Forestry Commission

Experiments on Lodgepole Pine Seed Origins in Britain

Roger Lines

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Summary

The range of lodgepole pine extends over 26 million hectares of north-west America, where climates vary from the bitter cold Yukon to the very mild Californian coast. It occurs from sea level to 3900 m in elevation. Over millions of years it evolved into a species which shows more variability than any other conifer.

Practical forest research aims to discover the most suitable origins for use on the wide variety of sites which occur in Britain. Seed origin experiments began in 1928, and over the next 45 years 90 experiments were planted on sites from Caithness to Cornwall. Altogether, 244 seed origins were tested some being the same in different years. Nursery tests gave information on many characters, some of which could be used to predict future performance. Three main groups of experiments were planted in 1937-42, 1969-71 and in 1972. Results from these are discussed at length, comparing performance both within and between groups of seed origins, and using regression analysis to show interactions across sites. The characteristics of trees from each of the main seed origin regions are discussed in detail.

No single origin possesses all the desired characters of fast growth rate, good stem form, stability against wind and snow, resistance to blasting winds, ability to suppress ground vegetation quickly, etc. One important use for lodgepole pine is in nursing mixtures with Sitka spruce, for which slow-growing Alaskan origins are best. For pure plantations the choice of seed origin is wider and depends on local factors.

Statistical note

The following convention has been followed when discussing the results of analysis of variance:

Significant *	=	*P* 0.05-0.01
Highly significant **	=	*P* 0.01-0.001
Very highly significant ***	=	$P<0.001$

Chapter 1

Introduction

Lodgepole pine (*Pinus contorta* Douglas ex Loud.) is the most widely distributed conifer in western North America. It is found on a remarkable range of site types and under climatic conditions varying from semi-desert to boreal peat bogs. This ecological tolerance and the fast growth of some seed origins has encouraged its wider use in European forestry. However, because adaptation of local ecotypes to each set of site conditions has become genetically fixed, when seed is used in another continent there is a considerable risk of choosing seed origins that are ill-adapted to their new environment. Many mistakes have been made in European forestry (not least in Britain) due to lack of knowledge of the inherent properties of the very varied seed origins that were commercially available. In addition, different origins of lodgepole pine have such different silvicultural properties that they can almost be considered as separate species. Each must be used in its correct role in silviculture, whether as a fast-growing pioneer, or as a bushy tree in mixture with spruce. Incorrect choice of origin by the forest manager for its role, site type and climatic province can lead to heavy financial loss. He also needs to know which origins can be used as substitutes should the most desirable ones not be available.

In some European countries lodgepole pine has become a controversial species, with huge areas (more than 300 000 ha) planted in northern Sweden since the end of the 1960s (Elfving, 1985), while its use in southern Sweden and in Finland is controlled by law, and so is used very sparingly. The two Forest Services in Ireland have adopted different policies about the use of the species and its origins and in Scotland there are several views on its correct place in forestry (e.g. Davies, 1980; Lines, 1980a; 1985). In New Zealand, it was used on colder sites because its frost tolerance is superior to that of *Pinus radiata*, and it was also much used to contain soil erosion on the upper slopes. Prolific natural regeneration later led to fears by conservationists and farmers that it would become a pernicious weed and it is no longer widely used for this purpose.

Although introduced to British arboriculture in 1853, widespread use of lodgepole pine in forest practice began only about 40 years ago. Because different seed origins perform almost as though they are different species, much disappointment was caused among forest managers, because of lack of reliable information about the characteristics of the seed origins available from forest nurseries at the time the plantations were established.

For most of the last 60 years, by far the largest proportion of all North American conifer seed used in Britain was bought by the Forestry Commission. This seed was used not only by Forestry Commission nurseries, but was also sold to the nurseries supplying the private sector with plants. Thus choice of seed origins by the Forestry Commission, based on the advice of Research Division, effectively controlled the origins used throughout Britain. Only in the last 15 to 20 years has seed been available from British stands in sufficient quantity to supply the major requirements – mainly of Sitka spruce. For lodgepole pine, most older stands were not of the seed origins that are now considered most desirable, nor were records of identity always available. The reliance on imported seed meant that in general only commercially available seedlots were used. Thus no seed came from Alaska until 1952 and the low-yielding muskeg stands on the Queen Charlotte Islands were also not tested widely until the 1970s. Use of commercial seed supplies carried with it the dangers of relying too heavily on the authenticity of origin provided by distant seed merchants. This could arise in two ways, either from simple mistakes in the identity of a seedlot, or from seed offered with an imprecise description of its origin, e.g. 'British Columbia' or 'Fraser River'.

Britain's lack of native conifers meant that exotic species were used on a far wider scale here than in any other European country. This applied particularly to lodgepole pine because it grew well on the poorest sites that could be released from agriculture on a large scale with little loss in food or wool production. As in northern Scandinavia, it outperformed native Scots pine on these sites and opened up a potential for a productive forest resource on an extensive area. Only the Irish Republic had an equally long history of commercial afforestation with lodgepole pine (Mooney, 1957).

