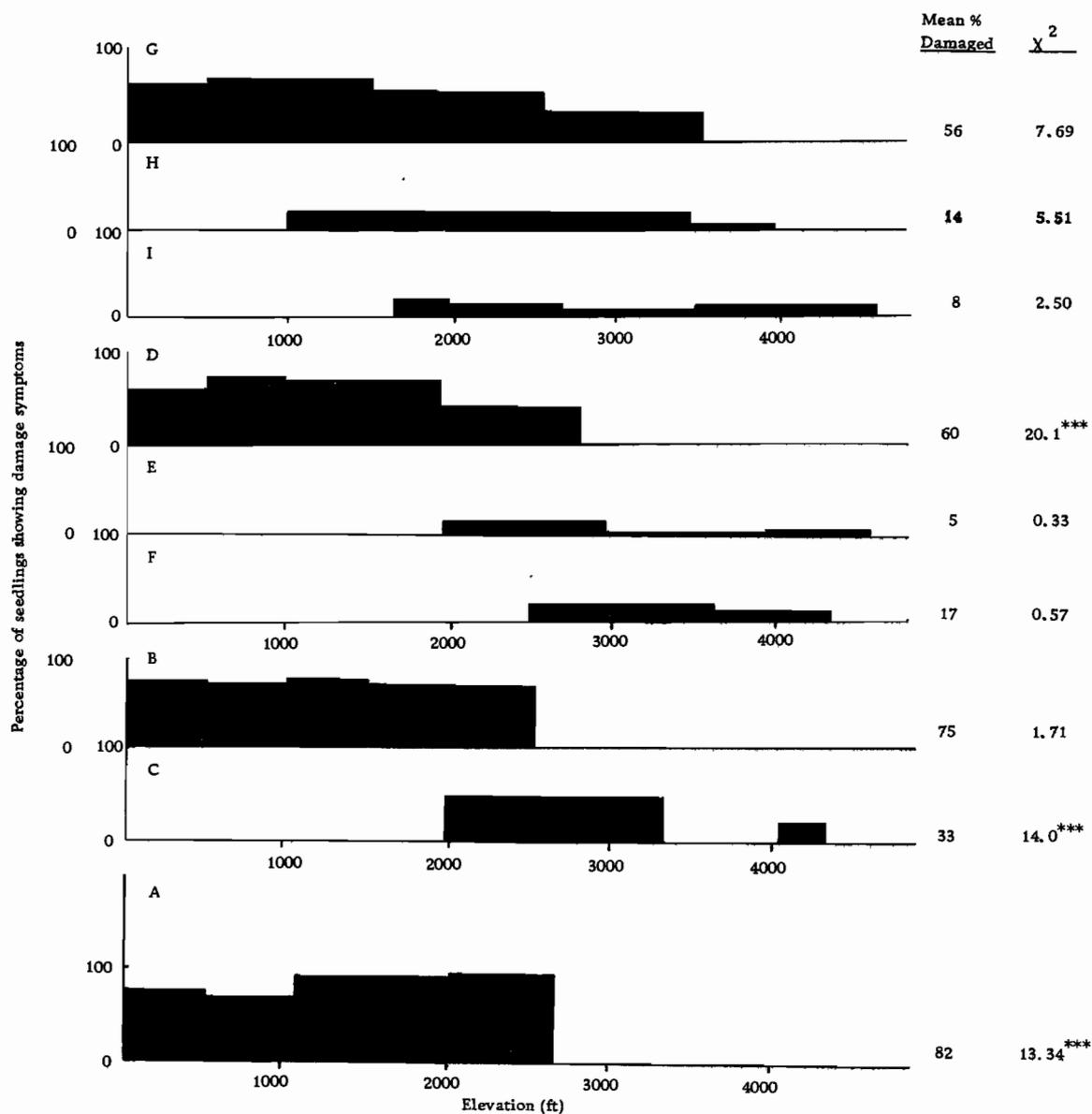


Figure 11. Percentage of seedlings showing cold damage symptoms by elevation classes within major locations.

## VI. DISCUSSION AND CONCLUSIONS

### Response to Stress Regimes

The reduction in height growth and advance in onset of dormancy were expected responses to increased moisture stress. It is difficult to compare results directly with those from published studies, since most workers have monitored stress through measurement of soil moisture rather than plant moisture. The former approach does not take into account variation in atmospheric conditions, which are equally important in determining PMS. However it is apparent that low levels of soil moisture tension are capable of affecting growth. For example, with Pinus sylvestris seedlings, allowing the soil to dry to a tension of 1.5 atm decreased dry weight production by 50% compared with a well-watered control (Sands and Rutter, 1959). Miller (1965) measured leaf water potential and needle elongation of potted Pinus taeda seedlings, and showed that growth was directly proportional to stress over the range of 3.6-10.2 atm PMS.

Using a rather severe cyclic regime involving rewatering when soil tension reached 15 atm, Lavender et al. (1968) showed that date of dormancy initiation in Douglas-fir seedlings was advanced by four weeks compared with controls and height growth reduced by two-thirds. Values for differences between the Moderate and Low stress

regimes in the present study were 10 days and 29% respectively (Table III).

The data regarding effect of watering regime on date of budburst (Table III) did not provide evidence of genetic variation among seedlots, and is of peripheral importance to this study. There may, however, be practical implications for treatment of planting stock in the year prior to outplanting on frost-prone sites. Guzev<sup>2</sup> (1958) reported that soil drought had the effect of advancing flushing date of fruit tree and oak seedlings in the following season, with particular emphasis placed on moisture regime during the period of bud formation. The effect observed is therefore not unprecedented.

The most important finding was that response to stress regime, in terms of budset and height growth, varied with seed source. This interaction, quantified as bud and height sensitivity, is an adaptive aspect of the annual growth cycle and is discussed in the following section.

#### Population Structure and the Adaptive Nature of the Observed Variation Patterns

Interpretation of the adaptive significance of intraspecific variation may be facilitated by considering the breeding system of the species in relation to its distribution and habitat heterogeneity,

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<sup>2</sup>Original not available.

since inferences may then be drawn regarding the potential effects of evolutionary factors such as natural selection, gene flow, and drift.

### The Breeding Unit in Douglas-fir

Douglas-fir is wind pollinated and largely outcrossing (Sorensen, 1971), and is essentially continuously distributed over much of its range. Pollen dispersal distance is large compared to that of seed, so that gene flow will take place primarily through transfer of male gametes (Tigerstedt, 1967), and the distance over which pollen movement may occur becomes an important factor in determining population structure. Sarvas (1967) estimated that in Scots pine (*P. sylvestris*) in Finland, approximately half of the pollen within a sub-population originated from outside sources. A "sub-population" was loosely defined as a fairly uniform stand some 0.5-2.0 hectares in extent, and is therefore comparable to a minor location in the present study. Evidence regarding actual distance traveled by pollen is varied. From the point of view of gene flow, however, it is probably of little importance whether it occurs between distance populations in a single generation or by transfer through a series of sub-populations.

Silen (1962) concluded that the great majority of pollen from an individual Douglas-fir was not transported very far, but that even in the center of a 3 x 15 mile treeless area in the Willamette Valley,

Oregon there was a high background pollen count in a year of good production. Apparently there is potential for pollen dispersal over considerable distances, particularly in mountainous regions where air turbulence could be expected. Gene flow may be further enhanced by the fact that individuals are reproductively mature for many years, so that the essentially stochastic process of pollen dispersal may lead to annual variation in the genetic constitution of the pollen cloud within a particular stand.

Pollination will, of course, only occur if female strobili are receptive at the time of a pollen influx, and reproductive isolation within continuous stands, due to climatically induced differences in flowering time, has been postulated. For example, Wells (1964) ascribed maintenance of a distinct ecotypic boundary within Ponderosa pine in northeastern California to a three-week difference in commencement of the growing season.

Data from a study of Douglas-fir by Silen (1963) show that date of maximum pollen shed is delayed approximately 13 days per 1000 ft. rise in elevation in the Washington and Oregon Cascades. However, since the same study determined that trees at a particular elevation shed pollen over a 20-30 day period, populations differing by as much as 2000 ft. were potentially able to interbreed. At least for this species, differences in flowering time may not constitute a very effective isolating mechanism.

From the above considerations it is appropriate to regard a wind pollinated seed collection of the type used in this study as a sample of the gene pool over an elevational range greater than the 250 ft. limits of a minor location, and probably of sites heterogeneous in terms of aspect, soil conditions, and vegetation competition.

Under this assumption, a low family component of variance relative to that determined for larger sampling units (Table IV) may be taken as indication that a character is adaptive for regional environmental factors, and conversely a large family component may be evidence that it is responsive to selection pressure heterogeneous on a scale smaller than the breeding unit.

Adaptation to Spatial Environmental  
Heterogeneity -- Theoretical  
Considerations

The concept of environmental grain (Levins, 1968) is helpful for discussion of the variation patterns exhibited by different characteristics. A given environment is said to be coarse-grained if spatial heterogeneity is great in relation to the tolerance of an individual genotype, and fine-grained in the reverse case.

Grain of a given environment is coarser for a small organism than for a larger one, implying that for a tree which undergoes great dimensional change over its lifespan, the environment will become increasingly fine-grained with time.

As an example, Owen (1953) studied Douglas-fir seedling establishment in a "bald" near Corvallis, Oregon. Oak scrub and grass were the principal vegetation components, and great heterogeneity of soil moisture, temperature, and light conditions were reported. Seed germinated well in grass but summer soil surface temperatures were lethal, whereas under the oak mortality occurred later in the year because of drought. Whether a seed fell into a grassy area or under scrub cover would have determined selection pressures operative at the early development stage. Selection for fitness at this time may be further enhanced by inter-seedling competition (Tigerstedt, 1967), since seed production may far exceed that necessary to maintain the population.

With each successive year's increase in size a young tree would be exposed to an increasing range of contrasting micro-environmental conditions and would itself begin to modify the latter. Therefore fitness should become more dependent upon adaptation to more regional (fine-grained) aspects of the environment. The most obvious of these is climate.

Namkoong et al. (1972) provided evidence in support of the above hypothesis, using data from the 1912 Douglas-fir heredity study (Munger and Morris, 1936). Within population genetic variance in height growth was relatively large in the early years, but decreased with time, whereas inter-population variance was low initially and subsequently increased.

### Nature of the Observed Variation Pattern

All characteristics were assessed on seed and young seedlings-- the stage of the life cycle at which an individual is smallest in relation to the micro-environmental matrix. This does not mean that all are responsive to similar selection pressures, however.

Phenology, growth, and hardiness are components of the seasonal growth cycle and remain operative throughout the lifespan, in contrast to seed related characteristics which are expressed only during the first growing season. It is reasonable to expect the former characters to show greater adaptation to the more fine-grained aspect of the environment, and the fact that epicotyl length is more closely correlated with source climate (p. 79) than is seed weight (p. 78) lends support to this contention.

### Adaptation of Factors Related to the Seasonal Growth Cycle

The observed decrease in period of active growth with increasing climatic extremity is expected, since the characteristics of a plant species are frequently determined by the most adverse conditions encountered (Bradshaw, 1965). Thus budset may be viewed as an external indication of the physiological changes required to withstand winter conditions. On average the first fall frost occurs some 60 days

later on the coast than at the nearest inner range location (Table IX), and budset must take place correspondingly earlier at the latter sites if damage is to be avoided.

