PROVENANCE VARIATION IN GRAND FIR
(*Abies grandis* Lindley)

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MPhil, 1992
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Acknowledgements

I am very grateful to my supervisor Dr. Richard Ennos, who offered constructive criticisms and guidance throughout the writing of this dissertation. Besides, the academic aspects of my work Richard has been extremely helpful during my stay in Edinburgh, for this I owe him a debt of gratitude. Dr. Douglas Malcolm offered very useful suggestions in the course of this work and this was highly appreciated.

I will also like to express my sincere thanks and profound gratitude to the Northern Research Station of the Forestry Commission. This work has been possible because of the access they granted me to their provenance trial plantations at Wark and Drummond Hill as well as the use of other facilities at the station. I will particularly like to thank Drs Samuel, Fletcher and Mckay, for the useful suggestions they offered in the course of this work. Mr Jim McIntyre of the Tree Improvement Branch of the station deserves an expression of my appreciation for the help he offered during my field work.

My thanks also go to my sponsors - the Institute of Renewable Natural Resources of the University of Science and Technology, Kumasi, Ghana who made my stay in Edinburgh and the persuance of this course possible. Mr J.G.K. Owusu my Departmental Head in the Institute deserves a special mention in this regard.

My friend and fellow postgraduate student Ayoub Khalil has been a real source of encouragement and help during this postgraduate programme, this is acknowledged and highly appreciated.To my other fellow postgraduate colleagues Cara, Thorunn and Laurel, I say thank you.

There are a number of other people who have in one way or the other been helpful to Christina and myself during our stay in Edinburgh and whose help we gratefully acknowledge, a special mention is made here of John and Margaret Maxwell and Roddy Darroch.

Finally, my thanks go to my wife Christina and little Yaw both of whom have had to cope with my long absence from home at times and all the other difficulties that we encountered in Edinburgh.

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List of Abbreviations

ALT - altitude in metres
ANOVA - analysis of variance
BC - British Columbia
BR - Branch angle
CI - Continentality index
cm - Centimetres
Dbh - Diameter at breast height 1.3 metres (overbark)
DF - Degrees of freedom
Drum - Drummond Hill
FT - Frost tolerance status
G * E - Genotype by Environment interaction
G/ha - Basal area per hectare
GP - growth potential
Grp - provenance group
Id - Idaho
IUFRO - International Union of Forest Research Organizations
KW - Kruskal-Wallis
LAT - Latitude (°)
LFF - Length of the frost free period in days
LONG - Longitude
LT - Temperature of the coldest month (°C)
MS - Mean annual snowfall in centimetres
MS - mean square
n.s. - Not significant at the 5% level
Ore - Oregon
PCA - Principal component analysis
PC - Principal component
P * S - Provenance by site interaction
Prov - Provenance
PROV ID - Provenance Identification Number
Scot - Scotland
SIG - Level of statistical significance
SP - Stability of performance
SS - Sum of squares
ST - Stem straightness

VC(%) - Variance component percentage
VR - Variance ratio
WA - Washington
WD - Wood density
Temp - Temperature

Abstract

Provenance variation in the growth potential, frost tolerance, pilodyn penetration (an indirect measure of wood density) and stem form of grand fir (*Abies grandis* Lindley) was studied in thirty two provenances from the range of the species and one provenance that has undergone a generation of adaptation in Scotland, at two contrasting sites in Britain - Wark and Drummond Hill.

There was wide variation in the growth potential among the provenances from the range of the species. Coastal provenances from Washington proved to be the sources with the best growth potential on the two sites. The provenance which has undergone a generation of adaptation in Scotland, 74(2002), had better growth potential than any of the provenances derived from direct transfer of seed and appeared to have developed into a land race. Evaluation of provenance * site interaction indicated that provenances from the coastal Washington range of the species had the best stability of performance over the two sites. Correlations between Dbh measurements in this study and earlier height assessments of the trials after three, six and ten growing seasons, at each of the two sites were highly significant and seemed to suggest that provenances with the best growth potential can be selected after six growing seasons.

The differences in growth potential were associated with differences in frost tolerance. Frost tolerance tests in ten provenances at a single date indicated that provenances from coastal Washington and British Columbia had relatively higher frost tolerance status than many of the other provenances, but the provenance with the highest frost tolerance status was from Idaho. The provenance 74(2002) had a relatively lower frost tolerance status. A regression of mean frost damage scores on the latitude of provenance origin showed that frost damage decreased with increasing latitude.

The pilodyn was used to measure wood density of provenances indirectly. Preliminary investigation to determine the necessity for taking multiple pilodyn measurements indicated that very little will be gained in accuracy from such measurements. The results of the pilodyn assessment showed that there was highly significant variation in wood density among provenances, both within and between sites. Faster-growing provenances generally, tended to have lower wood density than slower-growing provenances. However, some faster-growing provenances had relatively higher wood density than slower-growing provenances. Provenance * site interaction for pilodyn measurements between the sites was not significant.

Stem straightness assessments indicated that the ranking of the trait was very high in many provenances, although, provenances from southern coastal Oregon had relatively lower rankings for straightness on both sites. Provenance variation in branch angle was highly significant at each of the two sites. Provenances from higher altitudes and lower latitudes had comparatively wider branch angles than those from lower altitudes and higher latitudes. Thus the faster growing provenances from the coastal areas of the species range had relatively narrow branch angles. Provenance * site interaction for branch angle was highly significant.

Stem straightness and branch angle may not be traits of critical importance in provenance selection. Choice of provenances for higher growth potential and higher wood density, which will simultaneously select for narrower branch angles, can be based on provenances from the coastal Washington range of grand fir. Consideration may also be given to the provenance that has undergone a generation of adaptation in Scotland, due to the high growth potential and high wood density of this provenance.

CONTENTS

CHAPTER 1

INTRODUCTION

1.1 Utilisation of genetic variation in tree domestication

Tree species, like other biological organisms exhibit a wide degree of phenotypic variation. The variation results from their genetic constitution, the environment in which they grow, as well as the interaction between these two factors. Mutations, gene flow and natural selection are some factors that shape genetic variation. Environmental differences are due to climate, topography and soils to mention just a few of the factors and other biotic factors. The interaction between tree genotypes and the environment results in the development of phenotypes that are adapted to specific environments.

Domestication of trees in intensive forest management practice will be successful if this variation is recognised, understood and properly utilised. Trees growing in their natural habitat are adapted to that environment. Selection of such trees for use in forest production in their indigenous range may therefore not be as critical as when the same trees are introduced into another environment outside their natural range. Successful introduction of tree species into environments in which they do not normally grow requires that such trees are adapted to the new environment. Careless exploitation of variation in trees domesticated outside their natural habitat may be biologically and economically disastrous. Utilisation of the wrong provenances in a new environment may result in poorly adapted trees and may lead to poor yields or the production of poor products.

1.2 The need for and the role of provenance research in forest management

The sustained production and supply of wood for industrial and domestic use is a primary objective in forest management. The source of the wood is from the natural forest or man-made plantations. Continuous supply of wood as raw material for forest industries requires that the production base be replenished, through regeneration either artificially or naturally. Artificial regeneration which is a reliable method for sustaining forest production requires enormous investments. For example, between 1977 and 1980, it is estimated that the World Bank invested US$500 million in forestry, the greatest proportion of which went into forest plantation establishment (Evans, 1982). If such huge investments are to be justified then among other factors, there should be some guarantee that the planting material is of the best quality.

Provenance research is an aspect of forest management with the objective of locating suitable seed sources for specific environments. Wright (1976) defined provenance as the ultimate natural origin of a seedlot. Another definition by Burley (1969) was the geographic source of seed, plant material or plants from such a source. Sprackling and Mead (1975) outlined the objectives of provenance tests as the evaluation of plant material for adaption and genetic variability, to aid selection, propagation and breeding. In Callaham's (1964) words, provenance research defines the genetic and environmental components of phenotypic variability, with the practical objective of identifying provenances that will yield seed to produce well adapted and productive forest. Adaptation and productivity, among other factors may include the ability of provenances to withstand extremes in environmental conditions, rapid growth, good wood quality and good seed production (Burley, 1969; Rehfeldt, 1985). Provenance trials have short and long term objectives: in the short-term, the most productive and adapted sources can be used in reforestation programmes, while further screening and breeding will yield superior planting material in the long-term. The need for provenance research assumes greater importance particularly for species grown outside their natural habitat, if such introductions are to be successful (Larsen, 1956). The use of the right seed sources, together with proper forest management practices will improve the overall yield from the forest (Zobel and Talbert, 1984). Provenance research as an aspect of forest management therefore provides the means for greatly increasing the benefits flowing from intensive forest management to make the most of silvicultural investments and meet raw material demands and specifications (Daniels, 1984).

1.3 Factors affecting the amount of geographic variability in a species

Wright (1976) discussed four factors influencing the amount of geographic variability found within a species. The range of distribution of a species is identified as one of the important factors affecting the amount of variability within a species. Species like *Pinus contorta, Pinus ponderosa, Pinus sylvestris* and *Pseudotsuga menziensii*, that have wide distributional ranges also tend to have greater amounts of variability (Zobel et al., 1987; Critchfield, 1978). However, there are a few exceptions in which for some diverse reasons, species with large ranges exhibit very little variability. *Pinus resinosa,* is one example of such species. Although the species has a very wide range it shows little variability and this is believed to be due to a reduction in the species population size at some time in the past (Fowler and Morris, 1977). Other factors that affect the amount of geographic variability include the amount of environmental diversity encountered in a species range and discontinuities within the range. Species that do not encounter great climatic extremes in their in their habitat tend to be less variable than others growing in a habitat with wide environmental diversity. Thirdly, a species with a continuous range may have less genetic variability due to constant interchange of genes within the population, in contrast to geographically isolated populations.

1.4 Provenance testing: strategy and methods

Provenance testing dates back to more than 200 years but has been intensified within the last 40-50 years to identify suitable planting material for intensive reforestation and has become adjunct to tree improvement as a prerequisite to tree breeding effort (Niendstaedt, 1979). The number of provenances of a species that are tested is dependent on the available knowledge of the patterns of variation in the traits of interest. If little or nothing is known about a species then provenance collections over the entire range of the species is recommended, on the other hand if provenances of the required adaptation is suspected or known, then efforts to identify the most suitable provenances may be concentrated on specific regions within the range of a species (Callaham, 1964).

The distribution of a species will influence the methodology used to sample provenances (Fletcher and Barner, 1978). Generally, however, sampling is carried out parallel to major environmental gradients within the range of the species, for example, along specified degrees of latitude, on both sides of a mountain range or at specified intervals of elevation (Callaham, 1964). Within selected stands it is recommended that seed samples are taken from dominant and co-dominant trees (Callaham, 1964). Burley and Wood (1976) recommended that trees sampled within a stand should be at intervals of about 100m to avoid making collections from closely related individuals and also emphasised that seed collections are not made from isolated seed trees because of the high possibility of self-pollination. The number of trees that are sampled within stands will depend on variability in the characteristics of importance. In relatively homogenous stands Callaham (1964) recommended that 5-10 trees are sampled, while in heterogenous stands 25-50 trees are recommended. Generally, the selection of provenance samples has to be based on a larger number of trees rather than a few trees and the timing of seed collection should be carefully planned to coincide with years of abundant seed production (Burley and Wood, 1976).

Barner (1978) identified two types of provenance research based on the objectives of the research: provenance research on genecology and seed source studies. Provenance studies based on genecology deals with ecological variability and the influence of the environment as well as the reaction of different populations when transferred outside their natural range (Callaham, 1964). Seed source studies have a more limited scope. They seek to locate seed sources which in specified environments are superior in adaptability, production and wood quality.

Seed sources have an optimal range of environments to which they have become adapted by natural selection over a long period of time. Maladaptation may result when they are moved outside this environment. In provenance studies different seed sources of of a species are grown in a common environment, in which they are to be used and their performance is compared. Under a common environment, genetic variability can be observed and where patterns correspond to environmental gradients, adaptive variation is assumed (Rehfeldt, 1985).

Three phases with different objectives have been enumerated for provenance trials. Lines (1967) and Niendstaedt (1979) identified the phases outlined below, together with their objectives:

1. Broad Rangewide testing, with the objective of delineating regions in a species natural habitat with provenances having acceptable adaptation and productivity within the environment in which they are to be used.
2. Regional provenance test, with the aim of locating sub-regions within those identified in (1) above, containing provenances with superior productivity.
3. Testing of progenies from a limited number of provenances to determine the relative magnitude of variation among provenances and families from provenances.

1.5 Information derived from provenance trials

Provenance trials yield information on variation patterns over parts of a species range being studied. This information is useful for delineating seed zones. By relating variation patterns to environmental conditions of seed origin genecological information is obtained. Superior provenances from which breeding material can be obtained are identified by comparison among provenances. Genotype and environment interaction can be assessed where provenance trials cover more than one site. This assessment gives information on provenance performance over a range of sites and is useful in making seed deployment on specific sites if the optimum yield is to be realized from provenances. In addition provenance trials of a species yield information on juvenile-mature correlations which aids prediction on early selection for traits of interest (Niendstaedt, 1979).

1.6 Description of the biology of grand fir (*Abies grandis* Lindley)

1.6.1 The genus *Abies*

The genus *Abies* Miller belongs to the family Pinaceae. The species within the genus usually thrive well in a cool and humid climate (Anon, 1949). There are about 35-40 species included in this genus, these species are widely scattered throughout the forested regions of north and central America, Europe, Asia and north Africa, ten of the species in the genus are included in the coniferous flora of the United States of America (Harlow and Harrar, 1937). Grand fir (*Abies grandis* Lindley) is one of the *Abies* species found in north America.

1.6.2 General description

The trees attain heights of between 36-90 m in various parts of its natural range (Kirkwood, 1930; Sargent, 1905; Anon, 1949). Young trees have smooth grey bark which is blotched with resin blisters. Mature trees on the other hand have reddish-brown bark, deeply furrowed with thickness varying between 5-9 cm (see Fig. 1.1a). Crown shape differs with age. Young trees have spire-shaped crowns, while older ones have dome-shaped crowns. Tree appearance may differ depending on whether it

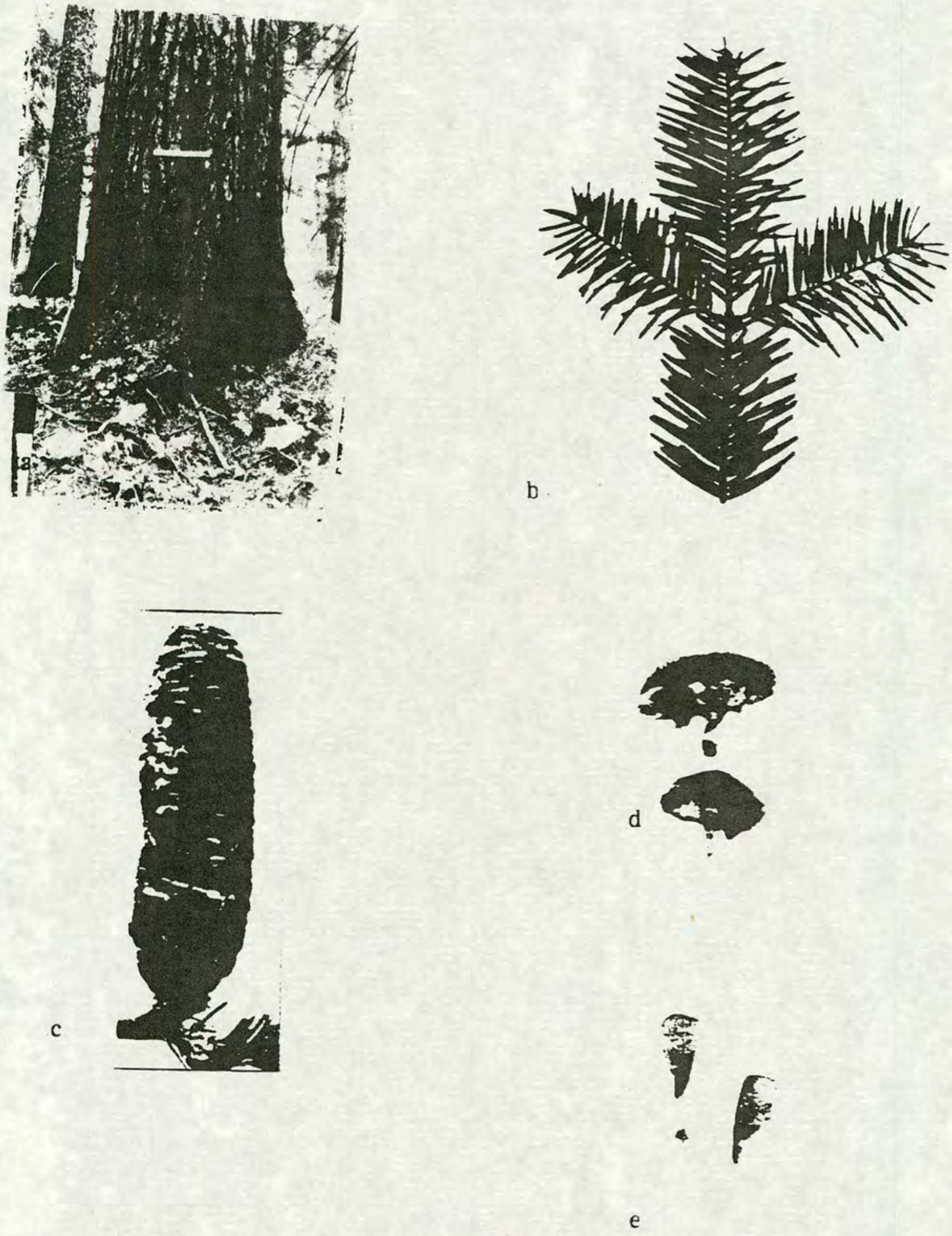


Figure 1.1 Diagram showing various morphological features of grand fir. **a.** bark. **b.** needles. **c.** cone. **d.** bracts. **e.** seed (Harlow and Harrar, 1937).

is growing solitary or in association with other trees. Trees growing in the open have few low very large branches, which turn upwards some 3-4m from the main stem. In the forest, old trees may have long slender branches hanging from mid-bole (Mitchell, 1972; Elias, 1980). Grand fir reaches maturity at about 200 years (Harlow and Harrar, 1937).

1.6.3 Botanical features

Sargent (1905) and Harlow and Harrar (1937) provide a botanical description of grand fir. The description below is taken mainly from these two authors.

1.6.3.1 Grand fir needles

The needles of grand fir are small, flexible, narrow and do not have leaf stalks (see Fig. 1.1**b**). Needle length varies with age. It ranges from 1.3-2.0 cm in young trees to 3.8-5.8 cm in older trees. Needle width is about 3 mm. The tips of the needles are either blunt or emarginate. Needles spread out in two ranks nearly at right angles to the branch. The upper surface of needles is dark green and lustrous, in contrast the lower surface is silvery white. Needles are often denser on the upper side of cone bearing branches.

1.6.3.2 Flowers

Staminate flowers are pale yellow, sometimes tinged with purple. Pistillate flowers are yellowish-green, with semi-orbicular scales and short oblong bracts, emarginate and denticulate at the obcordate apex and furnished with a strongly reflexed tip.

1.6.3.3 Cones and seed

The cones are long and cylindrical 6.4-10.8 cm in length (see Fig. 1.1**c**). The colour is yellowish-green to greenish-purple. The bracts are shorter than the scales (see Fig.1.1**d**), the shoulders are erose, rounded, truncate or cordate, terminating in a short spike-like tip. The seeds are about 9.5 mm long, with wings of about 19 mm long which are straw coloured (see Fig. 1.1**e**). There are about 77,000 seeds to the kilogram.

1.7 The silvics of grand fir

1.7.1 Associated species

Grand fir grows mostly in association with other species and occur in pure stands in a relatively limited area within its range. Franklin and Dryness (1969) included the species in the following vegetation zones of Washington and Oregon: the *Picea sitchensis* zone - in which the species occurs as a minor species; the *Tsuga heterophylla* zone in which grand fir is one of the major species, growing in association with *Pseudotsuga menziensii, Tsuga heterophylla, Thuja plicata, Picea sitchensis* and *Pinus monticola.* In the *Pinus ponderosa* zone, the species is reported to be confined mainly to moist sites. It occurs as a major species in a zone classified as the *Abies grandis* zone. In the Rocky Mountains Dwane and Green (1985) listed grand fir as occuring in the following forest types: the Larch forest in Montana, west of the continental divide and north of the Salmon River in Idaho; it is also found in the western Hemlock and white pine forest types. The most extensive pure stands are found in the Nezperce and Clearwater regions of Idaho (Foiles, 1959).

1.7.2 Reproduction

Seed production in grand fir begins at about 20 years and is reported to increase with age. The cones mature in September and seed dispersal which is mostly by wind and rodents is completed by the end of October of the same year. The average distance of seed dispersal has been reported as 46-60 m, with a maximum dispersal distance of about 120 m (Foiles, 1959; Fowells, 1965).

1.7.3 Germination and early growth

Natural regeneration of the species is variable. Foiles (1959) noted that germination under natural conditions seldom exceeds 50 percent. Embryo dormancy, injury to seed during dewinging and insect infestation are among the reasons assigned for low germination. Under nursery conditions, Lines (1974) and O'Driscoll (1978) reported variability in the germination of seeds from different geographic sources. Lower germination percentage for some seed sources was attributed to long storage of seeds and a high frequency of chlorophyll deficient cotyledons.

Seedling survival is critical under natural conditions, during the first two growing seasons. Fowells (1965), estimated that 40 percent of seedlings are lost in these seasons. Seedling mortality is caused by a number of factors including, the damping-off fungi, insolation and drought. Seedlings growing in full sunlight tend to survive better because of good root development. On the other hand seedlings growing under shade have slower root development, which makes them susceptible to drought mortality. Moderate overwood shade has been identified as a factor favouring initial survival. Under this condition seedlings of grand fir are reported to compete better with those of other species (Fowells, 1965; Seidel and Cooley, 1974).

1.7.4 Productivity of grand fir

Site quality appears to be an important factor affecting the productivity of grand fir. This is indicated in Table 1.1 which shows the relationship between height growth as an index of productivity, site quality and age.

Table 1.1 Relationship between site quality and height growth at different ages in grand fir (Fowells, 1965).

	Site index						
Age (years)	30	40	50	60	70	80	90
	(Height in metres)						
40	10	13	17	20	23	29	36
80	20	28	32	37	40	43	47
120	32	38	43	47	51	55	59
160	38	44	48	53	55	63	68

Annual height growth of 15-20 cm and 30-36 cm respectively have been reported for sites classified as of average and optimum potential. Within the coastal areas of distribution of the species annual height growth of 80-90 cm has also been reported (Fowells, 1965). Steinhoff (1978a) gave estimates of standing volume at 100 years as1250 m^3/ha.

1.7.5 Diseases and pest of grand fir in the natural range

The most important fungus of grand fir in its inland range is the Indian paint fungus (*Echinodontium tinctorum*). *Armillaria mellea* and *Poria weirii* are two root rot fungi that have been identified as affecting the species. Campbell and Hamm (1989) in a study on susceptibility to *Phytophthora* root rot fungi, rated grand fir as susceptible to the species. *Fomes annosus* has been identified as the most important cause of root rot of the species in the western Cascades Mountains (Steinhoff, 1978a).

Fowells (1965) identified some insects that affect grand fir. The spruce budworm (*Christoneura fumiferana*) and the tussock moth (*Hemerocampa pseudostugata*), both cause widespread defoliation and mortality in the species. The western balsam beetle (*Dryocoetus confusus*) and the grand fir engraver beetle (*Scolytus ventralis*) attack the species. The fir cone moth (*Barbara colfaxiana* var. *siskiyouna*) and the seed maggot (*Earomyia* spp.) are named as seed and cone destroyers of grand fir.

1.8 The geographic range of the species

Grand fir has its natural range of distribution in the northwestern United States and British Columbia in North America. Latitudinally, the range spans 39 °N-51 °N. The longitudinal limits are within 114 °W to 125 °W. Figure 1.2 which shows the areas of distribution of the species, indicates a split distribution. The coastal range of the species of the species, stretches from the eastern slopes of Vancouver Island in British Columbia and its adjacent mainland through coastal Washington and Oregon. This range spreads further into the Cascades in Washington and Oregon and further south along the coast to northern California. The inland range is found in southeastern British Columbia, through the northeastern tip of Washington, the outer mountain ranges of the continental divide in Montana, east central Oregon and west central Idaho (Steinhoff, 1978a).

1.9 A broad overview of the grand fir environment

A diverse range of environmental conditions are encountered within the areas of distribution of grand fir. Franklin and Dryness (1969) and Schaeffer (1978) provided an insight into the climatic conditions over the range. This section is based primarily on the reports of the above authors.

Precipitation and temperature which are two important factors for plant growth and distribution are affected by many factors within the grand fir range. The most important of these factors are proximity to the Pacific ocean and mountain barriers. A maritime climate characterises the coastal range of grand fir. Temperatures are mild, with narrow diurnal fluctuations of 6 °C to 10 °C. The winters are wet and mild. The summers are relatively dry and the frost-free period long. The total annual precipitation is within the range of 1700-3000 mm, 75% of which is available between March

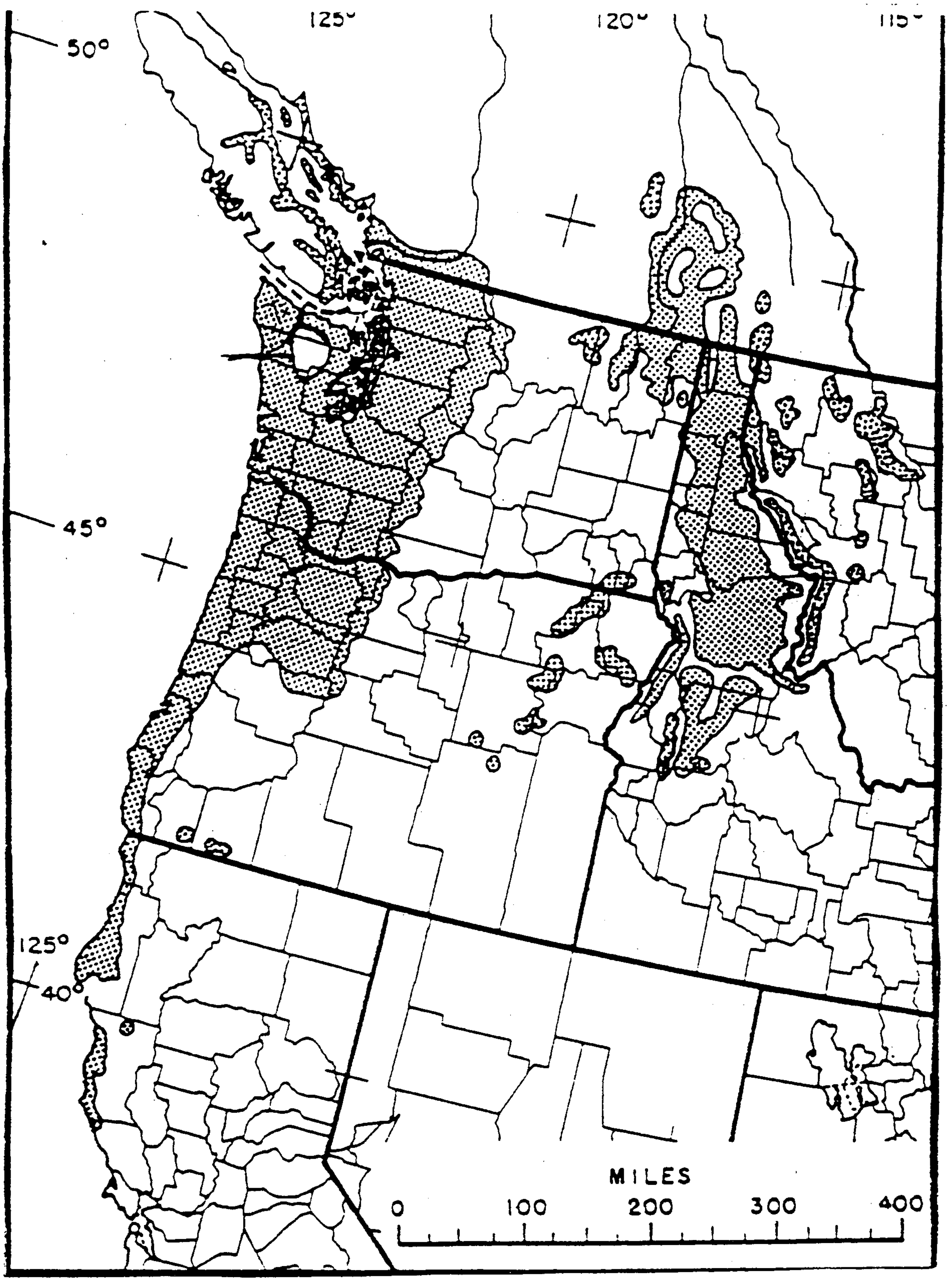


Figure 1.2 Map showing the range of distribution of grand fir (*A. grandis*).

and October. Within the Cascade Mountains, elevation is the major factor affecting climate. Precipitation decreases rapidly on both the eastern and western slopes of the Cascade Mountains.

The climate in the inland range is influenced by continental and maritime air-masses. Diurnal temperatures fluctuate between 10 °C to 16 °C. Annual precipitation and its distribution is lower compared to the coastal range. The annual precipitation is between 250-500 mm and a high proportion falls as snow. Table 1.2 gives an overview of some climatic indicators within the grand fir range.

Table 1.2 An overview of some climatic indicators in the grand fir (*A. grandis*) range (Schaeffer, 1978)

Part of Range/ Climatic Index	CI	MD	LT	LFF	MS
Coastal Vancouver Island	20	100	-10	240	<100
Coastal Washington	20	100	-10	240	<100
Coastal northern Oregon	20	300	-10	240	<100
Coastal southern Oregon	30	300	-10	240	<100
Eastern Cascades, Washington	40	300	-40	120	>500
Eastern Cascades, Oregon	40	500	-40	<120	>500
Western Cascades, Oregon	30	500	-30	<120	>500
Northeastern Washington	40	300	-50	<120	>100
West central Idaho	50	700	-50	<120	<100

Legend to Abbreviations.
CI = continentality index.
MD = mean annual water deficit in millimetres.
LT = temperature of the coldest month in (°C).
LFF = the length of the frost free period in days.
MS = the mean annual snowfall in centimetres.

1.10 Site factors in the grand fir environment

1.10.1 Temperature

The mean annual temperature within the grand fir range is about 10 °C, with a range of 6 °C-12 °C. Within the growing season - the consecutive days in which temperature is above 5 °C, the temperature is between 14 °C-19 °C. The mean length of the growing season varies in different parts of the range. In western Washington, it may be as long as 185 days; in northern Idaho it is between 60-140 days and in parts of eastern Oregon is less than 100 days. (Foiles, 1959; Fowells, 1965).

1.10.2 Precipitation

Precipitation decreases from the coastal to the inland range of the species. The mean annual precipitation is 2800 mm and 500 mm respectively in the two main areas of grand fir distribution. Within the coastal range with a general overall higher precipitation, there are variations in the amount of precipitation in different areas. For example, in British Columbia, it varies between 680-2800 mm in different areas (Schimdt, 1957). In western Washington, precipitation varies from 500 mm to over 2500 mm. In the inland range of the species, annual precipitation varies from 500-1270 mm in northern Idaho and 350-1015 mm in eastern Oregon. Snowfall increases from the coastal parts of the range to the inland areas, varying from a few centimetres along the coast to over 2000 cm within the inland parts of the range in Montana (Pfister et al., 1977).

1.10.3 Elevation

Grand fir is found at elevations varying from sea-level to over 1800 m. Along the coast in British Columbia, western Washington and Oregon, the elevation of the species varies from 0-300 m.The species is therefore found mostly at lower elevations along the coast. Within the Cascades, it occurs at an elevational range of 900-1500 m. Beyond this limit it is replaced by Pacific silver fir (*Abies amabilis*). Further inland grand fir occurs at an upper elevational limit of 1800 m and is replaced by subalpine fir (*Abies lasiocarpa*) above this limit (Steinhoff, 1978a).

1.10.4 Soils

The species grows on a diverse range of soils but is said to prefer moist soils with good drainage. Foiles (1959) listed the following soils on which grand fir occurs in the different parts of its range: deep rich alluvial soils along stream banks and valley bottoms, shallow exposed soils of mountain ridges, moist soils provided with seepage and pure pumice soils.

1.11 The need for provenance studies in grand fir (*A. grandis*) in Britain and objectives of study

Grand fir was introduced into Britain during the last century and has attracted attention because of its fast growth potential (Macdonald et al., 1957). The potential of the species for fast growth on good sites relative to other major species in Britain was reviewed by Aldhous and Low (1974). Like Sitka spruce and Douglas fir, other north American species introduced into Europe, the successful use of the species in plantation establishment will depend on the use of suitable provenances (Herman, 1987). Grand fir occurs over a wide range of ecological conditions, as a result large genetic differences are expected between populations adapted to these diverse conditions. With such a wide degree of ecological diversity, suitable populations can be identified through provenance trials on sites where the species is to be grown. This was the reason for this study which examined rangewide provenance variation in grand fir (*A. grandis*).