The main driving force behind the research programme was the demand from the Forestry Commission's Seed Branch and from forest managers for advice on suitable origins for use mainly as pure stands on exposed moorland and peatland sites, later for improved stem quality, and subsequently for their use in mixture with Sitka spruce during the major expansion of afforestation on poor moorland sites that started in the late 1940s.

The local ecotypes, which have evolved to fit its wide range of site conditions in North America, show differences in many characters. These include not only such obviously important ones as growth rate, form and frost and exposure tolerance but also large differences in phenology (flushing in spring and growth cessation in autumn), precocity and abundance of flowering, needle retention, branching characteristics, nutrient demand, forking, bark type and thickness, efficiency of suppression of ground vegetation, etc. No other species shows such a wide range of behaviour in Britain. Seed origin experiments in overseas countries (see Chapter 5), have further emphasised both its growth potential, in relation to the native Scots pine, particularly in northern Scandinavia (Hagner, 1985a) and very strong seed origin x site interactions.

Changes in forest practice, together with crop damage from exposure and climatic events, meant a progressive reassessment of the value of different seed origins. For example, susceptibility to damage by wind and snow is one of the main demerits of the faster-growing seed origins of lodgepole pine. The problem assumed major significance in the 1950s with the development of more intensive cultivation and heavier fertiliser applications, further accentuated by planting in the furrow bottom on mineral soils or on the top of high ridges on peatlands. South Coastal origins proved liable to develop a high proportion of trees with basal sweep and other fast-growing origins were affected to a lesser degree. No reliable silvicultural technique could be found to reduce this damage to an acceptable level and although most stands later became temporarily stabilised in the thicket stage, this was merely a prelude to catastrophic damage from a combination of wind and wet snow in the later thicket or early pole-stage. Assessments showed that damage was highly selective and that most interior sources and northern coastal ones suffered little damage at this later stage (see Chapter 15 for more detailed discussion of susceptible and resistant origins).

Later, changes in silvicultural practice away from planting pure lodgepole pine demanded origins that would be compatible in mixtures with Sitka spruce on poor sites. For this purpose lodgepole pine origins had to be efficient in suppression of ground vegetation and not grow so vigorously that they topped the Sitka spruce or too coarsely branched so that they interfered with the spruce crowns.

This Paper attempts to summarise and review the results from over 90 experiments covering a period of over 50 years of investigations into the place of lodgepole pine in British forestry. It is important to stress that this project was not an academic study, but a long series of practical field trials. Over the years, knowledge about variation within the species and the exploitation of this diversity for practical use in British forestry has grown slowly and in retrospect with many errors. The earliest crude division adopted by European foresters into 'Inland' and 'Coastal' strains (Forbes, 1928) paid too little attention to the complex patterns of variation that have evolved. These have been shown by Critchfield (1957) to exhibit both continuous variation, e.g. with latitudinal or elevational clines and discontinuous variation, e.g. on two adjacent but very distinct soil types.

As research progressed into the genetic variation in lodgepole pine, various lines of enquiry were followed. The earliest seed origin trials revealed some of the varietal differences on the broadest scale. In retrospect, too much attention was paid to investigating unrepresentative samples from the natural range and trying to extrapolate from insufficient data. By the early 1950s it was clear that a more detailed examination should be made of the natural populations and this was one of the minor objectives of the visit to North West America by R. F. Wood (1955). His acute observations showed some of the complexities in the pattern of natural variation which had not been appreciated before. By the early 1960s it had become evident that little progress could be made without importing a new comprehensive set of seed origins, each of which was to be located accurately, together with the elevation at which it was collected. In 1965, H. A. Maxwell and J. R. Aldhous (1967) made a detailed investigation of a large part of the natural range and had discussions on future seed supplies with all the main seed merchants. As a result of their visit, a collection of 80 seed origins was obtained. This formed the basis for the major series of seed origin trials. Later visits by R. Lines in 1968 and on various occasions by A. M. Fletcher served to investigate critical areas in more detail and to maintain contact with North American seed merchants.

The last major advance in our knowledge of the variation between origins of lodgepole pine came when the International Union of Forest Research Organizations (IUFRO) decided to include lodgepole pine in the range of species selected for testing on a world-wide scale. In a collaborative effort by many individuals and the Forest Services of Canada and the USA, 146 seed origins were obtained in 1966–68. An IUFRO Working Party was set up to organise the international trials (Lines, 1971) in 15 countries and much useful information on the results has been exchanged.

After over 50 years of investigation in seed origin experiments, it is now clear that no single seed origin possesses that combination of characters that would enable it to be used universally on all sites and for all silvicultural purposes in Britain. Progress in combining the most desired characteristics for British forestry may come from the current tree breeding programme (Faulkner, 1985). Little work has been done on the quality of timber produced by various origins on different sites, although this is now a factor tested in progeny experiments. A project to examine timber properties in samples taken from a 50-year-old provenance experiment in Wykeham has recently been undertaken at the University of Wales, Bangor (Marshall, 1989). Earlier studies were reported by Brazier (1980).