Bradshaw (1965) pointed out that adaptive modifications would frequently be operative too late if they were initiated by the environmental conditions for which they were adaptive, therefore permanent genetic adjustment within the population is necessary. This has evidently occurred in Douglas-fir since inner range seedlings set buds early even under good growing conditions.

Further regional differentiation is indicated by the greater bud and height sensitivity (Table V) of the inner range seedlings. This is interpreted as the capacity for limited plastic response superimposed upon the aspects of the growth pattern under more direct genetic control, and would allow growth to continue somewhat later in the season in a year when moisture is available, than in time of drought when growth cessation may have survival value.

Intra-specific variation in plasticity is apparent in many plants studied by Clausen et al. (1940), but the phenomenon has received little attention in tree species. Irgens-Moller (1967) noted that Douglas-fir from Arizona had the ability to flush repeatedly under long photoperiods, whereas seedlings from the northern Rocky Mountains set buds after a single flush no matter how favorable the growing conditions; since summer rainfall is a feature of the Arizona climate, it

was proposed that the intermittent flushing was an adaptation allowing use of periods of favorable soil moisture conditions.

While summer rainfall does not vary appreciably throughout northern California, evapo-transpiration is undoubtedly greater inland, where the moderating influence of the coastal fog is lacking, and the inner range seedlings may have evolved in a similar manner to those from the southern Rocky Mountains. It is interesting to note that, on the basis of cortical mono-terpene analysis, Zavarin and Snajberk (1972) found that Douglas-fir from the Sierra Nevada showed a greater affinity with var. glauca than with var. menziesii.

Similar intra-specific variation in growth pattern in relation to source moisture conditions have been reported for southern pine species. Woessner (1972) grew seedlings of Loblolly pine (P. taeda) from North Carolina and Texas under contrasting soil and moisture regimes and found that height growth was not significantly different under good conditions. Under stress, however, the Texas seedlings from a low summer rainfall environment grew less; i. e., in terms of the present study they showed greater height sensitivity. Since Texas seedlings survive well in plantings throughout the southern United States (Wells and Wakeley, 1966), it was suggested that growth reduction was an adaptive advantage in dry conditions. Terminal growth data from a six-year-old Slash pine (P. elliottii) provenance trial in northeastern Florida (Bengston et al., 1967)

demonstrated that differences in the proportion of annual growth made during the early and late part of the growing season was related to variation in the seasonal distribution of precipitation throughout the species range.

At least in the test environment there was no simple relationship between date of budburst and climatic variables such as the occurrence of spring frosts. Early flushing of the inner range seedlings (Table V) can be rationalized as an adaptation allowing early growth completion and, together with the late flushing of coastal seedlings from locations B and G, is in agreement with the conclusion of Clausen and Heisey (1958) that maritime races are characterized by later flowering because of the longer available growing season. The early flushing of seedlings from Santa Cruz (A) remains to be explained, however, since they were also the last to set buds at the end of the first growing season (Table V).

Clausen et al. (1940) studied variation in a range of species along an east-west transect at latitude  $38^{\circ}\text{N}$  in California, and concluded that coast range forms were generally capable of active growth throughout the year if conditions permitted. If a rest period did occur it was in late summer, new growth commencing with the advent of winter rains. Their study did not include any tree species but Monterey pine (P. radiata), native to the same region, exhibits this type of growth pattern, at least in the juvenile stages (Jacobs, 1937).

It is possible that early budburst of Douglas-fir from Santa Cruz may be ascribable to a similar weakly defined dormancy period.

Sweet (1965) noted that seedlings from Santa Cruz grew taller than expected on the basis of the relationship between provenance and climate exhibited in other parts of the species range. His data did not, however, indicate a significant difference in flushing date between Santa Cruz and more northerly coastal sources. The apparent discrepancy between the results of the two studies may be evidence of greater plasticity of Santa Cruz seedlings relative to those from further north, where climatic selection pressures have required more specific genetic adaptation. Latitudinal differentiation in the face of apparent north-south climatic uniformity is certainly indicated by the cold hardiness data (Table XII) and there is no reason to suppose that it could not have occurred for other aspects of the seasonal growth pattern.

Monterey pine and the Coast Redwood both occur in proximity to Douglas-fir in the Santa Cruz area, and it is known that both were formerly distributed further south than at present (Fielding, 1953; Munz and Keck, 1965). Therefore, it may also be that Douglas-fir is a relic of a more southerly population, with its integrity maintained by geographic isolation from populations to the north of San Francisco Bay.

The great regional difference in susceptibility to cold damage (Table XII) is paralleled by a reduction of mean winter temperature (Table IX), however this climatic factor varies very little with latitude along the coast, and yet a distinct cline for hardiness has developed. Differences in average winter conditions therefore do not adequately account for the pattern.

A plausible explanation is that low frequency occurrence of abnormally cold weather has acted as a catastrophic selection pressure. Since such weather would approach from the arctic regions, frequency as well as intensity of cold would reduce with decreasing latitude, allowing survival of an increasing proportion of sensitive genotypes.

The same argument may be applied to the elevational trends within major locations (Figure 11), since a given air mass would become colder with increasing elevation, and the resulting higher frequency of lethal temperatures would operate against reintroduction of sensitive genotypes through gene-flow.

The data in Table XII represent a decrease in damage of 5.5% per degree of latitude increase, for the coastal locations. This compares well with a figure of 4% per degree determined for samples from Oregon and Washington by Campbell and Sorensen (1973).

It appears that there is a continuous latitudinal cline for hardiness throughout the West Coast range of the species, though the

present study indicates a far greater rate of change associated with transition from the coastal climate.

### Adaptation of Seed-Related Characteristics

As noted these characters are only expressed over a short segment of the lifespan, when the individual is small in relation to micro-environmental heterogeneity. Phenotypic polymorphism may therefore be an adaptive strategy.

Certainly the within-minor location (family) variance for seed related characters is greater than that for growth and phenology (Table IV). For seed weight, cotyledon number, and cotyledon height the family component is of the same order as that for regions, while germination rate is even more variable. The significant regional contrast for each character (Table V) is due to an apparently linear change in mean value with distance from the coast. Figure 12 illustrates the pattern for seed weight data.

Assuming that fast initial growth is adaptive under hot or dry conditions, the larger seed, faster germination, greater number of cotyledons, and longer hypocotyls of inner range sources may be interpreted as a response to increased frequency of such micro-site conditions.

The clines for seed related characters do not show the abrupt curvilinear response to climatic change exhibited by height growth

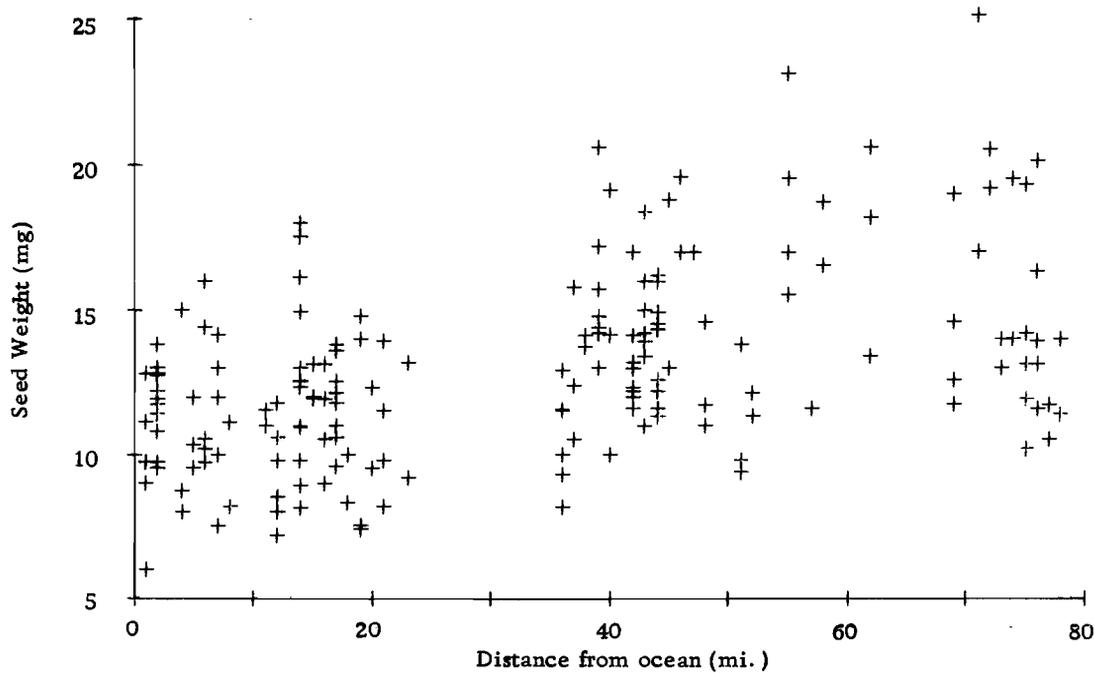


Figure 12. Variation of seed weight with distance from the ocean, by individual parent trees.

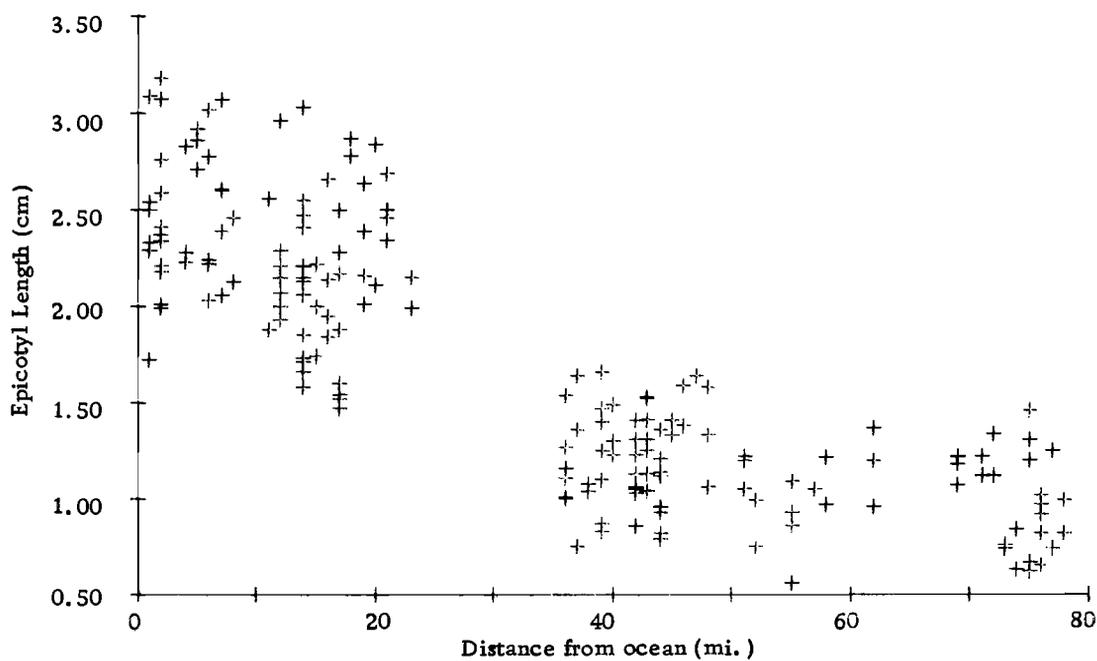


Figure 13. Variation of epicotyl length with distance from the ocean, by individual family means.