A broad objective of this work was to study rangewide provenance variation in grand fir, a possible underlying cause of the observed variation in one of the characteristics studied and relate these to the choice of provenances that may be suitable for reforestation and further screening. Fast growth potential resulting in high volumes of wood production is a highly desirable requirement for any species that is to be used for plantation establishment. Nevertheless, other characteristics relating to the quality of the wood produced, such as wood density and stem form, may equally be important. If provenance by site (P * S) interaction occurs, then the use of the correct provenance on a particular site will yield optimum benefits for wood production, hence knowledge of provenance by site interaction is essential. The study thus examined variation patterns in the growth potential, frost tolerance, stem form and wood density of grand fir on two sites with these objectives:

1. To identify seed zones containing provenances with high growth potential that can form the basis of a seed zone recommendation.
2. Examine provenance differences in growth potential between the two sites and determine the importance of P * S interaction.
3. Study provenance variation in frost hardiness as a possible underlying cause in the observed variation in growth potential of the provenance.
4. Examine provenance variation in pilodyn measurements as an indirect measure of wood density and stem form to determine how these traits relate to the most productive origins.

CHAPTER 2

2.1 Experimental Material

The experimental material consists of thirty three provenances. With the exception of two provenances, the remaining form part of IUFRO *A. grandis* provenance collections made in 1974 and 1976. Fletcher and Barner (1978) have discussed the background to the sampling method used in the collection of the provenances. Samples were collected from tree stands that were between 50 to 80 kilometres apart within the range of grand fir. Within a stand from which samples were collected, cones were taken from trees that were more than 50 metres apart to minimise the risk of half-sib mating. The trees from which samples were taken represented a range of ages, heights and diameter classes. The number of trees from which samples varied from stand to stand. Cone collection normally involved climbing of trees and picking of mature cones. However, in some cases collections were made from felled trees or shooting down of cone bearing branches using a gun and also from squirrel caches.

The details of the provenances with their locations of latitude, longitude and altitude of origin as well as the details of the trees from which samples were taken and the methods of collection were furnished by Fletcher (1986). Some of these details are presented in Table 2.1. The heights were within the range of 12-70 metres and diameter clases ranged between 20-120 centimetres. The approximate ages of trees from which samples were taken ranged between 20 and 150 years. The provenances representing the IUFRO collection are identified by numbers with the prefix 120-. Two provenances 74(7973)5 and 74(2002) have different identification numbers. The former is a commercial collection associated with provenances from coastal Washington. The latter, which originated from coastal British Columbia, has undergone a generation of adaptation in Craigvinean forest in Scotland. Provenances will be identified by their identification numbers (PROV ID).

The provenances are classified into one of nine groups. Provenances within a group were sampled from one of the eleven major vegetational zones within the range of grand fir (Fletcher, 1973). The classification of these zones are based on the climax vegetation (Franklin, 1965). Each of the vegetational zones has more or less similar geology, topogaphy, climate and major soil parent material. Grand fir has been recorded as a major species in four of these zones and a minor species in three. The

Table 2.1 Details of grand fir (*A. grandis*) provenances.

PROV ID	Group	Location	Lat(°N)	Long(°W)	Alt(m)	Number of trees sampled
12001	1	Darrington, Wa	48 16'	121 21'	400	25-30
12002	1	Tulalip,Wa	48 05	122 16'	30	20
12003	1	Elwha, Wa	48 04	123 38'	140	18
12004	1	Sequim, Wa	48 04'	122 54'	30	20
12005	1	Louella, Wa	47 59	123 02'	825	25+
12049	1	Shelton, Wa	47 11'	123 07'	40	25
12051	1	Pe Ell, Wa	46 38'	123 15'	125	20+
74(7973)5	1	Louella, Wa	47 55'	123 05'	600	_
12006	2	Leavenworth, Wa	47 41'	120 34'	760	20
12007	2	Leavenworth,Wa	47 39'	120 34	1200	20
12008	2	Cle Elum, Wa	47 20'	120 50'	825	20
12009	2	Cliffdell, Wa	46 55'	121 15'	945	21
12011	2	Clear Lake, Wa	46 37'	121 20'	945	19
12012	2	Trout Lake, Wa	46 07'	121 39'	945	16
12013	2	Parkdale, Wa	45 27'	121 39'	1040	20
12024	3	Usk, Wa	48 17'	117 16'	650	16
12016	4	Santiam Summit, Ore	44 26'	121 52'	1400	19
12018	4	Bend, Ore	43 59'	121 39'	1500	20
12020	4	Crescent, Ore	43 28'	121 57'	1375	30
12034	5	Dump Creek, Id	45 50'	116 01'	1190	7
12015	6	Sisi Butt, Ore	44 52'	121 48'	975	30
12019	6	Box Canyon, Ore	43 53'	122 01'	1310	30
12021	6	Prospect, Ore	42 56'	122 23'	1160	30
12040	7	Sayward, BC	50 20'	125 56'	25	22
12042	7	Courtney, BC	49 31'	124 52'	45	20
12043	7	Port Alberni, BC	49 18'	124 58'	25	22
12045	7	Nanaimo, BC	49 03	123 46'	30	20
12047	7	Sooke, BC	48 22'	123 47'	20	20
74(2002)	7	Craigvinean, Scot	50 00'	125 25'	0-150	-
12052	8	Pittsburgh, Ore	45 56'	121 10'	275	20
12053	8	Dallas, Ore	43 07'	123 23'	260	12
12056	9	Norway, Ore	43 07'	124 09'	60	20
12057	9	Gold Beach, Ore	42 28'	124 24'	45	21

Legend to Abbreviations
PROV ID - Provenance identification number; BC - British Columbia; Lat - Latitude of provenance origin; Scot - Scotland; Long - Longitude of provenance origin; Alt - Altitude of provenance origin; Wa - Washington; Ore - Oregon; Id - Idaho

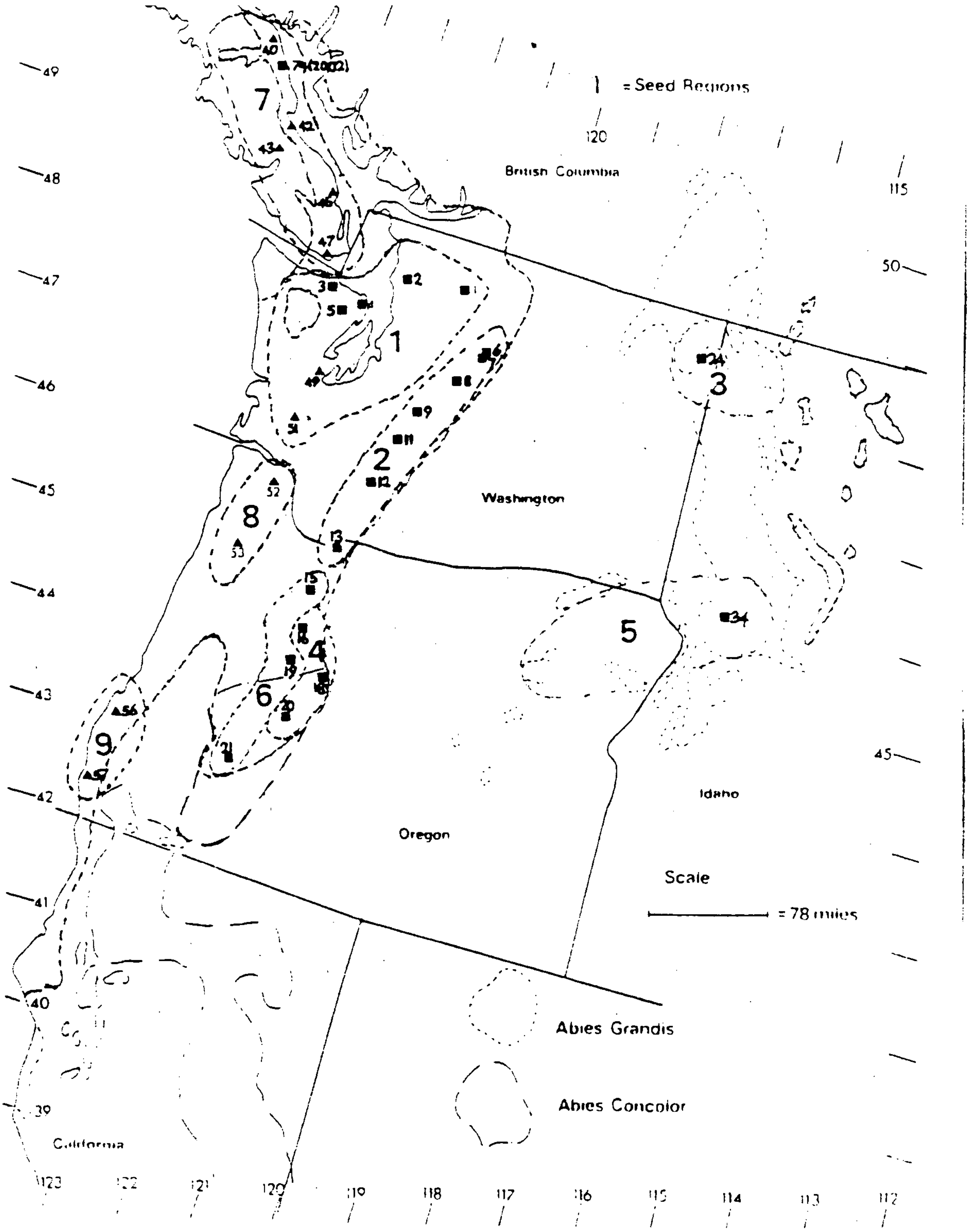


Figure 2.1. Map showing the location of grand fir (*A. grandis*) provenance groups represented in the experiment within the natural range of the species and the boundaries of the groups.

location of the provenances in the range of the species with the exception of 74(7973)5 and the groups with which they are associated are presented in Figure 2.1. Provenances in groups 1, 7, 8 and 9 are from the coastal areas in Washington, British Columbia and Oregon. Those in groups 2, 4 and 6 are located along the Cascades Mountains in Washington and Oregon. Groups 3 and 5, each represented by a single provenance, are found in northeastern Washington and west central Idaho.

The seeds of the provenances from which seedlings were obtained to establish the provenance experiments were sown in two batches in the nursery. The batches were sown a year apart. Provenances with identification numbers 12001 to 12034, together with 74(7973)5 and 74(2002) that formed part of the 1974 seed collection were sown in the nursery in 1976. Those with identification numbers 12040 to 12057 that were part of the provenance collection in 1976 were sown in the nursery in 1977. Thus at the time of planting of the seedlings on the experimental sites in 1979, seedlings of the two batches of provenances were 3 and 2 years old respectively.

2.2 Experimental Sites

The provenance trials of grand fir are established on twelve sites in Britain. These are shown in Figure 2.2 (Lines, 1986). The present study covers two of these sites, namely Wark and Drummond Hill both of which are experimental sites of the British Forestry Commission. These two sites were chosen because of the differences in exposure, soils and the growth performance of grand fir from earlier assessments. Wark is situated 6 kilometres southwest of Bellingham in Northumberland and Drummond Hill is located on the southside of Loch Tay near Aberfeldy in Tayside. The site conditions at each of the two which will simply be referred to as Wark and Drum in this study are summarised in Table 2.2.

Figure 2.2. Map showing Wark, Drummond Hill and ten other sites on which the grand fir (*A. grandis)* provenance experiments have been planted.

Table 2.2 Details of two experimental sites with grand fir provenance trials

	Site	
Detail	Wark	Drum
Grid reference	NY 799786	NN 711408
Latitude	55° 14'N	56° 54'N
Altitude (m)	201	200
Longitude	02° 34'W	04° 10'W
Rainfall (mm/yr)	1016	1270
Soil Type	Peaty gley	Surface water gley
General Topography	Even sloping ground with slight undulations	Concave sloping ground with slightly sloping terraces
Length of growing season (days)	176	176
Exposure	Moderate	Sheltered.
Vegetation	Mainly *Molinia carulea* with patches of *Juncus* species and other minor species	Various species of grasses, *Carex sp., Juncus sp., Pteridium sp., Hieraciu sp., Campanula rotundiflora, Ranunculus sp. and Stellaria sp*

2.3 Establishment of experiment and layout

The experiments were planted in 1979. Each of the two sites was given a single furrow ploughing at a spacing of 2.1 metres and Urea phosphate fertilizer applied at 375 kg/ha prior to the planting of the experiments on the sites. The experiments, using the planting material described in section 2.1, were laid out in three randomised complete blocks at each of the sites. The experimental layout at each of the sites are presented in Figures 2.3 and 2.4. Within a block each provenance was represented by a 25(5 *5) plants at a spacing of 2 metres in a square plot. The external boundaries of the experimental plots at each of the sites were planted with three rows of one provenance. Following planting, tending operations including hand weeding as well as weed suppression using herbicides and fertilizer application were made periodically until the plants became established in 1982.

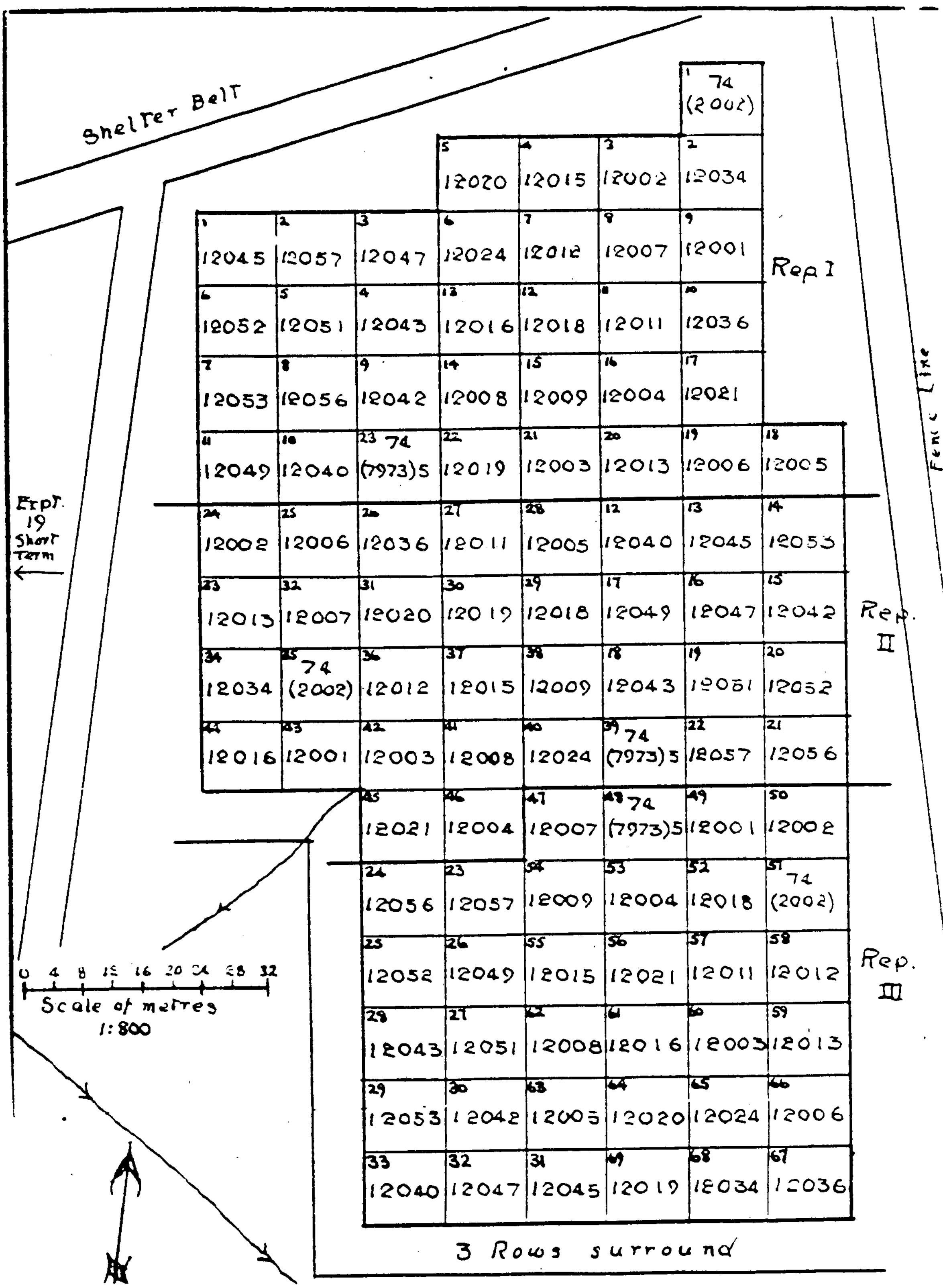


Figure 2.3. Experimental layout of grand fir (*A. grandis*) provenance trial at Wark.

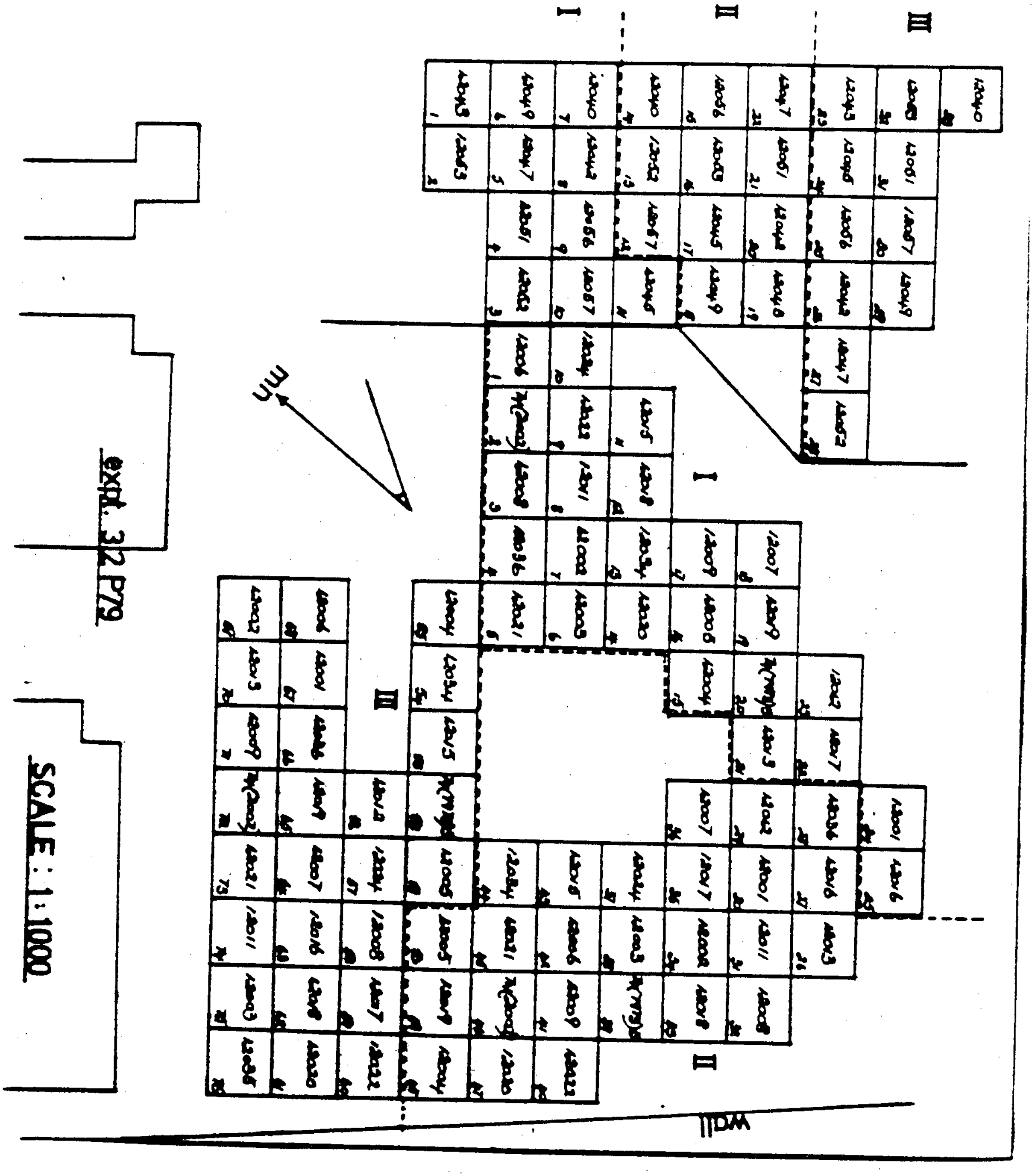


Figure 2.4. Experimental layout of grand fir (*A. grandis*) provenance trial at Drum.

CHAPTER 3

Provenance variation in the growth potential of grand fir (*A. grandis*)

3.1 Importance of growth potential of provenances and types of measurements

An important objective in provenance trials is to identify provenances with superior growth. The growth potential of provenances is assessed at various stages of the trial by height and diameter measurements. Height measurements are usually made in the early years of the assessments, but as provenances exceed heights of 2-3m, diameter measurements become a more reliable method of assessment (Burley and Wood, 1976). The economic value of a provenance is evaluated by the quality and quantity of timber produced per unit area (Lines, 1967). With height and diameter measurements, volume of wood produced per unit area can be derived. Basal area of wood produced per unit area can also be derived from diameter measurements at breast height. Both measurements can give a good indication of the growth potential of the provenances being assessed.

Provenance variation in the growth potential of grand fir (*A. grandis*) was studied in the thirty three provenances and two sites described in the previous chapter. The objective was to identify provenances that show superior growth and that can be recommended as seed zones from which seed could be procured for reforestation. From these regions further screening of provenances can be undertaken to identify suitable breeding material. The objective was pursued through the study of the growth potential and the interaction of the provenances described in chapter two with the two sites.

3.2 Methodology

3.2.1 Data collection

Over-bark breast height diameter (Dbh) measurements were made with a diameter tape on each of the inner nine trees covering an area of 36 m^2 in each provenance plot. The measurements were made to the nearest millimetre (mm). Among the nine trees from which the Dbh measurements were taken, the numbers of surviving and dead trees were counted at each of the two sites. The data for the Wark provenances were collected in May 1991 and that for the Drum provenances in April 1992. For each provenance the total basal area per plot was derived from the Dbh measurements. The relation $g = \pi d^2/4$, where;

g=basal area per tree

$\pi = 3.14$

d= Overbark diameter at breast height

was used to calculate the basal area for each tree. The basal areas of all the trees in a provenance plot were summed up to obtain the plot basal area. The plot basal area was taken to represent the growth potential of the provenance for an area of 36 m^2. This was then converted to basal area per hectare (G/ha), through multiplying by 10,000 m^2 and dividing by 36 m^2.

3.2.2 Arranging the G/ha data

For each of the two sites, the G/ha data was arranged in a hierachical manner as presented below;

Population
Group
Provenance.

A population consisting of 32 provenances from the range of grand fir, excluding the provenance that has undergone a generation of selection outside the range - 74(2002), constituted a block. Nested within this population were a number of provenance groups (refer to Table 2.1). Subsequently nested within the provenance groups were the individual provenances. The provenances within a group share geological, physiographic and vegetational zones in common (Fletcher and Samuel, 1990). Each provenance is characterised by a latitude, longitude and altitude.

3.2.3 Methods of analyses

3.2.3.1 Analysis of variance

To examine provenance variation at each of the two sites, a nested model of analysis of variance (ANOVA), from Sokal and Rohlf (1969) was employed. This model was to facilitate an examination of the magnitude of variance attributable to the various levels of variation and their relative importance in locating regions with provenances with superior growth potential. Thus besides, examining variation between the groups to which the provenances have been assigned and the provenances within these groups, the model also facilitated the assessment of variation among individual provenances irrespective of the group to which they have been assigned. The model is presented below;

$Y_{ijkl} = a + b_i + c_{ij} + d_{ijk} + e_{ijkl}$, where,
Y_{ijkl} is the l^{th} G/ha value of the k^{th} provenance in the j^{th} group of the i^{th} block
a is the parametric mean of the population,
b_i is the random contribution of the i^{th} block
c_{ij} is the fixed contribution of the j^{th} group of the i^{th} block
d_{ijk} is the random contribution of the k^{th} provenance in the j^{th} group of the i^{th} block
and e_{ijkl} is the error term of the l^{th} item of the k^{th} provenance in the j^{th} group in the i^{th} block

3.2.3.2 Analysis of tree survival and mortality counts

The survival counts between provenances was very high and consequently the mortality counts were very low at each of the two sites. With the relatively low mortality counts at each of the two sites, a chisquared test which could provide the appropriate statistical test for comparisons among provenances could not be used because many of the provenances had less than five dead trees (Campbell, 1974). The data for the provenances in a group were pooled to determine the possibility of making comparisons between provenance groups. After pooling the total group counts at Wark were still lower than could warrant a chisquared analysis. However, the pooled data for provenance groups at Drum was used in a chisquared analysis. Secondly survival and mortality counts data were pooled for each of the two sites and this was used in a chisquared analysis to compare survival and mortality of trees between the two sites. The objectives of these analyses were to determine whether provenance groups differ statistically from each other in mortality within and between sites and also whether mortality differences if they were evident provide a possible explanation for the poor performance of some provenance groups.

3.2.3.3 Regression analysis

A stepwise multiple linear regression analysis was used to examine the relationship between G/ha and the environmental variables of latitude, altitude and longitude of provenance origin. The objective of the analysis was to determine which of the environmental variables accounted for the greatest proportion of the G/ha variation of the provenances at each of the two sites and whether that could be used as an indicator to identify provenances of superior growth potential.

3.2.3.4 Principal component analysis (PCA)

Principal component analysis is a multivariate statistical method designed to reduce a large number of variables to a small number of indices which are linear combinations of the original variables (Manly, 1986). Each linear combination of the original variables identified by the analysis represents a component or a dimension in the body of data. Each of the identified components account for a certain proportion of the variation in the data. The components are identified in order of decreasing magnitude thus the first component account for the greatest proportion of the variation, followed by the second component and subsequent ones, until all the variation has been accounted for. Practical examples of this exploratory technique is presented by Newnham (1968) and Worrel (1987).

At the start of the analysis which is carried out on the covariance matrix of the original variables, all the variables are standardized to have a variance of one. This ensures that all the initial variables have equal weighting in the analysis. The variance of each principal component identified by the analysis is referred to as the eigenvalue or latent root of the component. These are weighted in comparison to the variance of original variables after standardization and depending on the total variance of all the variables, the percentage variance accounted for by each principal component is calculated as a ratio of the latent root of a component to the total variance of the standardized variables.

Principal components of latitude, altitude and longitude of provenance origin was calculated to find linear combinations of these variables. Any identified component will be orthogonal and could subsequently be used in a regression analysis. The identified components of latitude, altitude and longitude were therefore used in a regression analysis with provenance G/ha. This regression analysis facilitated a comparison with the earlier analysis on the individual variables to determine which of the two analyses provided a more suitable explanation for the observed variation in provenance basal area.

3.3 Results of ANOVA for G/ha at Wark and Drum

Results of the ANOVA of G/ha at the two sites are presented in Tables 3.1 and 3.2. With reference to these tables and subsequent ANOVA tables in this work, a variance ratio will be called significant if it's value is above the tabulated value for the F-distribution at the 5 percent level for the appropriate degrees of freedom. A variance ratio will be called highly significant, if it is above the tabulated value at the 1 percent level for the appropriate degrees of freedom. A non-significant (n.s.) variance ratio, is one that has a value less than the tabulated value at the 5 percent level. The usual ANOVA table has two additional VC (%) columns which refer to the percentage variance explained by the indicated source of variation. The first VC (%) column refers to the sources of variation attributed to the provenance groups and provenances within a group in a block, while the second is based on variation among provenances within a block, irrespective of the groups to which they have been assigned.

3.3.1 Results of ANOVA for provenance G/ha at Wark

Table 3.1 shows a highly significant difference between the provenance groups, accounting for approximately 50% of the observed variation in basal area per hectare, but there were no significant differences at the lower level of provenances within group. Provenances within the site are significantly different. Provenance variation explain 34.6% of the total variation. Variation within the experimental blocks was also significant indicating that the experimental design of completely randomised blocks was efficient in accounting for the heterogenous factors in fertility trends within the site.

From the overall group means presented in Table 3.3, it can be seen that group 1 with provenances located in northern coastal Washington, has the highest growth potential at this site. One other source, group 7 with provenances from coastal locations in British Columbia had above site average growth potential. In contrast, the seven remaining groups have growth performance below the site mean. Of these however, the coastal group 8 from northern Oregon had the best growth potential. The other coastal group from southern Oregon performed poorly.

Among the groups from the Cascade Mountains in Washington and Oregon, group 2 with provenances located on the eastern slopes of the Cascade Mountains in Washington, has better growth potential than its southerly counterparts on the west and east slopes of the Cascade Mountains in southern Oregon- groups 6 and 4 respectively. The inland provenances represented by groups 3 and 5 have relatively lower growth potential. The general pattern of G/ha variation that emerges from this site is a decrease in G/ha of the provenance groups from the coastal toward the inland areas.

3.3.2 Results of ANOVA for provenance G/ha at Drum

Similar to the results at Wark, Table 3.2 shows a highly significant difference between groups at Drum. Variation among provenance groups explained over 50% of the total observed variation. Similar to the trend observed at Wark, while provenances within group are not significantly different large differences exist among the individual provenances. The difference between provenances accounted for 33.7% of the total variation. The efficiency of the blocking in the experimental design is once again evident on this site. The block effect is significant and removes a little over 30% of the total variation.

The overall group means presented in Table 3.3 shows the superiority of group 1 provenances in G/ha performance. Additionally, groups 6, 7 and 9 show above average growth performance on this site. All other groups, have growth potential below the site mean. It must be noted, however, that the mean of group 8 is very close to the site mean. With the exception of group 6 located in the Cascades, the provenance groups with superior growth potential are all from coastal sources. Within the Cascade Mountains, group 6 from the western slope of the mountains in Oregon performs better than group 4, located on the eastern slope of the mountain in Oregon or the more northerly group 2 provenances in eastern Washington. Like Wark, the two inland sources groups 3 and 5 have relatively lower G/ha values compared to the other groups with the exception of group 4, which had poor performance on both sites.

Table 3.1 Results of ANOVA for provenance G/ha at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	1145.0	572.5	3.88	0.05	31.59	51.79
Grp	8	7039.0	880.0	4.21	0.01	48.55	-
Grp.Prov	23	4809.1	209.1	1.39	n.s.	11.54	-
Prov	31	11848.1	382.20	2.53	0.01	-	34.57
Plot	62	9349.8	150.8			8.32	13.64
Total	95	22342.9					

Table 3.2 Results of ANOVA for provenance G/ha at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	1919.8	959.9	4.19	0.05	31.37	53.53
Grp	8	12960.7	1620.1	6.46	0.01	52.94	-
Grp.Prov	23	5772.6	251.0	1.10	n.s	8.20	-
Prov	31	18733.3	604.3	2.64	0.01	-	33.70
Plot	62	14200.0	229.0			7.49	12.77
Total	95	34853.1					

Table 3.3 Provenance means of G/ha (m^2/ha) at each of the two sites

Group	PROV ID	Site Wark	 Drum
1	12001	31.30	72.90
1	12002	54.20	79.20
1	12003	45.80	68.70
1	12004	31.30	91.70
1	12005	52.10	87.50
1	12049	39.60	66.70
1	12051	45.80	70.80
1	74(7973)5	47.50	75.00
Group mean		43.50	76.60
2	12006	29.20	50.00
2	12007	43.70	60.40
2	12008	35.40	58.30
2	12009	25.00	66.70
2	12011	25.00	60.40
2	12012	22.90	64.60
2	12013	22.90	47.90
Group mean		29.20	58.30
3	12024	14.60	45.80
4	12016	12.50	41.70
4	12018	22.90	50.00
4	12020	16.70	31.30
Group mean		17.40	41.00
5	12034	22.90	47.90
6	12015	37.50	66.70
6	12019	27.10	66.70
6	12021	16.70	68.70
Group mean		27.10	67.40

Table 3.3 (cont.)

Group	PROV ID	Site Wark	 Drum
7	12040	43.70	77.1
7	12042	22.90	68.70
7	12043	29.20	58.30
7	12045	29.20	58.30
7	12047	43.70	81.20
Group mean		33.70	68.70
8	12052	35.40	79.20
8	12053	25.00	50.00
Group mean		30.20	64.60
9	12056	20.80	83.30
9	12057	27.10	77.10
Group mean		24.00	80.20
Site mean		31.30	64.80

3.4 Results of analysis of survival and mortality counts

Table 3.4 shows the percentage survival of the provenances at each of the two sites. Generally the survival percentages are high having a range of 81.5-100% at each of the two sites. Provenance performance may therefore be related to other factors other than survival. The results of the chisquared analysis for the provenance groups at Drum is presented in Table 3.5. The chisquare statistic is just significant at the 5% level, however it has to be noted that the expected values for six of the provenance groups is less than 5 which cast some doubt on the validity of the analysis. The results of the analysis between the two sites is presented in Table 3.6. There is a highly significant difference between the sites with Drum having higher mortality count than expected. Paradoxically, provenances on this site have a higher growth potential than at Wark. Thus higher growth potential of provenances on this site seem to compensate for higher than expected mortality.

Table 3.4 Percentage provenance survival at each of the two sites

Group	PROV. ID	% Survival Wark	% Survival Drum
1	12001	100.0	100.0
1	12002	96.00	100.0
1	12003	100.0	96.00
1	12004	96.00	96.00
1	12005	100.0	100.0
1	12049	100.0	96.00
1	12051	100.0	92.60
1	74(7973)5	96.00	100.0
2	12006	100.0	96.00
2	12007	100.0	100.0
2	12008	96.00	92.60
2	12009	100.0	96.00
2	12011	88.90	100.0
2	12012	100.0	96.00
2	12013	100.0	88.90
3	12024	100.0	96.00
4	12016	100.0	92.50
4	12018	100.0	88.90
4	12020	92.60	82.20
5	12034	100.0	92.6
6	12015	100.0	96.00
6	12019	100.0	85.20
6	12021	92.60	100.0
7	12040	92.60	96.00
7	12042	100.0	81.20
7	12043	92.6	88.90
7	12045	96.00	96.00
7	12047	100.0	96.00

Table 3.4 (cont.)