In the meantime the managerial solution is one of 'horses for courses', i.e. selecting origins with particular characters for particular site types and for different silvicultural roles and possible differential resistance to insects. The purpose of this Paper is to allow these choices to be made with increased understanding of a complex species.

Chapter 2

Distribution and variation within the natural range

The distribution of lodgepole pine is shown in Figure 1, and is described by Critchfield (1957) and Wheeler and Critchfield (1985). It is indicative of the lack of forestry interest in the scrubby coastal form that the earlier Critchfield publication shows the range terminating at Glacier Bay, Alaska. The outlying population at Yakutat, 140 miles further up the coast was discovered only during a seed collecting tour arranged in 1967 by the International Union of Forest Research Organizations. Aldhous (1976) reviews very fully the botanical and site variation in North West America with reference to British forestry.

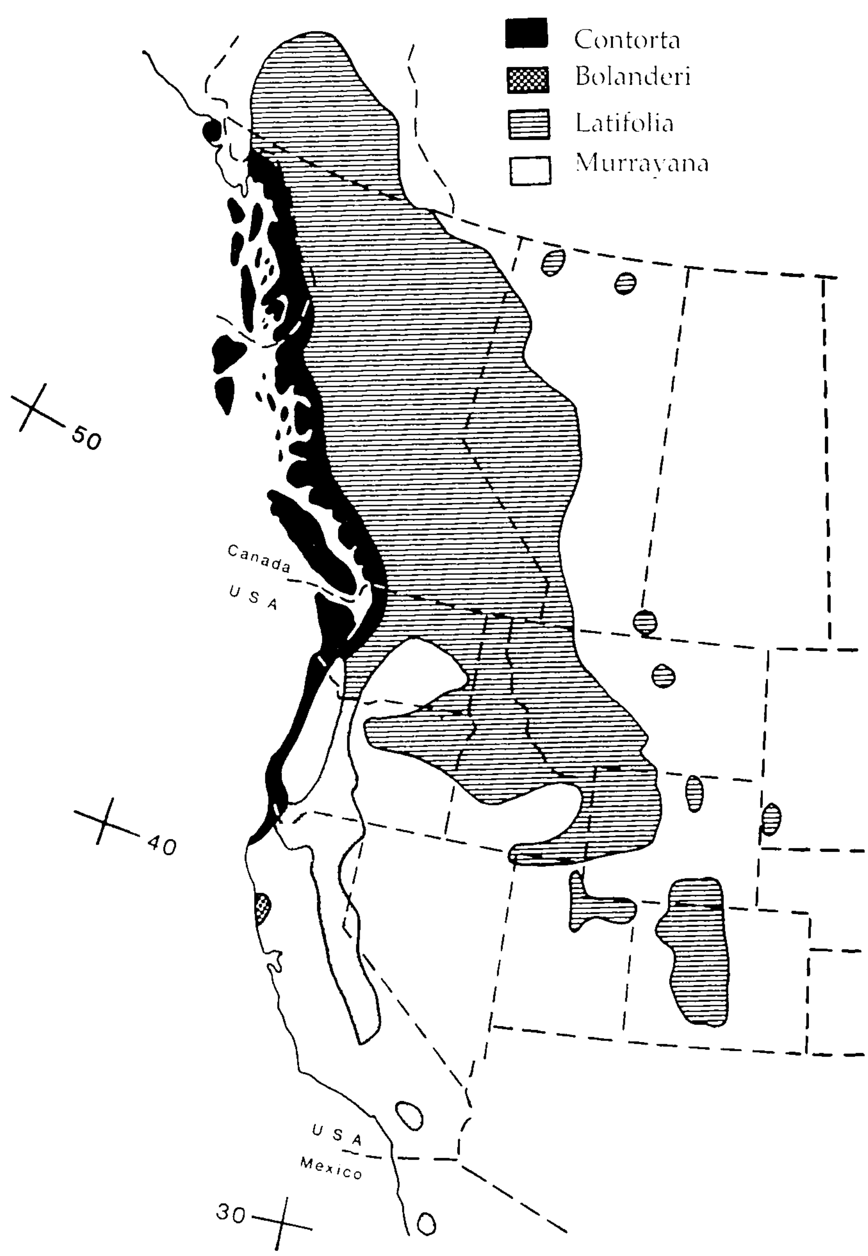

Figure 1. Map of lodgepole pine range (after Critchfield, 1957).

Lodgepole pine covers an area of about 6 million hectares in the USA and 20 million hectares in western Canada, mainly in British Columbia and Alberta, with extensive forests in the southern Yukon and a small eastern outlier in the Cypress Hills on the southern Alberta-Saskatchewan border. It reaches its northern limit at about 64° N in the Yukon near the permafrost zone, where there are some fine stands with individual trees up to 13 m tall at 32 years, even at an elevation of 650 m and with less than 300 mm of annual precipitation (Bartram, 1979).