(Figure 13), but since the species becomes increasingly restricted to higher elevations and north-facing slopes with distance from the coast, it is likely that this is because the average micro-environmental conditions in which the species is viable do not change as abruptly as the climate would indicate.

### Conclusions

For purposes of discussion frequent reference has been made to contrasts between seedlings from coastal and inner range sources, but it is not suggested that racial differentiation has developed to an extent where taxonomic distinction would be useful.

The various patterns are best considered as a system of clines in mean gene frequencies, with spatial rates of change differing according to the operative selection pressures. The nearest approach to a regional discontinuity occurs for height growth (Figure 13), bud-set, and cold hardiness. However, the population is continuously distributed across the transition zone, and in view of the potential ease of gene flow, it is likely that more intensive sampling would reveal the existence of a steep gradient for change in these characters. The Humboldt Redwood S. P. (location D) sample most closely approximated a transition site, and the seedlings set buds earlier, and were significantly shorter, than those from the other coastal locations (Table V).

### General Validity of the Seed Weight and Epicotyl Length Variation Models

An underlying assumption of provenance test procedures is that environmental effects are uniform for all sources and that observed variation is therefore genetic in nature. However, the seed from which plants are raised have developed under environmental conditions which may have been very variable, and there is often no way of distinguishing maternal environmental from genetic effects. Variation due to maternal effects must certainly be considered for the seed-related characteristics studied, and may even influence seedling growth (Rowe, 1964). It is also possible that observed variation patterns are due to specific interaction with the test environment.

Confidence both in the genetic nature of observed variation and in the general validity of results is enhanced if the latter are confirmed by independent studies. For seed weight and height growth there are data published which allowed comparison to be made.

#### Seed Weight

Variation in seed weight within the study area has been reported by Birot (1972) and Sweet (1965). Birot also presented a multiple regression model relating seed weight to longitude and elevation, thus providing a further opportunity for comparison of longitude and distance from the ocean as alternative location indices.

Differences in Models Used. Apparent year-to-year variation in seed weight may be determined using models based on the 1971 (present study) and 1968 (Biro, 1972) seed crops to predict weight for locations sampled in 1956 by Sweet (1965). Predictions and observed weights are given in Table XIV, together with a prediction of 1968 weights from the 1971 model. Direct comparisons of weights are not possible since different stands were involved in each collection.

Biro's model for "le groupe côtier méridional" was based on seedlots collected from the California Coast Ranges, southern Oregon, and the northern Sierra Nevada. Of the 26 seedlots, 21 were within the sampling area of the present study, and only these were used for comparative purposes.

Collection sites, together with those for Sweet's collection, were located on a 1:500,000 scale map, and the distance from the ocean thus determined (Table XIV).

In order to establish that omission of some seedlots did not significantly alter Biro's model, his calculations were repeated for the reduced data set (Model C, following page). Then the data were re-analyzed with latitude, distance, elevation and their interaction terms as potential independent variables. Distance alone accounted for 63% of the variation in seed weight, compared with 49% for elevation alone. The best model (D) was obtained by inclusion of the

Alternative Models of Seed Weight  
Variation with Location

Model A (see p. 71 )            n = 181        r = 0.57        r<sup>2</sup> = 0.475

Model B (Biro, 1972)            n = 26        r = 0.713        r<sup>2</sup> = 0.51

$$Y = 12703 - 1.553L + 0.092A$$

Y = 1000 seed wt (g) x 100

L = Longitude in minutes

A = Altitude in feet

Model C (Biro - reduced data set)            n = 21        r = 0.722        r<sup>2</sup> = 0.52

$$Y = 160.16 - 1.2025L + 0.000977A$$

Y = Seed wt. (mg)

L = Longitude in degrees

A = Altitude in feet

Model D (reduced data set)    n = 21        r = 0.81        r<sup>2</sup> = 0.65

$$Y = 10.059 + 0.1762D - 0.00108D^2$$

Y = Seed wt. (mg)

D = Distance from the ocean in miles

Table XIV. Comparison of Seed Weight Determined from 1956 and 1968 Collections, with Predictions from Models Based on 1968 and 1971 Data.

Seedlot No.	Latitude (°N)	Elevation (ft)	Distance from Ocean (mi.)	Observed Seed Wt. (mg)	Predicted Values			
					Model D (1968)	% Deviation	Model A (1971)	% Deviation
<u>1956 Crop (Sweet, 1965)</u>								
12	41.80	300	6	10.74	11.08*	+ 3.2	10.17	- 5.3
14	40.98	1600	88	18.61	17.20	- 7.6	17.72*	- 4.8
15	40.95	600	26	13.93	13.91*	- 0.1	13.46	- 3.3
16	40.92	1600	20	13.27	13.15*	- 0.9	12.27	- 7.5
17	40.92	700	11	12.62	11.87*	- 5.9	11.26	-10.8
18	40.23	1700	15	13.11	12.46*	- 5.0	11.74	-10.4
19	39.60	500	4	10.65	10.75	+ 0.9	10.65*	0.0
20	39.83	2500	40	15.63	15.38*	- 1.6	14.58	- 6.7
21	39.51	4500	45	18.67	15.80*	-15.4	12.85	-31.2
24	39.35	500	4	12.25	10.75	-12.2	10.75	-12.2
27	38.77	500	35	17.31	14.90	-13.9	15.10*	-12.7
28	38.65	500	2	11.04	10.41	- 5.7	10.67*	- 3.3
29	37.88	800	2	10.62	10.41*	- 2.0	10.90	+ 2.6
30	37.08	1000	3	13.96	10.54	-24.5	10.89*	-22.0
Mean Deviation					%	6.3		9.5
<u>1968 Crop (Biro, 1972)</u>								
1144	39.92	3000	30	14.86			12.90	-13.2
1145	39.80	5100	47	17.24			11.90	-30.9
1146	39.65	4500	56	19.04			13.72	-27.8
1147	39.50	200	5	10.93			10.89	- 0.4
1148	39.38	1800	22	12.37			13.03	+ 5.3
1149	38.83	3100	37	15.82			14.04	-11.2
1150	38.67	2350	33	11.87			14.34	+20.8
1127	41.95	3200	37	13.85			12.73	- 8.1
1128	41.85	400	12	13.35			11.11	-16.8
1129	41.80	2600	53	16.82			14.93	-11.2
1131	41.73	3300	58	17.65			14.65	-17.0
1132	41.72	3800	65	16.88			14.51	-14.0
1133	41.65	4100	37	14.23			11.72	-17.6
1134	41.28	3800	50	16.57			13.61	-17.9
1135	41.27	4800	50	14.23			12.11	-14.9
1138	40.92	1600	12	11.65			11.07	- 4.9
1139	40.90	3750	70	15.49			15.17	- 2.1
1140	40.90	2900	19	13.81			11.14	-19.3
1141	40.78	4300	48	16.90			12.90	-23.7
1142	40.72	3250	48	17.24			14.27	-17.2
1143	40.38	3900	56	15.34			14.28	- 6.9
Mean Deviation					%		14.3	

For locations within 25 miles of the coast, the mean deviations were: 1956 - Model D, 7.4%, Model A, 9.3%; and 1968 - Model A, 9.3%.

\* Best prediction

distance-squared term, which was also significant in the model (A) derived from 1971 date (p. 71). Sixty-five percent of the total variation was accounted for by Model D, an improvement on Model C, for the same data, which used longitude and elevation as independent variables and had an  $r^2$  value of 0.52.

The relatively higher  $r^2$  values obtained using the 1968 collection data, when compared with Model A ( $r^2 = 0.475$ ) may be due to the fact that the former were based on bulked samples from an average of 16 trees per location. Greater sampling variation is expected with the two trees per minor location scheme adopted in the present study.

Comparison of Predicted Values. Model D provided the best estimate of 1956 seed weights for eight locations, Model A for five, and both predicted the same value for the remaining location (24). Seed weight for the most southerly location (30) was considerably heavier than predicted by either model, and Model A was clearly less accurate for the high-elevation inner-range location (21).

Model D was based on the 1968 data, thus predictions for that year could only be made from the independently derived Model A. The deviations of predicted from observed values were again greatest for high-elevation inner-range locations. However, considering only samples within 25 miles of the coast, the absolute deviation was 9.3%, showing that predictions are equivalent in accuracy to those for the 1956 crop, based on Model A.

Since retention of all viable seed was necessary (p. 36) a small amount of empty seed in the 1971 samples may account for the predominance of under-estimates from Model A though it is clear that Model D also under-estimated the 1956 crop weights. Birot (1972) used a flotation method to clean his seed samples, while Sweet's (1965) data were based on samples cleaned to an average of 94.3% full seed.

For the low-elevation coastal locations the accuracy of prediction (within 10%) is evidence that environmental effects are either small or quite consistent from year to year. On the other hand, seed weight of inner range samples appears more variable over time, perhaps because of greater fluctuation in environmental factors such as drought or summer temperature conditions.

It is known that collection year can influence seed size in Ponderosa pine (Callaham and Hasel, 1958), yet Fielding (1964) found an intra-class correlation of 0.83 for weight of seed produced in a given year and location by Monterey pine clones. The latter observation indicates a high broad sense heritability for the character; therefore good repeatability should be expected in a predictable environment such as the fog-belt. The results indicate that this is so for Douglas-fir.

### Epicotyl Length

Since seedlings were raised under cultural conditions varying from normal nursery practice, and analysis was conducted on family means averaged over different watering regimes, the validity of the data as an indication of future growth potential must be considered. Sziklai (1966) reported a correlation of  $r = 0.895$  between first-year epicotyl length of growth-chamber-grown Douglas-fir seedlings and four-year total height, indicating utility of the measurement in principle.

Height growth data from Sweet (1965) provided an opportunity to compare epicotyl length values predicted by the location model (p. 72) with observed first- and second-year height growth of seedlings from the collection made in 1956 and raised in a nursery in New Zealand (Table XV).

Because of differences in environmental conditions, the data sets were not directly comparable, and the degree of correlation between observed total height and predicted epicotyl length was used to compare variation patterns (Figure 14).

The atypical nature of seedlot 30 (from Santa Cruz) has already been discussed (p. 97). Ignoring that sample, predicted epicotyl length is significantly correlated with both one- and two-year height. The variation pattern of container-grown seedlings is apparently quite comparable with that developed in a conventional nursery.

Table XV. Early height growth of Douglas-fir Seedlings of California origin when raised in New Zealand (after Sweet, 1965), and Predicted Epicotyl Length of the Same Sources Based on Growth at Corvallis, Oregon.