8	12052	100.0	96.00
8	12053	100.0	96.00
9	12056	81.50	96.00
9	12057	92.60	85.20

Table 3.5 Results of chisquared analysis of survival and mortality counts of provenance groups at Drum

Group	Trees Alive	Trees Dead	Total
1	211(203.75)*	5(12.25)	216
2	181(178.28)	8(10.72)	189
3	26(25.47)	1(1.53)	27
4	71(76.41)	10(4.59)	81
5	25(25.47)	2(1.53)	27
6	76(76.41)	5(4.59)	81
7	124(127.34)	11(7.66)	135
8	52(50.94)	2(3.06)	54
9	49(50.94)	5(3.06)	54
Total	815	49	864

DF = 8 Chisquare = 15.69 SIG = 0.05

*Numbers in brackets represent expected counts

Table 3.6 Results of chisquared analysis of survival and mortality counts between the two sites

Site	Trees Alive	Trees Dead	Total
Wark	839(827)*	25(37)	864
Drum	815(827)	49(37)	864
Total	1654	74	1728

DF = 1 Chisquare = 8.13 SIG = 0.01 *Numbers in brackets represent expected counts

3.5 Results of regression of provenance G/ha on latitude, altitude longitude of provenance and their first principal component

The results of the stepwise multiple linear regressions to explore the relationships between G/ha, the environmental variables of latitude (LAT), altitude (ALT) and longitude (LONG) as well as their principal components (PC) on the two sites, are presented below.

3.5.1 Results of multiple regression of G/ha on latitude, altitude and longitude of provenance origin at Wark and Drum

Tables 3.7 and 3.8 present the results of the stepwise multiple regression of G/ha on the environmental variables LAT, ALT and LONG of provenance origin, at each of the two experimental sites. There is a significant regression at Wark. The three variables account for about 25% of the variation in G/ha. Of these, however, only LAT is important, accounting for 22% of variation in G/ha of the provenances.

At Drum, the regression is highly significant, accounting for 32% of the observed variation but in contrast to Wark, ALT is the important environmental factor explaining 86% of the regression.

Table 3.7 Results of multiple regression of G/ha on LAT, ALT and LONG at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	3	1250.62	416.87	4.33	0.05	24.40
LAT	1	968.71	968.71	10.07	0.01	22.0
ALT	1	146.63	146.63	1.52	n.s.	1.30
LONG	1	135.28	135.28	1.41	n.s.	1.10
Residual	28	2693.91	96.21			
Total	31	3944.53				

Table 3.8 Results of multiple regression of G/ha on LAT, ALT and LONG at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	3	2418.9	806.3	5.90	0.01	32.20
LAT	1	357.8	357.8	2.62	n.s.	2.60
ALT	1	1806.3	1806.3	13.22	0.01	27.60
LONG	1	254.3	254.3	1.86	n.s.	2.00
Residual	28	3824.9	136.60			
Total	31	6243.8				

3.5.2 Principal components of latitude, altitude and longitude of provenance origin

Linear combinations of latitude, altitude and longitude upon which provenance G/ha was regressed was obtained using principal component analysis (PCA). The three components identified by the analysis are presented in Table 3.9. The components are identified by the latent vectors. Thus the first principal component (PC 1) can be represented by the equation,

$$\text{PC } 1 = 0.488\text{LAT} - 0.676\text{ALT} + 0.552\text{LONG},$$

and represents a contrast between latitude and longitude on one hand and altitude on the other. That is the component indicates that high latitude and longitude provenances are characterised by low elevation and vice versa. The latent root of the first component indicates that out of a total variance of 3 it accounted for 1.88 which is equal to 62.7% of the total variation accounted for by the three variables. Following Newnham (1968) method of ignoring any component with a latent root less than 1, only the first principal component (PC 1) was considered as important and used in the regression with provenance G/ha.

Table 3.9 Principal components of latitude, altitude and longitude of provenance origin

Latent vectors	1	2	3
Latitude (LAT)	0.488	0.768	0.415
Altitude (ALT)	-0.676	0.031	0.767
Longitude (LONG)	0.552	-0.64	0.534
Latent root	1.880	0.860	0.250
% Variation	62.70	28.71	8.33

3.5.2.1 Results of linear regression of G/ha on the first principal component of latitude, altitude and longitude of provenance origin at Wark and Drum

Multiple linear regression of G/ha on the first principal component reveals a highly significant relationship at both sites. The results of the analysis are presented in Tables 3.10 and 3.11. At both sites these analyses explained about the same percentages of variation accounted for by latitude at Wark and altitude at Drum.

Table 3.10 Results of linear regression of provenance G/ha on the first principal component of LAT, ALT and LONG of provenance origin at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	1	1069.96	1069.96	11.15	0.01	24.70
Residual	30	2879.18	95.97			
Total	31	3949.14				

Table 3.11 Results of linear regression of G/ha on the principal components of LAT, ALT and LONG of provenance origin at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	1	2145.6	2145.6	15.7	0.01	33.60
Residual	30	4098.2	136.61			
Total	31	6243.8				

3.6 Genotype *environment (G*E) interaction

3.6.1 Definition and Importance of G*E Interaction

Genotype by environment (G*E) interaction occurs when given genotypes, clones, families, provenances or species change in the rank of their performance in different environments or change in variation without change in rank over a number of sites (Zobel and Talbert, 1984; Wright, 1973). The environment consists of several factors, but in assessing G*E interactions, it is defined in terms of the cumulative effect of these factors as they affect tree growth (Zobel and Talbert, 1984).

A desired objective in tree improvement is the utilisation of genotypes that have stable and superior performance across a range of sites in establishing forest plantations or the matching of genotypes that are well adapted to particular sites, when fewer genotypes cannot be identified to suit a range of sites; it is only when such genotypes are identified and used that the optimum gains from seed sources can be realised (Shelbourne and Campbell, 1976). The study of G*E interactions is designed to achieve the above objective.

3.6.2 Assessment of G*E interaction

The assessment of G*E interaction in provenance experiments requires that the experiments are replicated at a minimum of two sites (Matheson, 1989). A large array of statistical techniques has been developed for assessment G*E interaction. Two of the most commonly used methods are; the analysis of variance and joint regression techniques (Burley and Wood, 1976; Freeman, 1973; Johnstone and Samuel, 1978). The analysis of variance technique, though useful for detecting and estimating the relative importance of G*E interaction in relation to the main effects does not give an indication of the relative contribution of the different genotypes to the interaction (Kaltsikes and Larter, 1970). The method is also of limited value when fewer genotypes and environments are involved in the investigation as it becomes insensitive in detecting interactions (Shelbourne, 1972).

The joint regression technique is a modified form of the analysis of variance that allows a more detailed examination of G*E interaction (Freeman, 1973). In addition to facilitating the detection of interaction when present, the method enables the assessment of the contributions of the individual genotypes to the interaction. The joint regression technique has led to the development of stability parameters - regression coefficient, deviation from regression, ecovalence and others (Skroppa, 1984). These stability parameters are used to measure the sensitivity of genotypes when grown across different sites.

The two widely used stability parameters are the regression coefficient and deviation from regression (Mergen et al., 1974; Fletcher and Samuel, 1990). These are derived from the regression of genotypic means over a number of sites on the environmental means of the genotypes. They also give an indication of a site's potential for a desired trait (Finlay and Wilkinson, 1963). An in depth discussion on the usefulness and limitations of the various stability parameters is given by Skroppa (1984), Freeman (1973) and Hardwick and Wood (1972). A major disadvantage of these stability parameters, particularly those based on regressions, is that they do not give any indication of specific environmental factors limiting the performance of genotypes in given environments (Knight, 1970). An important implication of of this is that experimental results should not be used to make generalizations and extrapolations to sites that are not covered by the experiment. Secondly, in assessing a genotype's adaptation, each environment has to be characterised by its critical environmental factors, considering a group of environmental factors affecting growth, in addition to the genotypes performance measured by its mean yield (Skroppa, 1984). Like the analysis of variance method, the joint regression technique is effective in examining G*E interaction if a large number of genotypes and environments are involved in the analysis. Skroppa (1984) recommends a minimum of five sites.

Two other methods that has been used in assessing G*E interaction are mentioned by Shelbourne (1972). These are the ranking of genotype means at each of different sites and the correlation between genotype means between pairs of environments. If genotypes have similar ranks over a number of sites, then the implication is that interactions are weak or absent. Changes in rank, as the above authors pointed out may be due to G*E interaction or experimental error, but where performance between replicates is not consistent between the different environments, then the presence of G*E interaction may be inferred. Correlation between genotypes at pairs of environments will give an indication of sites that can be said to be somehow similar.

For experiments replicated at a minimum of two sites, a graphical method proposed by Ekberg et al. (1983), enables the identification of genotypes that combine stability and high performance. These workers plotted what they referred to as the amplitude of performance - difference between provenance perfomance at the two sites - against the mean perfomance of the genotypes at the two sites. Genotypes with low amplitude are characterized as stable, that is they have relative consistent perfomance between the two sites. Their performance can simultaneously be observed from the graph. The preferred genotypes are those combining low amplitude with high performance.

3.6.2.1 Assessing provenance * site (P*S) interaction at the two sites

Provenance by site (P * S) interaction was analysed using an ANOVA model that considered site and provenance group as main effects and examined the interaction between them. The model for the analysis of P*S interaction is presented below;

$$Y_{ijklm} = u + a_i + b_{ij} + c_{ijk} + d_{ijkl} + (ac)_{ijk} + (ad)_{ijkl} + e_{ijklm}$$

Y_{ijklm} is the mth item of the lth provenance in the kth group in the jth block of the ith site.

u is the parametric mean of the population

a_i is the fixed treatment of the ith site

b_{ij} is the random treatment effect of the jth block of the ith site

c_{ijk} is the fixed treatment effect of the kth group in the jth block of the ith site

d_{ijkl} is the random treatment effect of the lth provenance of the kth group in jth block of the ith site

$(ac)_{ijk}$ is the interaction between the ith site and the kth group in the jth block

$(ad)_{ijkl}$ is the interaction between the ith site and the lth provenance of the kth group in the jth block

e_{ijklm} is the error term of the mth item of the lth provenance in the kth group in the jth block on the ith site.

Secondly, provenances were ranked in terms of their growth potential at each of the two sites. The changes in rank between the two sites were then illustrated graphically to determine how the provenance ranking changed between the two sites.

Finally the differences between provenance means at the two sites were calculated to represent a provenance's amplitude which is a measure of the relative stability of a provenance between sites. This amplitude was then plotted against the mean performance of the provenances between the two site in a scatter diagram. This diagram gave a pictorial representation of provenances that combined high stability with high growth potential.

3.6.3 Results of various assessments for P *S interaction at the two sites

3.6.3.1 Results of analysis of variance

The results of the ANOVA for P*S interaction is presented in Table 3.12. The table indicates no significant interaction between provenance and site. The interaction term is partitioned into site by group (Site*Grp) and site by provenance within group (Site*[Grp.Prov]), but neither component is statistically significant. The differences between the provenance groups and among the provenances are in agreement with the previous ANOVAs for each of the two sites. The difference between the sites is highly significant and account for 93% of the observed variation. The mean values of provenance group G/ha as well as those of the provenances in Table 3.3 indicate that Drum has a higher potential for the growth of grand fir than Wark. Comparison of G/ha means for provenance groups between the pair of sites show that almost all the groups have 100% better performance at Drum than Wark.

Table 3.12 Results of ANOVA for provenance*site interaction

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	4	3081.1	770.30	4.05	0.01	1.33	1.37
Grp	8	17508.2	2188.53	11.52	0.01	3.80	-
Grp.Prov	23	6824.4	296.7	1.56	n.s.	0.51	-
Provenance	31	24332.6	784.9	4.12	0.01	-	1.39
Site	1	54170.3	54170.3	285.1	0.01	93.23	96.04
Site*Grp	8	2544.3	318.0	1.67	n.s.	0.55	0.56
Site*(Grp.Prov)	23	3924.0	170.6	0.89	n.s.	0.29	0.30
Plot	124	23559.3	190.0			0.33	0.34
Total	191	111611.6					

3.6.3.2 The changes in growth performance ranks of provenances between the two sites

The changes in the growth performance ranks of provenances between the two sites is graphically illustrated in Figure 3.1. Generally the growth performance ranks of the provenances change between the two sites. Provenances can be grouped into one of four categories based on the degree of change in rank from Wark to Drum. The categories and provenances that fall into each of them are described below:

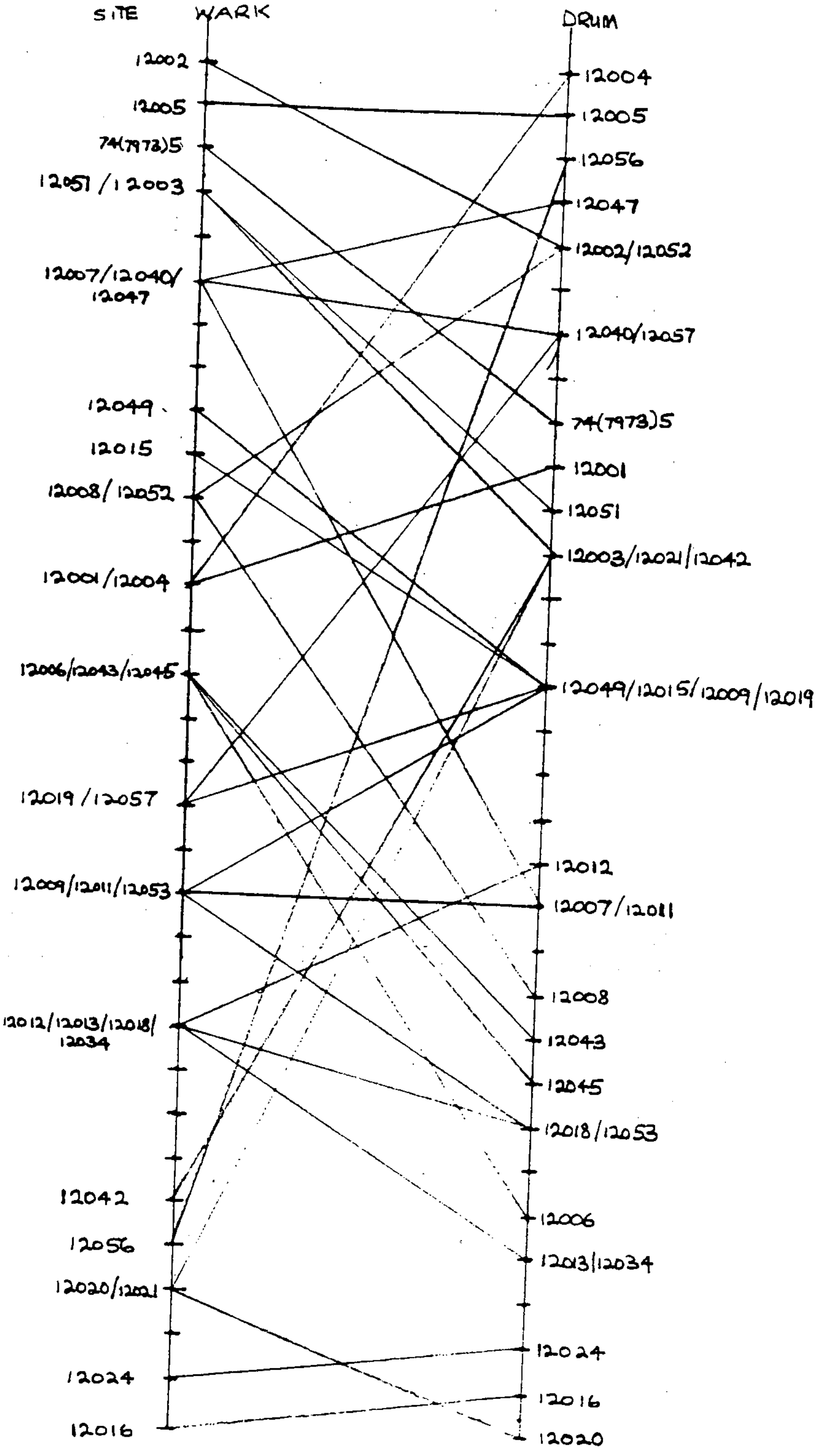


Figure 3.1 Changes in provenance growth potential ranks between Wark and Drum

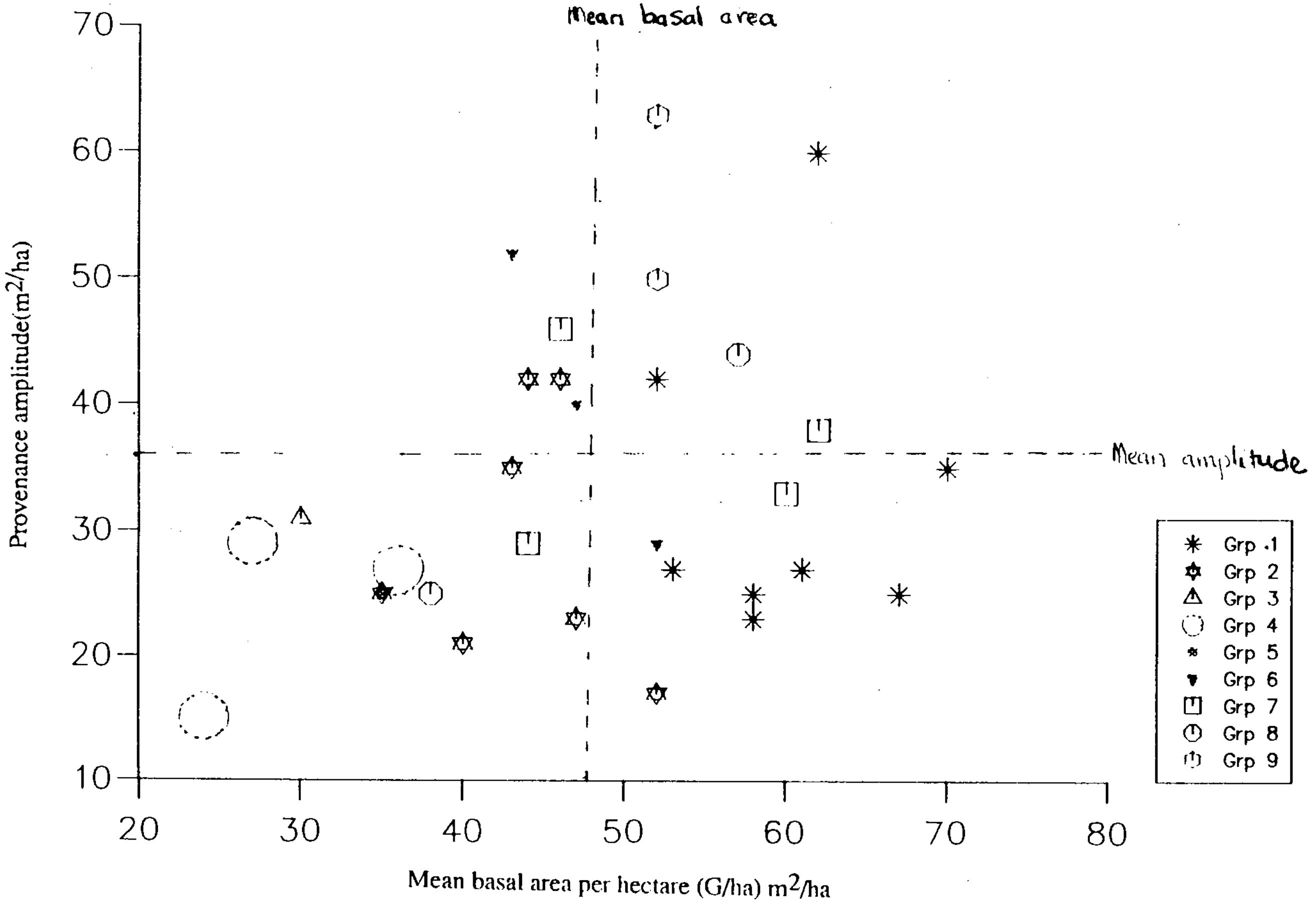
1. provenances that maintain their rank between the two sites - 12005 and 12011
2. provenances that show an increase or decrease of between 1 to 5 ranks between the two sites - 12001, 12002, 12009, 12012, 12013, 12015, 12018, 12016, 12019, 12020, 12024, 12034, 12040 and 12052.
3. provenances that exhibit an increase of six or more ranks between the two sites - 12004, 12021, 12042, 12056 and 12057.
4. provenances that show a decrease of six or more ranks between the two sites - 12003, 12006, 12007, 12008, 12043, 12045,12049, 12051, 12053 and 74(7973)5.

The changes in provenance ranks cannot be easily arranged on the basis of the groups to which the provenances belong, however, two features of the Figure 3.1 are noteworthy: provenances in group 1 are among the first thirteen ranked provenances on each of the two sites and secondly provenances in group 4 have consistently lower ranks at each of the two sites.

3.6.3.3 Graphical representation of the relationship between provenance amplitude and provenance mean G/ha between the two sites

A third method for examining the relative performance of the provenances between the two sites is presented in Figure 3.2. In this figure the difference between the means of a provenances G/ha for the two sites referred to as the amplitude of the provenance is plotted against the the mean performance of the provenance between the two sites. The figure facilitates an examination of provenances that combine both low amplitude and high growth potential. The diagram indicates that many of the provenances in group 1 match this description, though 12004 has a very large amplitude. Group 4 also have provenances with low amplitude but low growth potential. Between the other groups the provenances show a wide variation in combining low amplitude and high growth potential. For example in group 7 while two of the provenances combine relatively low amplitude with high growth potential, one has a low amplitude and low G/ha and the other has a high amplitude and low G/ha.

Figure 3.2 Scatter diagram showing the relationship between provenance amplitude and mean basal area per hectare (G/ha)



3.7 Comparison of the growth potential provenance 74(2002) with other provenances in group 7

The provenance 74(2002) which has undergone a generation of selection in Britain had the highest mean basal area per hectare (G/ha) among all the provenances on both sites. This provenance originated from British Columbia and is therefore associated with provenances in group 7 (refer to Fig 2.2). A generation of adaptation in Britain might have made it better adapted to this environment than the other provenances in its associated group hence the superior growth potential. In order to test the above speculation, provenance 74(2002) was considered as belonging to a group different from the other provenances in group 7. These two groups were compared in separate analysis of variance at each of the sites using the ANOVA model in Section 3.2.3. A second analysis using the ANOVA model in Section 3.5.2.1 combined the data from the two sites.

The results at the individual sites presented in Tables 3.13 and 3.14 indicate no significant differences between the two groups considered in the analyses. Also there were no significant differences among the provenances. In contrast the results presented in Table 3.15 indicate a highly significant difference among the provenances. Table 3.16 showing the mean G/ha of the provenances over the two sites indicate that provenance 74(2002) has superior growth potential to the other provenances in group 7. This appear to suggests that a generation of selection in the present environment has made the provenance better adapted to the two sites than the rest of the provenances with which it was associated with in the natural range of the species.

Table 3.13 Results of ANOVA comparing the growth potential of provenance 74(2002) to other provenances in group 7 at Wark.

Source	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	342.9	171.4	0.91	n.s.	10.26	21.90
Grp	1	1042.1	1042.1	3.86	n.s.	62.40	-
Grp.Prov	4	1078.1	269.5	1.44	n.s.	16.14	-
Prov	5	2120.2	424.0	2.26	n.s.	-	54.19
Plot	10	1870.7	187.1			11.20	23.91
Total	17	4333.8					

Table 3.14 Results of ANOVA comparing the growth potential of provenance 74(2002) to other provenances in group 7 at Drum

Source	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	1458.3	729.2	2.56	n.s.	19.26	41.27
Grp	1	2441.3	2441.3	7.35	n.s.	64.48	-
Grp.Prov	4	1328.3	332.1	1.17	n.s	8.77	-
Prov	5	3769.6	753.9	2.66	n.s	-	42.67
Plot	10	2838.0	283.8			7.50	16.06
Total	17	8065.9					

Table 3.15 Results of ANOVA comparing the growth potential of provenance 74(2002) to other provenances in group 7 at the two sites.

Source	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	4	1801.3	450.30	1.91	n.s	2.65	3.17
Grp	1	3336.7	3336.70	6.31	n.s.	19.67	-
Grp.Prov	4	2114.4	528.60	2.25	n.s.	3.12	-
Prov	5	5451.1	1090.22	4.63	0.01	-	7.68
Site	1	12192.2	12192.2	51.77	0.01	71.88	85.93
Site* Grp	1	146.7	146.70	0.62	n.s.	0.87	1.03
Site*(Grp.Prov)	4	291.6	72.90	0.31	n.s.	0.43	0.51
Plot	20	4709.1	235.5			1.39	1.66
Total	35	24592.0					

Table 3.16 G/ha means (m^2/ha) of provenance 74(2002) and other provenances in group 7 at Wark and Drum

PROV ID	Wark	Drum
74(2002)	54.20	100.0
12040	43.70	77.10
12042	22.90	68.70
12043	22.90	58.30
12045	29.20	58.30
12047	43.70	81.20

3.8 Prospects of early selection for provenance growth potential in grand fir

The rotation age of trees in forestry is very long compared to agricultural crops. As a result provenance trials that usually have to be conducted over a rotation age are very expensive. If selection for the most important traits could be made before the rotation age then the cost of conducting the research could be reduced. This could be achieved if the characteristics of great importance exhibit a strong correlation between young age and old age trees (Baa-Jen Jing, 1987).

In rangewide provenance trials one of the most important traits that need assessment is the growth potential of provenances to aid the delineation of broad regions in which provenances have acceptable productivity in the breeding zone (Niendstaedt, 1979). If such provenances can be located early in a trial then besides making savings in the cost of the research further screening and breeding of the species could be accelerated. The reliability of prediction of later growth performance from early assessments require extended periods to yield reasonably accurate information (Zobel and Talbert, 1984). Therefore, if correlations between growth potential are made at different ages, probably up to half the rotation period in a provenance trial it may be possible to reasonably make choices between provenances.

The grand fir provenance experiment on which the present work is based was established in 1979. Preliminary height assessments were made after 3- 6- and 10 years respectively. Height measurements were made on all the twenty five trees in the experimental plots at each of these ages. The results of the height assessments were reported by Lines (1978) and Fletcher and Samuel (1990). In this study, Dbh measurements were made at 12 and 13 years for the experimental trials at Wark and Drum respectively. With the height and Dbh data at the various ages it was possible to seek answers to the two questions below:

1. How early can provenance selection for superior growth performance be made ?
2. Is superior height growth performance of a provenance complementary with diameter growth ?

In order to answer these questions, correlations were calculated between mean height measurements at the different ages of assessment and the Dbh measurements made on each of the two sites. The correlation coefficients were then tested for significance.

The results of the correlation analysis are presented in Tables 3.17 and 3.18, r^2 values are indicated in brackets besides each of the correlation coefficients. There is a highly significant correlation between the Dbh and height measurements at the respective ages on each of the two sites and the amount of variation explained by the correlation as indicated by the r^2 values in brackets tend to increase with age. The highly significant correlations tend to suggest that superior height growth is complementary with diameter growth for the provenances. Secondly the increase in the regression coefficients gives an indication that the accuracy of predicting later performance from early performance increases with age. From the regression coefficients above, it appears that selection of the best provenances can be made at 6 years.

Table 3.17 Correlation coefficients for the relation between mean Dbh and mean height measurements at different ages in grand fir provenances at Wark

	Correlation coefficient (r^2)	DF	SIG
Dbh (12 years)			
Height (3 years)	0.74(0.55)	30	0.01
Height (6 years)	0.86(0.74)	30	0.01
Height (10 years)	0.89(0.74)	30	0.01

Table 3.18 Correlation coefficients for the relation between mean Dbh and mean height measurements at different ages in grand fir provenances at Drum

	Correlation coefficient (r^2)	DF	SIG
Dbh (13 years)			
Height (3 years)	0.82(0.67)	30	0.01
Height (6 years)	0.86(0.74)	30	0.01
Height (10 years)	0.86(0.74)	30	0.01

3.9 Discussion

3.9.1 Provenance variation in the growth potential of grand fir at the two sites

The ANOVA for each of the two sites have indicated that the greater proportion of the variation in provenance growth potential is explained by the groups to which the provenances belong and that variation among provenances within a group is not significant, however, there are differences between individual provenances. Coastal provenance groups generally have superior growth performance than other groups from elsewhere within the grand fir range.

Provenance group 1, with a location in northern coastal Washington (Refer to Fig. 2.1), has a better growth potential than any other provenance group at Wark. Group 7 with provenances located in British Columbia an area adjacent to the group 1 region has above site average growth potential. The remaining provenances groups have below site average growth potential. However, the coastal group 8 has a better growth performance than the rest. The only exception to the generally superior growth performance shown by the coastal sources is group 9, which is the most southerly coastal group from southern Oregon.

Among the inland sources, the provenance group located on the west of the Cascades in eastern Washington and northern Oregon - group 2, performs better than the southerly provenance groups along the mountain range - groups 4 and 6. The two groups located inland - groups 3 and 5, have a lower performance compared to the coastal groups. Groups 3 and 4 have the poorest growth performance at Wark. Provenance survival was generally very high on this site. Thus poor performance of any of the groups was not due to high mortality, but due to poor growth adaptation.

At Wark, the regression analysis suggests a relationship between growth potential as measured by G/ha and the latitude of provenance origin. Latitude explained 22% of the observed variation in provenance basal area. From Table 3.3, the apparent relationship is that groups from the high latitudes have better growth performance than the lower latitude sources. This seems particularly to be the case with the coastal group 1. A scatter diagram showing the relationship between G/ha and the latitude of provenance origin (Fig 3.3) elucidates this observation. Provenances from group 1 from relatively higher latitudes, generally have better growth performance relative to the other groups.

The analysis does not indicate any meaningful relationship between the growth potential and the other two environmental variables, altitude and longitude. The first principal component (PC1) of latitude, altitude and longitude is represented by the equation

$$PC\ 1 = 0.488LAT - 0.676ALT + 0.552\ LONG,$$

and indicates that latitude and longitude have an inverse relationship with altitude, that is as latitude and longitude of provenance origin increases the altitude decreases. A linear regression of the growth potential G/ha on PC 1 was highly significant indicating that the three factors collectively accounted for the observed variation in growth potential. The relationship between provenance G/ha and this component is illustrated in a scatter diagram in Fig 3.4. The figure indicates a discrimination between provenance groups on the basis of their location characterised by a linear combination of their latitude, altitude and longitude. The growth performance superiority of the group 1 provenances is evident from the diagram.

At Drum, the coastal provenance groups have relatively higher growth potential than the groups in the Cascade Mountains and those further inland. Three of the coastal groups of provenances namely, 1, 7 and 9 have above site average growth potential. The coastal group 8, though with a performance below the site average, has a mean very close to that of the site. The superior performance of the coastal groups is evident on this site.

Considering the growth performance of inland sources at Drum, group 6 from the western slopes of the Cascades in southern Oregon has a better growth performance than group 4, from the eastern slopes of the Cascades in Oregon and group 2 from the eastern slopes of the Cascades in Washington. Groups 3 and 5, from further inland have lower growth potential than the coastal groups. Provenances in group 4 have the poorest performance on this site. Mortality within provenances was relatively low and thus poor performance of any of the provenances might have been due to poor adaptation for growth on the site.

The regression analysis for the G/ha data on this site suggests a relationship between the growth potential and altitude. The relationship between provenance G/ha and altitude is illustrated in a scatter diagram in Figure 3.5. The superiority of the coastal sources from relatively lower altitudes than the rest of the groups, particularly those in groups 1 and 7 can be seen from this diagram. Alternatively, a regression of provenance G/ha on the PC 1 indicate a highly significant relationship. This relationship is illustrated by the scatter diagram in Figure 3.6. However, it has to be noted that both analyses account for nearly the same percentages of the observed variation in growth potential.

The growth performance patterns on the two sites tend to agree with each other with the coastal provenance groups emerging as having the best growth potential compared to the sources in the Cascade Mountains and those further inland. The magnitude of the differences in group G/ha values increases from Wark to Drum suggesting that the latter site has a higher potential for the growth of grand fir than the former, bearing in mind that measurements were made a year apart. Even though the growth performance of the provenances at Drum is higher than Wark, a chisquared analysis indicated that the mortality at Drum was higher than expected. Thus better growth on this site appears to compensate for the higher mortality.

Regressions of provenance growth potential on the individual environmental variables of latitude, altitude and longitude give conflicting results as to which of the variables will provide a better explanation for the observed differences. More importantly which of the variables could be used as a predictor of locating regions with provenances of superior growth performance. At Wark, latitude appears to be the important factor and explained only about 22% of the variation in the growth potential. At Drum, altitude, which explained a significant proportion of the variation in growth potential, accounted for only 27% of the variation. Results from the regressions of growth potential on the principal components appear to provide a better explanation for the observed differences than the variables considered individually. Nevertheless these regressions account for almost the same proportion of the variation as latitude and altitude do at each of the two sites.