On the coast it grows on sites that are too poor for its more demanding competitors (mainly Sitka spruce, Douglas fir and western hemlock) such as peat flats that are seasonally water-logged, rocky cliffs, dunes and dry, infertile gravels and sands in the Puget Sound. On southern Vancouver Island it can grow to a large tree on apparently bare, lichen covered, rock sheets by rooting deeply into crevices. On such sites it can withstand summer drought much more successfully than its competitors. At the southern end of its range in California, where it grows often in mixture with P. *muricata*, the stands on the coast extend to Point Arena near the town of Manchester at 39° N. Thirty miles to the north are the heavily compacted and extremely acid soils of the Mendocino White Plains, where so called 'Pygmy Forests' of *P. contorta* sub-species *bolanderi* occur (Critchfield, 1957). There is some debate about the taxonomic status of these populations, which are almost contiguous with stands of the sub-species *contorta* growing near the shore at an elevation only 100 m or so lower down. Wheeler and Critchfield (1985) state that 'this race is probably an edaphic ecotype derived from the contiguous coastal race'. Over much of its present range the coastal populations are effectively separated from the inland populations, either by high mountains in the north, or in the south by wide tracts not covered by coniferous forests. The main paths of gene exchange have been the through valleys such as the Skeena and Fraser River valleys in British Columbia, and the area to the east of the Puget Sound in Washington. There is little opportunity for gene exchange between most of the Alaskan populations on the coast and the Yukon ones of the interior at high elevations. However, on the basis of cone serotiny, Aldhous (1976) and Illingworth (1970) have suggested a coastal transition zone in south-east Alaska and adjacent British Columbia. Seed origins from the rain shadow area near Skagway have much lighter seed than the nearby coastal populations on high rainfall sites and behave somewhat differently from other Alaskan sources, which may indicate some influence of the interior populations from the Yukon. Throughout the coastal range it occurs nearly always at low elevations, though in the south of Vancouver Island it reaches 1500 m.

Ecological conditions in stands of lodgepole pine in the Yukon have been described by Nyland (1980), while the stands themselves have been investigated in detail by Hagner and Fahlroth (1974) and Bartram (1979) because of their great potential for use in the far north of Sweden. These origins are only of academic interest to British foresters.

In the interior of British Columbia and Alberta lodgepole pine occurs at elevations from 300 m to over 2000 m and as this species is highly adaptable to site variation, the vertical contrast is greater than the horizontal one, with important results on choice of seed origin. In northern British Columbia and western Alberta there are extensive areas of lodgepole pine of a rather uniform character resulting from lightning-induced fires (Pojar, 1985). In southern British Colombia and the Rocky Mountains, fire is again responsible for the subclimax stands that may extend as almost even-aged and nearly pure lodgepole pine forest over hundreds of square miles. The serotinous (i.e. closed) nature of the cones on a high proportion of the trees in this area ensures a large seed reserve and, after a fire has melted the resin bond of the cone scales, there may be up to 6 million germinable seeds per hectare (Ackerman, 1966) released on a site with no other competitors. In some cases, growth stagnation results in the 'dog's bristle' stands at extreme overstocking (see Plate 11 in Aldhous, 1976). In areas subject to repeated fires, e.g. where forest borders the dry interior grassland, there is strong selection pressure to fire-resistant ecotypes. These develop thick, corky bark at an early age (see Chapter 17).

Stands of lodgepole pine are less common in the Cascade Mountains of north Washington, while in the southern Cascades, particularly on the drier east slopes and on the plateaux of Deschutes and Klamath Counties in Oregon, extensive pure stands again occur at an elevation of 1500 m. Lodgepole pine forms extensive forests in the Intermountain and Rocky Mountain regions of western Montana, Wyoming and Colorado, usually at elevations over 1000 m and up to 3000 m. Lodgepole pine reaches its upper limit of 3900 m in the southern Sierra Nevada. Volland (1985) summarised the information on the ecological status of lodgepole pine in the United States. It has three ecological niches: 1. as a seral species to more shade tolerant trees; 2. as a relatively stable codominant with one or more other species; and 3. as the only tree-layer dominant.

Fire plays a major role in its success, together with the serotinous (closed cone) cone habit in the Rocky Mountains, but it can also form extensive pure stands, e.g. on dry pumice soils in central Oregon in populations that are mainly non-serotinous.

Lodgepole pine is most closely related to Jack pine (*Pinus banksiana* Lamb.) whose natural range extends from 65° N on the Mackenzie River in the North West Territories to Nova Scotia. The ranges overlap in central Alberta and above 60° N in the North West Territories. In these areas hybridisation has occurred, since the species cross easily (Righter and Stockwell, 1949). There is little evidence for hybrid vigour in the progeny.