Source	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi. )	Total Height (in. )		Predicted length (cm)
					1 yr.	2 yr.	
12. Berteleda	41. 80	124. 07	300	6	3. 14	21. 6	2. 69
14. Lamoine	40. 98	122. 43	1600	88	2. 22	11. 8	1. 14
15. Willow Creek	40. 95	123. 65	600	26	2. 91	15. 9	1. 88
16. Six Rivers	40. 92	123. 80	1600	13	3. 70	19. 2	2. 24
17. Mad River	40. 92	123. 92	700	11	3. 48	20. 3	2. 40
18. Miranda	40. 23	123. 87	1700	15	4. 29	22. 3	2. 19
19. Dehaven	39. 60	123. 80	500	2	5. 49	24. 8	2. 67
20. Mendocino N. F.	39. 83	123. 05	2500	40	3. 40	18. 6	1. 51
24. Jackson S. F.	39. 35	123. 72	500	4	5. 18	24. 5	2. 60
27. Middletown	38. 77	122. 68	1500	33	3. 98	17. 3	1. 95
28. Stewart Point	38. 65	123. 37	500	2	5. 17	24. 5	2. 57
30. Santa Cruz	37. 08	122. 25	1000	2	8. 22	30. 2	2. 40

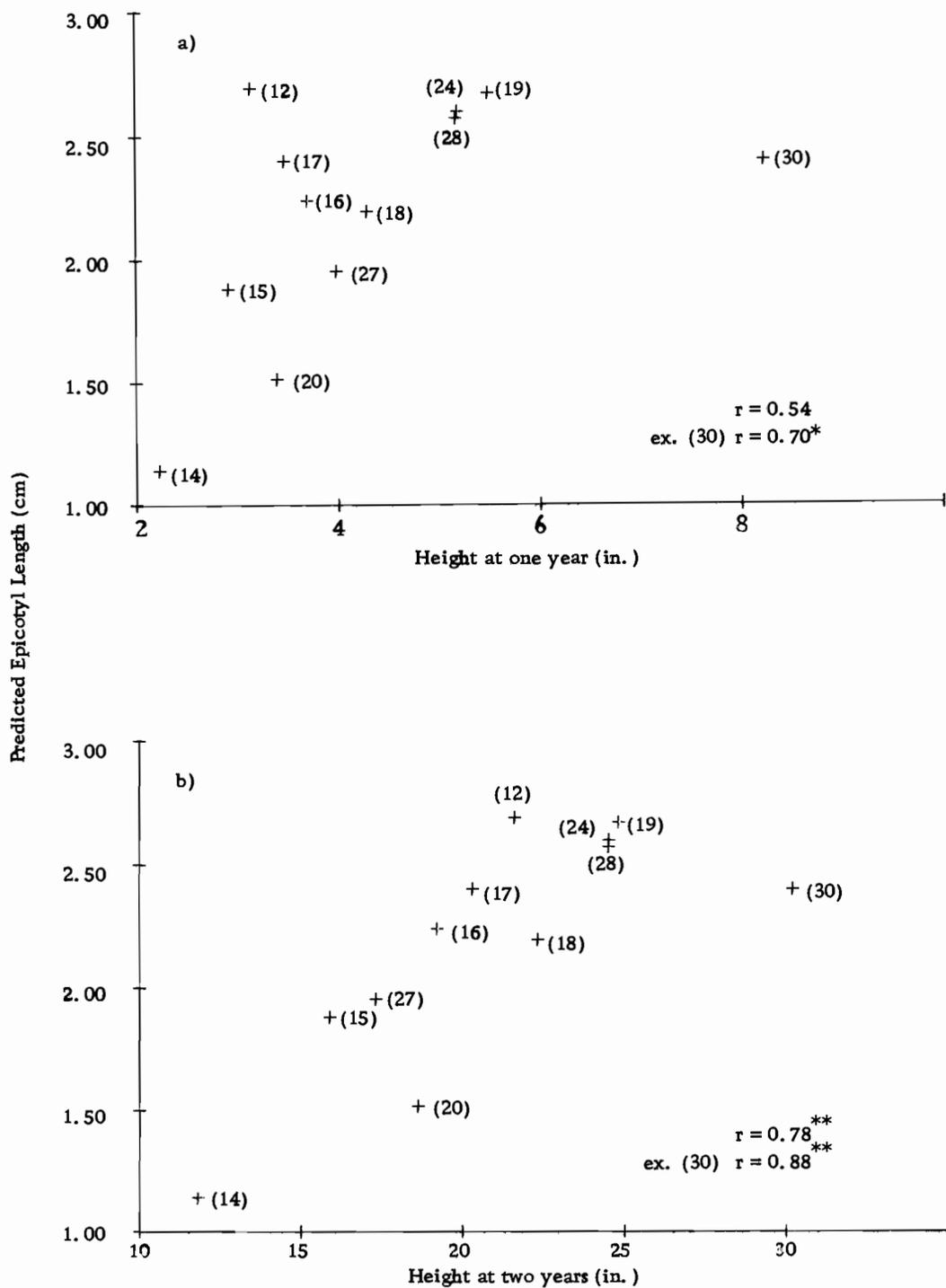


Figure 14. Correlation of predicted epicotyl length with a) one-year, and b) two-year height growth in New Zealand (Sweet, 1965).

The improvement of the correlation with second-year growth ( $r = 0.88$  c. f.  $r = 0.70$ ) may have important implications for progeny screening, since testing under stress has allowed first-year expression of genetic variation which is masked by the fertile well-watered nursery conditions. A further possible reason for the poorer correlation with first-year growth is that the total height included seed size effects, and possibly some component due to germination rate, while the technique used in the present study minimized both these effects.

### Implications for Seed Movement

#### Definition of Seed Zones

Observations on one-year-old seedlings are obviously not a valid basis for firm recommendations regarding seed zone boundaries. Nevertheless, certain relationships between the current zoning system<sup>3</sup> (Buck et al., 1970) and the seedling variation pattern are apparent.

- 1) The results of this study confirm the desirability of defining the North Coast Redwood (Series 090) and the North Coast Interior (Series 300) as separate regions (Figure 3), and eliminating seed movement between them.

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<sup>3</sup>For definition of the system sub-divisions, see p. 16.

2) Within Series 090 growth data do not fully support the rule that, seed from a particular seed collection zone being lacking, that from an adjacent zone should be used. Thus seedlings from zone 091 (location G) were more similar to those from 095 (location B) than were either to 093 (location D). An earlier map produced by Schubert (1966) shows zone 093 as being included in a westward extension of the "coast range Douglas-fir" to the coast at Cape Mendocino. Although seedlings from D were faster growing than more typical Series 300 samples (Table V), some such distinction may be warranted, as movement of 093 seed north or south could result in a loss of productivity.

Caution should also be exercised with respect to the movement of zone 097 (location A) seed to more northerly planting sites, at least without preliminary trials. The apparent plasticity of growth of these seedlings might result in productivity gains if planted further north, but this must be weighed against the increased chance of freezing damage.

3) Within Series 300 some division into sub-regions seems justified since seedlings from zone 301 (H) and zone 312 (E) grew marginally faster than those from further east in zone 321 (I) and zone 371 (F) respectively. It may be that movement of seed from west to east in this region would result in improved growth with little

attendant risk of increased susceptibility to drought or cold damage.

4) Restriction on north-south movement of seed within regions should be subject to local assessment of the probability of low temperature damage, since there was little indication that early growth would be affected by movement well in excess of the current 50-mile zone limits.

5) Apart from cold hardiness at the two most northerly locations (D and G), and possibly height growth at G (Figure 7), there was little evidence of elevational differentiation in the Series 090 samples. Within the Series 300 adherence to elevational sub-zones may be more important (Figure 8). The pattern of growth variation with elevation differed among the major locations (Figure 7), so it is not possible to generalize regarding the desirable magnitude of elevational tolerances, but the present 500 ft. range specification seems adequate.

#### Use of Californian Douglas-fir as an Exotic

It is clear that coastal seedlings are potentially faster growing than those from a relatively short distance inland, but whether this potential will actually be realized at a particular exotic planting site will depend upon the frequency of damaging climatic conditions.

Of all the aspects of climate, growth was most highly correlated with the annual range in mean monthly temperature. At the coast this

is in the order of  $14^{\circ}\text{F}$  (Table IX)-- $47^{\circ}\text{F}$  in winter and  $61^{\circ}\text{F}$  in summer. The low summer temperature is due to the moderating influence of fog. Biologically this acts to reduce evapo-transpiration, and sites are more mesic than would be expected for an area with July-September rainfall of less than one inch (Appendix Table III). Presumably coastal sources would grow well on sites with higher summer temperatures but a different precipitation pattern.

The limiting effects of summer drought were not fully explored in this study, as no evidence regarding differential survival ability was obtained. The coastal seedlings did not show the plastic growth response to stress exhibited by the inner range seedlings. The latter's capacity to go dormant under stress is presumably adaptive, but may result in poor productivity, while the coastal sources should be better able to maintain productive growth rates if they are able to survive. In regions where periodic drought is anticipated, samples from zone 093 (location D) are worth testing, since they exhibit some of the inner range characteristics with only a small reduction in growth compared to the fastest growing sources.

Sensitivity to winter cold places a more serious limitation on the planting of coastal Californian sources, since a December temperature of  $-7^{\circ}\text{F}$  caused severe damage when seedlings were raised at Corvallis, Oregon ( $44^{\circ}38'\text{N}$ ). Of the coastal samples, those from above 2500 ft. in the north of the region (locations G and D) were

the most hardy (Figure 11), and may be useful in areas with a low but significant probability of cold temperatures. Since all coastal locations produced some seedlings that survived undamaged, and these were not obviously slower growing, selection for hardiness may produce worthwhile gains.

Many coastal seedlings did not set buds until well into September, and so would be susceptible to even mild fall frosts. At least some samples did, however, show the late flushing habit for which coastal sources from further north are favored in Europe.

The trial included several seedlots from Oregon, Washington, and British Columbia (Appendix Table I), and those from coastal sites north of latitude  $45^{\circ}\text{N}$  set buds earlier and made less height growth than the Californian samples.

Because of their low growth potential inner range Douglas-fir sources are not likely to be of widespread use. On sites where their drought hardiness characteristics might be valuable, some other species may be more suitable, while cold hardiness may be obtained with less sacrifice of productivity by planting more northerly coastal sources.

#### Use of Juvenile Characteristics in Seed Source Identification

The economic consequences of planting seedlings of an unsuitable

provenance are potentially serious, and the development of early tests for confirming seedlot origin has received attention (Allen, 1961; Bouvarel, 1961).

Because of the general uniformity of within region juvenile characteristics, extensive testing would be required to distinguish samples at the major location level. The data indicate, however, that if a seedlot may correctly be assumed to originate somewhere in northern California, the source region may be identified with reasonable certainty, using a three-stage procedure:

- 1) With the possible exception of the most southerly (Santa Cruz) population, collection year appears to have little effect on mean seed weight of coast region samples. Expected weight of a putative coastal seedlot may therefore be predicted from either Model A or D (p. 104) and compared with the observed value. A deviation of less than 10% would be good evidence of the validity of source information, with larger deviations suggesting the desirability of further testing.