Comparing regressions of provenance G/ha on the individual environmental variables or their principal components and the analysis of variance, the latter analysis tend to give the best indication of locating regions with provenances with the best growth potential. The amount of variation accounted for by the groups to which the provenances belong which was nearly 50% of the total variation at Wark and a little over 50% of the variation at Drum, suggesting that the choice of provenances with the best potential will depend on the groups to which the provenances belong. On this basis, while coastal provenances generally have higher growth potential, the best coastal group appears to be group 1 from coastal Washington.

The above discussion has indicated that grand fir exhibit variation in its growth potential. Some provenances, notably from coastal locations, generally have higher growth potential than those from elsewhere within the range. This observed variation appears to be related to the size of the species range, the environmental diversity encountered by different populations of the species within the range and discontinuities in the range of the species (Wright, 1976).

The provenances represented in the study cover a latitudinal range of 42° - 50 °N and an altitudinal range of 25 - 1500m. With such a wide range of latitude and altitude, variation among different populations of the species should be expected. Populations along the coast are adapted to a maritime climate, in contrast inland provenances grow in a more continental climate (Franklin and Dryness, 1969; Schaeffer, 1978).

Variation in climate is related to tree growth and distribution and follows a continuous pattern, therefore individual trees growing under a climatic regime should show continuous variability of inherent climatic adaptation (Burley, 1965). As a result of this adaptation, different populations are expected to be different. In the introduction of these plants into another environment, it is imperative that some climatic matching be made between geographic origin of seed and the sites on which they are to be planted though a perfect match cannot be achieved (Lines, 1965). Nevertheless, greater success in survival and growth which are marks of adaptation can be expected when the climate of provenance origin fairly corresponds with that of the planting site (Haddock, 1965; Rehfeldt, 1985).

The latitude of provenance origin and that of the environment in which it is to be used is another factor closely associated with climatic matching, because as Mergen et al. (1974) noted, latitude adjusted for differential altitude reflect many of the climatic factors associated with tree population differentiation. Thus Zobel et al. (1987), referring to the growth of *Pinus contorta* in Norway and Sweden, indicated that the best provenances are those originating from similar latitudes within the range of the species that is 54° -56 °N and 63 °N respectively.

If these principles are ignored in the search of suitable geographic seed origins, then provenances selected are likely to result in failed plantations with a knock-on consequence of the loss of huge financial investments. Similarly a species which could have provided provenances that could yield productive forest may be abandoned due to the use of the wrong provenance as was the case with the early introductions of *Pinus contorta* in Britain (Herman, 1987).

The inherent climatic adaptation of the coastal provenance groups of grand fir particularly those from coastal Washington and British Columbia, as well as their greater proximity to the latitudes of the planting sites than any of the other provenance groups may provide an explanation for their superior growth performance. In comparing climates between provenance origin and planting environments, Fairbairn (1968) recommended the use of the length of the growing season between the two areas which as he explained gives a natural correlation of the numerous climatic factors. The use of such an index seems to reasonably explain the better performance of the coastal groups from Washington and British Columbia. The length of the growing season in the coastal Washington area is estimated as 186 days (Fowells, 1965). Each of the two sites represented in the study is estimated to have a growing season of length 176 days. (Fletcher and Samuel, 1990). In contrast, provenance groups from inland areas are adapted to growing seasons of relatively shorter lengths ranging between 100 - 140 days (Fowells, 1965; Foiles, 1959).

Some inland provenances have better growth performance on both sites. These provenances include 12007, 12015 and 12019. Their relative adaptations may be explained in terms of the fact that within broad areas with more or less similar climatic conditions, discontinuities which may be edaphic, climatic or elevational may occur resulting in different adaptations between these populations and other found in such areas (Burley, 1965)

The principle of climatic matching does not have a strictly universal application as instances of provenances having adaptations to maritime climate have been reported to do well when cultivated in continental climates. Steinhoff (1978b) working on grand fir provenances in Idaho reported that a coastal source from Washington had a 50% superior performance than other provenances that originated from the local area. In Germany and France, the superior performance of the coastal provenances of grand fir from coastal Washington have been reported (Kleinschmit, 1986; Birot and Couviour, 1986). This provenance group has perhaps developed genotypes that have a broad adaptations to a range of environments as safeguard in surviving in a variety of envronments (Niendstaedt, 1975).

Differences in provenances may be due to other factors besides climate. One of such factors is altitude. Zobel and Talbert (1984), in formulating rules for the movement of provenances, indicated that high elevational provenances should not be moved to low elevational environments. However, they also noted that high elevation provenances from lower latitude can often be moved successfully to lower elevations at high latitudes. The growth performance of the high elevational sources from groups 4 and 6 does not agree with the above rule. These high elevation provenance groups do not perform well at the relatively low elevational sites of 200m at each of the two sites. Group 4 provenances have poor performance among all the groups on both sites.

These two provenance groups are located on the east and west slopes of the Cascade Mountains in Oregon. They are found in a region in which *Abies grandis* intergrades with *Abies concolor*. While the group 4 provenances perform very poorly on both experimental sites, the group 6 provenances improve markedly in their growth performance from Wark to Drum. Whether integradation has an effect on the growth performance of these provenances is beyond the scope of this study. However, it probably may be the underlying reason for the poor performance of these provenances.

Provenance selection for growth potential using early growth as a predicter of late performance improves with age. The results have indicated that growth performance of provenances may reasonably be predicted at the end of six growing seasons. While such an early screening may lead to the reduction in the financial cost in conducting the research as well as accelerate further screening and breeding of suitable provenances it may also carry the limitation of not yielding information on provenance adaptability in the event of extremes in environmental factors which may occur once in the rotation of the trial plantation (Zobel and Talbert, 1984).

The proper utilisation of genetic variation in tree domestication is based on the recognition and understanding of variation of the desired traits in the species of interest. The study of provenance variation in the growth potential of grand fir has indicated that provenance group origins from areas of similar climate and latitude to the two sites Wark and Drum, have a better growth performance on each these sites. The use of the variation between sites has to be based on a comparison of performance between sites, thus a knowledge of provenance by site interaction will be invaluable.

3.9.2 Provenance*Site Interaction

The analysis of variance examining the presence of interactions between provenance and site indicated no interaction. The differences between the sites however was highly significant. Variation between the two sites explained the greatest proportion of the observed variation between provenance groups and among provenances. The performance of the groups considering the pair of means for each of the groups between the two sites (Table 3.3) was in almost all cases more than a hundred percent better from Wark to Drum. The latter site has a higher potential for the growth of grand fir.

Although the analysis of variance indicated no interaction between provenance and site the changes in provenance growth performance rank between the two sites appear to suggest that the provenances interact with the sites. Among the thirty two provenances only two - 12005 and 12011 maintained their ranks between the two sites. The remaining thirty provenances changed their growth potential ranks by varying degreess between Wark and Drum. Provenances 12004, 12021, 12942, 12056 and 12057 had a marked increase in rank between the two sites. Among these 12056 and 12057 belong to group 9, the most southerly coastal group among the groups represented in the provenance experiment. Their response to better site conditions indicate their sensitivity to site conditions and suggest that they cannot do better on a relatively poor site. The other provenances 12004, 12021 and12042 which are from different provenance groups show the same kind of tendency as the two provenances mentioned above.

In contrast to these, provenances 12007, 12008, 12006, 12043, 12045 and 12052 exhibit a marked decrease in growth rank between the two sites. These provenances have higher ranks on the poor site. The remaining provenances do not tend to change very markedly in rank as those that have been discussed above. Provenances in group 1 have consistently higher ranks at each of the two sites in contrast to those in group 4 which have the lowest ranks on both sites.

Figure 3.2 relates provenance amplitude to the mean performance. This figure gives a clear indication of the provenances that maintain relative consistent growth performance between the two sites. Two perpendicular lines representing the mean amplitude and the mean provenance performance divides the figure into four quadrants. Provenances that have high growth potential and maintain relative consistent performance between the two sites are located in the fourth quadrant and include 12002, 12003, 12005, 12007, 12040, 12047, 12049, 12051 and 74(7973)5. With the exception of 12040, 12047 and 12007, all the remaining provenances belong to group 1. 12040 and 12047 are found in group 7, while 12007 is a member of group 2. Group 1 thus emerges as the best group from which provenances can be selected on the basis of their growth potential and consistent performance across the two sites, while group 7 appears to be the second most important group. These conclusions tend to reinforce earlier results obtained from the analysis of variance for each of the two sites.

The methods used to assess provenance * site interaction may have their limitations. The fact that only two sites were covered in this study rendered that analysis of variance insensitive in detecting interactions between provenance and site. However, the diagram illustrating the changes in rank between the two sites did show that most of the provenances changed rank between the two sites suggesting possible interaction between provenance and site. Nevertheless a limitation of the method appear to be that an increase or decrease in the rank of a provenance does not give a useful clue of how its performance compares with those of other provenances. For example, 12003 and12007 show a decrease in rank from Wark to Drum. Based on this decreased rank it will appear that these provenances do not have a high performance on the better site - Drum. In contrast the relative magnitude of the change in growth performance of these provenances between the two sites as measured by the amplitude is very small. Their growth potential between the two sites is also very high compared to many of the other provenances. Comparatively, provenance 12021 which shows an increase in rank from Wark to Drum has a relatively low growth potential. The third method for examining interactions which relates the amplitude to the provenance mean appear to be the best among the three methods since it facilitates a comparison between provenances for stability and better growth performance.

The identification of provenances that are suitably adapted to provide sources of seed for reforestation is an important objective in a rangewide provenance test. However, where differences exist between planting sites it is appropriate that provenances are also screened for adaptation to specific sites. This will ensure that the right sources are assigned to the appropriate sites to ensure optimum productivity from provenance deployment on sites (Zobel and Talbert, 1984).

An examination of provenance by site interaction in this study has indicated that provenances change in their growth rank potential between the two sites. Provenances in the group 1, however, maintain a consistent growth performance between the two sites. Thus over these sites the best provenance choices can be made from the group 1 provenances. The fact that the results cover a range of two sites has the implication that extrapolation to other sites has to be made with great caution since the factors limiting growth on other sites may be different from those of these sites (Skroppa, 1984; Knight, 1970). An earlier work by Fletcher and Samuel (1990) on the same provenance experimental series covering twelve sites, including the two sites covered in this work, indicated the superiority of the group 1 provenances across the range of sites studied. That study, which is in agreement with the present study covering only two sites, confirms the finding that the best provenances are from the provenance group located in coastal Washington.

3.9.3 The development of a land race of grand fir

Zobel and Talbert (1984) defines a land race as a population of individuals that has become adapted to a specific environment in which it has been planted. The development of a land race as these authors explained follows the introduction of a species to an environment outside its natural range. The pressures imposed by natural selection operate on the individuals of the introduced population such that only adapted genotypes are able to survive and grow well in the new environment. These individuals can then be selected and used for planting in the new environment to which they have adapted. They further noted that selection could be done after a one generation in the new environment but the best adapted individuals are usually obtained after several generations of selection. Hall (1990) working on Sitka spruce (*Picea sitchensis)* on several sites in Newfoundland noted the probable development of a land race of the species in that environment. He observed that the average performance across a range of sites was poor in comparison to the local black spruce and white spruce but then he also noted that on the productive sites some individuals of Sitka spruce grew faster than the local species. Following this observation he was of the opinion that the individuals showing faster growth may constitute a land race developing in the species which could be exploited through selection and breeding.

The importance of land races in introduced species is that due to their superior performance they could be used to improve production from the forest. Zobel et al. (1987) explained that their use constitute the easiest and best way of making quick and large genetic gain in the use of exotic species, apparently due to the fact that land races combine both adaptability and high productivity. They provide several examples from species like *Pinus patula, Cupressus lusitanica, Gmelina arborea* and *Pinus elliottii* in which land races have been reported to have superior performance than than other imported provenances.

The grand fir provenance 74(2002) originated from British Columbia and is associated with the provenances in group 7. It has undergone a generation of selection at Craigvinean in Scotland and has the highest growth potential than any of the provenances represented in the provenance experiment considered in this study. Statistical analyses to compare this provenance with the other provenances with which it may be associated but had not undergone any selection in the present environment at each of the two sites yielded negative results. However, a second analysis combining data from the two sites did indicate that there are differences among all the provenances considered in the analysis.

The best overall growth performance of this provenance may be attributed to the fact that it has undergone a generation of selection in the present environment. Thus it appears the provenance has developed into a land race by the definition above. This provenance therefore deserves attention in the selection of provenances based on superior growth performance.

Figure 3.3 Scatter diagram showing the relationship between provenance growth potential (G/ha) at Wark and latitude of provenance origin

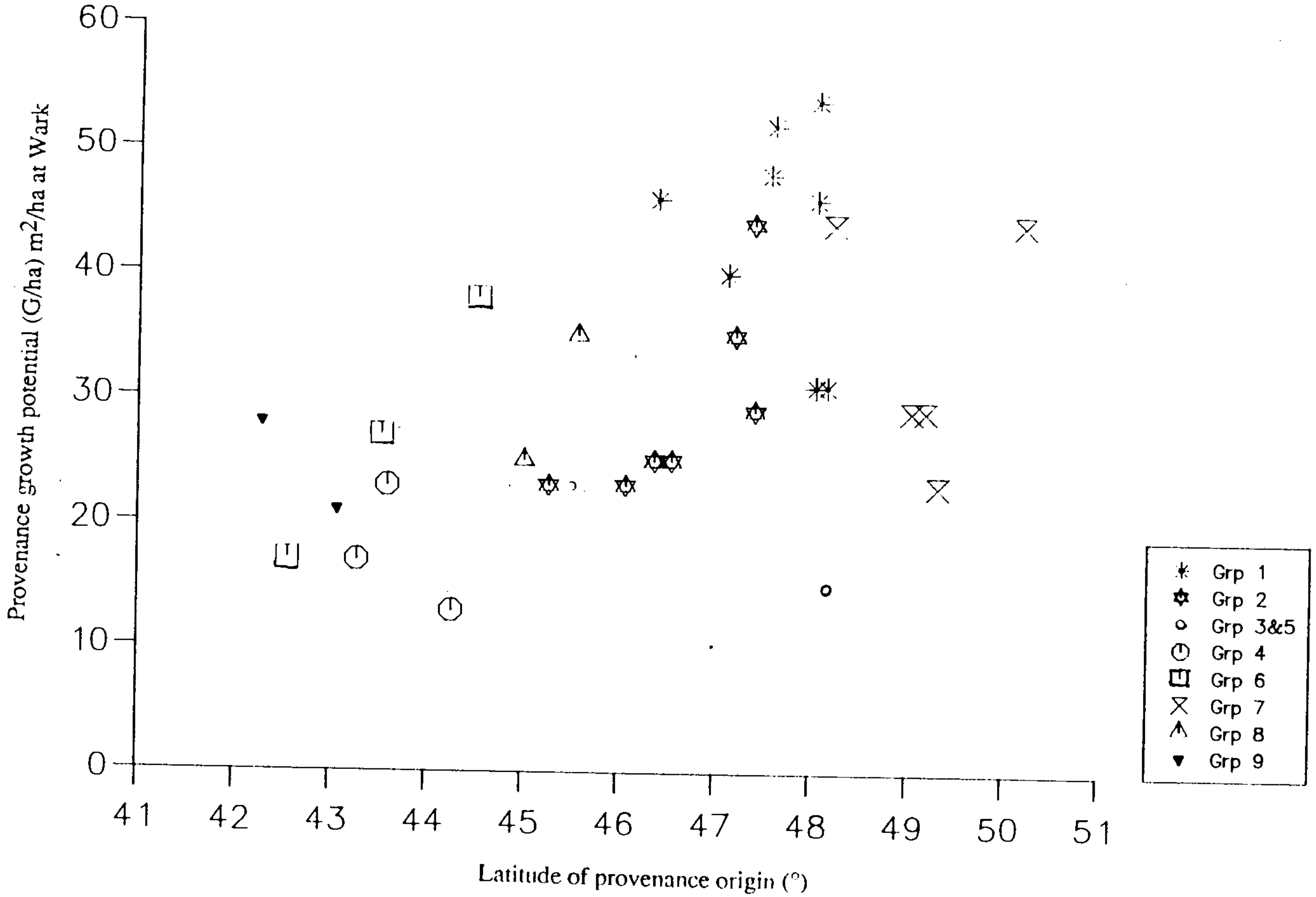


Figure 3.4 Scatter diagram showing the relationship between provenance growth potential (G/ha) at Wark and the first principal component of latitude, altitude and longitude of provenance origin.

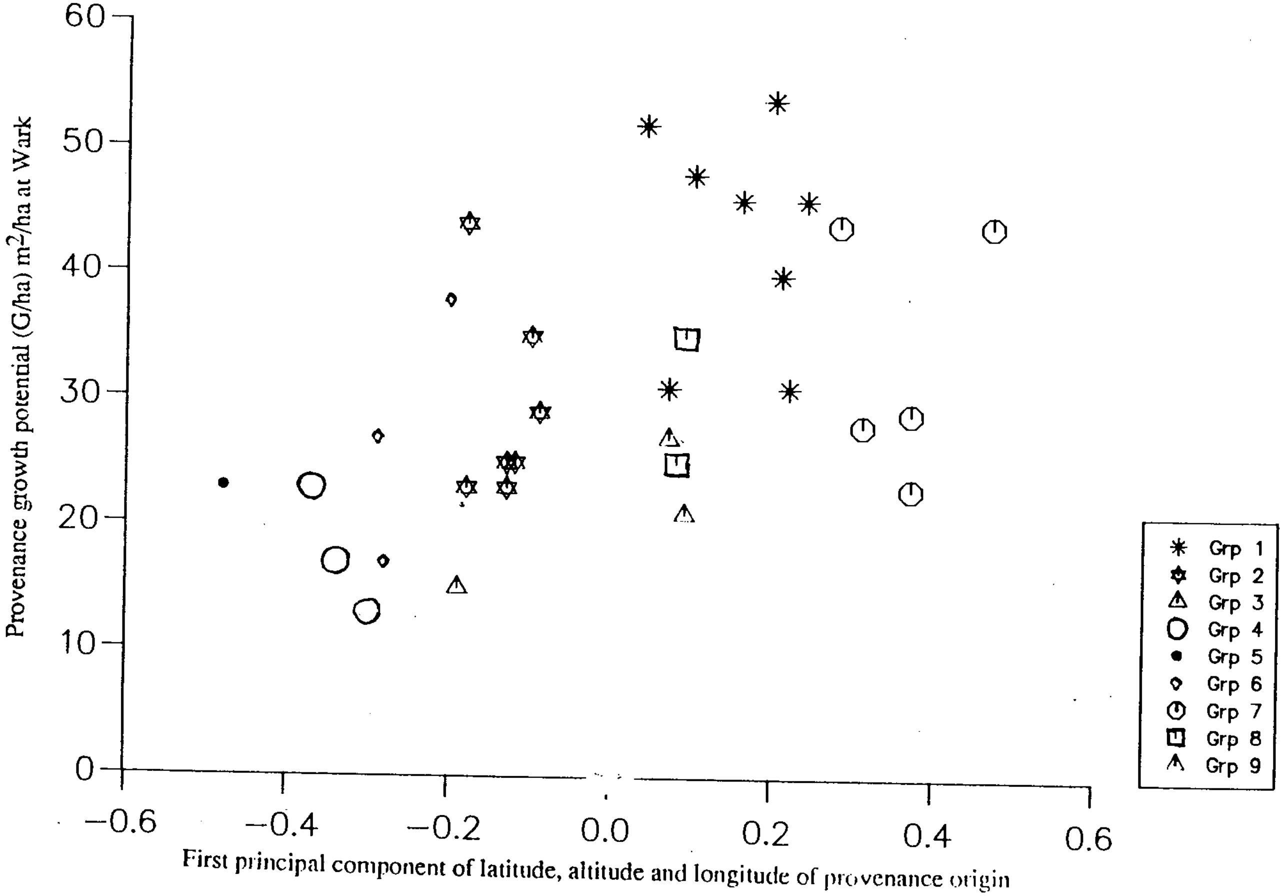


Figure 3.5 Scatter diagram showing the relationship between provenance growth potential (G/ha) at Drum and altitude of provenance origin

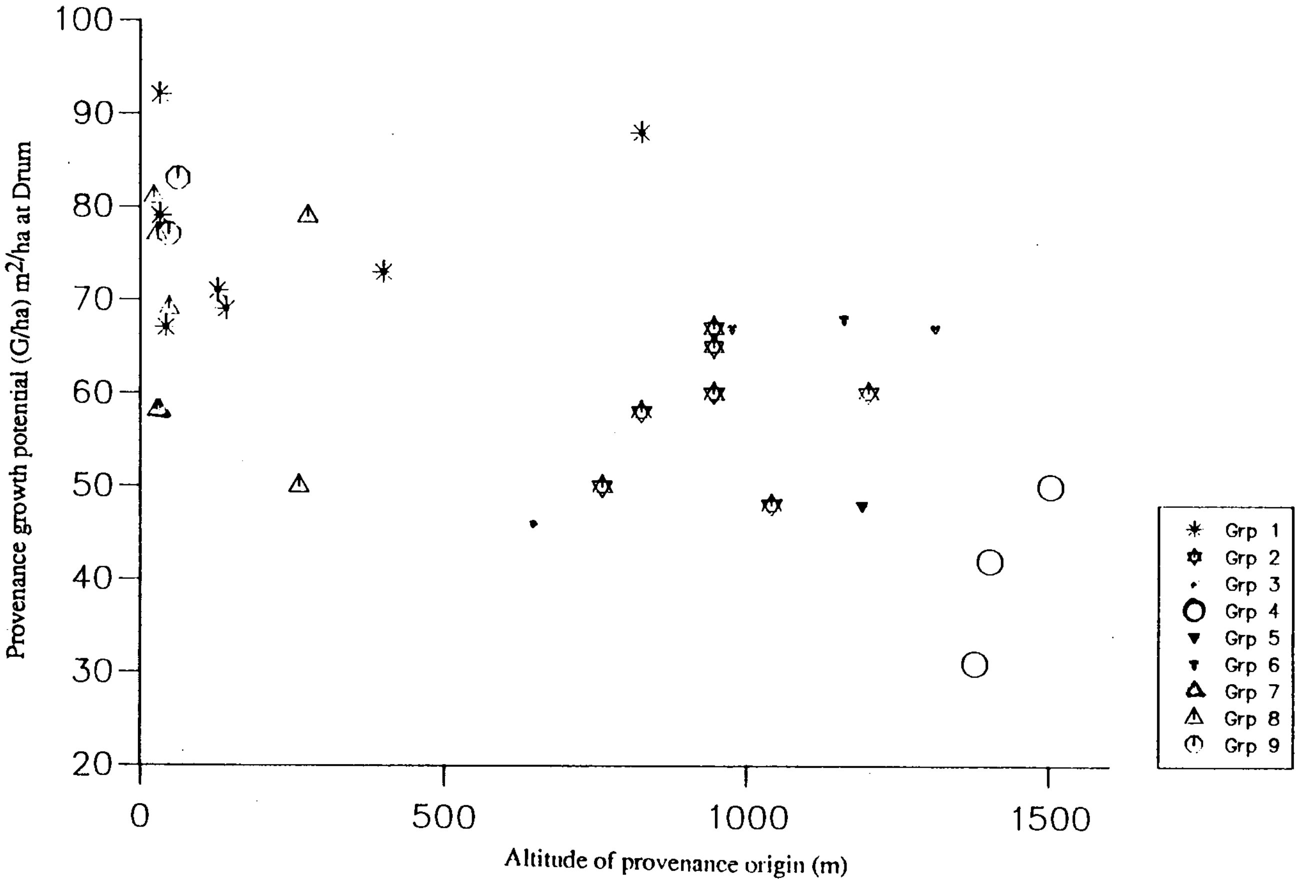
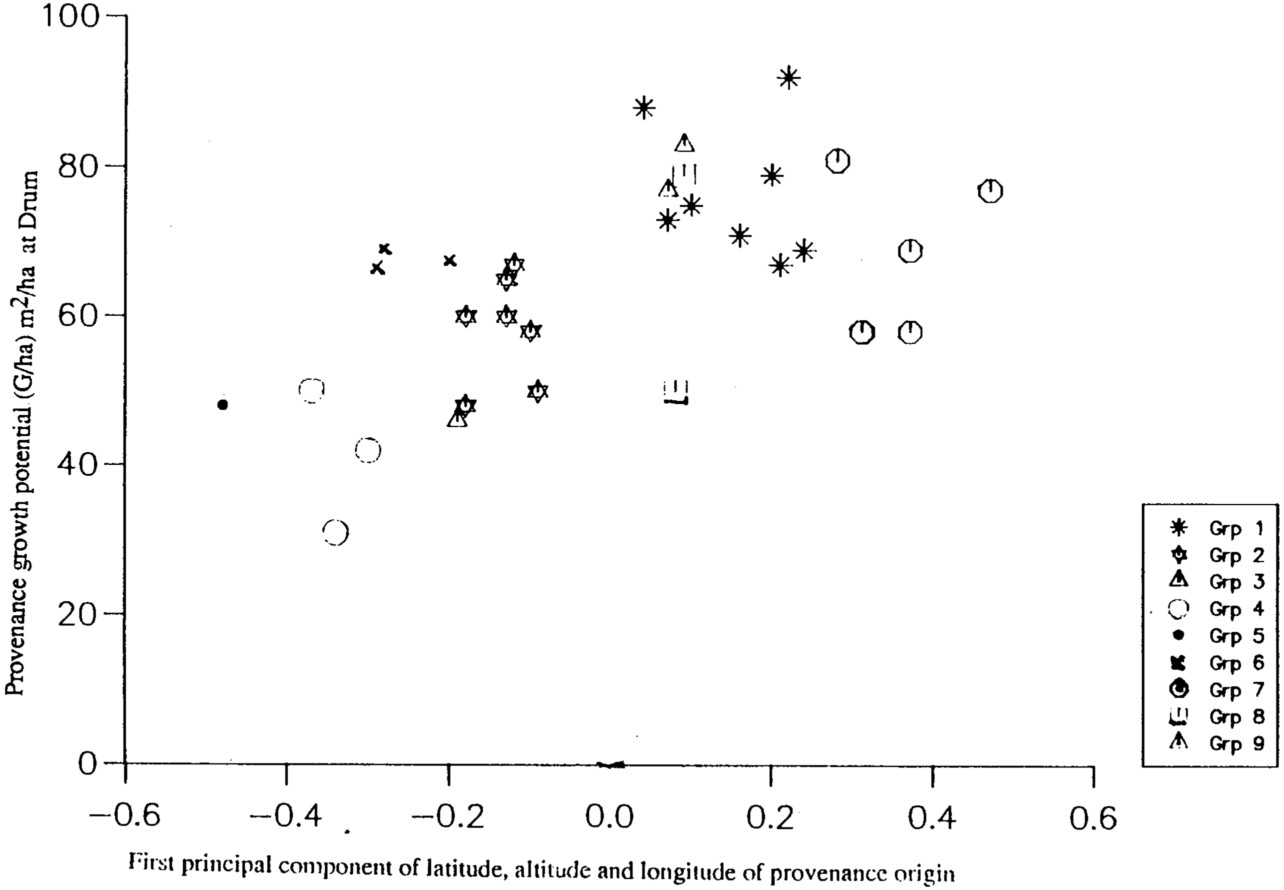


Figure 3.6 Scatter diagram showing the relationship between provenance growth potential (G/ha) at Drum and the first principal component of latitude, altitude and longitude of provenance origin.



CHAPTER 4

Provenance variation in frost hardiness of grand fir (*A. grandis*)

4.1 Introduction

A study of provenance variation in the growth potential of grand fir in chapter three has shown substantial differences between the different provenance groups. Environmental factors of latitude, altitude and longitude of provenance origin have accounted for a proportion of the observed variation. However, these factors do not explain all the observed differences as the analysis of variance and regression analysis have shown. With provenances from such a wide and diverse range, one factor that may be of importance in explaining the observed differences in growth potential is the variation in frost hardiness of the provenances. This section of the study attempts to examine provenance differences in frost hardiness of some provenances from the various provenance groups and possibly relate this to the observed variation in growth potential of the provenance groups.

4.2 Frost hardiness

Frost hardiness is defined by Glerum (1976) as the lowest temperature below freezing to which a tree can be subjected without damage to its tissues. For trees growing in environments in which freezing occurs, frost tolerance is a prequisite for survival and growth. Lack of adaption to frost injury will result in stunted growth and the attendant loss in the amount of wood produced in forest plantations. The search for suitable provenances for reforestation in environments in whch freezing occurs should therefore ensure that selected provenances are well adapted to resist frost damage in the environments into which they are introduced.

Seasonal variation in frost hardiness has been described for some species (Huystee et al., 1967; Sakai, 1966; Glerum, 1976; Cannell and Sheppard, 1982). The trends indicate that hardiness rythms or internal factors (Weiser, 1970), enable trees to take cue from the environment at the end of the growing season and the onset of the cold season to initiate physiological mechanisms that facilitate resistance to cold temperatures. The frost hardiness of tissues increases to a maximum level with decreasing environmental temperature, it then levels off at a plateau after the lowest temperatures have been attained; as the environmental temperature increases with the approach of a new growing season, the tissues deharden - move from a frost resistant to a frost susceptible state. Although this described trend generally applies to all the species for which they have been described, there are specific differences relating to each particular species with respect to the timing of the sequence of hardening and dehardening.

The initiation and subsequent development of frost hardiness in the tissues of a tree species is affected by a complex array of factors. Alden and Herman (1971)have furnished a comprehensive literature review on these factors. Among others, decreasing photoperiod and temperature have been identified as major factors affecting the development of frost hardiness. Weiser (1970) pointed out that decreasing photoperiod at the end of the growing season results in the initiation of frost hardiness and that subsequent development of cold injury resistance in woody plants is dependent on decreasing temperature. In *Picea abies* and *Pinus sylvestris* Christersson (1978) noted that the two factors mentioned by Weiser (1970) resulted in the development of frost hardiness. Also in *Pseudotsuga menziesii*, Schuch et al. (1989) reported that photoperiod was an important factor affecting the development of frost hardiness in the species. Elevation and latitude of origin have been reported as being inportant factors in predicting frost hardiness in *Pinus radiata* (Menzies et al., 1981). Among the coniferous species growing along the Pacific Northwest Coast and the Cascade Mountains in North America, differences in frost hardiness for species at different latitudes and elevations have been reported. Sakai and Weiser (1973) reported that along the coast frost hardiness of species increased with increasing latitude but in comparison to trees growing in the Cascade Mountains, those growing in coastal areas were reported to be less hardy.

4.3 Measurement of frost hardiness

Frost hardiness is generally measured by subjecting whole seedlings or excised tissues to a range of freezing temperatures, testing whether the seedlings or excised tissues are dead or alive and determining the temperature that kills 50% of the samples. Several methods for testing viability of seedlings or excised tissue have been proposed. Timmis (1976) provides a summary of the various methods which he classifies into one of four categories: morphological, chemical, physiological and electrical.

The morphological method utilizes visual assessment of the degree of the damage done to tissues after they have been subjected to freezing treatments and left for a certain period of time to manifest symptoms of damage, usually browning of tissues. A subjective scoring system is usually employed to assess the extent of the frost damage (Jonsson et al., 1981; Maronek and Flint, 1974; Nilsson and Eriksson, 1986). Besides being subjective, other disadvantages of the method are that it is time consuming and requires a lot of experimental material. These drawbacks notwithstanding, the method has often been used to corroborate the results obtained from some of the other methods. Timmis(1976) used results from the visual assessment method to compare the results for evaluating some of the other methods. Murray et al. (1989) found that the results obtained from the visual scoring method for assessing frost damage was in agreement with an electrical assessment method that they used. A similar result was reported by Maronek and Flint (1974).

4.4 Preliminary investigation to determine temperatures for testing shoot frost hardiness in grand fir

The range of temperatures over which excised tissues may be tested for frost hardiness is not easy to determine, particularly, when working with provenances from such a diverse environment as that of grand fir. Parker (1955) found that grand fir needles were resistant to freezing temperatures as low as -55 °C, but his work was based on one tree from an elevation of about 845m. For this reason and the fact that he was working on a tree in the local environment of the species, the range of temperatures over which he conducted his work cannot be used in this study. To get an idea of the range of temperatures that may be suitable for testing frost hardiness, this preliminary investigation was undertaken. A second but less important objective was to determine whether there was any indication of difference in frost tolerance of the tested provenances.

4.4.1 Materials and Methods

Five of the thirty three provenances included in the study were selected for this investigation. These provenances represented a range of latitudes and altitudes within the range of grand fir. Details of the samples are given in Table 4.1.

Table 4.1 Details of provenances represented in preliminary test to determine temperatures for freezing tests

PROV ID	Latitude(°N)	Altitude(m)
12005	47 11'	825
12053	45 01'	260
12018	43 39'	1500
12020	43 21'	1375
12021	42 56'	1160

4.4.2 Shoot sampling and freezing tests

Four batches of shoot samples were collected from each of the five provenances listed above. Each batch consisted of ten shoots, each shoot taken from a different tree within a provenance plot. Each shoot was taken from a second year's growth and was 5cm long. The shoot samples were collected on February 4, 1992. Freezing tests were completed within a week of collection of the material. During the testing period samples were kept in black polythene bags and stored in a cold room at 4 °C.