The early history of the species has been discussed by Wheeler and Critchfield (1985) and Critchfield (1985). Lodgepole pine has probably been present in the western North American forests for millions of years, but no trees could have survived on the vast area covered by the Wisconsin ice-sheet during the last glacial period, ending about 12 000 years ago (Critchfield, 1985). Populations in areas to the south of this line, i.e. approximately 46-48° N, were influenced to a rather small extent by the glacial influences to the north, and have had ample time to become stabilised in their adaptation to local climates. The populations now found north of the glacial border have presumably arisen from migration northwards and/or from northern stands of trees that survived in glacial refugia. These are known to have existed in the Yukon and east of the Rocky Mountains, where the annual precipitation was too low to allow snow accumulation, as well as on the Pacific coast. For example, Warner *et al.* (1982) showed that some pockets of lodgepole pine persisted throughout the last glacial period on the Queen Charlotte Islands.

These northern populations have had far fewer generations to become adapted to their present site characteristics, yet all the evidence points to their being well adapted to particular site factors and such genetic characters as time of flushing, frost hardiness, etc., exhibit a fixed pattern when seed is transferred to countries as far away as New Zealand or North Sweden. In general, seed origins from high elevations (above 1500 m) or high latitudes (above 56° N) grow slowly in Britain, while origins from latitudes as low as 43° N on the USA coast can survive on coastal sites in Britain at 55° N and even as far as 62° N in the Faroes. On the other hand, edaphic ecotypes, such as the dwarf trees of ssp. *bolanderi* growing on the Mendocino White Plains give progeny very similar to those from tall trees of ssp. *contorta* on the nearby coast when both are grown in Britain.

A general principle in seed transfers from the native range to a new environment is to match the climatic regions as closely as possible (Larsen, S., 1956). Wood (1955) pointed out that in practice there is considerable freedom, 'we can often take our seed from regions further south and a good deal warmer than our own, thereby getting faster growth than if we confined our attention to equivalent latitudes'. Strict climatic matching is seldom possible, as even if annual means for temperature and rainfall can be matched, seasonal variation may be very different. As an example of the approximate nature of climatic matching, seed origins from Prince George, BC can grow well in the British maritime climate, although the best climatic match for Prince George is that of Moscow. Aldhous (1976) gives other examples of sharp local adaptation occurring alongside more gradual clinal trends with latitude or continentality. The quality of adaptability (the ability to grow well on a wide range of sites) is of greatest importance to the forest manager. This subject is discussed further in Chapter 9. Aldhous (1976) has noted that seed in bulk is often collected from an area rather than a point source and that within a 20 mile radius of the town of Salmon Arm, BC, several forest associations occur, giving ecotypes that have developed on sites varying from the dry valley bottom, frequently affected by fire, to montane forests with heavy snow fall and adequate growing season moisture. Differences in aspect can also have a large influence on local site types.

Studies on variation in the natural range

David Douglas collected the scrubby coastal form (later often called 'shore pine') sub-species *contorta* Doug. at Cape Lookout near Tillamook, Oregon in 1825 and in 1826 at Cape Disappointment, Washington (Douglas, 1914). He considered that it had no future in British forestry in comparison with the alternative magnificent forests of Douglas fir, western hemlock and western red cedar, with which he was now familiar. 'Little can be said in favour of this tree, either for ornament or as a useful wood.' On his return journey to Hudson's Bay he walked through extensive forests of the interior form in north east Washington, British Columbia and Alberta without recognising it as the same species. In his Journal under the heading *Pinus banksiana*, he notes 'a common tree in the mountainous districts of the Columbia River in 48° Lat., 118° W Long., and in the valleys of the Rocky Mountains ...'. This species was well known by then from its extensive distribution in eastern Canada, but it does not occur along this part of his route and he must have confused *P. contorta* sub-species *latifolia* with Jack pine.

The two interior forms, sub-species *latifolia* Engelm. and sub-species *murrayana* Balfour were first collected in the 1850s. Another coastal form (sub-species *bolanderi*, Parlatore), which grows on the Mendocino White Plains in northern California, was collected by Bolander in 1866.

There was considerable disagreement about the taxonomy of lodgepole pine during the next 50 years. From the viewpoint of the taxonomist, the similarity of the floral organs throughout the range led to its being classified by Sudworth (1908) in the official manual of the US Forest Service as a single polymorphous species. Practical foresters in North America and Europe were influenced more by the huge differences in growth rate and tree form of progeny from different parts of its range and preferred a division into two or more taxa. The situation was not eased by the fact that for many years all seed from the inland part of the range was sold in Europe as 'var. *murrayana*', despite the large differences in performance between trees from the Oregon Cascades and the Interior Wet Belt of British Columbia, for example. Biochemical tests now allow clear distinction between trees from these regions.

Although there are good older accounts of lodgepole pine forests in some parts of its range (Clements, 1910; Mason, 1915; Whitford and Craig, 1918; Moss, E. H., 1953 and Halliday and Brown, 1943), the first detailed study of natural variation throughout a major part of its range was made by Critchfield (1957). He studied mainly the morphology and anatomy of the needles and cones of trees from 40 seed origins, though he also investigated several characteristics of the seedlings. This can be considered as the first comprehensive seed origin trial of this species in North America. He concluded that the species should be split into four sub-species, as noted above.