An inner range origin would be confirmed by a mean seed weight in excess of 13 mg since this is heavier than any coastal mean (Table V). High elevation inner range trees may, however, produce light seed, and none of the regression models are adequate for prediction in this case.

- 2) Of the other seed related characters, cotyledon number appears to be the most useful discriminant. It is not likely to be

affected by test environment, as is the germinative pattern, and so may be determined from relatively small samples without comparison with a series of known controls.

Excluding locations D and E, each coastal major location mean cotyledon number was significantly less than that determined for those from the inner ranges (Table V). A mean number of less than seven cotyledons per seedling is evidence for a coastal origin.

3) If doubt still remains, then first-year growth in comparison with seedlings of known origin should resolve the issue. A sub-optimal cultural regime should be followed, and either date of final budset or final epicotyl length assessed. A preliminary study indicated that, under stress, the ranked date of first budset correlated well with that of final setting under nursery conditions. If this is so, it may not be necessary to test over a full growing season.

Under such conditions the controls should fall into distinct regional groups, and the unknowns be classified accordingly. Growth significantly different from either group (e. g. , location D, Table V) would indicate a transition zone origin, or that the seedlot came from outside the area.

Identification by multivariate analysis has been suggested by Sweet (1965), and was successfully used by Squillace (1966) to distinguish among Slash pine sources. In the present case, however, the regional differences are so distinct that the simpler procedure

suggested above should be adequate. A principle component analysis based on all ten variables assessed was no more useful in discriminating between regions than was the single variable epicotyl length.

## VII. SUMMARY

1. The study demonstrates marked adaptive differentiation within the Douglas-fir population in northern California. For all characters assessed, excepting date of budburst, the primary contrast was between samples from the coastal fog-belt and those from the inner ranges. More minor variation patterns were related to elevation within major locations (growth and cold hardiness) and latitude (cold hardiness).

Seedlings from coastal locations set buds later; grew taller; were less cold hardy; and had less capacity to go dormant in response to moisture stress than did those from inner range locations. Coastal samples were also characterized by smaller seeds, slower germination, and seedlings with fewer cotyledons and shorter hypocotyls.

2. Characteristics related to the annual cycle of growth and dormancy showed greater adaptation to source climate, and thus differed more between regions, than did those related to seed. Regional effects for epicotyl length and time to budset were ten times greater than family variances, but for seed weight, cotyledon number, and cotyledon height both estimates were of the same order. Furthermore, the regression of epicotyl length on source climate accounted for 76% of family variation,

compared with 41% for seed weight. A hypothesis is presented which accounts for the different variation patterns exhibited by these two groups of characters:

Growth, phenology, and hardiness are all characteristics which are expressed throughout the lifespan, and are subject to climatic selection pressures operative over areas as large or larger than the breeding unit. This results in adaptation on a regional scale, with changes in gene frequency mapping climatic variation. Thus the gradient of the cline for height growth is steepest over the inner margin of the fog-belt where climate changes most rapidly with distance.

On the other hand, seed related characteristics are only directly expressed over the first growing season, when micro-environmental conditions constitute more severe selection pressures than do climatic factors per se. A polymorphic population should therefore be maintained to the extent that the micro-environment is heterogeneous. The clines in mean values for these characters represent corresponding gradients in average micro-environmental conditions, which are related, but not necessarily proportional to, climatic change.

3. Regression models were developed relating the seed weight and epicotyl length data to source location. In each case the most important single location index proved to be the distance from the ocean.

The equations were solved for locations sampled in previous studies, and predictions compared with published observed values.

It appears that seed weight samples from near the coast are relatively consistent from year to year (within 10%), but this is not the case with inner range samples. Greater fluctuation in annual weather conditions is a possible cause of the latter observation.

Two-year height of seedlings raised in a nursery in New Zealand showed a highly significant correlation with epicotyl length predicted for the same locations. This result is important in that it shows that the observed variation pattern did not result from specific interaction with the rather unconventional test procedures. Since predictions were more highly correlated with second than first year total height, the method offers the possibility of shortening the initial screening period in progeny and provenance tests.

4. The results generally confirm the applicability of the present seed zoning system as a basis for movement of Douglas-fir seed within northwestern California. In particular, care should be taken to eliminate transfer between the two designated physiographic and climatic regions.

The rule that seed from an adjacent zone should be used if stock from the planting zone is not available may not always be optimal, and this is discussed in relation to the growth of seedlings from zones 093 and 097.

Within Series 300, some division into sub-regions is indicated by the marginally faster growth of seedlings from sites in the west of the region. Seed could possibly be moved from west to east, but movement in the reverse direction would result in loss of productivity.

There is little biological basis for the current 50 mile latitudinal zone limits, and elevational sub-zoning might be relaxed in Series 090, but seems more important within 300. Because of their fast growth, coastal sources should be useful for plantation establishment as exotics. The coastal region is characterized by a low annual temperature range, but sources should grow well in regions with higher summer temperatures if sufficient soil moisture is available. The major limiting factor may be their susceptibility to winter cold injury, and in this regard the testing of high elevation samples from the north of the region is suggested.

The inner range sources seem less useful since their cold hardiness can be matched by coastal samples from further north, and it is doubtful whether they would outproduce alternative species on dry sites.

6. Under the assumption that a claim for northern California origin is valid, a three-stage procedure for confirming the regional origin of a seedlot is outlined.

As a first step, the seed weight on location model may be used to predict weight for the putative source. A low weight in good agreement with the prediction would confirm a claim of coastal origin. Mean weight in excess of 13 mg would indicate that the source was somewhere in the inner ranges. Secondly, a sample may be germinated and mean cotyledon number determined. If this is less than seven per seedling then a coastal origin is again indicated. Thirdly, if still in doubt, seedlings could be raised for the first growing season in a test with controls from each region, and height growth or budset assessed.

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## APPENDIX

Appendix Table I. Location Data and Family Character Means (untransformed).

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi. )	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
A	7	37.13	122.18	640	2	11.9	39	7.17	1.52	145	21.3	24	40	2.01	3.53
	8			650	2	9.7	7	6.17	1.18	151	28.7	12	15	2.34	3.52
	9			680	2	12.2	29	7.32	1.42	144	25.3	18	24	2.21	3.63
	10			720	2	13.8	78	6.95	1.32	144	22.4	-6	-19	2.59	3.91
	11			730	2	13.0	49	7.10	1.47	151	24.6	0	22	2.37	3.83
	12			760	2	11.7	30	7.11	1.16	152	27.0	-1	22	3.07	4.23
	13			760	2	10.8	22	6.78	1.28	159	26.4	5	15	3.18	4.46
	14			800	2	9.5	51	5.97	1.02	152	28.2	11	18	2.76	3.78
	15			830	2	12.7	9	6.88	1.17	148	20.5	18	29	1.99	3.17
	16			100	1	9.7	51	6.30	1.12	155	29.7	2	-24	2.50	3.63
	17			150	1	11.1	20	6.89	1.27	138	25.1	15	44	2.29	3.56
	18			180	1	12.8	6	6.67	1.51	145	24.2	14	29	2.33	3.84
	19			150	1	9.7	29	6.83	1.48	147	26.9	-1	50	2.54	4.03
	20			450	2	12.8	8	6.56	1.33	146	21.4	-7	-7	2.41	3.73
	21			500	2	11.4	29	7.17	1.40	139	20.0	-18	-82	2.18	3.58
	22			1750	4	15.0	40	6.75	1.56	139	19.6	7	31	2.23	3.79
	23			1750	4	8.7	17	6.42	1.14	143	29.5	5	18	2.28	3.42
	24			1950	6	16.0	18	6.45	1.31	140	22.8	15	29	2.24	3.56
	25			1950	6	14.4	30	6.47	1.01	146	24.9	7	27	2.22	3.23
	26			2250	6	10.5	29	6.89	1.03	149	18.5	1	14	2.03	3.06
	27			2500	7	13.0	4	6.72	1.36	146	28.8	7	27	2.60	3.96
	28			1250	7	14.1	41	7.07	1.16	161	27.4	5	-13	2.61	3.77
	29			2600	14	12.5	18	6.96	1.19	132	18.2	15	38	1.71	2.89
	30			2700	14	12.5	7	6.92	1.43	141	24.4	2	33	2.41	3.84
	31			2650	14	12.3	89	6.50	1.53	132	18.5	20	35	1.73	3.26
	32			2750	14	8.1	45	6.76	1.08	140	19.6	-4	6	1.85	2.93
	33			2700	14	9.8	22	7.30	1.19	147	20.2	-8	18	2.55	3.74

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
B	60	39.38	123.60	1450	23	13.2	42	7.33	1.28	141	29.4	7	-22	2.15	3.43
	61			1500	23	9.2	24	6.44	1.02	135	28.5	12	10	1.99	3.01
	62			2000	21	8.2	23	7.33	1.04	147	26.8	7	7	2.50	3.54
	63			2000	21	11.5	75	7.16	1.42	129	28.5	19	46	2.34	3.75
	64			2500	21	13.9	37	7.17	1.48	144	34.3	-4	-12	2.46	3.95
	65			2500	21	9.8	55	6.94	1.10	150	29.5	14	17	2.69	3.79
	66			1750	20	12.3	81	6.94	1.86	147	37.6	0	16	2.84	4.70
	67			1750	20	9.5	49	6.39	1.37	145	28.6	4	21	2.11	3.48
	68			1450	19	7.4	42	5.96	1.20	148	28.5	1	22	2.64	3.83
	69			1450	19	14.8	46	6.83	1.32	134	28.5	12	21	2.39	3.70
	70			1200	18	8.3	51	6.11	1.12	154	28.7	-3	32	2.87	3.99
	71			1200	18	10.0	51	7.11	1.12	145	32.5	-4	7	2.78	3.90
	72			900	17	12.5	36	6.61	1.23	130	32.1	18	41	2.28	3.51
	73			850	17	12.1	38	7.56	1.34	149	34.5	18	37	2.50	3.87
	74			400	14	11.0	51	6.92	1.40	143	36.5	16	22	2.47	3.87
	75			400	14	10.9	31	6.83	1.45	156	39.6	-4	27	3.03	4.48
	76			50	5	10.3	16	7.39	1.21	151	34.7	-1	17	2.71	3.92
	77			200	1	6.0	5	6.07	1.05	152	30.0	3	25	3.09	4.14
78	200	1	9.0	21	6.33	1.14	135	31.3	4	47	1.72	2.85			
C	49	39.28	122.83	3100	43	16.0	78	7.39	1.55	111	27.3	22	14	1.52	3.07
	50			3100	43	15.0	26	8.05	1.60	116	29.6	4	17	1.53	3.13
	51			2050	48	11.7	45	7.00	1.23	92	27.7	-3	36	1.33	2.55
	52			2050	48	14.6	42	7.06	1.50	96	26.0	38	75	1.06	2.56
	53			4100	51	9.4	46	6.75	1.23	95	28.2	24	48	1.20	2.43
	54			4150	51	13.8	46	8.19	1.44	103	27.4	41	30	1.05	2.48