Four arbitrary temperatures (-5,-15,-25 and -36) including two extremes of freezing treatments were chosen for the test. The samples of ten shoots for each of the provenances were subjected to each of these treatments in an unlit programmable freezing cabinet. The freezing chamber of the cabinet is constructed from high grade stainless steel with welded vapour tight seams. The chamber designed to simulate frost has an air circulation system generated by a series of fans. The air is drawn through the heating and cooling elements of the chamber and recirculated back into the chamber ensuring minimum temperature gradients. Humidity in the chamber is produced by introducing water vapour in the form of steam. The rates of cooling and warming as well as the duration of freezing were controlled by an in-built computer program of the freezing cabinet

A set of samples given a temperature treatment was cooled from room temperature to 1 °C in one hour, then from 1 °C to the set minimum temperature at 5 °C per hour. The set minimum temperature was then maintained for three hours. After this period the samples were heated back to 1 °C at 10 °C per hour and finally to room temperature in one hour. After the freezing treatment the samples were mounted in sand trays and kept on a mist bench for a fortnight for damage symptoms to develop fully.

4.4.3 Visual assessment and analysis of frost damage scores

A subjective visual scoring system was devised to assess the degree of damage to frosted shoots. The scores ranked from 1 to 5 depending on the proportion of needles on an excised shoot that had turned brown after cold temperature treatment and being kept on mist benches for 14 days. Table 4.2 gives a description of the damage scores that were used for the assessment.

Table 4.2 Criteria used to assess damage to frosted shoots

Damage score	% of brown needles
1	0
2	1 - 25
3	26 - 50
4	51 - 75
5	76 - 100

4.4.4 Analysis and Results of preliminary test

The damage scores were analysed using a two-way analysis of variance model presented below;

$Y_{ijk} = m + a_i + b_j + (ab)_{ij} + e_{ijk}$ where,

Y_{ijk} is the k^{th} item in the subgroup representing the i^{th} group of treatment a(temperature) and the i^{th} group of treatment b(provenance),

m is the parametric mean of the population,

a_i is the fixed treatment effect of the i^{th} group of treatment a(temperature),

b_j is the fixed treatment effect of the i^{th} group of treatment b (provenance) and

e_{ijk}, the error term of the k^{th} item in subgroup ij.

The preliminary results presented in Table 4.3 indicated highly significant differences between the four test temperatures, but no significant differences between the provenances used in this study. There was very little damage done at temperatures of -5 °C and -15 °C as the mean damage scores presented in Table 4.4 show. On the other hand the temperature of -36 °C proved to be lethal to the shoots of all the provenances. The temperature that revealed a greater variability between the provenances was -25 °C, as Figure 4.1 indicates.The fact that there were no significant differences between the provenances may have been due to the the small number of replicates used in the study.

Table 4.3 Results of ANOVA for frost damage scores

SOURCE	DF	SS	MS	VR	SIG
Temperature(Temp)	3	289.375	96.458	95.94	0.01
Provenance(Prov)	4	6.080	1.52	1.50	n.s.
Temp*Prov	12	16.600	1.38	1.37	n.s.
Residual	180	181.900	1.01		
Total	199	493.955			

Table 4.4 Mean damage scores of provenances at the four test temperatures

	Temperature (°)				
Prov	-5 °C	-15 °C	-25 °C	-36 °C	Mean damage score
12005	1.8	1.4	2.3	4.5	2.5
12053	1.4	1.1	2.9	4.4	2.5
12018	1.1	1.1	2.8	4.1	2.3
12020	1.2	1.3	3.6	4.0	2.4
12021	1.9	1.3	3.6	4.0	2.8
Mean damage score	1.5	1.2	3.0	4.2	

4.5 Testing frost hardiness in ten provenances

4.5.1 Choice of test temperatures and provenances

Based on the results of the preliminary tests presented in Section 4.4.4 and the fact that the shoots were very likely dehardening for the current seasons growth at the time of the second test, a temperature range of -18 °C to -27 °C, at intervals of 3 °C was chosen to study provenance variation in ten provenances drawn from the entire range represented in the experiment. Nine provenances from each of the provenance groups and 74(2002), were selected for this study. The details of the provenances are presented in Table 4.5.

Table 4.5 Provenances represented in test to assess frost hardiness in grand fir

PROV. ID	Latitude(°N)	Altitude(m)
12002	48 05'	30
12040	50 20'	25
74(2002)	50 00'	150
12006	47 41'	760
12016	44 26'	1400
12019	43 53'	1310
12052	45 56'	275
12057	42 28'	45
12024	48 17'	650
12034	45 50'	1190

4.5.2 Shoot sampling and freezing test

5 batches of shoots each consisting of 20 shoots, each of length 5cm and of second year's growth, were collected from each provenance. The samples were collected on March 12, 1992. A batch of provenance samples consisting of samples from each of the provenances was subjected to each of the four temperatures (-18 °C, -21 °C, -24 °C and -27 °C). One batch of provenances was used as a control. During the testing period, the samples were kept in black polythene bags and stored in a dark room at 4 °C. The freezing treatments were the same as those for the preliminary investigation, described in Section 4.4.2. The frosted shoots were left on mist benches for 14 days for symptoms of damage to appear completely. The scoring system outlined in Table 4.2 was used in assessing the damage to the shoots. Plate 4.1 provides a visual presentation of the scoring scale that was used for the assessment. Plates 4.2-4.5 show pictures of the frosted shoots.

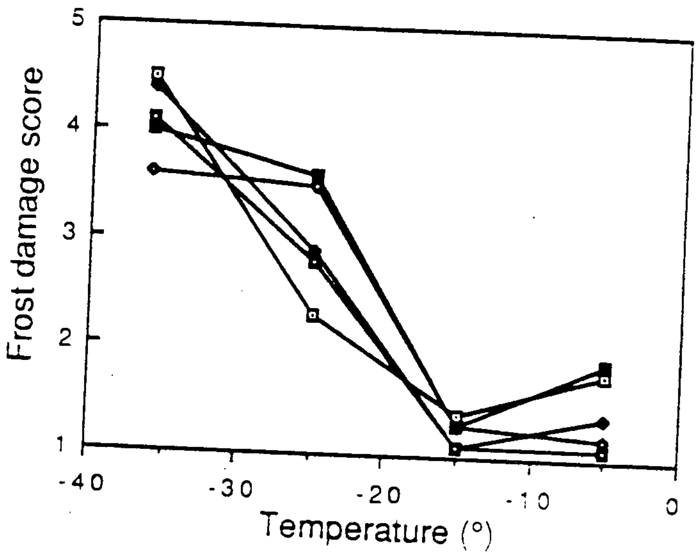


Figure 4.1 Variability between frost damage scores of five grand fir provenances at four test temperatures

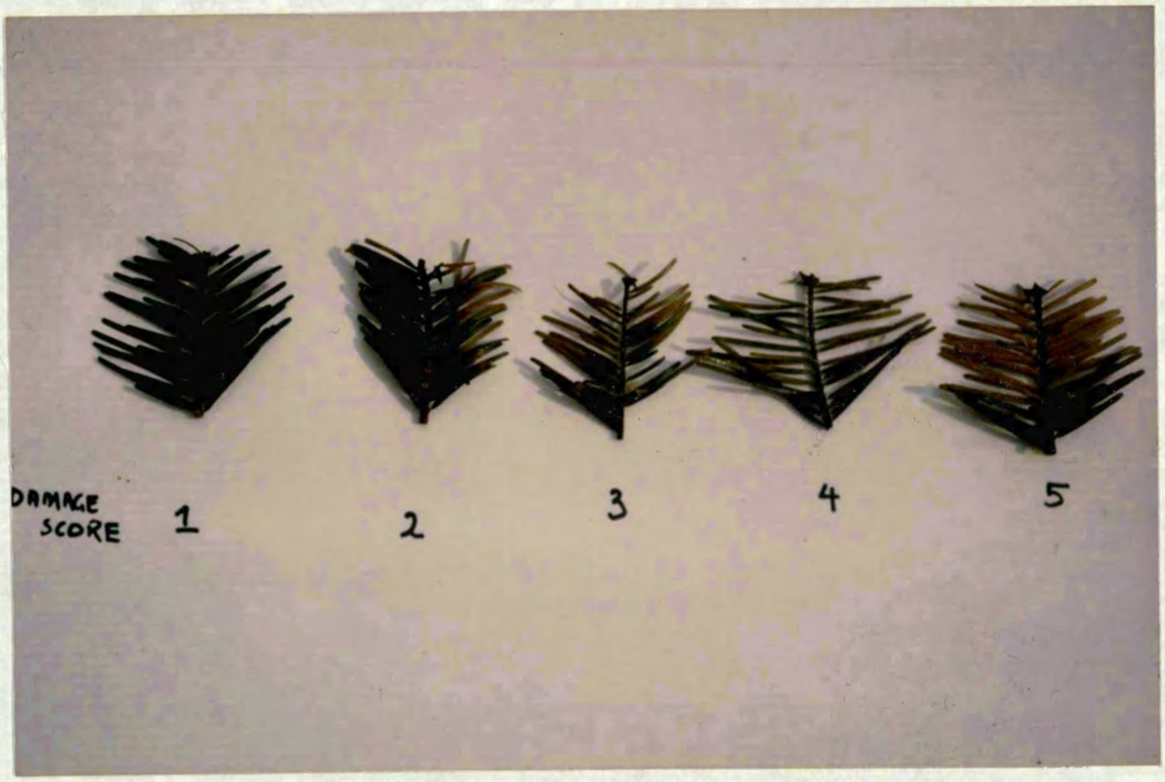


Plate 4.1 Visual presentation of the scoring scale used to assess damage to frosted shoots in ten provenances of grand fir (*A. grandis*)

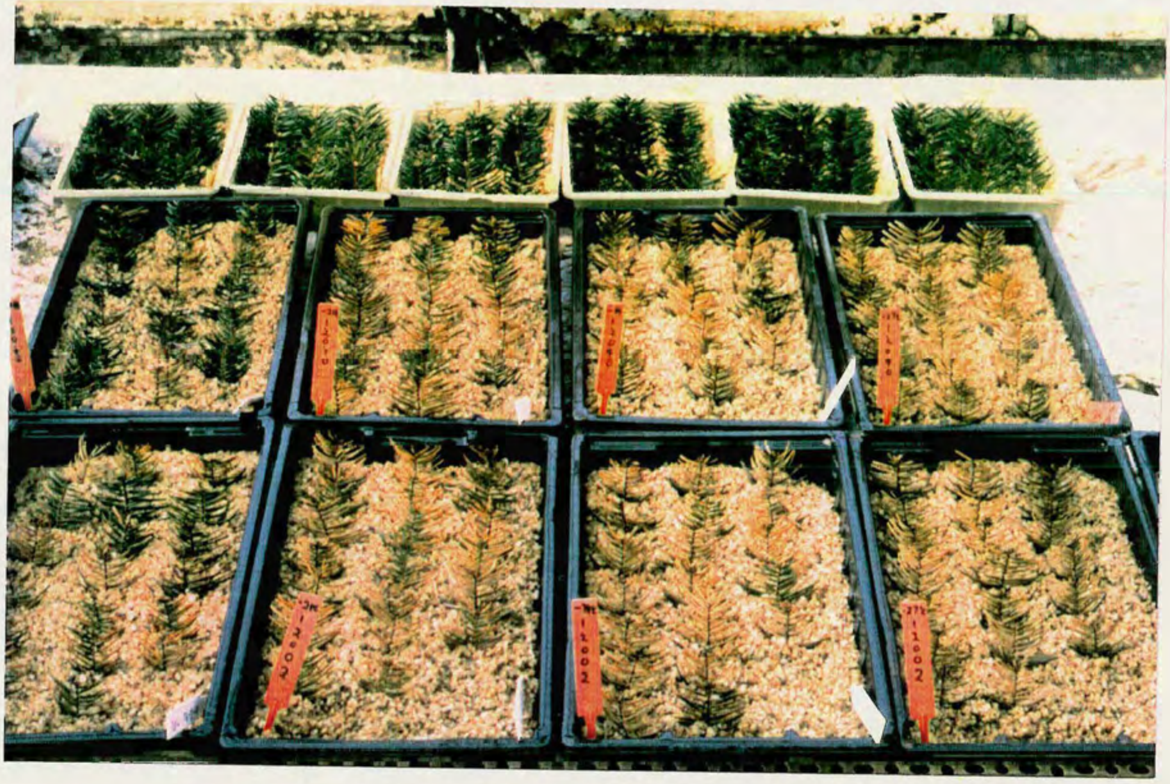


Plate 4.2 The plate shows the frosted shoots of the coastal provenance 12002 (front row, trays from left to right contain shoots frosted at -18 °C, -21 °C, -24 °C and -27 °C and kept on a mist bench for 14 days). SECOND ROW, shows frosted shoots of the coastal provenance 12040, with trays containing treatments at temperatures same as described for provenance 12002 above. THIRD ROW, shows the trays containing the control shoots, kept at 4 °C.

Plate 4.3 The plate shows the frosted shoots of the coastal provenance 12052 (front row, trays from left to right contain shoots frosted at -18 °C, -21 °C, -24 °C and -27 °C and kept on a mist bench for 14 days). SECOND ROW, shows frosted shoots of the coastal provenance 12057, with trays containing treatments at temperatures same as described for provenance 12052 above. THIRD ROW, shows the trays containing the control shoots, kept at 4 °C.

Plate 4.4 The plate shows the frosted shoots of the coastal provenance 12034 (front row, trays from left to right contain shoots frosted at -18 °C, -21 °C, -24 °C and -27 °C and kept on a mist bench for 14 days). SECOND ROW, shows frosted shoots of the coastal provenance 12024, with trays containing treatments at temperatures same as described for provenance 12034 above. THIRD ROW, shows the trays containing the control shoots, kept at 4 °C.

Plate 4.5 The plate shows the frosted shoots of the coastal provenance 12016 (front row, trays from left to right contain shoots frosted at -18 °C, -21 °C, -24 °C and -27 °C and kept on a mist bench for 14 days). SECOND ROW, shows frosted shoots of the coastal provenance 12019, with trays containing treatments at temperatures same as described for provenance 12016 above. THIRD ROW, shows the trays containing the control shoots, kept at 4 °C

Plate 4.6 The plate shows the frosted shoots of the coastal provenance 74(2002) (front row, trays from left to right contain shoots frosted at -18 °C, -21 °C, -24 °C and -27 °C and kept on a mist bench for 14 days). SECOND ROW, shows frosted shoots of the coastal provenance 12006, with trays containing treatments at temperatures same as described for provenance 74(2002) above. THIRD ROW, shows the trays containing the control shoots, kept at 4 °C.

4.5.3 Analysis of frost damage data

Two analysis of variance models were used to analyse the the data for frost damage scores. The first approach was to use a two-way ANOVA model to examine variation in provenances, temperatures and their interaction. The model used for analysing the preliminary data in Section 4.4.4 was used:

$Y_{ijk} = m + a_i + b_j + (ab)_{ij} + e_{ijk}$

where temperature(a) and provenance(b) were treated as fixed treatment effects.

The second model placed emphasis on the provenances at each of the temperatures seperately. The model used was:

$Y_{ij} = m + a_i + e_{ij}$ where,

Y_{ij} is the j^{th} item of the i^{th} provenance,

m is the parametric mean of the population and

e_{ij} is the error term of the j^{th} item of the i^{th} provenance.

4.5.4 Results of the ANOVA for the frost damage scores in ten provenances of grand fir

The ANOVA examining frost damage variations among the ten provenances at the various temperatures as well as the interaction between these two factors is presented in Table 4.6. The mean damage scores at each of the temperatures is presented in Table 4.7. The results of the ANOVA at each of the four test temperatures is presented in Table 4.8.

Considering provenances and temperatures together in an ANOVA indicated highly significant differences between provenances, temperatures and the interaction between the two factors. The results of the second analysis in Table 4.8 similarly indicated highly significant differences among the provenances. Examination of Table 4.7 shows that at a temperature of -18 °C, the provenances 12040, 12002, 12016 and 12034 had damage scores representing less than 50% damage. All the remaining provenances at this temperature sustained more than 50% frost damage. Of these however, 12019 and 12052 had relatively lower frost damage score. At the temperature of -21 °C, only two provenances 12040 and 12034 had less than 50% frost damage. Provenance 12002 and 12024 had relatively lower damage scores than the remaining provenances, although all these provenances had more than 50% frost damage. At the lowest temperatures of -24 °C and -27 °C the degree of damage to shoots increased. The damage score was more than 50% in almost all the provenances with the exception of 12034 at -24 °C. But even at these lower temperatures some differences in frost damage susceptibility are apparent. At -24 °C, 12040 had the lowest score compared to the remaining nine provenances. Other provenances with lower scores at this temperature are 12019, 12052 and 12057. At the lowest temperature of -27 °C, 12040 and 12024 had lower damage score than the other provenances. There was no damage evident at the control temperature of 4 °C indicating that the observed differences in the provenances at the other four temperatures was due to the frost treatments.

The mean damage scores over all the temperatures appears to give an indication of differences among the provenances. Two provenances 12040 and 12034 tend to have lower scores relative to the other provenances at most of the temperatures. The former is a provenance with location in British Columbia while the latter is located in Idaho. Another pattern from the overall mean scores also emerges among the coastal provenances. Within these the frost damage scores increases from north to south. The most southerly provenance 12057 has the highest damage score among all the ten provenances over the four test temperatures. The provenance 74(2002) which has undergone a generation of selection in Britain and is reported to have come from a similar location as 12040 also had a very high damage score second only to 12057 among the coastal provenances.

Comparing provenances from the Cascade Mountains, the southern Oregon sources 12016 and 12019 do not appear to be different from each other in their frost damage score as they tend to have about the same score but 12006 from the Cascade Mountain in Washington tend to have a higher damage score than these provenances. The provenance 12024 also appears to have a comparatively higher frost damage score than the southern Oregon provenances. The provenance from Idaho however, had the lowest frost damage score among all the sources indicating that it was the most frost hardy provenance among all the provenances.

The general pattern that emerges from this frost tolerance test is that along the coast frost hardiness of provenances decreases from north to south. Within the Cascade Mountains, southern provenances appear to be more frost tolerant than northern provenances, while further inland the southern provenance from Idaho is more hardy than the northern provenance from Washington.

Table 4.6 Results of ANOVA for frost damage scores in ten provenances of grand fir

SOURCE	DF	SS	MS	VR	SIG
Provenance	9	157.225	17.469	16.30	0.01
Temperature	4	1467.56	366.89	342.37	0.01
Prov*Temp	36	226.140	6.282	5.86	0.01
Residual	950	1018.05	1.072		

Total	999	2868.975

Table 4.7 Mean damage scores of ten provenances at five temperatures

	Temperature (°C)					Mean damage score
PROV ID	4(control)	-18	-21	-24	-27	
12002	1.05	1.40	3.25	4.40	5.0	3.08
12040	1.00	1.70	2.95	3.95	4.10	2.74
74(2002)	1.00	3.75	3.95	4.65	4.75	3.62
12006	1.00	4.40	4.15	4.60	4.20	3.67
12016	1.00	2.65	3.95	4.50	4.45	3.24
12019	1.00	3.25	3.55	4.00	4.60	3.38
12052	1.10	3.15	3.70	4.25	4.35	3.31
12057	1.10	4.30	4.50	4.05	5.00	3.79
12024	1.00	4.00	3.20	4.15	4.10	3.29
12034	1.00	2.15	2.05	2.55	4.40	2.43
Mean damage score	1.03	3.08	3.53	4.11	4.50	

Table 4.8 Results of ANOVA for frost damage scores of ten provenances at each of four temperatures

SOURCE	DF	MS (-18 °C)	MS (-21 °C)	MS (-24 °C)	MS (-27 °C)
Provenance	9	16.56**	9.96**	7.38**	2.26**
Residual	190	2.158	1.822	1.313	0.28

** $p < 0.01$

4.6 Discussion

The main objective in provenance studies is to locate provenances that are adapted and productive in the environment in which they are to be planted (Callaham, 1964). Provenances to be grown in environments in which freezing occurs need to have adaptation to avoid or resist frost damage. Such an adaptation will result in good growth and high productivity. Campbell and Sorenson (1973) found that frost injury was directly related to height and diameter growth in seedlings of *Pseudotsuga menziesii*.

Two factors influence the chance of frost damage to trees growing in a cold environment. These are the inherent levels of frost hardiness of the trees and changes in environmental factors such as the occurence of frost (Cannel and Sheppard, 1982). As these authors found in their studies on *Picea sitchensis*, the inherent frost hardiness of trees is not static but fluctuates daily and seasonally. This fluctuation is in response to changes in environmental factors like photoperiod and temperature. The changes in environmental factors cannot be controlled but in contrast the choice of provenances with the required frost hardiness adaptation to daily and seasonal environmental fluctuations can be controlled through careful selection.

All provenances may possess the ability to resist frost damage but the lack of proper timing to invoke the physiological mechanisms that may lead to frost damage resistance particularly for provenances growing outside their natural habitat may lead to cold injury (Weiser, 1970). Due to their geographic origins, provenances have varying adaptations to daylength exposures. This adaptation affects their inherent timing of periods in which growth is stopped. If this period is not well synchronised with the environmental factors in a new environment but coincides with periods of low temperatures, then such provenances will be liable to repeated frost damage and hence stunted growth. Similarly, if periods in which active growth is initiated is not well tuned to that of the new environment, frost damage may result (Rehfeldt, 1985; Lines, 1987). Thus in the selection of provenances, it is imperative that seed sources from geographic origins with adaptations of inherently high degree of frost resistance and the requisite timing of physiological mechanisms to escape or avoid frost damage in the environments in which they are to be planted are used.

In the previous chapter, large differences in the growth potential of grand fir provenance groups were found between and within each of two sites. On each site the provenance group with the best growth performance was about a 100% better than the poorest provenance group. The differences in the growth potential have been related to the locations of the provenaces in analyses of variance. While such analyses have explained some proportion of the variation as attributable to the groups to which the provenances belonged, it does not explain all the variation.

Differences in inherent levels of frost hardiness of the provenances may an provide additional explanation of the observed variation in the growth potential. The frost hardiness test in ten provenances was conducted with the above fact in mind. Although a provenance selected to represent a group may not be fully representative of the frost tolerance characteristics of all the provenances within the group, the results have given an indication that frost tolerance levels may be one of the underlying reasons for the poor performance of some of the provenances.

The mean frost damage scores of the nine provenances from the range of grand fir which gives a general indication of the frost tolerance status of the provenances over the tested temperature was regressed on the latitude of origin of the provenances. The relationship graphically illustrated in Figure 4.2**a** shows the regression equation and the regression coefficient. The apparent relationship is that the frost damage score decreases with increasing latitude. A second regression of mean frost damage score of the coastal provenances and their latitude of origin is shown in Figure 4.2**b**. This presents a strong relationship between the frost damage score and the latitude of origin. The damage score decreases with increasing latitude. This is in agreement with observations made in *Picea sitchensis* (Cannell and Sheppard, 1982). Sakai and Weiser (1973) also noted that along the Pacific Northwest Coast in America frost hardiness of many species increased with increasing latitude.

This pattern of inherent variation in frost hardiness among the coastal provenances may provide an additional explanation for the observed differences in growth potential. On each of the two sites the provenance groups in Washington and British Columbia had superior performance to those in northern and southern coastal Oregon. Observations made on the flushing pattern of grand fir in Britain and the Netherlands indicate that coastal provenances from southern Oregon are the earliest flushing provenances among all the other sources (Lines, 1987; Kranenborg, 1986). Rau and Weisgerber (1986) have also reported that provenances from this origin had the highest damage among other tested in Germany. In *Picea sitchensis*, Cannel and Sheppard (1982) found that a southern coastal provenace from latitude 42° 53 °N and longitude 124° 28 °W flushed early and ceased growth later at the end of the growing season and was thus more liable to fost damage than provenances from a more northerly latitude. Provenance 12057 originates from latitude 42° 28' and longitude 124° 24'W. It may thus exhibit a similar growth pattern to the corresponding *Picea sitchensis* provenance and will therefore be liable to frost damage on frosty sites. This appears to be the case with the provenance at Wark, the more frosty of the two sites, where the provenance had a very poor growth performance. In contrast, it had an exceptionally relative superior performance at Drum. The region of southern coastal Oregon may not therefore be suitable for the choice of provenances.

Inland populations of many species in North America are supposed to be more frost hardy than coastal populations (Sakai and Weiser, 1973). In contrast, the results of the frost damage scores of the grand fir provenances from the coastal and inland areas of the species range does not seem to agree with this general observation. However, the provenance 12034 from Idaho appears to be an exception. This provenance is the most frost tolerant among the ten provenances that were tested, indicating that it has an inherently high level of frost tolerance. Larsen (1978) working on a grand fir provenance trial based on the IUFRO seed collection reported a similar result that a provenance from Idaho was very resistant to late frost. The relatively poor growth performance of this provenance may therefore be attributed to other factors other than frost tolerance, perhaps its continental climatic adaptation.

The provenance 74(2002) which has undergone a generation of selection in Britain had relatively high frost damage score compared with 12040 which is also a provenance from British Columbia the region from which 74(2002) is reported to have originated. Edwards(1953) observed that seedlings from seeds of *Picea sitchensis* collected in Britain were unusually frost tender. In view of this earlier observation and the high frost damage score of this provenance it may be worthwhile to conduct further studies on the frost tolerance of this provenance.

The frost hardiness investigation has provided a complementary study to the earlier investigation on the growth potential of grand fir provenances. As pointed out previously, growth potential and frost tolerance adaptations are essential in the choice of provenances. The two studies have indicated the suitability of provenances from coastal Washington and British Columbia as they appear to combine both adaptations. The sampling of needles for the frost hardiness, was conducted only once. The results of frost tolerance is therefore based on scores of hardiness at one point in time. Because of daily and seasonal fluctuations in the levels frost hardiness sampling and testing for hardiness in the different seasons may give more information on frost hardiness of grand fir provenances. The provenance 74(2002) has a high growth potential but a further study on its frost hardiness status is essential because of the limitation on the study imposed by testing for frost hardiness at one point in time. Similarly, further studies on the daily and seasonal variation in frost hardiness of provenances from Washington and British Columbia will yield more information on making suitable provenance choices within these two groups.

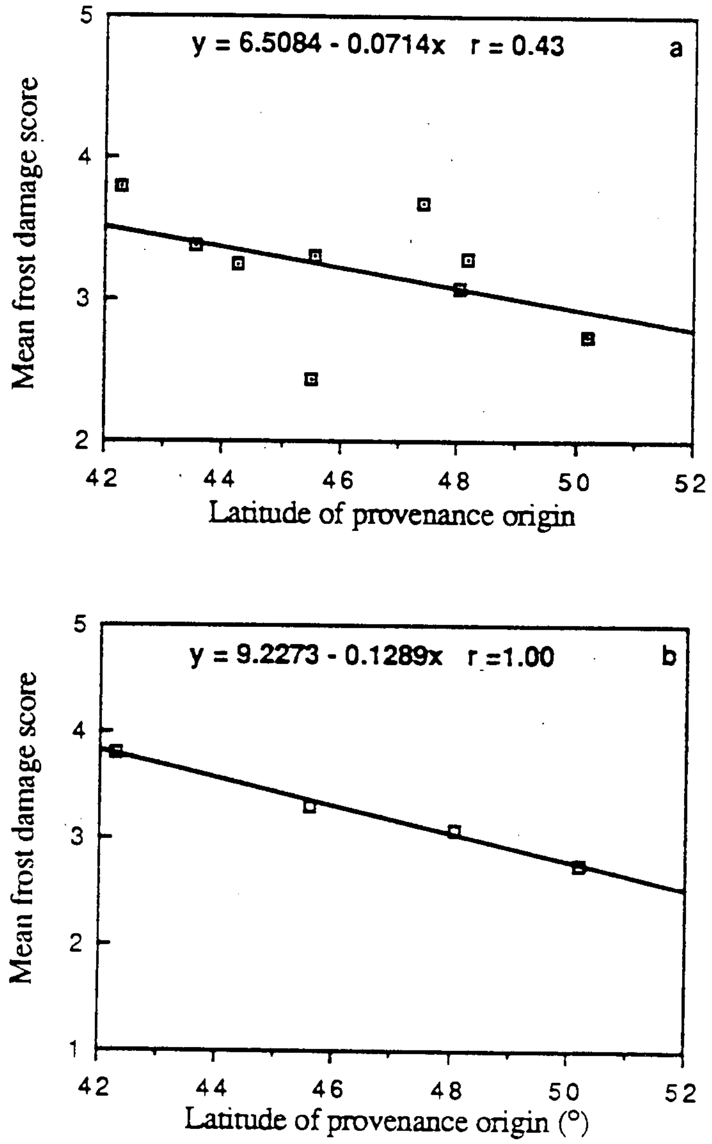


Figure 4.2 Relationship between mean frost damage score and latitude of provenance origin. **a.** in nine provenances from entire range of grand fir. **b.** in four coastal provenances of grand fir.

CHAPTER 5

Provenance variation of pilodyn penetration as an indirect measure of wood density in grand fir (*A. grandis*)

5.1 Introduction

Wood density is the weight of wood expressed per cubic volume. Its importance as a characteristic influencing nearly all wood products has been recognised (Zobel and Talbert, 1984). In solid wood products, the strength properties are generally positively correlated with wood density; similarly pulp yields and quality are related to wood density (Koch, 1972; Armstrong, 1953; Lavers, 1969). The establishment of large forest plantations with attention focussed primarily on growth potential characteristics of tree species but not wood quality traits including wood density, may result in the production of high volumes of wood with inferior wood quality, resulting in economic loss in a forest plantation enterprise (Ladrach, 1986). Therefore the search for planting material for plantation establishment should put some emphasis on the quality of the wood produced and its suitability for the desired end use. One of the several options available for controlling the density of wood grown as a raw material is the utilisation of geographic variation in wood quality (Stahl, 1988). Provenance variation in wood density has been well documented (Zobel and Talbert, 1984; Dorman, 1976; Ladrach, 1986; Posey et al., 1970; Bryam and Lowe, 1988). Wood density may differ for provenances growing in-situ and when grown under plantation conditions (Talbert and Jett, 1981). For provenances used as exotics an evaluation of wood density may therefore assume greater importance.

Grand fir is a species which generally has low density wood. Growing in-situ a wood density estimate of 445 kg/m^3 has been reported (Mullins and Knight, 1981). As an exotic in Britain, Brazier (1973) estimated the nominal specific gravity as 0.31. Because of its generally low wood density, the utilisation of provenances with high wood density as well as acceptable wood yield will be of importance. This chapter has the objective of studying the patterns of variation in wood density in the grand fir provenances and relating them to the growth potential on the two sites mentioned in chapter two, to find provenances that may combine both high growth potential and better wood density. Pilodyn penetration into standing trees will be used as an indirect measure of wood density.

5.2 Wood density variation within trees

Within-tree variation in wood density both radially and longitudinally has been described. Panshin and De Zeeuw (1980), classify variation in wood density in the radial plane into three types;

1. increase in density from the pith to the bark.
2. decrease in density outward from the pith to a certain growth ring and then an increase toward the bark.
3. decrease from the pith to the bark.

The first pattern of variation is the most common found in tree species among the three. In *Pinus taeda*, Zobel and Talbert (1984) reported a trend in wood density variation similar to the first classification. Increase in wood density from the pith towards the bark has been similarly reported for *Pinus patula*, (Ladrach , 1986) and *Pinus radiata* (Cown, 1974). Brazier (1967) and Wood (1986), both working on *Picea sitchensis*, reported a decrease in wood density from the pith up to a certain growth ring limit and then an increase toward the bark. Koch (1967) noted a similar trend in radial wood density variation for *Prunus serotina*. In some conifers, wood density decreases from the base of the tree to the top, but in others, there in no marked decrease with height. Spurr (1954) noted a pronounced decrease in wood density from the base of the tree to the top in Jack pine. Wood (1986) could not establish a relationship between tree height and wood density in Sitka spruce.

5.3 Anatomical features and wood density

The anatomical features of wood have an influence on density. The proportion of earlywood to latewood as well as juvenilewood to maturewood affects the density of wood. Cells formed in the early period of active growth during the growing season constitute earlywood, while those laid down by the cambium towards the end of the growing season constitute latewood. While the former is characterised by large-lumen, thin-walled cells, the latter has smaller-lumen, thick-walled cells. Trees with a high proportion of latewood cells tend to have higher wood density than those with a high proportion of earlywood cells (Butterfield and Meylan, 1980). Trees that inherently produce latewood early in the growing season will have an overall higher density than those producing them late in the growing season (Zobel and Talbert, 1984). The relative proportion of juvenile and maturewood also influences the wood density. Juvenilewood generally occur in the first 10-20 annual growth rings but varies with species. This wood has low density and strength properties, therefore a high proportion in wood will result in lower wood density (Senft, 1986).

5.4 Other factors affecting wood density

The effect of growth rate of a tree on the wood density is variable depending on the species and the environment, including soil properties, moisture availability and other factors (van Buijtenen, 1986; Cown, 1974). For species in the genera *Abies* and *Picea*, faster growth is believed to result in lower wood density (Zobel and Talbert, 1984). In *Picea sitchensis*, Brazier (1970) noted that vigour or faster growth resulted in lower wood density. He found that the proportion of earlywood to latewood was high within the growth rings and thus resulted in lower density wood. Ladrach (1986) working on tropical pines found no significant relationship between wood density and growth rate in *Pinus patula, Pinus oocarpa*, and *Pinus kesiya.* For *Prunus serotina*, Koch (1967) reported a finding similar to that of Ladrach (1986).

Wood density varies for provenances and between sites, but provenance and site interaction has been found to be negligible (Wright, 1990; Barnes et al., 1977). These authors reported a significant correlation between wood density and site temperature. Wright (1990) reported also a significant relationship between wood density and provenance altitude and latitude. Stahl (1988) reported site differences in wood density across a range sites for *Pinus sylvestris.* He found that wood density was low at high altitude and latitudes. As noted previously, the effect of growth rate on wood density is variable depending on the species, but for trees of the same age growing on a more or less uniform site, Zobel and Talbert (1984) noted that the trees with faster growth rate may have higher or lower wood density because of the large between tree variation in wood density.