Wood (1955) spent 9 months studying the coastal forests of British Columbia and the Pacific coast of the USA, making many important observations about the ecological 'fit' of several species, including lodgepole pine, in relation to their seed transfer to British conditions. A later study by Roche (1962) was concerned primarily with the coastal populations of British Columbia, though he used the Critchfield collection of 22 provenances growing at Placerville, California to study needle width and length. On the basis of the ratios of length to width Roche distinguished three major regions (*contorta*, *latifolia* and *murrayana*). The mean of the *bolanderi* region was not significantly different from that of the *contorta* region.

Critchfield (1980b) summarised many newer studies of variation in natural stands. The most relevant to British conditions are those by Smithers (1961), Roche (1966), Illingworth (1971, 1975) and Aldhous (1976). These authors drew attention to the complexity of behaviour, morphology, cone and seed characteristics and so on, within the area of each sub-species. Thus, although scrubby trees of the sub-species *contorta* are common on rocky cliffs and muskegs, trees on Vancouver Island may exceed 30 m in height and 61 cm in diameter and Critchfield quotes reports of even larger trees on the Queen Charlotte Islands. In British Columbia and the Washington Cascades, trees 40 m tall and 76 cm in diameter have been recorded. Hagner (1985b) claimed that a tree 40.5 m tall and 42.7 cm diameter growing in Manning Park, BC, was the tallest lodgepole pine in the world. Diameter growth in old trees appears to continue for much longer on trees of the sub-species *murrayana* in the southern Sierras, than on trees of the sub-species *latifolia* (Critchfield, 1980a). The largest trees recorded by Pardo (1978) were 33.5 m x 183 cm in diameter and 27.7 m x 206 cm in diameter, both in the Californian Sierras. This pattern of very large diameter growth in relation to moderate growth in height for the *murrayana* sub-species appears to be inherited, judging from results in British experiments. Wheeler and Critchfield (1985) give the most comprehensive recent summary of the botanical characteristics of the four sub-species, which is not repeated here, as it is not directly relevant. Detailed morphological measurements noted in Chapter 16 show that large variations are found among different seed origins within the sub-species in British experiments, though they follow broadly the same pattern as in the native stands.

Differences in the biochemistry of terpenes in wood resin (Smith, 1964), leaf resin (von Rudloff and Nyland, 1979; von Rudloff and Lapp, 1987) and stem cortical resin (Forrest, 1980, 1981 and 1987) have been used to characterise different populations or regions of the natural range and also to estimate the degree of introgression with *Pinus banksiana* (Pollack and Dancik, 1985). Wheeler and Guries (1982) also used isozymes to investigate the genetic similarity of 34 populations. This technique provides information on the genetic history of a species, since isozymes are valuable genetic markers that seem to carry no selective advantage and thus act in a neutral manner.

Chapter 3

Seed zones

For practical purposes, it is necessary to divide the natural range into seed zones as lodgepole pine shows such wide variation in its morphology, rate of growth, resistance to exposure, etc. Ideally, seed from each zone should perform predictably within certain limits, when planted on specified sites in Britain. Even with the information from a large number of seed origin experiments scattered throughout upland Britain this is an ambitious aim. It relies on the assumption that the performance of the progeny from a stand at, say, Fort Fraser, BC, is typical of all stands in the Fort Fraser area. Even if this were true, how far around Fort Fraser would one find similar performance by different seed origins?

One approach is to examine the climatic variation within the native range and fix zones based on this, often using topographic features, such as mountain chains, to act as zonal borders though political boundaries are not ignored. This has long been the method used in the USA for Douglas fir zonation following the pioneer work by Isaac (1949). His scheme was superseded by the North West Forest Tree Seed Certification Scheme (NWFTSC, see Figure 2a) in Washington and Oregon, while in British