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
	55			4150	51	9.8	57	7.60	1.30	108	28.0	14	45	1.22	2.52
	56			4300	52	12.1	63	6.99	1.29	92	28.6	31	41	0.99	2.28
	57			4200	52	11.3	55	7.45	1.31	79	27.5	9	56	0.75	2.06
	58			2700	48	11.0	33	7.17	1.14	124	24.9	- 8	14	1.58	2.72
	59			2300	47	17.0	20	7.73	1.69	113	27.6	9	32	1.64	3.32
D	80	40.23	123.90	850	17	9.6	34	6.83	1.18	140	27.2	13	15	1.54	2.73
	81			850	17	13.6	29	6.83	1.33	140	28.4	6	23	2.17	3.49
	82			900	17	13.8	86	6.75	1.56	123	19.9	20	44	1.60	3.17
	83			900	17	11.0	45	7.03	1.30	136	24.2	15	41	1.88	3.18
	84			1350	17	11.8	56	6.83	1.38	129	26.7	- 6	13	1.47	2.85
	85			1350	17	10.6	47	7.50	1.48	134	23.7	11	45	1.52	3.00
	86			3300	16	9.0	45	7.17	1.12	146	31.3	0	35	2.14	3.26
	90			2750	16	11.8	45	8.07	1.22	141	28.0	9	28	2.66	3.88
	91			2750	16	13.1	14	8.24	1.47	137	27.9	- 3	13	1.84	3.31
	92			2450	16	10.5	52	6.83	1.18	132	22.3	11	18	1.95	3.13
	93			2450	16	13.1	30	7.33	1.52	140	20.6	8	36	1.74	3.26
	94			2150	15	12.0	64	6.39	1.59	139	25.4	20	45	2.22	3.81
	95			2150	15	11.9	37	7.46	1.32	139	24.2	22	51	2.00	3.32
	96			1450	14	18.0	42	7.84	1.46	111	23.9	- 1	31	1.58	3.04
	97			1450	14	8.9	42	6.72	1.29	147	29.8	2	40	2.15	3.44
	98			1200	14	14.9	43	7.94	1.61	144	30.1	- 5	4	2.21	3.82
	99			1200	14	16.1	64	7.93	1.49	136	25.9	3	6	2.21	3.71
	100			950	14	17.5	33	7.72	1.63	121	26.0	18	25	2.13	3.76
	101			900	14	16.1	36	7.28	1.54	127	27.1	27	53	2.06	3.61

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (*N)	Longitude (*W)	Elevation (ft)	Distance from Ocean (mi. )	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
	102			650	14	13.0	26	7.39	1.38	117	19.2	26	20	1.66	3.04
	104			400	19	14.0	82	7.00	1.66	136	24.5	10	46	2.16	3.82
	105			400	19	7.5	45	6.89	1.55	130	22.1	-26	-18	2.01	3.56
E	87	40.38	123.38	3400	43	13.9	75	6.56	1.52	112	24.7	27	57	1.41	2.93
	88			2400	46	17.0	89	7.72	1.58	99	25.1	19	44	1.38	2.96
	89			3650	43	11.0	65	7.22	1.22	105	27.5	33	50	1.04	2.27
	206			2400	46	19.6	80	7.05	1.98	122	21.3	13	22	1.59	3.57
	207			2900	45	18.8	90	7.17	1.63	97	23.8	4	28	1.33	2.96
	208			3000	45	13.0	67	7.55	1.43	121	26.9	0	5	1.41	2.84
	209			3100	44	11.6	31	7.06	1.91	107	22.8	25	51	0.79	2.70
	210			3100	44	14.9	90	7.67	1.72	91	23.7	3	35	0.93	2.65
	211			4000	42	13.2	79	6.61	1.61	94	24.0	54	65	1.13	2.75
	212			4000	42	14.1	90	7.06	1.76	87	24.3	15	29	0.86	2.62
	213			4000	42	12.2	88	7.00	1.31	107	26.0	14	43	1.23	2.54
	214			4650	42	12.0	62	6.86	1.35	102	29.1	57	73	1.02	2.40
	215			4650	42	11.6	39	6.78	1.46	100	25.8	43	49	1.03	2.49
	216			4200	42	13.0	49	7.13	1.52	116	28.1	17	37	1.31	2.83
F	197	40.33	123.00	4400	55	19.5	54	7.83	1.50	89	27.3	20	32	1.09	2.59
	198			4400	55	15.5	57	7.28	1.82	87	25.9	22	45	0.56	2.38
	199			4000	55	17.0	91	7.61	1.91	83	25.5	20	39	0.93	2.84
	200			4000	55	23.1	66	8.05	1.74	78	22.5	6	20	0.86	2.60
	201			2650	62	13.4	75	7.11	1.55	100	28.9	29	55	1.37	2.92
	202			2650	62	20.6	72	7.44	1.79	104	27.2	2	43	0.96	2.76

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
	203			2650	62	18.2	73	7.72	1.81	95	26.4	- 9	42	1.20	3.01
	204			3700	58	18.7	56	7.48	1.42	102	26.7	33	46	1.22	2.67
	205			3650	58	16.5	55	7.45	1.63	101	26.1	32	53	0.97	2.60
G	109	41.78	124.00	700	11	11.5	80	6.61	1.43	128	30.1	2	36	1.88	3.31
	110			700	11	11.0	36	7.22	1.11	152	37.3	7	44	2.56	3.66
	111			3600	12	8.0	22	6.72	1.14	149	30.3	10	17	2.07	3.21
	112			3600	12	8.5	64	7.24	1.19	141	37.4	- 2	28	2.29	3.47
	113			3600	12	11.8	56	7.39	1.29	136	36.0	22	21	1.93	3.23
	114			3100	12	10.6	45	7.27	1.27	138	31.7	13	20	2.15	3.42
	115			3100	12	7.2	33	7.04	0.82	147	35.0	- 9	-17	2.96	3.79
	116			2600	12	9.8	9	6.79	1.27	135	32.7	5	-13	2.00	3.27
	117			2200	12	7.2	49	6.29	1.16	134	30.0	16	36	2.21	3.37
	118			1000	6	9.7	49	7.06	1.34	152	32.8	- 6	-17	3.02	4.37
	119			1400	6	10.2	56	6.53	1.11	152	31.6	3	29	2.78	3.90
	120			1750	7	10.0	47	6.44	1.34	163	29.5	- 9	21	3.07	4.41
	121			1700	7	7.5	49	6.83	1.21	143	34.4	- 3	-12	2.39	3.60
	122			1650	7	12.0	68	6.53	1.58	142	35.9	10	29	2.06	3.64
	123			2000	8	8.2	57	7.22	1.16	147	33.1	2	22	2.46	3.62
	124			2000	8	11.1	52	7.39	1.32	146	34.9	- 2	-16	2.13	3.45
	126			150	5	9.5	75	7.00	1.61	149	31.6	2	12	2.92	4.52
	127			150	5	12.0	52	6.56	1.53	150	35.5	- 2	4	2.86	4.39
	128			100	4	8.0	48	6.13	1.32	161	29.0	2	12	2.83	4.15

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
H	131	41.87	123.47	1300	43	18.4	74	7.39	1.79	100	25.2	8	0	1.25	3.04
	132			1300	43	14.2	80	7.38	1.47	112	22.7	20	44	1.31	2.78
	133			1300	43	13.4	92	7.39	1.54	111	23.3	44	51	1.13	2.68
	134			1600	40	10.0	52	7.00	1.32	108	27.6	29	50	1.23	2.56
	135			1600	40	19.1	52	7.28	1.95	109	23.5	12	24	1.49	3.43
	136			1650	40	14.1	46	7.39	1.68	104	28.2	38	40	1.30	2.98
	137			1850	39	13.0	81	7.16	1.61	101	21.6	31	22	0.87	2.47
	140			4450	36	8.2	30	7.84	0.98	101	27.0	12	39	1.11	2.09
	142			4000	36	9.3	40	6.71	0.99	101	24.4	25	43	1.27	2.26
	143			3800	36	11.5	16	7.00	1.16	97	22.6	2	23	1.01	2.17
	144			3800	36	12.9	33	6.61	1.41	101	25.4	9	8	1.16	2.57
	145			3650	36	10.0	33	6.83	0.98	114	23.3	3	16	1.54	2.53
	146			3650	36	11.6	63	7.43	1.34	105	28.8	15	34	1.00	2.34
	147			3200	37	10.5	40	6.55	1.12	107	25.3	24	45	1.36	2.47
	148			3200	37	12.4	19	7.28	1.20	121	31.8	- 1	- 8	1.64	2.84
	149			2750	37	11.6	75	7.28	1.68	102	22.1	25	67	1.05	2.73
	150			2700	37	15.8	71	7.50	1.72	81	30.9	0	55	0.75	2.47
	151			2200	38	13.7	44	8.00	1.50	91	23.7	26	55	1.08	2.58
	152			2200	38	14.1	12	7.55	1.44	110	23.2	24	47	1.04	2.48
	153			3300	44	16.0	27	7.56	1.42	103	24.9	46	40	1.14	2.56
	154			3300	44	14.5	85	6.78	1.61	99	22.5	11	39	1.36	2.97
	155			3300	44	12.2	81	7.39	1.63	92	24.8	38	26	0.82	2.45
	156			3300	44	12.6	64	7.44	1.61	70	17.9	- 3	54	0.96	2.57
	157			3300	44	11.3	18	7.00	1.41	100	20.3	- 4	51	0.96	2.37
	158			3300	44	16.2	6	7.56	1.64	94	23.3	17	13	1.12	2.75
	159			3300	44	14.3	71	7.44	1.46	101	23.2	11	28	1.21	2.67

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Height (cm)	Total Height (cm)
	160			1300	39	20.6	54	8.17	1.95	89	25.2	6	43	1.10	3.05
	161			1300	39	15.7	52	7.72	1.79	118	27.3	-1	43	1.47	3.27
	162			1350	39	14.2	62	6.83	1.60	102	25.4	11	42	1.25	2.84
	163			1250	39	17.2	91	7.92	1.88	114	27.8	33	45	1.66	3.55
	164			1250	39	14.4	69	7.57	1.99	99	20.0	2	9	1.40	3.39
	165			1050	39	14.8	52	7.07	2.07	91	25.6	16	32	0.83	2.89
	166			1000	42	17.0	42	7.45	1.83	112	21.7	12	28	1.41	3.24
	167			1050	42	12.3	46	7.41	1.52	108	22.4	27	64	1.06	2.58
I	171	41.93	122.78	4900	78	11.4	31	7.06	1.50	107	29.3	14	36	0.99	2.49
	172			4850	78	14.0	49	6.94	1.40	96	27.6	34	26	0.82	2.22
	173			4550	77	10.5	47	7.33	1.50	98	20.1	23	55	1.25	2.75
	174			4550	77	11.7	95	7.83	1.69	66	22.9	-16	-33	0.74	2.44
	175			4500	76	16.3	93	7.50	1.72	76	23.4	11	53	0.82	2.55
	176			4500	76	13.9	73	7.17	1.57	84	22.9	32	76	0.92	2.49
	177			4500	76	20.1	83	8.22	1.81	81	27.1	23	31	1.02	2.84
	178			4100	76	13.1	82	7.22	1.32	84	31.7	14	22	0.65	1.97
	179			4100	76	11.6	49	7.01	1.21	86	31.9	28	42	0.97	2.18
	180			3800	75	13.1	37	7.59	1.42	83	24.5	2	26	0.62	2.03
	181			3800	75	14.2	64	7.72	1.35	70	26.9	3	-43	0.67	2.02
	182			3500	74	19.5	42	7.61	1.57	67	28.1	13	55	0.63	2.19
	183			3500	74	14.0	19	7.78	1.52	86	21.0	8	20	0.84	2.36
	184			3200	73	14.0	83	7.67	1.43	70	22.8	2	40	0.74	2.16
	185			3200	73	13.0	67	7.61	1.67	81	22.4	15	26	0.76	2.45