5.5 Measurement of wood density using the pilodyn

Wood density is an important timber characteristic that requires investigation in tree improvement programmes. However, because the conventional methods of assessing this important characteristic are time consuming and expensive, it is often not assessed (Cown, 1978). This may lead to the establishment of large areas of forest plantations that subsequently produce wood of inferior quality for the desired end use.

Wood density is usually determined by taking wood samples of increment cores with an increment borer. The volume of the core samples are determined by immersion in a fluid and measuring the volume of fluid displaced by the samples. The mass of the samples are determined by drying in an oven at predetermined temperatures to standard moisture content and measuring the weight of the dried samples. The density of the samples can then be determined from the volume and mass measurements. Alternatively, X-ray scanning techniques can be used to determine the density of wood from samples (Koch, 1972; Adams et al., 1990).

The above methods for the determination of wood density yield better estimates but are time consuming, expensive and may require destructive sampling. They are therefore impossible to use when a large number of genotypes have to be screened very quickly for wood density in the field. A method that gives relatively a less accurate measure of wood density than the methods described above but facilitates a fairly rapid assessment of wood density for a large number of trees in the field is the use of the pilodyn (Cown, 1978; Adams et al., 1990). The pilodyn is a hand-held instrument that measures wood density indirectly in the outer rings of standing trees. It injects a spring-loaded striker pin into the wood. The depth of penetration of the striker pin is inversely propotional to the wood density and is read off a scale on the body of the instrument. Features of the instrument are shown in Plates 5.1 and 5.2.

The pilodyn is particularly useful in young stems where bark removal is easy and rapid, but in contrast it can be time consuming in older trees with thick bark which will have to be removed with a chisel. Additionally the instrument causes negligible damage to standing trees compared to the removal of increment cores (Cown, 1978)

Plate 5.1 The pilodyn: showing the body of the instrument and the pin.

Plate 5.2 The pilodyn: showing the scale that registers the depth of pin penetration in millimetres.

5.6 The pilodyn and wood density

An indirect relationship between outerwood density and pilodyn penetration has been established and widely reported in the literature. Cown (1978) found a significant correlation ($r = -0.96$) between pilodyn measurement and outerwood density in 10 year-old clones of *Pinus radiata.* In the same work, he studied the relationship between outerwood density and pilodyn penetration for 25 trees of a 31 year-old plantation of the same species and reported a significant correlation of -0.81. Working on *Pinus taeda*, Taylor (1981) found a significant correlation ($r = -0.81$) for the two characteristics mentioned above in a 21 year-old plantation. Similar findings have been reported by Micko et al. (1982), for *Picea glauca* (a significant correlation of -0.83), Gough and Barnes (1984) in *Pinus elliottii* (a significant correlation of -0.87), Adams et al. (1990) for *Pseudotsuga menziesii* (a significant correlation of -0.90). All these findings suggest that the pilodyn can be used sucessfully to assess the outerwood density.

These correlations were all based on pilodyn measurements taken under bark - after a strip of bark had been removed. Micko et al. (1982) compared correlations based on readings taken underbark and overbark. They noted that correlation based on the latter was lower, but still significant. Gough and Barnes (1984) compared correlations between pilodyn penetration and outerwood density to pilodyn penetration and whole tree density in *Pinus elliottii.* They found the correlation between pilodyn penetration and whole tree density to be the lower of the two. Nevertheless the relationship was significant. Wood (1986) reported a similar finding with a highly significant correlation between pilodyn penetration and whole tree density in *Picea sitchensis.*

The pilodyn may facilitate the rapid screening of density of a large number of trees in the field but for more accurate wood density estimates the traditional methods for determining wood density will be indispensable. The interpretation of pilodyn measurements between narrow limits may be subject to error due to the relative insensitivity of the scale of the pilodyn which makes it impractical to make measurements within the limits of less than 0.5mm (Cown, 1978), though small differences between pilodyn values may represent large differences in wood density. For example, in *Pinus radiata* Cown (1978) indicated that 1mm difference may represent a difference in density of 20 kg/m^3.

There are conflicting opinions on the number of pilodyn readings that should be taken on each tree. Gough and Barnes (1984) found a close correlation between two readings on the same tree. Similarly, Sprague et al. (1983) reported little within tree variability in needle penetration with readings varying within 1mm on each tree. In contrast, Micko et al. (1982) and Taylor (1981) found considerable differences between readings taken on the opposite sides of the same tree and thus recommended that multiple readings be taken. The differences might have arisen because of the different tree species on which these were working. These differences in opinion on the number of reading that need to be taken, suggest that perhaps for different species the necessity of taking multiple readings need to be assessed.

5.7 Assessing the need for multiple pilodyn measurements in grand fir

Eighty provenance plot boundary trees of grand fir were randomly chosen and two pilodyn measurements made underbark on the opposite sides of each tree. These measurements were made at breast height or as close as possible to breast height. A 6 joule pilodyn with a 2.5 mm needle shown in Plate 5.1was used. The readings were taken to the nearest 0.5 mm

The measurements were analysed using the analysis of variance model from shown below from Sokal and Rohlf (1969);

$Y_{ij} = m + A_i + E_{ij}$, where,

Y_{ij} is the j^{th} item of the i^{th} pilodyn penetration group,

m is the mean pilodyn measurement for the population,

A_i is the random contribution of the i^{th} pilodyn penetration group,

and E_{ij} is the error term of the j^{th} item of the i^{th} group.

The results of the analysis is shown is Table 5.1 below.

Table 5.1 Results of ANOVA for pilodyn penetration of 80 grand fir trees

SOURCE	DF	SS	MS
Tree	79	878.736	11.123
Residual	80	135.357	1.692
Total	159	1014.111	

Based on the results of the analysis of variance, the repeatability of the measurements was calculated using the concept and relationship from Falconer (1989) and Falconer (1983) based on intraclass correlation shown below;

$r = A / A + B$ (1)

where r is the intraclass correlation,

A is variance component between trees, represented by the tree mean square (MS) in the ANOVA table above,

B is the variance component within trees represented by the residual mean square (MS) in the ANOVA table above.

The variance component of pilodyn measurements between trees has a within tree component and is represented by the relationship,

B + 2A where B represents the within tree variance component and the coefficient of the between tree variance is due to the fact that two readings were taken on each tree. Therefore the between tree variance component A is calculated as follows,

$A = (11.123 - 1.692)/2 = 4.7155.$

The repeatability of the pilodyn measurements as represented by the intraclass correlation (r) based on equation 1 is calculated as,

$r = 4.7155/4.7155 + 1.692 = 0.736.$

This high intraclass correlation (r = 0.736) suggests that little will be gained in accuracy from multiple measurements with the pilodyn measurements in the trees of grand fir (Falconer, 1989). As a rule and in agreement with the findings of Gough and Barnes (1984) and Sprague et al. (1983), the within tree pilodyn measurements were within 1mm of the other and consequently had a high correlation. Pilodyn measurements of the provenances were therefore limited to one underbark reading at breast height or as close as possible to breast height.

5.8 Data collection and analysis of pilodyn measurements

Pilodyn measurements were made on the inner nine trees in each of the 25(5*5) provenance plots on each of the two sites. A single pilodyn measurement was taken after a strip of bark had been removed at breast height or as close as possible to breast height. The measurements were made to the nearest 0.5mm. For each plot the mean pilodyn value was calculated and used in the subsequent analysis of variance. The means were used in the analysis following Cown's (1978) suggestion that errors imposed on the interpretation of pilodyn values due to the relative insensitivity of the scales of the instrument in making distinctions between values within narrow limits will tend to be negligible when means of a large number of samples are used instead of the use of single tree values which will result in larger errors.

The pilodyn data was arranged in a hierachical manner as follows;

Population

Group

Provenance.

The three categories have the same definition as explained in Section 3.2.2. A nested anova model similar to that described previously in Section 3.2.3.1 was used to analyse the pilodyn data. The provenance 74(2002) was included in this analysis. This was to make possible a comparison between the pilodyn measurements of this provenance and those of the other provenances. Due to the fact that this provenance has undergone a generation of selection outside the range of the species it was assumed that it belonged to a group different from those of the other provenances. The objective of the analysis was to determine the relative contributions of the various levels of variation into which the provenances have been partitioned.

Secondly a covariance analysis based on the nested model was computed. The growth rate of a tree may be linearly related to the wood density. If this assumption is true in the case of grand fir, then it will be expected that pilodyn measurements at breast height will be linearly related to the radial growth as measured by diameter at breast height - Dbh. In order to determine whether such a relationship existed in grand fir provenances, a covariance analysis combining analysis of variance and regression techniques based on the nested model used above was computed. By putting Dbh into the analysis as a covariate it was possible to determine whether it had any influence on the pilodyn values and also the nature of the relationship and whether the pattern of change was different from that found in pilodyn values that had not been adjusted for differences in Dbh.

A third analysis of variance based on the model in Section 3.6.2.1 attempted to seperate the differences of the main effects provenance groups and site as well as the interaction between these two factors.

5.9 Results

5.9.1 Results of ANOVA and covariance analysis for pilodyn measurements at Wark

The results of the analysis of variance and covariance for pilodyn measurements are presented in Tables 5.2 and 5.3. The means of the pilodyn values from the two analyses are presented in Table 5.6. The results in Table 5.2 indicate highly signficant differences within provenance groups and among provenances. In contrast there are no significant differences among the provenance groups. The block effects are also highly significant.

An examination of Table 5.6 shows differences in mean pilodyn values among provenances and within provenance groups. Provenance 12042 has the lowest mean pilodyn value while 12051 has the highest mean value. Provenances with relatively lower mean pilodyn values include 12056, 12057, 12001, 12004, 12005, 74(2002), 12011 and 12013. On the other hand provenances 12051, 12018, 12015, 12040 and 12052 have relatively higher mean pilodyn values. The pilodyn means of the remaining provenances vary between those of these two sets of provenances. The mean values of provenances within groups 2, 7 and 10 generally appears to be lower than those in the other groups.

The pattern of the results of the covariance analysis is similar to that of the analysis of variance. The result of this analysis is presented in Table 5.3. After adjustment in pilodyn values for differences in Dbh, the block effects are still highly significant. There are no significant differences between the provenance groups. Significant differences are however found among provenances within groups and among provenances. The significance of differences among provenances within groups is not at as high a probability level as it was prior to the adjustment for the covariate. The covariate removes a highly significant proportion of the variation in the pilodyn measurements. This seems to indicate a linear relationship between Dbh and the pilodyn values.

The adjusted pilodyn means of provenances are presented in Table 5.6. In general, provenance mean pilodyn values are adjusted either downwards or upwards. A close examination of the table shows that provenances in groups 1, 7 and 10 which have relatively fast growing provenances on this site, generally, have their pilodyn values adjusted downwards. In contrast the other provenances with relatively slower growing provenances have pilodyn values adjusted upwards. This suggests a positive relationship between mean pilodyn values and Dbh.

5.9.2 Results of ANOVA and covariance analysis for pilodyn measurements at Drum

The results of the analyses of variance and covariance are presented in Tables 5.4 and 5.5. The mean pilodyn values for the respective analysis are presented in Table 5.6. The results of the analysis of variance indicates highly significant differences in pilodyn values among provenances within groups and among provenances. There are no statistically significant differences among blocks and provenance groups.

Provenance 12042 has the lowest mean pilodyn value while provenance 12051 has the highest mean pilodyn value among all the provenances as the pilodyn means in Table 5.6 indicate. Provenaces with relatively lower pilodyn measurements include 12002, 12005, 12006, 12008, 12009 and 12045. In contrast provenances 12012, 12015 12018 and 12019 have relatively high mean pilodyn values. The remaining provenances have their mean pilodyn values varying between those of these two sets of provenances. There is a wide variation among provenances and thus no pattern of differences is clearly evident from the table between fast and slow growing provenances.

The covariance analysis shows highly significant differences among provenances within groups and among provenances. There are no significant differences between provenance groups and between blocks. The covariate removes a highly significant proportion of the variation in the pilodyn measurements. The adjusted pilodyn means presented in Table 5.6 indicate that mean values of provenances from groups 1, 7, 8, 9 and 10 which are relatively fast growing generally decrease, while those of the other groups that are relatively slow growing increase. The adjustments in the pilodyn mean values of the two sets of provenances suggest a positive relationship between Dbh and the pilodyn values as at Wark.

5.9.3 Results of ANOVA for provenance * site interaction for pilodyn measurements

The results of the analysis of variance examining variation between provenances, sites and the interaction between the two factors is presented in Table 5.7. The results indicate highly significant differences between blocks, sites and provenances. The interaction term partitioned into interaction between site and provenance groups and site and provenance within group is not significant.

The significant differences among provenances within groups and among provenances is in agreement with the results of the separate analysis computed for each of the two sites. The greatest proportion of the variation is however, accounted for by the differences between the two sites. The site factor accounted for approximately 60% of the total variation. A comparison of means between the two sites suggest that mean pilodyn values generally increased from Wark to Drum

Table 5.2 Results of ANOVA pilodyn measurements at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	27.717	13.859	12.36	0.01	66.94	77.55
Grp	9	25.098	2.789	0.95	n.s.	13.47	-
Grp.Prov	23	67.450	2.933	2.62	0.01	14.17	-
Prov	32	92.548	2.892	2.57	0.01	-	16.18
Plot	64	71.717	1.121			5.410	6.27
Total	98	191.983					

Table 5.3 Results of covariance analysis for pilodyn measurements at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	27.7025	13.85	14.90	0.01	41.12	45.36
Grp	9	32.5639	3.618	1.85	n.s	10.74	-
Grp.Prov	23	44.9134	1.953	2.11	0.05	5.80	-
Prov	32	77.4773	2.421	2.61	0.01	-	7.93
Covariate(Dbh)	1	13.3338	13.334	14.39	0.01	39.59	43.67
Plot	63	58.3745	0.9266			2.75	3.03
Total	98	191.9723					

Table 5.4 Results of ANOVA for pilodyn measurements at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	5.199	2.599	2.23	n.s.	22.58	35.45
Grp	9	41.654	4.628	1.52	n.s.	40.20	-
Grp.Prov	23	69.898	3.039	2.43	0.01	26.40	-
Prov	32	111.552	3.486	2.79	0.01	-	47.55
Plot	64	79.749	1.246			10.82	17.00
Total	98	195.501					

Table 5.5 Results of covariance analysis for pilodyn measurements at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	5.198	2.599	2.23	n.s	14.42	19.10
Grp	9	44.267	4.919	1.57	n.s	27.29	-
Grp.Prov	23	72.185	3.138	2.69	0.01	17.41	-
Prov	32	116.452	3.64	3.12	0.01	-	26.76
Covariate (Dbh)	1	6.199	6.199	5.31	0.05	34.40	45.56
Plot	63	73.551	1.167			6.48	8.58
Total	98	196.501					

Table 5.6 Means of pilodyn penetration from ANOVA and covariance analysis for pilodyn measurements from the two sites

PROV ID	Wark	Wark*	Drum	Drum*
12001	16.074	16.231	17.963	17.967
12002	16.224	15.431	16.444	16.333
12003	17.298	16.727	18.145	18.047
12004	16.225	16.137	17.768	17.478
12005	17.130	16.361	16.667	16.377
12049	16.630	16.767	18.664	18.660
12051	19.474	18.995	19.576	19.313
74(7973)	17.532	16.922	18.691	18.551
Mean	17.073	16.692	17.990	17.841
12006	16.540	15.567	16.242	16.489
12007	17.519	17.301	17.114	17.297
12008	16.519	16.608	16.437	16.497
12009	16.438	16.681	16.876	16.995
12011	16.066	16.250	18.000	18.098
12012	16.675	16.904	18.806	18.886
12013	16.099	16.406	17.554	17.809
Mean	16.550	16.674	17.290	17.439

* Represent mean pilodyn value adjusted for the covariate (Dbh)

Table 5.6 (cont)

PROV ID	Wark	Wark*	Drum	Drum*
12024	17.450	17.989	17.429	17.814
12016	16.743	17.341	16.722	16.972
12018	18.195	18.633	18.811	18.979
12020	17.140	17.438	17.473	18.053
Mean	17.360	17.804	17.669	18.001
12034	17.875	18.273	17.941	18.227
12015	18.290	18.020	19.202	19.247
12019	16.663	16.820	18.788	18.582
12021	16.962	17.547	19.370	19.550
Mean	17.305	17.462	19.120	19.126
12040	18.127	17.546	18.145	17.995
12042	14.550	14.754	15.626	15.302
12043	16.827	16.712	17.382	17.403
12045	15.960	15.713	16.223	16.370
12047	16.686	16.372	17.241	16.914
Mean	16.376	16.219	16.923	16.797
12052	18.301	18.168	18.338	18.099
12053	16.609	16.994	18.026	18.169
Mean	17.445	17.556	18.182	18.134
12056	15.492	15.596	17.209	16.866
12057	15.687	15.609	17.415	17.010
Mean	15.590	15.602	17.317	16.938
74(2002)	16.221	16.193	17.742	17.694

* Represent mean pilodyn values adjusted for the covariate (Dbh)

Table 5.7 Results of ANOVA for Provenance * Site interaction for pilodyn measurements

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	4	32.437	8.109	7.07	0.01	15.17	16.83
Grp	9	50.957	5.662	1.32	n.s	10.59	-
Grp.Prov	23	98.325	4.275	3.73	0.01	8.00	-
Prov	32	149.282	4.665	4.07	0.01	-	9.68
Site	1	31.528	31.528	27.49	0.01	58.98	65.43
Site*Grp	9	12.99	1.444	1.26	n.s.	2.70	3.00
Site*(Grp.Prov)	23	29.717	1.292	1.13	n.s.	2.42	2.68
Plot	128	146.754	1.147				2.38
Total	97	402.714					

5.10 Discussion

5.10.1 Provenance variation of pilodyn penetration of grand fir

The wood of grand fir is described as light, with low density. Estimates of wood density of trees growing in-situ have been given as 445/kg m^3 (Mullins and Knight, 1981). Grown as an exotic in Britain, Brazier (1973), estimated the nominal specific gravity (oven dry weight/ green weight) of ten trees per site, for ten sites as 0.31. He reported a wide variation in wood density between the sites. The range of specific gravity variation being 0.22-0.39. In their review of the potential of grand fir in Britain, Aldhous and Low (1974) noted that the species has faster growth rates on good sites. This faster growth rates achieved by the species tend to result in the wood produced being of inferior quality (Kleinschmit, 1978). In discussing the choice of provenances for reforestation, Fletcher and Samuel (1990), speculated that the use of slower growing provenances on better sites may result in the production of timber of higher density. As a result of this speculation, the present study related the outerwood density as measured by pilodyn penetration to the growth potential measured by the basal area per hectare (G/ha) rank, with the view of determining whether some meaningful relationship existed between the two traits.

The analysis of variance for growth potential of provenances at Wark in chapter 3 indicated significant differences among the provenance groups but not between provenances within a group. The results of the ANOVA for the pilodyn measurements from this site in the previous section in contrast show significant differences between provenances within groups. This contrast between the two analyses seems to suggest that fast or slow growing provenances can have either relatively higher or lower wood density.

The relationship between mean pilodyn values and the growth potential ranks of provenances at Wark is shown in a scatter diagram in Figure 5.1. The figure indicates a wide degree of variation among provenances for pilodyn mean values irrespective of the growth potential rank. Figure 5.1 can be divided into three regions based on the growth potential ranks of the provenances for the purpose of making comparisons among the provenances. Each region starting from the highest ranked provenance can have at least ten provenances. Within the first region with the ten highest ranking provenances for growth potential, there is a wide variation in the mean pilodyn values. Provenances 12002, 12005 and 74(2002) have relatively lower pilodyn values compared to provenances 12040 and 12051. The pattern of differences is similar for the remaining regions. Comparison between regions also indicate that some of the fastest growing provenances can have relatively lower pilodyn values compared with slow growing provenances, similarly, the converse is true. Thus for the provenances growing on this site provenances with faster growth rates have either higher or lower wood density because of the large among provenance variation in wood density (Zobel and Talbert, 1984).

The covariance analysis after making adjustment for differences in diameter (Dbh) thus removing the effects of differences in growth rates indicated significant differences among provenances within groups and among provenances. The adjusted means which gives estimates of pilodyn values unaffected by differences in growth rates in the provenances generally increased or decreased when compared with the unadjusted mean values in Table 5.6. Faster growing provenances in groups 1, 7 and 10 had their pilodyn mean values generally adjusted downwards while relatively slow growing provenances had pilodyn mean values adjusted upwards. With the covariate removing a significant proportion of the variation in pilodyn measurements, the directions of the adjustments in the mean values of the fast and slow growing provenance appear to suggest an inverse relationship between the growth rates as measured by Dbh and wood density as measured by the pilodyn. Therefore faster growing provenances tend to have lower wood density while slower growing provenances have relatively higher wood density. An examination of the unadjusted mean pilodyn values suggest that some of the faster growing provenances have lower mean pilodyn values than some slower growing provenances. Thus while adjustment for the covariate removes a significant proportion of the variation in pilodyn measurements the pattern of differences in the adjusted and unadjusted mean pilodyn values does not seem to be different. For practical purposes of making selection among provenances based on the pilodyn values the adjusted means will be of limited value due to the fact that the density of the wood produced is better represented by the unadjusted pilodyn mean values. Nevertheless, the covariance analysis has given an indication that the rate of growth as well as other factors may influence the density of wood.

At Drum, the analysis of variance for growth potential indicated significant differences among provenance groups. There were no significant differences between provenances within groups. In contrast for pilodyn measurements significant differences are among provenances within groups and not between groups. The contrast between the two analyses similar to the results obtained from the data for Wark, suggest that growth potential and pilodyn measurements may not be directly related.

The relationship between pilodyn measurement and the growth potential ranks of provenances is illustrated in Figure 5.2.. As shown in this figure there are large differences in pilodyn values between provenances. Faster growing provenances may have comparable or lower pilodyn values than slower growing provenances. Thus like the observation made among provenances at Wark faster gowth may result in lower or higher wood density for provenances growing on a more or less uniform site (Zobel and Talbert, 1984).

On this site, the covariance analysis after making adjustment for differences in diameter indicated that significant differences existed among provenances within groups and among provenances for pilodyn values. The covariate removed a significant proportion of the variation in pilodyn measurements. Adjustment for differences in growth rates resulted in the pilodyn means of faster growing provenances in group 1, 7, 8, 9 and 10 decreasing while the means of slower growing provenances generally increased as a comparison between unadjusted and adjusted mean pilodyn values in Table 5.2 indicate. Thus suggesting a positive relationship between Dbh and mean pilodyn values.

The covariance analysis has indicated that the density of grand fir is affected by the growth rate and other factors. The results in this study which suggested that increase growth rate may result in lower wood density in grand fir is in agreement with similar results reported in *Pinus patula* (Zobel et al, 1987). Similarly, in *Picea sitchensis* Brazier (1967) noted a decrease in wood density with increasing growth rate.

Besides the growth rate several other factors might have resulted in the variation in the wood density of the provenances as measured by the pilodyn on each of the two sites. Zobel et al. (1987) mention moisture availability and distribution within a site, the moisture content of the soil, soil fertility, elevation and latitude of provenance origin and the intensive management of a species as factors contributing to the changes in the wood density of introduced species.

There is a highly significant difference in pilodyn values between the two sites. At Drum where grand fir has a higher growth potential, the mean pilodyn values of provenances are generally higher than corresponding values at Wark. It has to be borne in mind that the values for Drum will tend to be a bit exaggerated because of the year differences in the taking of measurements between the two sites. Brazier (1973) reported differences in the wood density of grand fir growing on different sites. The differences in wood density is perhaps due to differences in the soils between the two sites. Wark has a peaty gley soil while Drum has a surface water gley soil. Differences in wood density between sites have similarly been reported in *Pinus sylvestris* (Stahl, 1988).

There are a few provenances which show a decrease in pilodyn values between the two sites. These include 12005, 12006, 12007 and 12008. All these provenances have higher growth potential at Drum than at Wark and yet show a decrease in pilodyn values. It therefore appears that for these provenances wood density may increase with increased growth rate. Provenance 12002 a faster growing provenance maintained relatively low pilodyn values between the two sites and seemed to have relatively inherently high wood density. Similarly, provenance 74(2002), one of the fastest growing provenances at Wark, has a relatively low mean pilodyn value. Its pilodyn value is comparatively higher at Drum but in relation to some of the other provenances it has a lower pilodyn value. Provenance 12042, which has the lowest mean pilodyn values on both sites also appears to have an inherently high wood density. In contrast, provenance 12051 which also has a high growth potential, has very high pilodyn values on both sites. It has the highest pilodyn values among all the provenances on each of the two sites and seems to be an inherently low density provenance.

The interaction between provenance and site was neglible in the study. Although the results are in agreement with works by (Wright, 1990) and Barnes et al. (1977), the use of the analysis of variance method may not have been sensitive in determining interactions between provenance and site since only two sites were covered (Skroppa, 1984). For example, from an examination of Figures 5.1 and 5.2, provenances in groups 2 and 6 change markedly in their mean pilodyn values between the two sites indicating some sort on interaction at least between these provenances and the sites. Therefore a more useful approach to examining provenance * site interaction will be the covering of a large number of sites.

Pilodyn measurements are indirectly related to outerwood density as studies in other species have indicated (Cown, 1978; Taylor, 1981; Adams et al., 1990). In this work, pilodyn measurements were made at breast height or as close as possible to breast height. These measurements may therefore be related to the outerwood density at breast height as studies in other species have indicated. However, wood density may not be uniform along the bole of a tree as Spurr (1954) indicated in Jack pine. There was a decrease in wood density from the base to the top of the tree. In such a case a single measure of wood density taken at breast height may not give a good reflection of the whole tree density. In other species however, pilodyn values at breast height have been shown to have significant correlations with whole tree density (Gough and Barnes, 1984; Wood, 1986). Therefore pilodyn measurement at breast height may perhaps give a good indication of the whole tree density in grand fir. The reliability of the use of the pilodyn for the rapid assessment of wood density is suggested by the high intraclass correlation (0.734) of pilodyn measurements between trees of grand fir. This indicate that the pilodyn could be used for the rapid assessment of wood density in the species. A further work which relates pilodyn measurements to the whole tree density of grand fir may be useful in assessing how accurately breast height pilodyn measurements assess whole tree density.

The choice of provenances that combine high growth potential with high wood density in grand fir may be possible due to the fact that some provenances with fast growth have relatively higher wood density. Simultaneous selection for the two traits can therefore be concentrated on provenace groups with a high growth potential. Thus selection's can be made within group 1 which has provenances with the highest growth potential. The land race 74(2002) which is among the fastest growing provenances should be considered because of it relatively higher wood density. The limitation on the density of the wood produced from grand fir will appear to depend on the site on which the species is grown. The evidence from this study suggest that the density of wood produced from sites with high potential for tree growth may be lower. The choice of sites on which the species is planted will therefore be critical. Even on sites with high potential for growth there is still the possibilty of selecting provenances that have inherently high density and high growth potential like provenance 12002 or a provenance that shows an increase in wood density on a site with high potential for growth such as provenance 12005.

The study considered only two sites with large differences in the potential for growth. The changes in pilodyn values may therefore be very abrupt. A further study looking at differences in pilodyn values across a range of sites with gradual changes in

Figure 5.1 Scatter diagram showing the relationship between mean pilodyn measurements and the growth potential rank of provenances at Wark

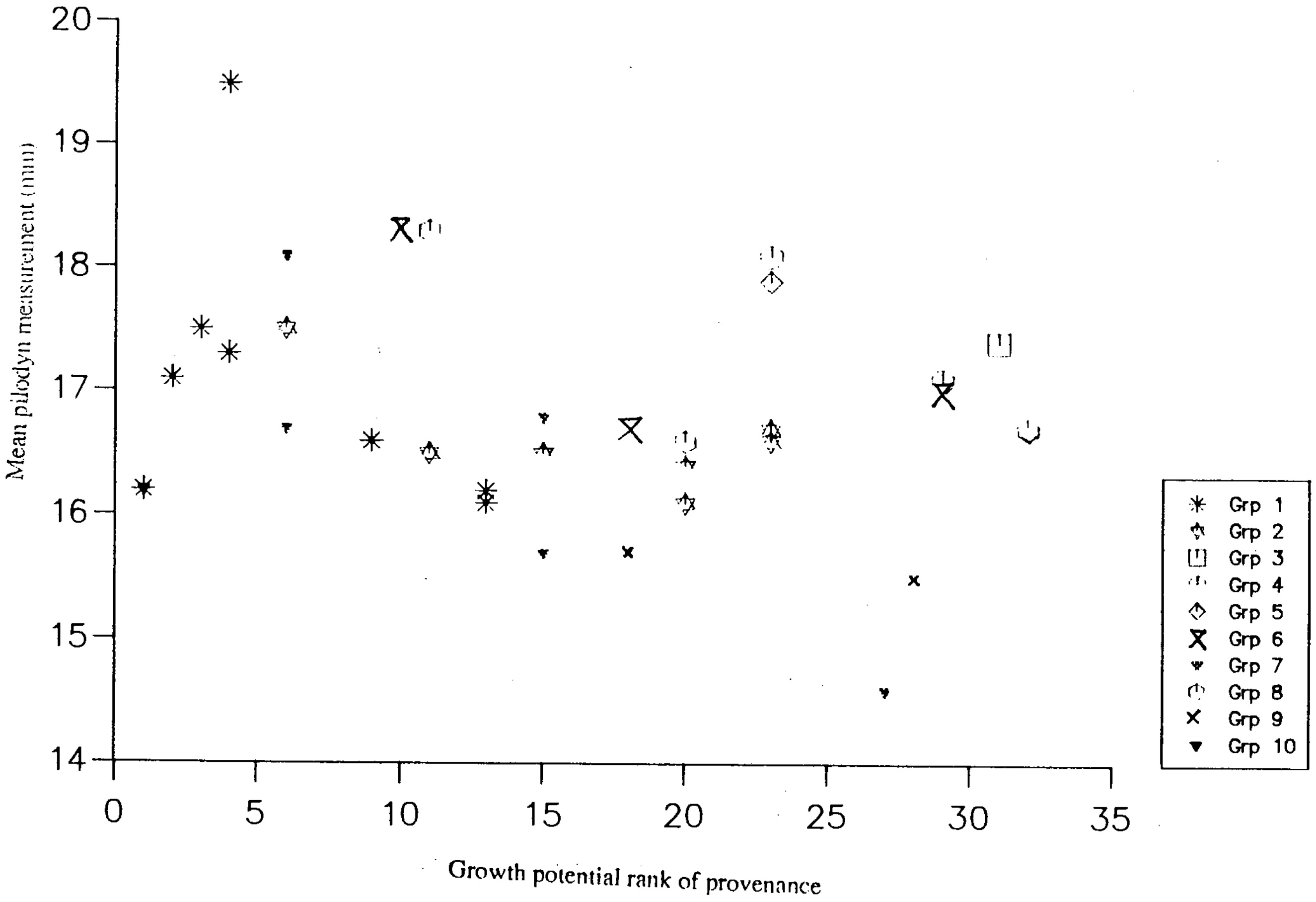
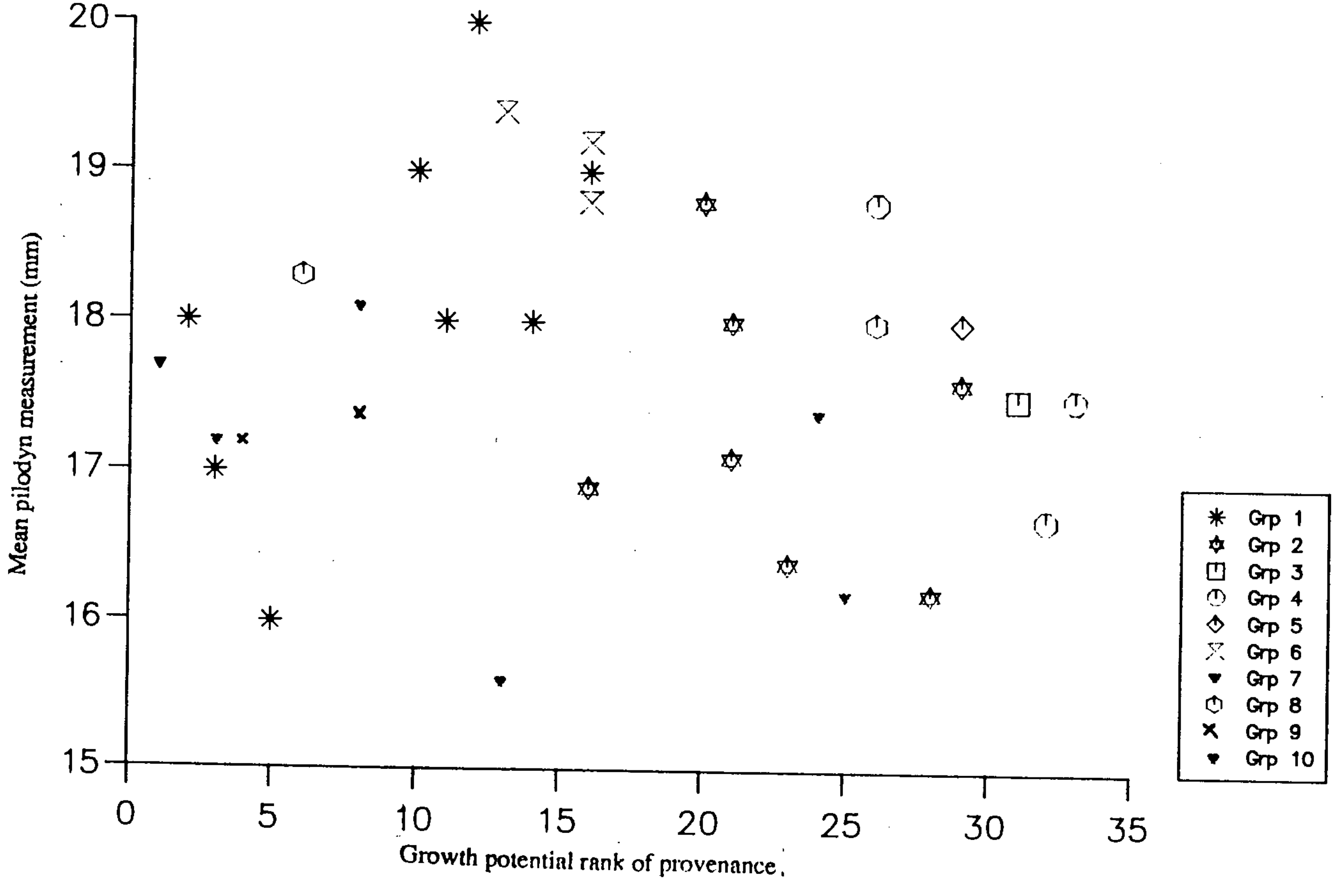


Figure 5.2 Scatter diagram showing the relationship between mean pilodyn measurements and the growth potential rank of provenances at Drum



the growth potential of grand fir may yield more information on the choice of site for high productivity and higher wood density.