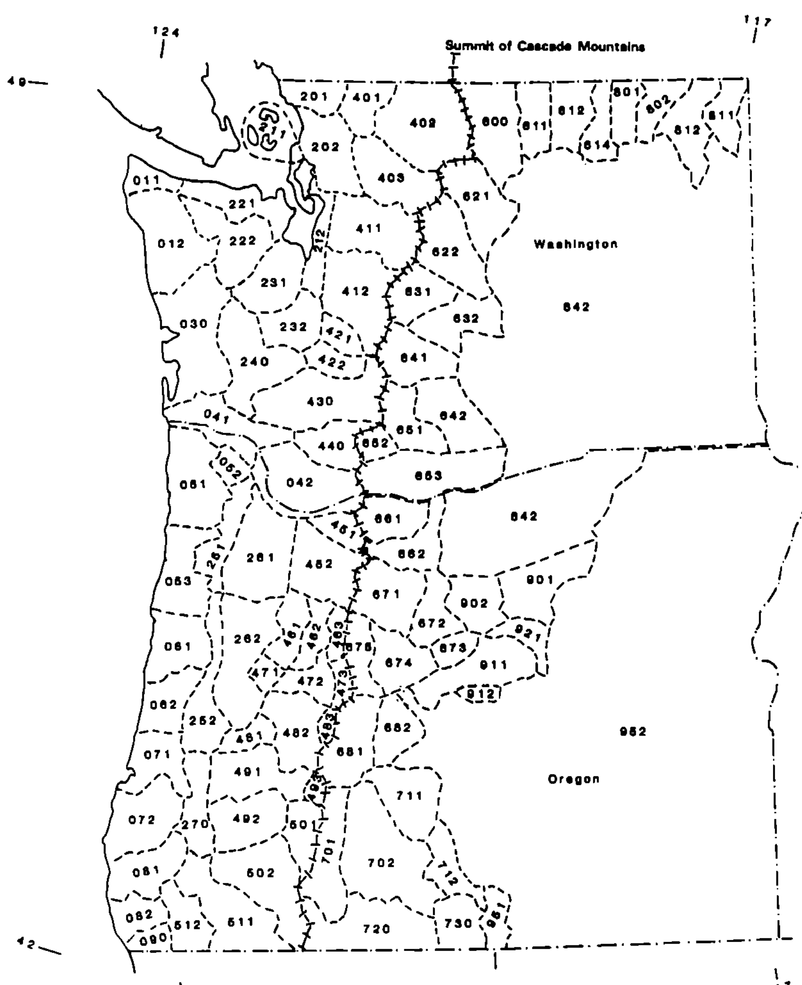

Figure 2a. Tree seed zones for Washington and Oregon, USA.

Columbia, Dobbs *et al.* (1976) published a similar scheme, the British Columbia Forest Tree Seed Zones (BCFTS, see Figure 2b). Aldhous (1976) describes the background of these zonations in more detail. Both are based on Douglas fir, though they are used for all species. In Europe similar zonations have been used by EEC countries for their native species, though in Germany for example, different zone maps are used for different species.

In Britain, from 1921 to 1956 all seedlots were given a serial number that gave no indication of its geographical origin, except by reference to annual lists that were circulated internally. In 1957 a new seed identification code was devised (Matthews, 1958) in which identity numbers were allocated with the crop year, followed by the Seed Region in brackets. Seed Region numbers were taken from the Oxford Decimal Classification. If the seed was from a known locality in that region a further number was added, e.g. 62(7114)1 meant seed was collected in crop year 1962 from Terrace (1) in the Skeena/Bulkley River region (7114). If seed were bulked from say Terrace and Hazelton it would be given the number 62(7114). Twenty-four major seed collecting Regions for North West America were devised (see Figure 2c), based partly on climatic regions, on Isaac's maps and on experience gained in 1952–53 by R. F. Wood (1955) in the coastal part of the range. This zonation lasted from 1957 until 1983, when it was replaced by a revised one based more closely on the NWFTS and the BCFTS regions.

An alternative way of creating seed zones is to examine biological or biochemical characteristics of the trees themselves and use computers to show where statistically significant differences arise between the populations sampled. Clearly this method can only be effective when fairly large numbers of sample populations are used. An early study by Jeffers and Black (1963) used only nine seed origins, but nevertheless produced distinct groupings into North Coastal, South Coastal, Interior BC, with a Cascades origin, ssp. *murrayana* standing out as very different from these. A later study with 30 seed

Figure 2b. Tree seed zones for British Columbia, Canada.

origins, using cluster analysis, and based on height at 15 years on two sites in British Columbia (Ying *et al.*, 1989), showed that only three seed regions could be distinguished in British Columbia: Coastal, Coast–Interior Transition and Central–Southern Interior. Wheeler and Guries (1982) used biochemical markers (isozymes) of 32 seed origins of lodgepole pine to show genetic similarity. Cluster analysis showed close grouping between Yukon and northern British Columbia populations, which were distinct from those of Central and Southern BC. Von Rudloff and Lapp (1987) used a similar cluster analysis to give eight groups from the 681 trees sampled for terpene types from 111 sites. Forrest (1980, 1981, 1987) used shoot monoterpenes to characterise 150 seed origins. With this large number he was able to delimit 14 terpene regions (see Figure 2d). Although the analyses for Forrest's 1980 paper were made on shoots taken from trees growing in Britain, subsequent work by Forrest (1981) using shoot material from the native range has confirmed the strict inheritance of terpene types, which show virtually no effect of varying site conditions, including transfer from North America to Europe.