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Appendix Table I. (Continued)

Major Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
I	186	41.93	122.78	2750	72	19.2	39	7.11	1.58	96	19.0	34	44	1.34	2.92
	187			2750	72	20.5	33	7.77	1.97	91	25.3	14	38	1.12	3.09
	188			2300	71	25.1	31	8.05	1.77	75	25.4	11	33	1.12	2.89
	189			2300	71	17.0	60	7.33	1.49	99	21.6	16	50	1.22	2.71
	190			1900	75	10.2	94	7.39	1.87	90	24.7	40	36	1.31	3.18
	191			1900	75	19.3	68	7.22	1.65	114	21.6	25	44	1.46	3.11
	192			1900	75	11.9	83	6.89	1.82	108	22.9	32	52	1.20	3.02
	193			1700	69	11.7	58	7.06	1.60	112	30.8	34	36	1.22	2.82
	194			1750	69	12.6	60	7.17	2.05	100	25.7	16	17	1.22	3.27
	195			1700	69	14.6	53	7.49	1.43	108	19.3	36	43	1.07	2.50
	196			1700	69	19.0	54	7.39	1.87	103	25.1	15	55	1.18	3.04

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Appendix Table I. (Continued)

Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi. )	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)
<u>California</u>															
Little Sur	6	36.33	121.80	1000	5	19.6	19	7.27	1.80	117	17.2	0	18	1.84	3.64
Jenner	34	38.45	123.12	100	1	9.2	0	7.00	1.24	144	24.9	15	33	2.45	3.69
	35			100	1	8.4	11	6.39	1.31	142	21.9	13	34	2.22	3.53
	36			100	1	9.6	27	7.08	1.22	144	22.7	15	24	2.70	3.93
Las Pasadas	37	38.57	122.52	1700	36	12.1	35	6.89	1.23	136	24.0	7	29	1.71	2.98
	38			1700	36	13.9	18	7.41	1.29	124	24.8	32	17	1.45	2.74
	39			1700	36	14.0	54	7.17	1.08	129	25.5	12	22	1.53	2.62
	40			1700	36	15.6	58	7.00	1.35	120	18.6	25	34	1.27	2.62
Napa Valley	41	38.57	122.52	400	31	15.2	36	7.50	1.52	136	22.9	7	34	1.92	3.44
	42			750	31	17.5	41	7.17	1.32	139	21.1	-7	12	2.01	3.33
	43			750	31	11.6	49	7.39	1.10	140	13.6	-4	11	1.57	2.67
Boggs Mt.	44	38.83	122.63	3100	37	10.6	41	7.11	1.08	142	22.7	-26	31	1.28	2.37
	45			3000	37	14.5	44	7.83	1.33	122	26.0	4	29	1.16	2.49
	46			2950	37	13.6	77	7.72	1.41	107	25.0	-18	25	1.59	3.00
	47			2950	37	16.0	78	7.61	1.58	117	18.5	-7	42	1.16	2.74
	48			3000	37	9.9	29	6.78	1.12	128	24.3	14	43	1.41	2.53
Mad River	106	40.90	123.93	550	9	8.3	84	6.78	1.23	150	35.5	10	8	2.46	3.70
	107			550	9	10.4	71	6.94	1.15	144	31.1	13	25	2.08	3.23
	108			600	9	8.8	39	7.00	1.12	150	26.5	-2	38	2.35	3.47
Siskiyou Fork (Highway #199)	129	41.78	123.78	1100	21	17.9	49	7.33	1.94	109	29.4	15	20	1.56	3.50

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Appendix Table I. (Continued)

Location	Seedlot No.	Latitude (°N)	Longitude (°W)	Elevation (ft)	Distance from Ocean (mi.)	Seed Weight (mg)	Germination (% at 7 days)	Cotyledon No.	Cotyledon Height (cm)	Days to Budset	Days to Budburst	Bud Sensitivity	Height Sensitivity	Epicotyl Length (cm)	Total Height (cm)	
<u>Oregon</u>																
Brookings	(2)*	4	42.05	124.28	80	1	-	-	7.33	1.47	149	29.6	- 6	15	2.48	3.95
Medford	(4)	79	42.37	122.87	2700	75	-	-	7.23	1.31	85	22.5	20	8	1.05	2.36
Canary	(2)	139	43.92	124.03	100	5	-	-	6.33	1.10	146	31.0	10	43	2.39	3.49
MacDonald Forest	(4)	103	44.63	123.20	1900	37	-	-	7.17	1.46	125	27.7	13	37	1.45	2.91
Cloverdale	(2)	138	45.22	123.90	20	5	-	-	6.61	1.24	129	32.9	- 2	4	1.72	2.96
Mollalla	(4)	1	45.27	122.32	3400	80	-	-	6.72	1.40	87	25.9	10	47	0.90	2.30
<u>Washington</u>																
Forks	(2)	168	47.95	124.37	350	10	-	-	7.21	1.12	115	37.0	13	51	1.11	2.23
Shelton	(2)	5	47.95	123.10	10	50	12.5	-	6.95	1.41	111	23.4	15	47	1.30	2.71
<u>Vancouver Island</u>																
Sugar Loaf	(4)	141	48.55	123.93	3200	28	6.8	-	6.22	0.89	114	27.0	38	42	1.24	2.13
Parksville	(2)	3	49.20	124.28	-	55	-	-	7.05	1.23	103	36.6	17	22	1.63	2.86
Jeune Landing	(2)	2	50.30	127.43	-	15	-	-	6.50	1.30	115	30.0	16	4	1.60	2.90

\* Number of trees in sample, where > 1.

## Appendix Table II

Supplemental Information, and Sample Calculations for  
Analysis of Variance of Seed and Seedling  
Characteristics (Table IV)

Correlation of Major Location Means and Variances  
for Each of Ten Characters

Character	$r^*$	Transformation adopted	$r$ (transformed data)
Seed Weight	0.67	Square root	0.42
Germination (% at 7 days)	-0.33	None	
Cotyledon No.	-0.15	None	
Cotyledon Height	0.25	None	
Budset	-0.34	None	
Budburst	0.05	None	
Bud Sensitivity	0.91	Natural log.	-0.30
Height Sensitivity	-0.07	None	
Epicotyl Length	0.91	Square root	-0.05
Total Height	0.76	Square root	0.12

\* At 5% level, critical  $r$  (7 d. f.) =  $\pm 0.666$

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Computation of Coefficients for the Components of  
Variance (nested analysis with unequal numbers)

Source of Variation	<u>Analysis of Variance</u>	
	d. f.	Expected Mean Square
Regions (R)	$R - 1$	$\sigma^2 + K_1' \sigma_{RMm}^2 + K_2' \sigma_{RM}^2 + K_3 K_R^2 \frac{a/}{R}$
Major locations in regions (M)	$\sum M_i - R$	$\sigma^2 + K_1' \sigma_{RMm}^2 + K_2' \sigma_{RM}^2$
Minor in Major in Regions (m)	$\sum \sum m_{ij} - \sum M_i$	$\sigma^2 + K_1' \sigma_{RMm}^2$
Trees in Minor in Major in Regions (Residual)	$N - \sum \sum m_{ij}$	$\sigma^2$
Total	$N - 1$	

$$\frac{a/}{K_R^2} = \sum \frac{\alpha^2}{R-1} \quad \text{since R effects are fixed.}$$

Number of Observations by Sampling Levels

		<u>Major Locations in Regions</u>	<u>Minor in Major Locations</u>	<u>Trees in Minor Locations*</u>	
Coastal	4	A	9	5(2), 4(2), 2(4), 1(1)	= 27
		B	10	2(9), 1(1)	= 19
		D	12	2(10), 1(2)	= 22
		G	10	3(3), 2(3), 1(4)	= 19
Inland	5	C	6	4(1), 2(2), 1(3)	= 11
		E	8	3(1), 2(4), 1(3)	= 14
		F	4	3(1), 2(3)	= 9
		H	15	4(1), 3(5), 2(6), 1(3)	= 34
		I	<u>11</u>	4(1), 3(2), 2(8)	= <u>26</u>
		<u>9</u>			<u>181</u>

\*Numbers in parentheses indicate the number of minor locations containing the respective sample sizes.

Let the number of observations for each class or sub-class be as follows:

- There are  $n$  . . . . total observations
- In each Region ( $R_i$ ) there are  $n_i$  . . . observations
- In each Major Location ( $M_{ij}$ ) there are  $n_{ij}$  . . observations
- In each Minor Location ( $m_{ijk}$ ) there are  $n_{ijk}$  observations

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Table for Computation of Coefficients

S. S.	$\sigma^2$	$\sigma^2_{RMm}$	$\sigma^2_{RM}$	$\sigma^2_R$	d. f.
$\frac{(n_{\dots})^2}{n_{\dots}}$	1	$\frac{\sum n_{ijk}^2}{n_{\dots}} = 2.49$	$\frac{\sum n_{ij\cdot\cdot}^2}{n_{\dots}} = 23.01$	$\frac{\sum n_{i\cdot\cdot\cdot}^2}{n_{\dots}} = 90.64$	1
$\frac{\sum R_{i\cdot\cdot\cdot}^2}{n_{i\cdot\cdot\cdot}}$	1	$\sum \left( \frac{\sum n_{ijk}^2}{n_{i\cdot\cdot\cdot}} \right) = 4.99$	$\sum \left( \frac{\sum n_{ij\cdot\cdot}^2}{n_{i\cdot\cdot\cdot}} \right) = 45.96$	$n_{\dots} = 181$	$R - 1 = 1$
$\frac{\sum RM_{ij\cdot\cdot}^2}{n_{ij\cdot\cdot}}$	1	$\sum \left( \frac{\sum n_{ijk}^2}{n_{ij\cdot\cdot}} \right) = 21.70$	$n_{\dots} = 181$	$n_{\dots} = 181$	$\sum M_i - R = 7$
$\frac{\sum RMm_{ijk}^2}{n_{ijk}}$	1	$n_{\dots} = 181$	$n_{\dots} = 181$	$n_{\dots} = 181$	$\sum \sum m_{ij} - \sum M_i = 76$

$$\frac{\sum n_{ijk}^2}{n_{\dots}} = \frac{451}{181} = 2.49$$

$$\frac{\sum n_{ij\cdot\cdot}^2}{n_{\dots}} = \frac{4165}{181} = 23.01$$

$$\sum \left( \frac{\sum n_{ijk}^2}{n_{i\cdot\cdot\cdot}} \right) = \frac{221}{87} + \frac{230}{94} = 4.99$$

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$$\Sigma \left( \frac{\Sigma n_{ij}^2}{n_{i\dots}} \right) = \frac{(27^2 + 19^2 + 19^2 + 22^2)}{87} + \frac{(11^2 + 14^2 + 9^2 + 34^2 + 26^2)}{94} = 45.96$$

$$\Sigma \left( \frac{\Sigma n_{ijk}^2}{n_{ij\dots}} \right) = \frac{99}{27} + \frac{37}{19} + \frac{43}{19} + \frac{42}{22} + \frac{27}{11} + \frac{28}{14} + \frac{21}{9} + \frac{88}{34} + \frac{66}{26} = 21.70$$

$$\frac{\Sigma n_{i\dots}^2}{n_{\dots}} = \frac{87^2 + 94^2}{181} = 90.64$$

### Computation of Coefficients

For the coefficient in the  $p^{\text{th}}$  column and  $r^{\text{th}}$  row in the table, subtract the value in the table of the  $p^{\text{th}}$  column and  $(r-1)^{\text{th}}$  row from the value of the cell in the  $p^{\text{th}}$  column and  $r^{\text{th}}$  row, and divide by the degrees of freedom for the  $r^{\text{th}}$  row.