The pilodyn may facilitate the rapid screening of density of a large number of trees in the field but for more accurate wood density estimates the traditional methods for determining wood density will be indispensable. Thus while the study have given some indication wood density variation in grand fir a complementary study based on the traditional methods for measuring wood density may yield more accurate estimates of wood density in grand fir.

CHAPTER 6

Provenance variation in stem straightness and branch angle of grand fir (*A. grandis*)

6.1 Introduction

Tree form is an important characteristic which merits an assessment in the search for provenances for reforestation. Zobel and Talbert (1984) indicated that the easiest way to improve wood quality is to develop straighter trees that also have smaller limbs growing at right angles to the tree bole. While these authors were referring to the improvement of tree form through breeding, the screening of provenances for good form within the context of the above authors will be desirable. This chapter of the study therefore concentrate on two tree form traits, stem straightness and branch angle.

6.2 Stem Straightness

Deviations of tree stems from straightness may be classified as lean, crook, twist or sweep, any of these abnormalities in stem straightness reduces the commercial value of the useful part of the stem through the formation of compression wood (Ehrenberg, 1970). Butterfield and Meyland (1980) enumerated a number of disadvantages in timber due to the formation of compression wood. These include:

1. Low tensile strength, modulus of elasticity and impact strength.
2. Relatively higher longitudinal shrinkage than that of normal wood.
3. Inferior paper making properties.

Compression wood therefore has inferior wood properties and in provenance screening, provenances that are likely to produce compression wood due to poor stem form have to be identified and avoided for large-scale planting.

Three kinds of deviations in stem straightness, namely crooks (sinuosity), sweep and lean have usually been assessed either subjectively or through a form of measurement. Kieding and Olsen (1965) and Stahl et al. (1990) both used subjective assessments in examining stem straightness. Perry (1960) counted the number of crooks per unit length of stem to assess straightness. Shelbourne (1963) used the deflection of stems from a straight rod in making an assessment on stem straightness.

6.3 Branch angle

Branch angle which is a measure of the divergence of branches from the main stem greatly modifies tree form and has effects on wood quality. The branch angle is initially determined by the angle of branch elongation during primary growth. Further changes in angle during the life of a branch occurs after the branch has thickened. The subsequent changes may be the result of downward bending due to an increase in the branches own weight, an external load or due to the formation of reaction wood (Jankiewicz and Stecki, 1976). The stresses imposed by these factors may cause a general increase in branch angle annually. Formation of new leaves every year exerts some weight and result in an increase in angle which subsequently decreases following reaction wood formation (Zimmermann and Brown, 1971).

For the production of wood with high quality, trees with wider branch angles are more desirable than those with very narrow branch angles. Branches with wider angles are more easily shed and easily occluded and have less knot volume than branches with narrow angles (Ehrenberg, 1970; Kramer and Kozlowski, 1979). Knots are a source of degrade in wood because the wood in and around knots sometimes have high cellulose and resin content and are in some ways similar to compression wood (Zobel et al., 1987). Branches with wider angles have been reported to result in lower knot size than those with narrow angles in some species. In longleaf pine reported studies indicate that wider branch angles resulted in smaller knot size (Koch, 1972). The branch diameter which is also related to the size of knots has been reported to be influenced by the branch angle. Studies in loblolly pine and slash pine indicated that branches making wider angles had smaller diameters. Bozzuto and Wilson (1988) in their studies on the branching characteristics of Red maple trees found a significant relationship between branch angle and branch diameter. Wider branch angles associated with smaller branch diameter will lead to smaller knot sizes and hence wood of high quality.

6.4 Data collection on stem straightness and branch angle

6.4.1 Ranking stems for straightness

A ranking method based on that used by Keiding and Olsen (1965) was used to assess stems for crooks, The four ranks that were used in scoring the straightness of stems are defined below;

Rank 4:	Absolutely straight without any crooks.
Rank 3:	Straight but with a crook near the base of the tree.
Rank 2:	Two crooks discernible in the main stem
Rank 1:	More than two crooks discernible on the main stem.

The severity of the crooks has not been classified as either small or pronounced, because in most cases, the degree of crookedness was more or less the same, that is the deviation from the vertical was not very marked. Based on the four ranks defined above, the straightness of each of the nine inner trees in each provenance plot was subjectively assessed up to about 50cm below the leader.

6.4.2 Branch angle measurements

Branch angle measurements were made on one branch in the whorl at breast height or nearest to breast height. The branch angle measured with a protractor to the nearest 5° is defined as the angle between the branch and the main stem.

6.5 Analysis of stem straightness and branch angle data

The stem straightness data was analysed using the Kruskal-Wallis (KW) one-way analysis of variance by ranks. The KW test is a non-parametric test that does not rely on the statistical distribution of the data. The stem straightness rank data was not normally distributed and therefore the KW analysis of variance by ranks was appropriate for the analysis of the data. The KW test calculates an analysis of variance for ranked variables by means of an H- statistic. At known degrees of freedom and specified levels of probability, the significance of the H-statistic can be tested. With k samples and the number of individual observations in each sample greater than 5, the H-statistic with k-1 degrees of freedom is well approximated by a chi-square distribution (Siegel and Castellan, 1988).

For each of the two sites variation between provenances was examined in a KW analysis of variance by ranks. Then secondly, an analysis was carried out based on the provenance groups. These two approaches enabled comparisons to be made between individual provenances and also among provenance groups. The proportions of stems within the lower two ranks for straightness used for assessment (1or 2) and the upper two ranks (3 or 4) were also calculated to give a general overview of stem straightness variation among the provenances and also determine which provenances had a high proportion of poorly ranked stems.

The branch angle data was arranged and analysed in a similar manner as that used for the growth potential data in Sections 3.2.2 and 3.2.3.1. A nested ANOVA model was used to analyse branch angle data from the two sites. The use of the nested ANOVA model was to facilitate an examination of the magnitude and importance of the various levels of variation into which the provenances have been partitioned.

The relationships between branch angle and latitude, altitude and longitude of provenance origin, as well as the principal components of these variables were explored in multiple regression analyses. These analyses were done with the objective of determining how the environmental variables considered individually and together as a principal component accounted for the variation in branch angle.

Provenance* Site interaction was examined in an ANOVA, using the model in Section 3.6.2.1 to determine whether there were any changes in branch angle between sites.

6.6 Results of Kruskal-Wallis ANOVA for stem straightness ranks at the two sites

6.6.1 Results of Kruskal-Wallis ANOVA for stem straightness ranks at Wark

The results of the KW ANOVA for stem straightness at Wark is presented in Tables 6.1.1 and 6.1.2. The results in Table 6.1.1 is based on the stem straightness ranks of the thirty two provenances from the grand fir range while the results in the Table 6.1.2 is based on ranks of the provenances groups. There are highly significant differences among provenances as the results in Table 6.1.1 indicates. Many of the provenances have medians of 4 but provenances 12006, 12007, 12021, 12047, 12053, 12056 and 12057 have median ranks of 3. The average ranks for the provenances put on a scale of 1-32 indicate that many of the provenances with median ranks of 3 are at the lower end of the scale. Table 6.1.3 which shows the proportions of stems of each of the provenances in rank 1 or 2 and 3 or 4, indicate that many of the provenances with median ranks of 3 have a relatively high proportion of their stems ranked either 1 or 2. These provenances have the percentages of their stems in ranks 1 or 2 indicated against them: 12057(40%), 12056(23%), 12006(27%), 12047(15%) and 12053(11%). On the otherhand provenance 12007 with a median rank of 3 has only 4% of its stems ranked 1 or 2. The higher proportion of the stems of this provenances are therefore ranked 3 or 4. The median rank of 3 suggests that rank 3 was the predominant rank among stems ranked 3 or 4. Provenances 12003, 12040, 12045 and 12051 have median ranks of 4 but have a relatively high proportion of their stems ranked either 1 or 2 as Tables 6.1.1 and 6.1.3 indicate.

The results in Table 6.1.2 also show highly significant differences among the provenance groups. With the exception of groups 8 and 9 all the other provenances have medians of 4. The average stem straightness ranks ordered on a scale of 1-9 indicate that groups 8 and 9 have the two lowest average ranks

6.6.2 Results of Kruskal-Wallis ANOVA for stem straightness ranks at Drum

The results of the KW ANOVA for stem straightness ranks at Drum is presented in Tables 6.2.1 and 6.2.2. The H-statistic in the former table indicates a highly significant differences between provenances. All the provenances have medians of 4. The average stem straightness ranks ordered on a scale of 1-32 indicates differences among provenances. Provenances 12004, 12002, 12056 and 12057 are at the lowest end of the average rank scale. Table 6.2.3 shows the proportions of stems for each of the provenances ranked 1 or 2 and 3 or 4. With the exception of provenance 12056 all the other provenances have less than 10% of their stems ranked between 1 or 2.

The results of the analysis of variance based on provenance groups in Table6.2.2 similarly indicates significant differences among the groups. All the groups have medians of 4 but the average ranks ordered on a scale of 1-9 indicate that groups 3 and 9 have the lowest average ranks.

Table 6.1.1 Results of Kruskal-Wallis ANOVA for stem straightness of provenances at Wark

PROV ID	Median rank	Average rank
12001	4.0	16
12002	4.0	20
12003	4.0	26
12004	4.0	29
12005	4.0	18
12049	4.0	13
12051	4.0	22
74(7973)5	4.0	15
12006	3.0	31
12007	3.0	25
12008	4.0	12
12009	4.0	2
12011	4.0	10
12012	4.0	8
12013	4.0	17
12024	4.0	9
12016	4.0	14
12018	4.0	5
12020	4.0	11
12034	4.0	2
12015	4.0	1
12019	4.0	4
12021	3.0	24
12040	4.0	23
12042	4.0	5
12043	4.0	7
12045	4.0	21
12047	3.0	28
12052	4.0	19
12053	3.0	27
12056	3.0	30
12057	3.0	32

H = 108 (adjusted for ties) DF=31 SIG =0.01

Table 6.1.2 Results of ANOVA for stem straightness of provenance groups at Wark

Group	Median rank	Average rank
1	4.0	7
2	4.0	5
3	4.0	4
4	4.0	3
5	4.0	1
6	4.0	2
7	4.0	6
8	3.0	8
9	3.0	9

H = 49.95 (adjusted for ties) DF = 8 SIG = 0.01

Table 6.1.3 Proportion of stems ranked (1 or 2) and (3 or 4) for straightness at Wark

PROV ID	Prop (1 or 2)	Prop (3 or 4)
12001	0.15	0.85
12002	0.04	0.96
12003	0.26	0.74
12004	0.12	0.88
12005	0.04	0.96
12049	0.07	0.93
12051	0.15	0.85
74(7973)5	0.08	0.92
12006	0.27	0.73
12007	0.04	0.96
12008	0.00	1.00
12009	0.04	0.96
12011	0.00	1.00
12012	0.00	0.89
12013	0.07	0.93
12024	0.04	0.96
12016	0.00	1.00
12018	0.04	0.96
12020	0.04	0.96
12034	0.04	0.96
12015	0.00	1.00
12019	0.00	1.00
12021	0.08	0.92
12040	0.28	0.72
12042	0.04	0.96
12043	0.08	0.92
12045	0.15	0.85
12047	0.15	0.85
12052	0.07	0.93
12053	0.11	0.89
12056	0.23	0.77
12057	0.40	0.60

Prop - proportion of stems falling into rank categories indicated.

Table 6.2.1 Results of Kruskal-Wallis ANOVA for stem straightness of provenances at Drum

PROV ID	Median rank	Average rank
12001	4.0	19
12002	4.0	28
12003	4.0	13
12004	4.0	31
12005	4.0	1
12049	4.0	8
12051	4.0	6
74(7973)5	4.0	28
12006	4.0	8
12007	4.0	2
12008	4.0	24
12009	4.0	4
12011	4.0	2
12012	4.0	25
12013	4.0	27
12024	4.0	26
12016	4.0	6
12018	4.0	14
12020	4.0	21
12034	4.0	12
12015	4.0	16
12019	4.0	22
12021	4.0	8
12040	4.0	8
12042	4.0	15
12043	4.0	20
12045	4.0	4
12047	4.0	8
12052	4.0	23
12053	4.0	17
12056	4.0	32
12057	4.0	30

H = 87.26 (adjusted for ties) DF =31 SIG = 0.01

Table 6.2.2 Results of Kruskal-Wallis ANOVA for stem straightness of provenance groups at Drum

Group	Median rank	Average rank
1	4.0	7
2	4.0	4
3	4.0	8
4	4.0	3
5	4.0	1
6	4.0	5
7	4.0	2
8	4.0	6
9	4.0	9

H = 35.19 (adjusted for ties) DF = 8 SIG = 0.01

Table 6.2.3 Proportion of stems ranked (1or 2) and (3 or 4) for straightness at Drum

PROV ID	Prop (1 or 2)	Prop (3 or 4)
12001	0.07	0.93
12002	0.07	0.93
12003	0.04	0.96
12004	0.08	0.92
12005	0.00	1.00
12049	0.00	1.00
12051	0.00	1.00
74(7973)5	0.07	0.93
12006	0.00	1.00
12007	0.00	1.00
12008	0.04	0.96
12009	0.00	1.00
12011	0.00	1.00
12012	0.04	0.96
12013	0.00	1.00
12024	0.04	0.96
12016	0.00	1.00
12018	0.00	1.00
12020	0.00	1.00
12034	0.00	1.00
12015	0.00	1.00
12019	0.09	1.00
12021	0.00	1.00
12040	0.00	1.00
12042	0.00	1.00
12043	0.00	1.00
12045	0.00	1.00
12047	0.00	1.00
12052	0.00	1.00
12053	0.04	0.96
12056	0.12	0.88
12057	0.04	0.96

Prop - proportion of stems falling into rank categories indicated.

6.7 Comparison of stem straightness of provenance 74(2002) and provenances in group 7 at the two sites

Provenance 74(2002) was compared to the other provenances in group 7 in a KW analysis of variance to determine how the stem straightness rank of this provenance compares with those of the other provenances in the provenance group to which it is related. The result of the analysis are presented in Tables 6.3 and 6.4 for each of the two sites. There are no significant differences between provenance 74(2002) and the provenances in group 7 at each of the two sites as Tables 6.3 and 6.4 indicate. The average ranks of the provenances ordered on a scale of 1-6 show that provenance 74(2002) has comparatively higher average rank on both sites. The results from both sites suggest that the provenance has good stem form ranking compared to those of the other provenances in group 7.

Table 6.3 Results of Kruskal-Wallis ANOVA for stem straightness ranks of provenance 74(2002) and provenances in group 7 at Wark

PROV ID	Median rank	Average rank
12040	4.0	5
12042	4.0	1
12043	4.0	2
12045	4.0	4
12047	3.0	6
74(2002)	4.0	3

H = 9.92 (adjusted for ties) DF = 5 SIG = n.s.

Table 6.4 Results of Kruskal-Wallis ANOVA for stem straightness ranks of provenance 74(2002) and provenances in group 7 at Drum

PROV ID	Median rank	Average rank
12040	4.0	3
12042	4.0	4
12043	4.0	6
12045	4.0	1
12047	4.0	5
74(2002)	4.0	1

H = 3.75 (adjusted for ties) DF = 5 SIG = n.s.

6.8 Results of ANOVA for provenance branch angle at the two sites

6.8.1 Results of ANOVA for provenance branch angle at Wark

The results of the analysis of variance for provenance branch angle at Wark is presented in Table 6.5. There are highly significant differences between provenance groups and also between blocks. In contrast provenances within groups are not significantly different from each other, however, there are highly significant differences between provenances. Provenance groups accounted for 64% of the total variation.

The mean branch angle values for the provenances are presented in Table 6.7. From this table, provenance groups from the Cascades Mountains - groups 2, 4 and 6, seem to have comparatively wider branch angles than provenance groups from coastal sources - 1, 7, 8 and 9. Similarly, group 5 provenances from the inland part of the species range have wider branch angle than the coastal provenance groups. In contrast group 3 from the inland part of the range has a similar mean branch angle to the coastal groups. Among the provenances, 12019 has the widest mean branch angle - 80.48°, while provenance 12042 had the narrowest angle - 62.22°.

6.8.2 Results of ANOVA for provenance branch angle at Drum

The results of the of the analysis of variance for branch angle at Drum are presented in Table 6.6. There are significant differences at all the levels tested. The provenance groups are significantly different from each other. In contrast to the results obtained at Wark, provenances within groups are highly significantly different from each other. There are also highly significant differences among provenances. Similarly the effect of blocking is highly significant. Like the results obtained at Wark, the greatest proportion of the variation in branch angle resides between the groups which explain 54% of the total variation.

The mean branch angle values shown in Table 6.7 indicate the provenance groups from the inland areas of the grand fir range generally have higher branch angles than provenance groups from the coastal areas. The inland provenance groups including groups 2, 4, 5 and 6 have have branch angle means greater than that for the site. In contrast, group 3 has a mean value less than that for the site. Among the coastal groups only group 8 has an above site average branch angle value.

6.8.3 Results of ANOVA for provenance * site interaction for branch angle

The results of the analysis of variance examining variation among provenances and sites as well as their interaction is presented in Table 6.8. The results indicate highly significant differences between the provenance groups and the sites. There is significant interaction between provenance and site. The interaction term is partitioned into site and group interaction and site and provenance within group interaction. The interaction between group and site is significant while the interaction between site and provenance within group is highly significant. Similarly there is a highly significant difference between the blocks at the two sites. The provenance group factor explains the greatest proportion of the total variation. Besides this factor, site and block effects are the two other factors explaining a relatively larger proportion of the remaining variation.

An examination of Table 6.7 shows that with a few exceptions, branch angle increases from Wark to Drum. The few provenance with a decrease in branch angle between the two sites include 12005, 12007, 12008, 12015, 12019, 12020 and 12057. In some groups, increase in the branch angle between the two sites in about 2° but in others the magnitude of the change is relatively larger. Comparison between provenances in group 2 on one hand and provenances 12049, 12051, 12042 and 12043 may illustrate this observation. Similarly, among the provenances that show a decrease in branch angle between the sites, 12019 exhibits a marked decrease.

Table 6.5 Results of ANOVA for branch angle at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	136.42	68.21	10.71	0.01	28.91	56.49
Grp	8	1216.25	152.03	16.29	0.01	64.43	-
Grp.Prov	23	214.70	9.34	1.47	n.s	3.96	-
Prov	31	1430.95	46.16	7.24	0.01	-	38.23
Plot	62	395.0	6.37			2.70	5.28
Total	95	1962.36					

Table 6.6 Results of ANOVA for branch angle at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	55.764	27.883	4.65	0.05	23.70	39.19
Grp	8	508.648	63.581	3.15	0.05	54.03	-
Grp.Prov	23	464.801	20.209	3.37	0.01	17.17	-
Prov	31	1155.449	37.273	6.22	0.01	-	52.38
Plot	62	371.758	5.996			5.10	8.43
Total	95	1400.971					

Table 6.7 Provenance means of branch angle (°) at the two sites

Group	PROV ID	Wark	Drum
1	12001	70.92	73.15
1	12002	67.84	65.00
1	12003	67.47	69.70
1	12004	68.89	70.35
1	12005	68.70	68.33
1	12049	69.63	74.31
1	12051	67.41	74.23
1	74(7973)5	64.63	68.52
Group mean		68.82	70.41
2	12006	73.52	75.09
2	12007	71.48	70.92
2	12008	74.56	72.02
2	12009	71.30	73.63
2	12011	70.55	72.04
2	12012	70.61	74.72
2	12013	70.74	72.62
Group mean		71.82	72.96
3	12024	67.04	70.19

Table 6.7 (continued)

Group	PROV ID	Wark	Drum
4	12016	73.33	76.97
4	12018	74.63	75.21
4	12020	75.61	73.82
Group mean		74.05	75.21
5	12034	72.78	72.75
6	12015	77.96	74.33
6	12019	80.48	72.78
6	12021	73.70	75.55
Group mean		77.47	74.12
7	12040	68.16	70.88
7	12042	62.22	69.28
7	12043	64.74	69.28
7	12045	65.37	69.10
7	12047	65.00	67.20
Group mean		65.11	69.38
8	12052	70.37	72.89
8	12053	67.22	72.62
Group mean		68.70	72.71
9	12056	68.13	71.30
9	12057	68.93	67.74
Group mean		69.49	69.53
Site mean		70.24	71.78

Table 6.8 Results of ANOVA for provenance * site interaction of branch angle

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	4	188.971	47.243	7.54	0.01	14.37	24.14
Grp	8	1401.481	175.185	14.46	0.01	53.27	-
Grp.Prov	23	278.624	12.112	1.93	0.05	3.68	-
Prov	31	1680.105	54.197	8.64	0.01	-	27.69
Site	1	56.106	56.106	8.95	0.01	17.06	28.66
Site*Grp	8	122.207	15.276	2.44	0.05	4.65	7.80
Site*(Grp.Prov)	23	382.923	16.649	2.65	0.01	5.06	8.51
Plot	124	777.393	6.269			1.91	3.20
Total	191	3207.705					

6.9 Results of regression of branch angle on latitude, altitude and longitude of provenance origin and their principal components

6.9.1 Results of multiple regression of branch angle on latitude, altitude and longitude of provenance origin at Wark and Drum

The results of a stepwise multiple regression of branch angle on latitude, altitude and longitude of provenance origin at each of the two sites are presented in Tables 6.9 and 6.10. The results of the regression at Wark shown in Table 6.9 is highly significant and explains 63.6% of the total variation in branch angle. Among the three environmental variables latitude and altitude of provenance origin have significant regressions with branch angle. Longitude of provenance origin however, does not have a significant regression with branch angle.

The results of the regression of branch angle on the three environmental variables of provenance origin at Drum presented in Table 6.10 is highly significant and explains 33.4% of the variation in branch angle. Like the results of a similar regression of branch angle on these variables at Wark, latitude and altitude of provenance origin have significant regressions with branch angle. However the effect of longitude is not significant.

6.9.2 Results of linear regression of branch angle on the first principal component of latitude, altitude and longitude of provenance origin

The results of the linear regression of branch angle on the first principal component of latitude, altitude and longitude of provenance origin are presented in Tables 6.11 and 6.12. The regression of branch angle on the first principal component at Wark presented in Table 6.11 show a highly significant results. The first principal component explains 59% of the variation in branch angle. Similarly the regression of branch angle on the first principal component at Drum indicates a highly significant relationship. The component explains 31% of the variation in branch angle.

Table 6.9 Results of multiple regression of branch angle on latitude, altitude and longitude of provenance origin at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	3	315.4	105.125	18.92	0.01	63.40
LAT	1	189.3	189.3	34.05	0.01	38.20
ALT	1	126.1	126.1	22.68	0.01	25.20
LONG	1	0.014	0.014	0.00	n.s.	0.00
Residual	28	155.6	5.56			
Total	31	471.0				

Table 6.10 Results of multiple regression of branch angle on latitude, altitude and longitude of provenance origin at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	3	86.80	28.926	5.65	0.01	33.4
LAT	1	49.60	49.60	9.69	0.05	18.9
ALT	1	37.10	37.10	7.25	0.05	14.50
LONG	1	0.10	0.10	0.01	n.s.	0.00
Residual	28	143.40	5.12	66.60		
Total	31	230.20				

Table 6.11 Results of linear regression of branch angle on the first principal component of latitude, altitude and longitude of provenance origin at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	1	283.6	283.6	45.44	0.01	58.90
Residual	30	187.31	6.24			
Total	31	471.0				

Table 6.12 Results of linear regression of branch angle on the first principal component of latitude, altitude and longitude of provenance origin at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)
Regression	1	76.90	76.90	15.06	0.01	31.30
Residual	30	153.20	5.106			
Total	31	230.1				

6.10 Comparison of branch angle of provenance 74(2002) and provenances in group 7 at the two sites

6.10.1 Analyses of variance to compare branch angle variation in provenance 74(2002) and the provenances in group 7

The branch angle of provenance 74(2002) was compared to those of the provenances in group 7 to examine how branch angle variation in this provenance compares to those of the provenances with which it shares more or less similar location within the grand fir range. The comparison was done in an analysis of variance with the model in Section 3.2.3.1. Provenance 74(2002) was assumed to have come from a group different from group 7 to which the other provenances belong. Each of the two groups with the respective provenances nested in them were then compared in the analysis of variance, to determine whether provenance 74(2002) was different from the other provenances. The model also facilitated the comparison among the provenances as individuals. A second analysis of variance based on the model in Section 3.6.2.1 was aimed at examining provenance differences and their interaction with site.

6.10.2 Results of analyses of variance

The results of the analysis of variance for branch angle variation in provenance 74(2002) and the other provenances in group 7 for the two sites are presented in Tables 6.13 and 6.14. The mean branch angle values for the two sites are presented in Table 6.15. The results of the interaction between these provenances and site is presented in Table 6.16.

At Wark there is no significant difference between provenance 74(2002) and the other provenances considered as two separate groups as Table 6.13 indicate. There are significant differences between provenance within groups and among provenances. Block effects are also significantly different. The means of branch angle for all the provenances in Table 6.15 seem to indicate that provenance 74(2002) has the same branch angle as the other provenances considered as a group.

The results, for the Drum site in Table 6.14 show highly significant differences among provenances within groups and among provenances. In contrast the results indicate that 74(2002) is not significantly different from the other provenances considered as a group. The effect of blocking is also not significantly different. The mean branch angle values in Table 6.15 indicate that the provenances in group 7 considered as a group have wider branch angle than provenance 74(2002).

The result of the analysis examining the interaction between provenance and site presented in Table 6.16 indicate a highly significant interaction between provenance within group and site. There are significant differences among provenances within group and among provenances. There are no significant differences between the two groups, among the sites or between the blocks. The mean branch angle values in Table 6.15 suggest an increase in the branch angles of the provenances in group 7 while the branch angle of provenance 74(2002) decreases from Wark to Drum.

Table 6.13 Results of ANOVA for branch angle of provenance 74(2002) and the provenances in group 7 at Wark

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	27.969	13.985	4.95	0.05	41.00	49.94
Grp	1	4.409	4.409	0.342	n.s.	12.93	-
Grp.Prov	4	51.544	12.886	4.55	0.05	37.78	-
Prov	5	55.953	11.1906	3.96	0.05	-	39.96
Plot	10	28.261	2.826			8.29	10.09
Total	17	112.182					

Table 6.14 Results of ANOVA for branch angle of provenance 74(2002) and the provenances in group 7 at Drum

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	2	20.546	10.273	1.91	n.s.	13.46	21.10
Grp	1	25.803	25.803	0.74	n.s.	33.82	-
Grp.Prov	4	139.324	34.831	6.46	0.01	45.65	-
Prov	5	165.127	33.025	6.13	0.01	-	67.83
Plot	10	53.911	5.391			7.07	11.07
Total	17	239.583					

Table 6.15 Branch angle means of provenance 74(2002) and provenances in group 7 at each of the two sites

PROV ID	Wark	Drum
12040	68.34	71.01
12042	62.22	69.37
12043	64.74	69.84
12045	65.33	69.08
12047	65.00	67.26
74(2002)	65.19	64.63

Table 6.16 Results of ANOVA for provenance * site interaction of branch angle

SOURCE	DF	SS	MS	VR	SIG	VC(%)	VC(%)
Block	4	46.440	11.610	2.78	n.s.	11.18	14.43
Grp	1	25.946	25.946	1.98	n.s	24.99	-
Grp.Prov	4	52.223	13.056	3.13	0.05	12.57	-
Prov	5	78.169	15.634	3.75	0.05	-	19.43
Site	1	9.528	9.528	2.28	n.s.	9.18	11.84
Site*Grp	1	4.525	4.525	1.08	n.s	4.36	5.62
Site*(Grp.Prov)	4	139.999	35.00	8.39	0.01	33.71	43.50
Plot	20	83.446	4.172			4.02	5.18
Total	35	362.107					

6.11 Discussion

6.11.1 Stem straightness variation in grand fir provenances

Grand fir provenances show variation in stem straightness at each of the two sites considered in the study. At Wark many of the provenances have a very high proportion of their stems in ranks 3 or 4. This is generally the case with the group 1 provenances. Among this group many provenances have more than 80% of their stems ranked 3 or 4, which indicate very good form. Many of the provenances among the remaining provenances in the other groups similarly have higher proportion of stem in rank 3 or 4. There are a few provenances however, with a higher proportion of their stems ranked between 1 and 2. These provenances include 12006, 12040, 12045, 12051, 12053, 12056 and 12057. The last four provenances in the above list belong to provenance groups 8 and 9 from coastal northern and southern Oregon and have comparatively poor stem straightness compared generally with the other provenance groups.

At Drum stem straightness variation pattern among the provenances appears to be different from that observed at Wark. The proportion of stems with very good form that is with rank 3 or 4 is generally above 90% for all the provenances. Provenance 12056 is the only exception to this trend in stem straightness among provenances. It has more than 10% of its stems in the straightness ranks of 1 or 2. The provenance 74(2002) has very good stem form on each of the two sites. The average stem form on both sites is very high compared to those of the provenances in group 7.

The effect of site on stem straightness cannot be easily assessed but it appears that the proportion of stems with poor straightness ranks for some provenances is comparatively high at Wark than at Drum. This is particularly so for the provenances in groups 8 and 9. The relatively low average stem straightness ranks of provenances in groups 8 and 9 on both sites suggest however that these provenances may have inherently poor form.

The relatively poor stem straightness of the provenance from the Oregon coast is in agreement with studies on the stem form of *Pinus contorta* from the same coast planted in Scotland (Lines, 1987). This suggest that seed sources from this coast may not give trees of good stem form. In other species for example *Pinus caribaea* and *Pinus contorta* stem form is reported to be defective when these species are grown in environments outside the species range (Zobel et al., 1987). In contrast it appears that the stem form will not be a very important trait in the choice of provenances of grand fir in the present environment. Faster growing provenances have very good stem form and can be used for reforestation.

6.11.2 Branch angle variation in grand fir

The branch angle of provenances in grand fir varies as indicated by the results of the analysis of variance. The analysis of variance for each of the two sites suggest that the greater proportion of the variation in branch angle is among the provenance groups. This level of variation explaining 64% and 54% of the total variation in branch angle for Wark and Drum respectively.

At Wark the inland provenance groups generally had wider branch angles than provenance groups from the coastal sources. A stepwise regression of branch angle on latitude, altitude and longitude of provenance origin indicate significant relationships with latitude and altitude. Similarly, the regression of branch angle on the first principal component of these environmental variables was highly significant. The analysis of variance and the regression analysis of branch angle on the individual variables as well as the first principal component of these variables throw some light on the nature of variation in the branch angles of grand fir provenances. Generally, provenance groups from higher latitudes and lower altitudes have relatively narrower branch angles than groups from lower latitude and higher altitude. The regressions of branch angle on latitude, altitude and the first principal component are graphically illustrated in Figure 6.1**a**, 6.1**b** and 6.2. There is a decrease in branch angle with increasing latitude and an increase with increasing altitude as Figure 6.1**a** and 6.1**b** indicate. The relationship between branch angle and the first principal component of latitude, altitude and longitude in Figure 6.2 shows a discrimination among provenance groups based on their location. Therefore, at Wark, faster growing provenance groups from the coastal areas have comparatively narrow branch angles.

The pattern of provenance variation in branch angle at Drum appears to be similar to that at Wark. The greatest proportion of the variation in the trait resides among the groups. However, there are differences among provenances within groups and also among the provenances. Like the trend in variation observed at Wark, inland provenance groups generally have wider branch angles than the coastal provenance groups. The regression of branch angle on latitude, altitude and longitude of provenance origin indicated significant relationships with the first two variables. Similarly, branch angle had a highly significant regression with the first principal component of these variables. These relationships are graphically illustrated in Figure 6.3**a** which indicates a negative relationship between branch angle and latitude of provenance origin, Figure 6.3**b** which shows a positive relationship between the two variables and Figure 6.4 which shows a descrimination between the coastal and inland provenance groups.

There were significant differences in branch angles between the two sites and significant interaction between site and provenance. Drum, the site with the higher potential for growth, had provenances with wider branch angles than Wark the site with the lower potential for growth. The between site variation may be partly explained by the year lag between the measurements at the sites. This may particularly be the case where the difference in branch angle for a provenance between the pair of sites is not very large, for example considering provenances in group 2. Formation of new leaves during the years interval may have resulted in an increase in the weight of branches of the provenances at Drum and consequently an increase in the branch angle (Zimmermann and Brown, 1971). However, significant interaction between provenance and site also suggests that for other provenances, differences in branch angle between sites may have been due to other factors like the genetic or environmental control of the trait. Provenance 12005 for example, appears to be a source with inherently narrow branch angles as its branch angle does not vary much between sites.

The provenance 74(2002) is not significantly different from the other provenances in group 7. This suggest that this provenance, which originally came from the coastal areas of British Columbia like the other provenances from the coastal areas, has relatively narrower branch angle. The provenance, unlike the other provenances in group 7, does not show an increase in branch angle from Wark to Drum and appears to be a source with inherently narrow branch angle like provenance 12005.

Provenance branch angle variation may have some implication on the quality of wood produced by the provenance. In slash and loblolly pine it has been reported that branches with wide angles generally have small diameters (Koch, 1972). Wider branch angles resulting in smaller branch diameters will lead to a lower knot volume in wood and hence a higher wood quality (Koch, 1972). The wood in and around knots sometimes has low cellulose content and is in some ways similar to compression wood (Zobel et al., 1987). Compression wood has lower strength properties (Butterfield and Meylan, 1980) and hence if narrow branch angles result in higher knot volume, then provenances with such angles will not be desirable for wood production. The relatively narrow branch angles of the faster growing coastal provenances however, does not necessarily indicate that wood produced by these provenances will have a higher knot volume. The branch angles will have to be considered together with the number of branches per whorl and the diameters of these branches. A high branch diameter to stem diameter ratio for example will indicate a higher knot volume (Murphy and Pfeifer, 1990; Campbell, 1961).

In *Pinus contorta*, Kranenborg and Kriek (1978) reported that fast growing provenances had branches with larger diameters than slow growing provenances and therefore concluded that selection for fast growth will result in the selection for relatively larger branches. Observations in the field indicated that the faster growing provenances of grand fir have relatively larger branch diameters thus the selection of these provenances for faster growth will also lead to the selection for larger branch diameters. Further studies on the branching characteristics of the faster growing provenances will therefore be appropriate.

Branch angle has been reported to be an inherited trait in slash pine and loblolly pine (Koch, 1972). The pattern of variation in the trait at the two sites with distinctive differences between coastal and inland provenances appear to suggest that branch angle may be under genetic control in grand fir. This observation however can be better established in a progeny test.

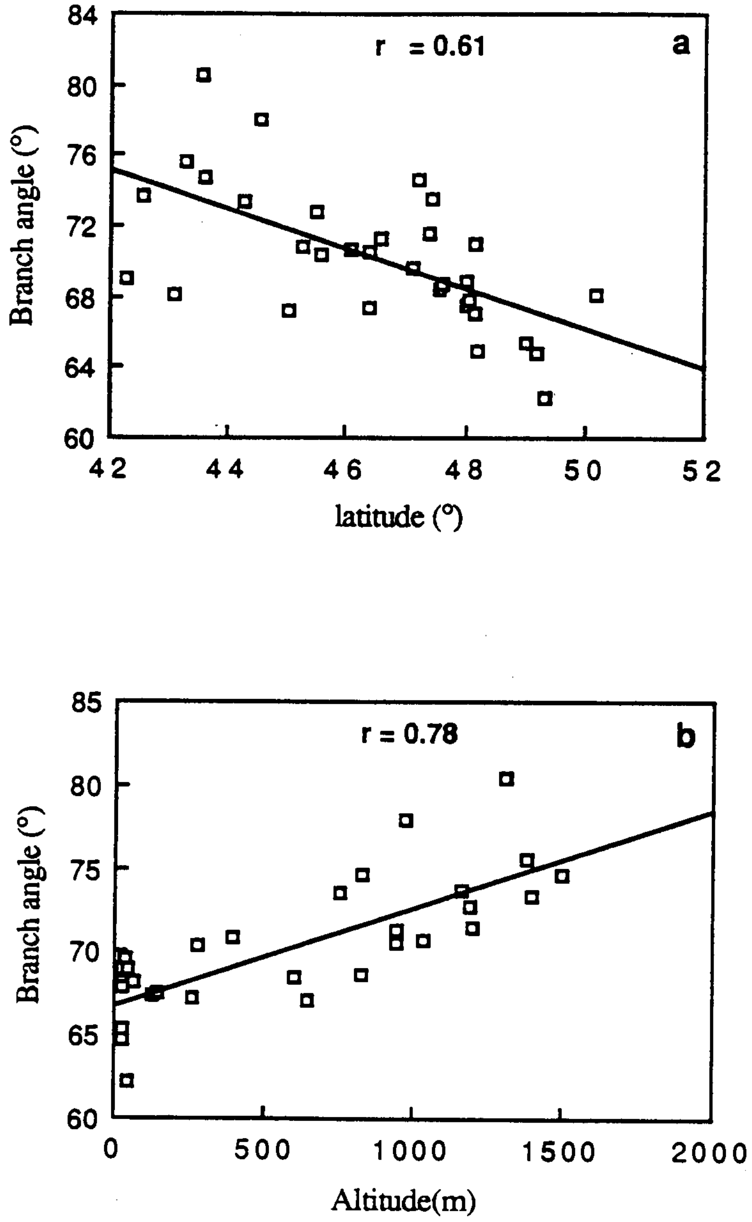
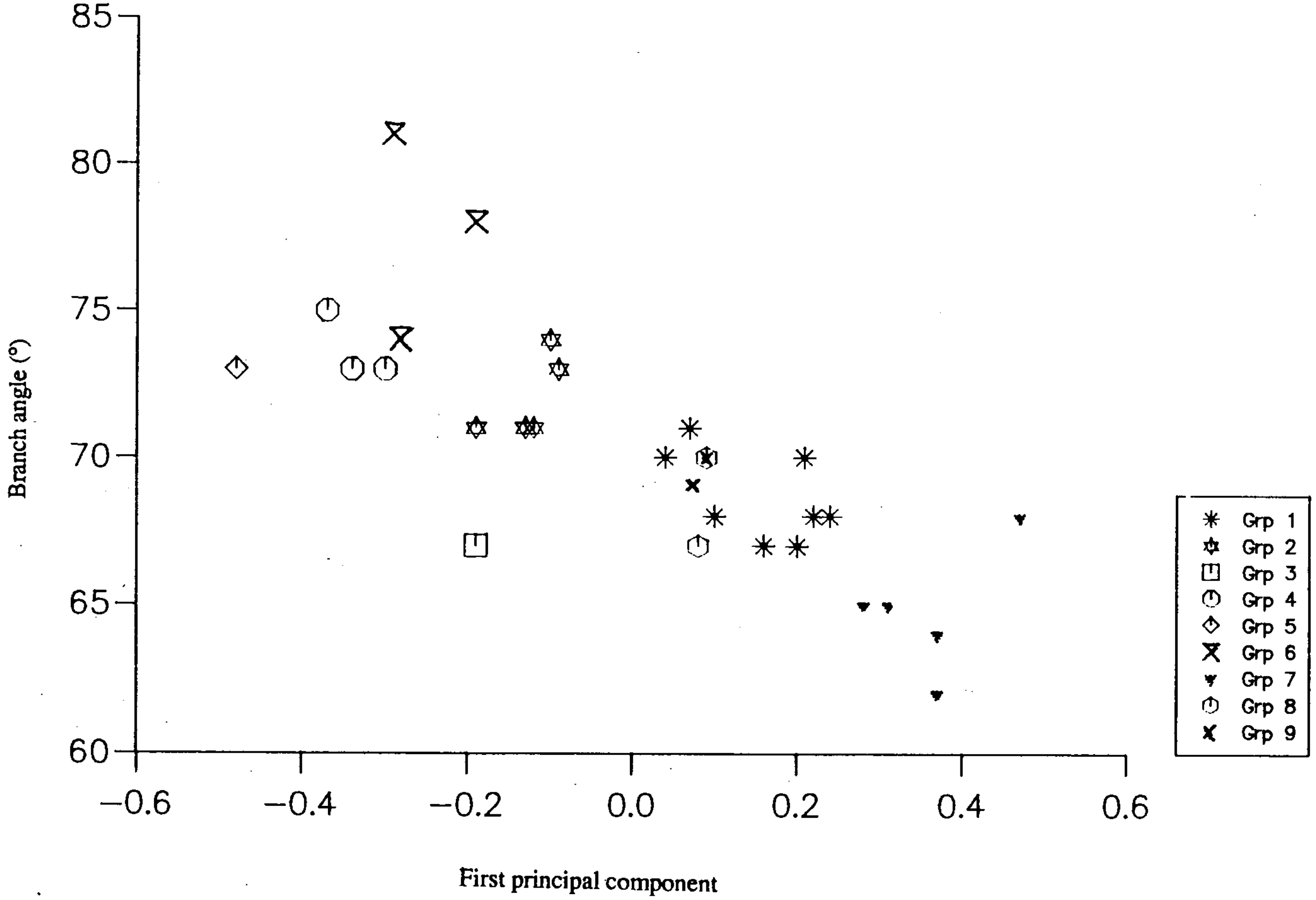


Figure 6.1. Relationship between branch angle **a** - and latitude of provenance origin at Wark **b** - and altitude of provenance origin at Wark. Regression line and values of regression coefficients (r) are shown.

Figure 6.2 The relationship between branch angle and the first principal component of latitude, altitude and longitude of provenance origin at Wark



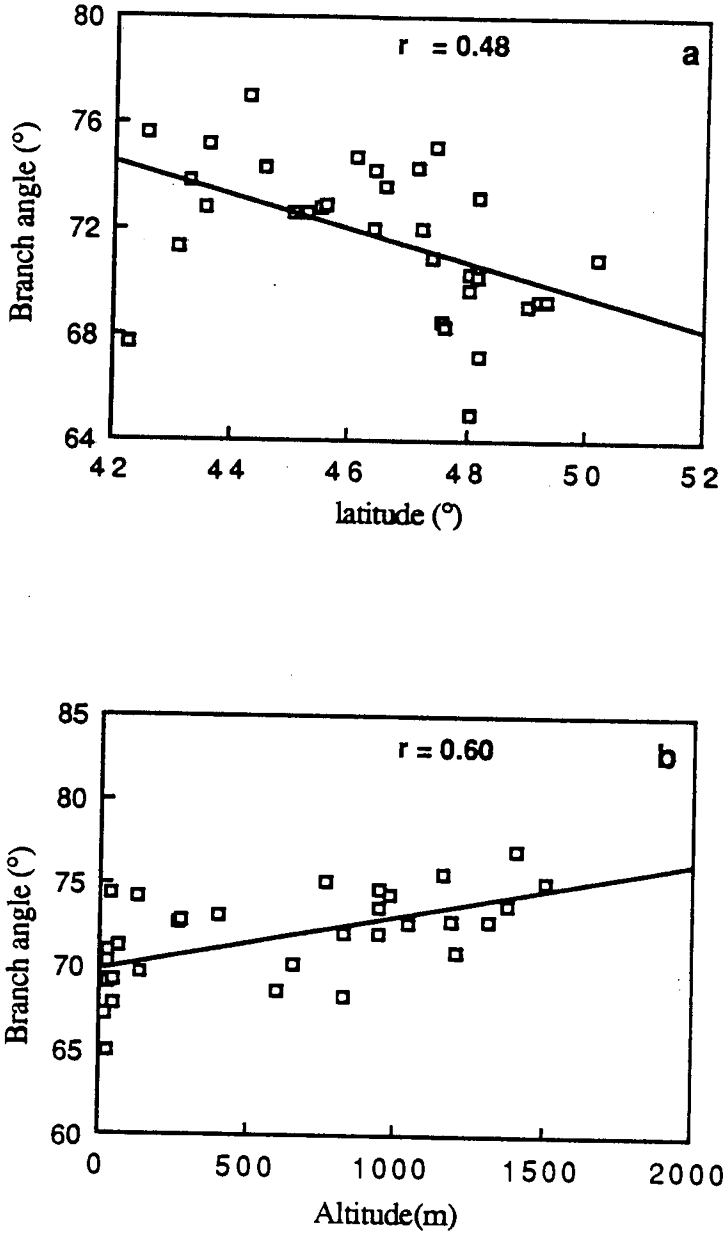
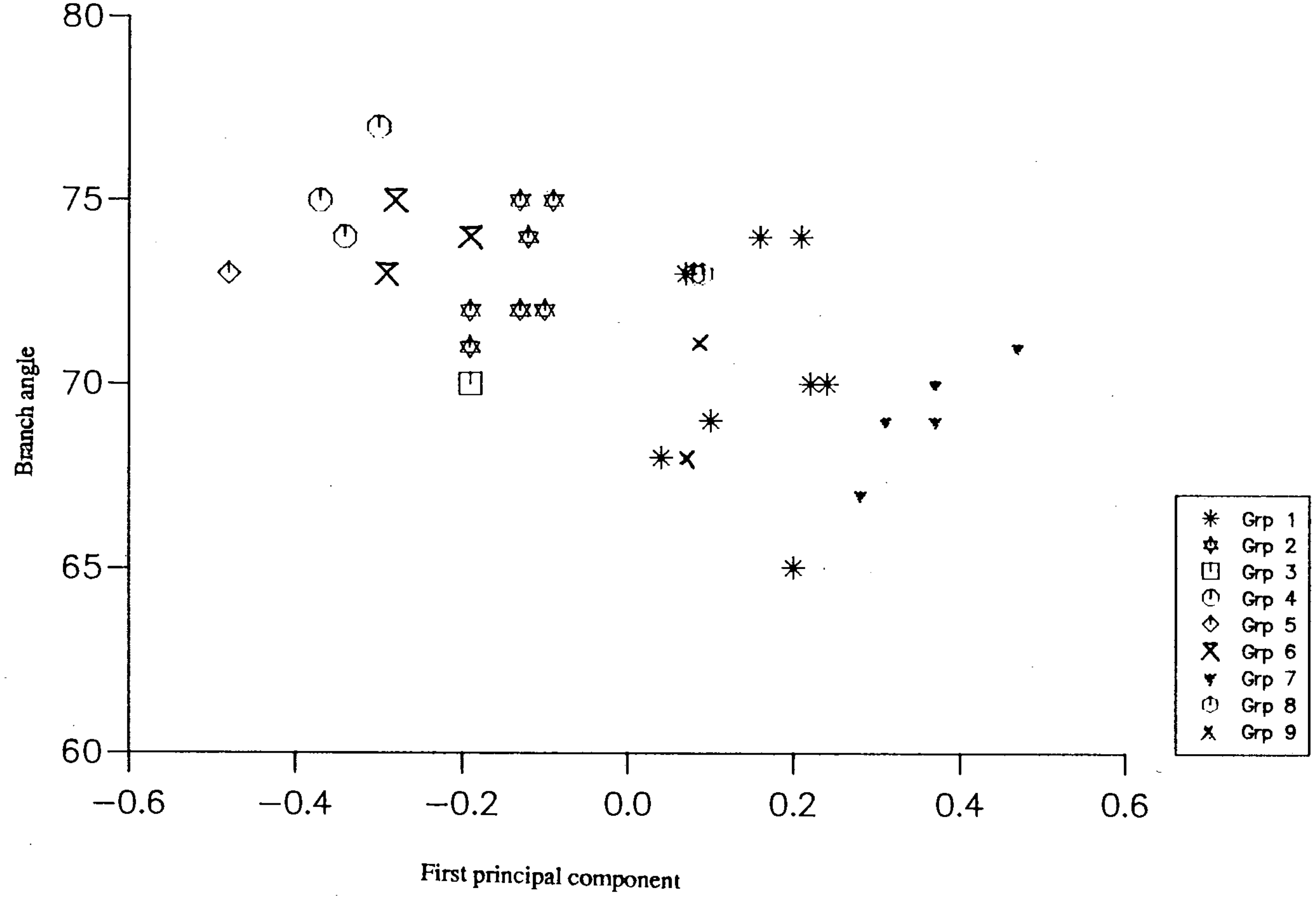


Figure 6.3. Relationship between branch angle **a** - and latitude of provenance origin at Drum **b** - and altitude of provenance origin at Drum. Regression line and values of regression coefficients (r) are shown.

Figure 6.4 The relationship between branch angle and the first principal component of latitude, altitude and longitude of provenance origin at Drum



CHAPTER 7

General discussion and conclusions

7.1 General discussion

Provenance variation studies have the objective of evaluating plant material from different geographic origins for adaptation and productivity with the objective of selecting planting material that will give adapted and productive forest in the environment in which they are to be grown (Sprackling and Mead, 1975; Callaham, 1964). In a rangewide provenance test, the main objective is the delineation of regions within the range of the species in which provenances have the requisite adaptation and productivity in the environment in which they are to be planted (Niendstaedt, 1979). The evaluation of some characteristics of grand fir in this study has yielded information that may be used to locate provenance regions with populations that are adapted and productive in the environment in which the test is conducted.

The provenances from different parts of the range of grand fir have good survival on each of the two test sites. However, there are large differences in the growth potential of the provenance groups from different locations within the range of the species. Provenance groups from coastal areas generally have higher growth potential than provenance groups from elsewhere within the grand fir range. Among the several factors which might have contributed to this variation in growth potential, frost hardiness was investigated. The indication is that frost hardiness increases with increasing latitude. This is especially so in the case of coastal provenance groups. Among these sources, groups with high growth potential apparently had high frost tolerance status. A study of variation in wood density indicated that provenances within groups showed a wide degree of variation in this trait and that some faster growing provenances had high wood density. The wood density of provenances generally decreased with increase in the site growth potential. Stem straightness of provenances was generally excellent. Faster growing provenances however, tend to have comparatively narrow branch angles than slower growing provenances. One provenance included in the trial which has undergone a generation of adaptation in the present environment appears to have developed into a land race. The growth potential of this provenance compared equally or better than the best provenances on each of the two sites over which this study was conducted. The wood density of this provenance was comparatively higher and the stem straightness was excellent. The frost tolerance status was apparently very low. Like the other coastal provenances, this provenance which originally came from the coastal area of the species range had relatively narrow branch angle.

There were also indications of how early provenances with high growth potential could be selected. Although the prediction of early selection improves with age, indications were that provenances with high growth potential could be selected after six growing seasons. Height measurements from earlier assessments were significantly correlated with diameter measurements in this study, suggesting that the use of height assessment gave a good indication of the growth potential of grand fir.

Provenance variation is a product of genetic and environmental factors as well as the interaction between these two factors (Zobel and Talbert, 1984). The differences in the growth potential of the different populations of grand fir may be attributed to these factors. Growing in a more or less uniform environments at each of the two sites Wark and Drum, large differences existed among the provenance groups. The provenance groups with the highest growth potential at Wark for example, had more than a 100% better performance than that with the worst performance. These differences within site may be attributed to genetic differences among the provenances. The populations may have been different from each other as a result of mutations and genetic recombinations that has occured among them over a long period of time (Burley, 1965). The variation between coastal and inland populations of grand fir may also be associated with the inherent growth potential of these populations (Lines, 1987). Within the natural range of grand fir, coastal populations are known to achieve higher growth than inland populations of the species (Kirkwood, 1930; Sargent, 1905)

The environment is another factor that may have played a role in the variation in the growth potential of the provenances. Growing on a surface water gley soil at Drum, the provenances have higher growth potential than growing on a peaty gley soil at Wark. The growth potential of grand fir as a species is reported to increase with increase in the site potential (Fowells, 1965). The environmental climatic adaptations due to their origins may also explain the variation in the growth potential of the provenances (Burley, 1965). Coastal provenances have better growth potential possibly due to their maritime climatic adaptation which corresponds with that of the present environment in which they are growing, in contrast inland provenances have continental climatic adaptation and thus are not probably well adapted to the present environment in which they are growing (Schaeffer, 1978; Franklin and Dryness, 1969; Zobel et al., 1987). The interaction between provenance and site among the grand fir provenances is borne out by the fact that the relative performance of the provenances to each other varied between the two sites.

Frost tolerance is a requisite adaptation for provenances to be grown in environments in which freezing occurs because without this adaptation trees may not survive or where they survive their growth may be stunted leading to loss in productivity (Glerum, 1976). Provenance variation in the frost tolerance of grand fir seems to suggest that for some provenances there is perhaps a relationship between frost tolerance and the growth potential. This may be the case with the most southerly coastal provenances from Oregon. At Wark, the more frosty of the two sites covered in the study, those provenances which have low frost tolerance status have very low growth potential presumably due to repeated frosting. To the contrary at Drum, a less frosty site compared to Wark, the growth potential of these provenances is comparatively very high. While these coastal provenances may have inherently high growth potential, this may be limited by their inability to resist frost damage. In contrast to the southern coastal provenances from Oregon, northern coastal provenances from Washington and British Columbia appear to have high frost resistance status which perhaps is one of the factors underlying their high growth potential. One inland provenance from Idaho appear to have high resistance to cold damage but has a lower growth potential, which is probably genetic in origin, since inland populations of grand fir do not achieve the same growth rates as the coastal populations within the natural of the species (Harlow and Harrar, 1937).

Wood density is another important trait in the search for suitable provenances of a species because of the relationship between this trait and the strength properties of wood (Koch, 1972). The density of wood from trees grown outside their natural range may be different from that of the same species growing within their natural habitat (Zobel et al., 1987). It is thus of importance that this trait is assessed for introduced provenances. The traditional methods for assessing wood density while indispensable may not be appropriate when large numbers of trees from different populations have to be fairly rapidly screened for this trait. The pilodyn may therefore facilitate a rapid method for assessing wood density (Cown, 1978; Adams et al, 1990).

Grand fir growing within part of the natural range produces wood descibed as light in weight with an air-dried density of 443kg/m^3 (Mullins and Knight, 1981). Growing as an exotic in Britain Brazier (1973) estimated the wood density at 12% moisture content as 310kg/m^3. The screening of provenances so as to utilise those with high wood density is therefore essential. The study has indicated the apparent possibility of making selections for both fast growth rate and high wood density. Wood density variation in grand fir seems to be under genetic and environmental control. Some provenances tend to have high wood density irrespective of their growth potential when a comparison is made between the two sites. Provenance

12002 is one of such provenances. The effect of site is however evident among many of the provenances. The density of the wood produced by the provenances appears to decrease with an increased site potential for growth. Thus provenances generally have lower wood density at Drum than at Wark. Within a site however, faster growing provenances may have higher wood density.

The stem straightness of many of the provenances at each of the two sites is generally excellent. Between the two sites however, a comparatively large number of provenances have a higher proportion of stems with poor form at Wark than at Drum. The relatively poor form of the provenances in group 9 may be genetic in origin as provenances of *Pinus contorta* from the Oregon coast have also been reported to have poor form when grown in Scotland (Lines, 1987). However the differences in stem straightness between the two sites also appear to suggest an element of environmental influence. Branch angle variation seem to indicate genetic differences in this trait among provenances within and between sites. On both sites provenance groups are characterised by distinctive branching patterns as the branch angle values suggest. Low latitude and high altitude provenances tend to have wider angles than high latitude and low altitude sources. The general trend in branch angle variation among provenances between the two sites generally appear to the same but there are also some differences among provenances between the sites. Provenances in group 7 for example showed a marked increase in branch angle from Wark to Drum. Coastal provenances with faster growth potential like provenances from the inland range of grand fir generally have very straight stems but their branch angles are comparatively narrower than those of inland populations.

A land race is a population of individuals that has become adapted to a specific environment in which it has been planted (Zobel and Talbert, 1984). The provenance 74(2002) that has undergone a generation of selection in the present environment in which the provenance trial is conducted appear to have become adapted to this environment and hence by the above definition developed into a land race. Its adaptation is borne out by the fact that the growth potential of the provenance is either the highest or among the highest at each of the two experimental sites.The wood density of this provenance as measured by the pilodyn is high compared to many of the slow growing provenances but decreases with an increase with the sites growth potential like many of the other provenances with high growth potential. The stem straightness is excellent, although like the other coastal provenances its branch angle is narrow compared to those of inland provenances. The frost tolerance status appears to be very low but will need further investigation, in view of the high growth potential of this provenance.

Provenance trials take a long time to conduct and are therefore expensive. If sources with high growth potential can be located earlier in a rangewide provenance trial then the cost of the trial may be reduced and further screening of provenances from adapted regions accelerated. Correlations of the Dbh data in this study with those of earlier height assessments in grand fir (Lines, 1987; Fletcher and Samuel, 1990) suggest that the provenances with the high growth potential can be identified after about six growing seasons. The significance of the correlations between diameter and height measurements also suggests that height measurements used in the earlier assessment gives a good reflection of provenance growth performance. The usefulness of early selection based on growth potential may however be limited if much is not known about other characteristics such as the wood density of the provenances. The provenances that are selected early based on growth potential may not therefore have all the desirable characteristics for the objective for which they are to be used.

7.2 The choice of provenances in grand fir

The successful utilisation of provenance variation in intensive reforestation programmes will be dependent on knowledge of the variation in the provenance traits that will be of interest to the programme (Cheng et al., 1985). The variation in four characteristics of grand fir that have been considered in this study should therefore aid in the location of provenances that have the suitable adaptations for the traits considered. The selection of provenances will depend on the objectives for which they are to be used (Lines, 1987). For the production of wood for lumber and pulp for example fast growth rates, high wood density and good stem form will all be desirable characteristics in chosen provenances. Provenances may not have all the desirable characteristics in which case compromises will have to be made among the traits for the optimum gains that can be realised (Rehfeldt, 1985).

The growth potential of provenances will be a trait of primary importance for wood production. In the rangewide grand fir provenances considered in this study the variation in the growth potential is between provenance groups that share more or less similar locations (Fletcher and Samuel, 1990). Thus coastal provenances have higher growth potential than inland provenances. The search for provenances with high growth potential should therefore be directed towards the coastal areas of the species range. Among the coastal provenance groups, the growth potential, stability of growth performance between sites and the the frost tolerance status will be important considerations in making selections. Taking these three factors into consideration, coastal provenance group 1 from Washington seems to be the best among the coastal provenance groups. Another coastal region which may be considered is that of the group 7 provenances in British Columbia. A second stage of provenance study with the objective of concentrating on provenances in a sub-region within the range of a species (Niendstaedt, 1979) can therefore concentrate on these regions in the coastal range of grand fir.

The single provenance 74(2002) that has undergone a generation of selection in the present environment and appears to have developed into a land race should also be given attention in the choice of provenances for planting and further screening. The fact that it has undergone a generation of selection in the present environment has the implication of an adaptational advantage in the selection pressures that operate in the environment (Zobel et al., 1987) over the other provenances that also have high growth potential but are being tested for the first time in the present environment. Its frost tolerance status which however, appears to contradict the high growth performance, will require further investigation.

Wood density which is a trait of comparable importance as the growth potential of provenances show variation among the provenances. This variation is among provenances within a group. Thus some provenances with high growth potential have higher wood density than those with low growth potential. The implication of the nature of wood density variation for the choice of provenances is that selections can be based on provenances within a group with high growth potential. Choices can thus be made among provenances within the coastal Washington provenance group. Provenance 12002 for example, appear to have inherently high wood density. Although the density decreased from Wark to Drum, it was still comparatively higher than those of many of the other provenances. Similarly provenance 12005 also appears to have high wood density. The density of this provenance increased with an increase in the site potential for growth. Provenance 12042 from group 7 may be another population that may be of interest. Although the growth potential was low at Wark, it increased at Drum. This indicated that on a better site this provenance can have high growth potential. The wood density of this provenance compared to the other provenances was lower on both sites. The limitation on the density of wood produced by grand fir will not generally be dependent on the use of faster growing provenances but rather on the sites on which the faster growing provenances are planted although a fast growing provenance like 12051 have low wood density irrespective of the site on which it is planted.

Stem straightness does not appear to be a characteristic of importance in the choice of provenances in grand fir. The provenances with high growth potential also have excellently straight stems. However it seems that provenance group 9 will have to be avoided due to its relatively poor form on each of the two sites. Fast growing provenances in group 1 have generally comparatively narrow branch angles than the inland provenance groups. The branch angles of provenances within group 1 are however generally over 60° and are not very acute angles. While it may be necessary to make further study on the branching characteristics of the best provenance groups in relation to the influence of this trait on wood quality in subsequent screening, the relatively narrow branch angles will have to be compromised for high growth potential and high wood density. This will also have to be the case with provenance 74(2002).

7.3 Conclusions and recommendations

The study of provenance variation in the growth potential, wood density and stem form of grand fir has indicated there are differences among provenances in relation to the above characteristics. This variation can be exploited through careful selection of provenances for the utilisation of the species for the production of wood in a reforestation programme. Some provenances with comparatively high growth potential also tend have high wood density. The straightness of the stems of the species is generally excellent and will not interfere with selection of provenances based on growth potential or wood density. Provenances with high growth potential and high wood density do not however have the widest branch angles. Nevertheless their branch angles are not very acute and will therefore have to be compromised in the selection for high growth potential and high wood density. The provenance group from coastal Washington which tend to have high growth potential and wood density also seem to have very high frost tolerance status. The characteristics of provenance groups considered in this study which will aid in making selections among provenances from different regions within the range of grand fir are summarised in Table 7.1.

The following recommendations are made on the choice of provenances of grand fir for wood production in the short-term and further screening for tree improvement in the species:

1. The best provenance region of the species is that occupied by the provenance group 1 in the coastal Washington range of the species. Provenances within this group have the best overall growth performance and stability of performance.

2. Provenance 12002 within provenance group 1 has high growth potential and inherently high wood density. It may therefore be used for planting in the short-term while further screening in carried out on the wood density and the branching characteristics.

3. 12005 is another provenance within group 1 with high growth potential and high wood density. The increase in wood density with an increase in the growth growth potential recommends it as a provenance for selection. Further screening of this provenance will therefore be appropriate.

4. Provenance 12042 shows an increase in growth potential with an increase in the site potential and coupled with its relatively high wood density may be a population that may have to be screened for improvement.

5. The provenance 74(2002) which appears to have developed into a land race is also recommended for planting and further investigations.

6. The frost tolerance status of the provenances in group 1 and provenance 74(2002) need to be assessed further with regards to variation between seasons.

7. Provenances in group 9 from southern coastal Oregon range of grand fir are not recommended for planting because of the instability of their performance, relatively poor form and the low frost tolerance status.

8. Among the coastal group 1 provenances 12051 has a high growth potential but seem to have an inherently low wood density and will therefore not be a suitable provenance.

9. Grand fir provenances with high growth potential and high wood density may produce wood of relatively low density when planted on a site with a high potential for growth. Sites on which the best provenances are planted should therefore be chosen carefully and further investigation on the effect of site on the density of wood over a range of sites need to be conducted.

Table 7.1 Ratings of chracteristics of grand fir provenance groups from a rangewide provenance trial

Grp	GP	SP	WD	ST	BR	FT	General Remarks
7	4	2	4	4	3	4	Growth potential of the group very high. Stem straightness is excellent and branch angle is high. Frost tolerance status of the group is very high comparable to that of group 5. Wood density is high but the stability of growth performance is low.
1	4	4	3	4	3	3	Growth potential of the group very high Stem straightness is excellent , branch angle is high. Frost tolerance status of the group is high. Wood density is generally high but varies widely among provenances. Performance of group very stable.
8	3	2	2	2	3	2	Growth potential of the group high Stem straightness is generally low, branch angle is high. Frost tolerance status is low. Wood density is low. Stability of performance is low
9	3	1	4	2	3	1	Growth potential of the group variable between sites Stem straightness is generally low, branch angle is high. Frost tolerance status is the lowest among all the groups. Wood density is high. Stability of performance is very low
2	2	4	4	4	4	1	Growth potential of the group low. Stem straightness is excellent , branch angle is high. Frost tolerance status of the group is very low. Wood density is generally very high Performance of group very stable
4	1	4	2	4	4	2	Growth potential of the group is very low. Stem straightness is excellent , branch angle is high. Frost tolerance status of the group is low. Wood density is low. Performance of group very stable

Table 7.1 (continued)

Grp	GP	SP	WD	ST	BR	FT	General Remarks
6	3	1	2	4	4	2	Growth potential of the group high Stem straightness is very high and branch angle is very high. Frost tolerance status is low. Wood density is very low. Stability of performance is very low.
3	1	4	2	4	3	2	Growth potential of the group is low Stem straightness is excellent and branch angle is high. Frost tolerance status of the group is low. Wood density is generally low. Performance of group very stable
5	2	4	1	4	4	4	Growth potential of the group is high Stem straightness is excellent and branch angle is high. Frost tolerance status of the group is very high. Wood density is low. Performance of group very stable
74(2002)	4	_	3	4	2	1	Provenance has undergone a generation of selection in the present environment. The growth potential is very high and the wood density is high. The stem straightness is excellent but the branch angle narrow. The frost tolerance status is low.

Rating of characteristics 4 = very high. 3 = high. 2 = low. 1 = very low

Legend to abbreviations

Grp - provenance group

GP - growth potential

ST - Stem straightness

FT - Frost tolerance status

SP - Stability of performance

WD - Wood density

BR - Branch angle

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