(If n... occurs in both the  $r^{\text{th}}$  and  $(r-1)^{\text{th}}$  rows of the  $p^{\text{th}}$  column, then  $K = 0$ , and the component does not appear in the mean square expectation.)

From the table:

$$K_1'' = (4.99 - 2.49) / 1 = 2.50 \quad K_2' = (45.96 - 23.01) / 1 = 22.95$$

$$K_3 = (181 - 90.64) / 1 = 90.36 \quad K_1' = (21.7 - 4.99) / 7 = 2.387$$

$$K_2 = (181 - 45.96) / 7 = 19.29 \quad K_1 = (181 - 21.7) / 76 = 2.096$$

### Example - Analysis and Components of

Variance:  $\sqrt{\text{Epicotyl Length}}$

<u>Source of Variation</u>	<u>d. f.</u>	<u>M. S.</u>	<u>Expected Mean Square</u>
Regions (R)	1	9.461***	$0.011 + 2.50 \sigma^2_{RMm} + 22.95 \sigma^2_{RM} + 90.36 K^2_R$
Major Locations in Regions (M)	7	0.094***	$0.011 + 2.39 \sigma^2_{RMm} + 19.29 \sigma^2_{RM}$
Minor in Major in Regions (m)	76	0.017*	$0.011 + 2.10 \sigma^2_{RMm}$

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<u>Source of Variation</u>	<u>d. f.</u>	<u>M. S.</u>	<u>Expected Mean Square</u>
Families in Minor in Major in Regions (F) (Residual)	96	0.011	0.011
Total	180		

Solutions:  $\sigma^2 = 0.011$        $\sigma^2_{RMm} = 0.0029$        $\sigma^2_{RM} = 0.0039$

$K^2_R = 0.1035$

Satterthwaite's Approximate F-test  
Procedure (Ostte, 1963)

Because sample sizes are unequal, the coefficients of components of variance differ for the EMS at each sampling level. The F-ratio is still appropriate as a test of  $H_0: \sigma^2_{RMm} = 0$ , but not for  $H_0: \sigma^2_{RM} = 0$ , or  $H_0: K^2_R = 0$ .

To allow computation of an approximate F-ratio, each EMS is replaced by a synthetic linear combination:

$$L = a_1 MS_1 + a_2 MS_2 + \dots + a_k MS_k$$

where  $a_i$  are constants.

Degrees of freedom associated with L are estimated by:

$$\hat{v} = \frac{L^2}{(a_1 MS_1)^2 / v_1 + (a_2 MS_2)^2 / v_2 + \dots + (a_k MS_k)^2 / v_k}$$

where  $v_i$  represent the degrees of freedom associated with  $MS_i$  ( $i = 1 \dots k$ ).

Sample Calculation ( $\sqrt{\text{Epicotyl Length Data}}$ ):

Consider Regions/Major-Locations-in-Regions

$$\text{MS ratio: } \frac{\sigma^2 + 2.50\sigma_{\text{RMm}}^2 + 22.95\sigma_{\text{RM}}^2 + 90.36K_{\text{R}}^2}{\sigma^2 + 2.39\sigma_{\text{RMm}}^2 + 19.29\sigma_{\text{RM}}^2} = 100.7$$

Synthetic Mean Squares -  $L_{\text{R}}/L_{\text{RM}}$ :

$$\frac{1.163\sigma^2 + 2.843\sigma_{\text{RMm}}^2 + 22.95\sigma_{\text{RM}}^2 + 90.36K_{\text{R}}^2}{1.189\sigma^2 + 2.843\sigma_{\text{RMm}}^2 + 22.95\sigma_{\text{RM}}^2}$$

$$= \frac{0.026(\text{MS}_{\text{F}}) + 0.163(\text{MS}_{\text{RMm}}) + 1(\text{MS}_{\text{R}})}{1.189(\text{MS}_{\text{RM}})} = 9.464 = 84.7$$

Estimated d. f. :

$$\hat{v}_{\text{R}} = \frac{9.494^2}{[(.26)(.011)]^2 / 96 + [(.163)(.017)]^2 / 76 + 9.461^2 / 1} = 1$$

$$\hat{v}_{\text{RM}} = \frac{1.1118^2}{[(1.189)(0.094)]^2 / 7} = 7$$

Degree of freedom estimates are dependent upon magnitude of the mean squares, and therefore vary for each character. However, in no case did the estimate cause an integer change in the value given in Table IV.

Appendix Table III. Meteorological Data<sup>+</sup> Summary for Stations Representative of Major Locations.

Major Location	Station	Station Elevation	Days from Jan. 1st datum			Mean Temperature (°F)				Precipitation (in. x 100)				
			Last spring < 28°F	First fall < 28°F	Period > 28°F	Annual	Hottest Month	Coldest Month	Annual Range	Jan. -March	April-June	July-Sept.	Oct. -Dec.	Annual
G	Crescent City*	40	10	360	350	52.6	58.2	46.4	11.8	3175	970	319	2537	7000
H	Happy Camp*	1000	78	329	251	55.9	73.4	47.6	25.8	2298	533	124	1956	4911
I	Siskiyou Summit	4485	130	315	185	46.8	64.0	31.8	32.2	836	461	122	851	2270
D	Scotia*	139	7	355	348	54.9	61.5	47.7	13.8	2271	573	63	1794	4701
E	Forest Glen*	2340	125	288	163	51.2	68.4	35.5	32.9	2723	695	126	2001	5545
F	Platina*	2260	104	298	194	55.6	75.3	37.1	38.2	1427	369	71	1548	3415
B	Willitts*	1348	94	294	199	54.6	66.7	44.3	22.4	2493	440	52	2324	5309
(60-65)														
B	Fort Bragg*	80	9	351	343	52.9	57.4	47.8	9.4	1910	463	78	1347	3798
(66-78)														
C	Lake Pillsbury*	1740	130	281	150	55.0	71.2	41.2	30.0	2533	359	69	2488	5449
A	Santa Cruz*	125	27	349	322	57.1	63.2	49.1	14.1	1519	314	54	953	2840
(7-21)														
A	Ben Lomond*	720	37	337	299	56.0	64.6	45.9	18.7	3253	517	70	1687	5527
(22-33)														

\* In this and the subsequent table, denotes stations used in preliminary correlation analysis (Appendix Table V).

<sup>+</sup> Derived from U. S. Weather Bureau records (1964; 1960-70).

Appendix Table IV. Meteorological Data Summary for Subsidiary Location Stations, and Those Used in Preliminary Climatic Analysis.

Family No.	Station	Station Elevation	Days from Jan. 1st datum			Mean Temperature (°F)				Precipitation (in. x 100)				
			Last spring < 28°F	First fall < 28°F	Period > 28°F	Annual	Hottest Month	Coldest Month	Annual Range	Jan. - March	April - June	July - Sept.	Oct. - Dec.	Annual
6	Carmel Valley*	425	31	348	318	57.0	65.5	48.6	16.9	912	215	14	621	1762
34-36	Fort Ross*	116	0	365	365	54.5	59.3	49.5	9.8	2348	587	89	1591	4615
37-40, 44-48	Angwin*	1815	94	348	255	57.0	71.7	43.5	28.2	2098	441	51	1386	3976
41-43	St. Helena*	225	50	339	289	58.3	70.4	45.7	24.7	1788	337	42	1117	3284
106-108	Eureka*	43	5	365	360	51.6	56.1	47.0	9.1	1892	581	127	1392	3992
-	Fort Bragg Avn.	61	15	363	348	52.2	56.7	47.6	9.1	1905	528	65	1524	4022
-	Potter Valley*	1015	92	317	225	58.3	73.4	43.5	29.9	2180	525	68	1636	4409
-	Hilts*	2900	128	287	159	49.4	69.1	30.7	38.4	906	292	121	895	2214
1	Estacada	375	75	324	249	52.0	65.3	39.0	26.3	2052	1044	428	2122	5646
2	Port Alice	50	-	-	-	49.0	61.0	39.0	22.0	3741	1584	1077	5246	11648
3	Parksville	250	-	-	-	47.0	61.0	36.0	25.0	1033	476	384	1333	3226
4	Brookings	80	38	355	317	53.4	59.5	47.1	12.4	3442	1218	300	3180	8140
5	Shelton	22	-	-	-	51.1	64.3	38.4	25.9	2526	783	418	2702	6429
79	Medford WB	1312	86	305	219	52.6	72.0	35.4	36.6	732	355	99	792	1978
103	Corvallis	207	58	321	263	53.0	66.6	39.4	27.2	1589	544	220	1598	3951
138	Cloverdale	20	54	331	277	51.7	60.4	42.2	18.2	3244	1336	589	3269	8438
139	Canary	93	71	326	255	51.9	60.8	43.2	17.6	3317	1137	451	3079	7984
141	Cowichan Lake	-	-	-	-	49.0	63.0	35.0	28.0	2647	917	521	3083	7168
168	Forks	322	93	318	225	49.2	60.0	38.7	21.3	4412	1683	929	4595	11619

Appendix Table V. Correlation Matrix for Climate/Location Data, 18 Stations within the Study Area.

	Latitude	Elevation	Distance	Last frost	Frost-free period	Mean temperature	Hottest temperature	Coldest temperature	Temperature range	April-Sept. precipitation
Elevation (ft)	.34									
Distance (miles)	.39	.89								
Last spring frost (days from Jan. 1st)	.28	.91	.86							
Frost-free period	-.28	-.91	-.85	-.99						
Temperature (°F)										
Mean annual	-.64	-.24	-.07	-.09	.13					
Mean hottest month	.05	.71	.82	.80	-.77	.44				
Mean coldest month	-.47	-.91	-.82	.83	.84	.48	-.51			
Range in monthly means	.28	.92	.94	.94	-.92	.02	.89	-.84		
Precipitation (in.)										
April-Sept.	.55	-.13	-.30	-.14	.15	-.50	-.36	-.05	-.20	
Total annual	.33	-.01	-.23	.11	-.12	-.29	-.12	-.06	-.04	.82

Critical  $r_{(16, 1\%)} = \pm 0.59$