Table 1 compares the nine main seed collecting regions, comprising a total of 21 subregions, which have been used in this Paper. It will be seen that taxonomically the Coastal regions are all ssp. *contorta*, except for the Californian ssp. *bolanderi*. Regions 3 to 8 are all ssp. *latifolia*. The Washington Cascades seedlots are of the Cascades terpene type ssp. *murrayana* though from their silvicultural behaviour and morphology, they may represent an introgression with ssp. *latifolia*. The Oregon Cascades seedlots are clearly ssp. *murrayana*. The terpene typing method is invaluable as a

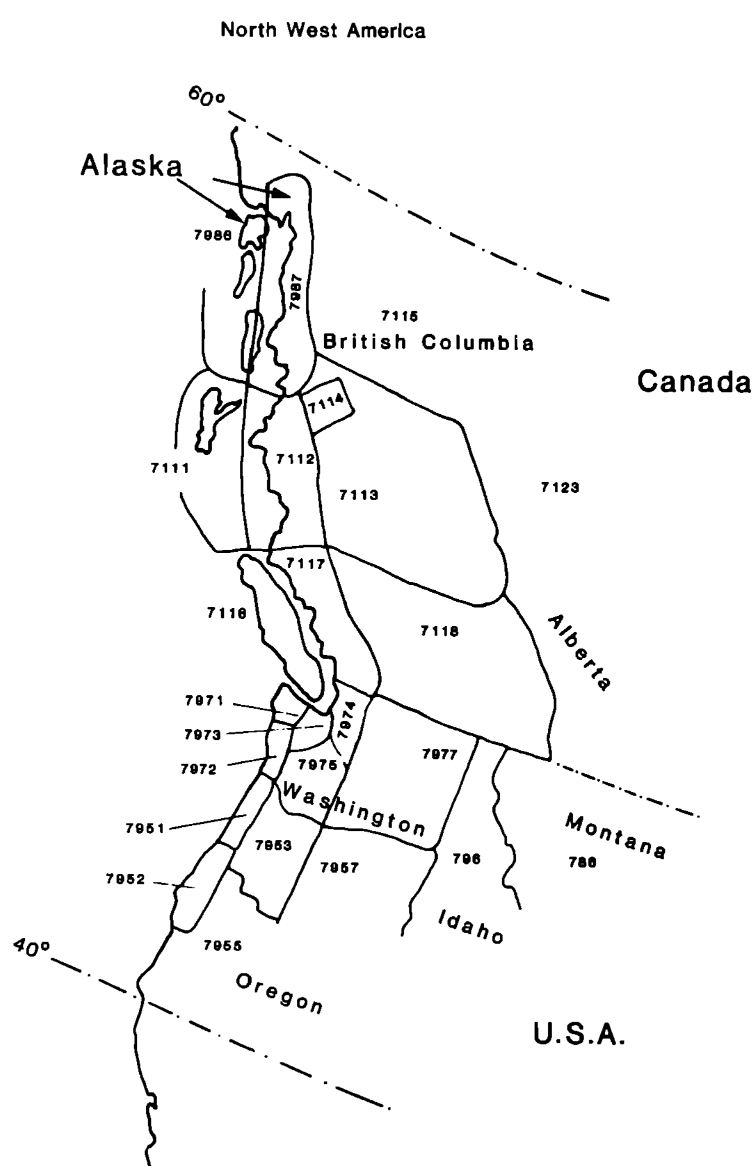

Figure 2c. Forestry Commission seed collecting regions in NW America.

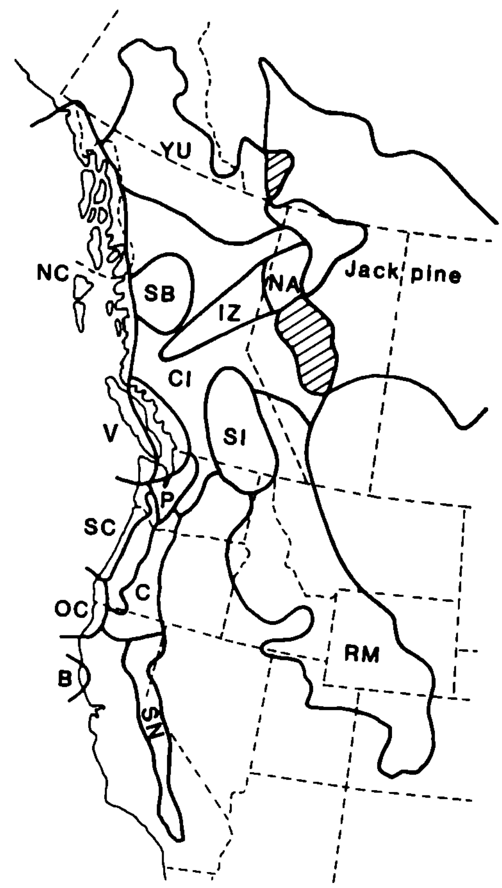

Figure 2d. Terpene regions of Forrest (1980) also showing overlap with Jack pine range.

technique for natural grouping of seed origins, for deciding where the boundary should lie between adjacent groups, for checking the identity of stands whose records of seed identity have been lost, for investigating possible association between individuals showing morphological differences and their genetic make-up (e.g. as hybrids with *Pinus banksiana*) and for indicating probable post-glacial biogeographical movements. Over a large part of its range, these terpene regions correspond rather well with the regions used by the NWFTS and the BCFTS and also with the 1957 Forestry Commission Scheme. However it is clear from seed origin experiments that within some terpene regions wide differences are found in inherent vigour. For example, the North Coastal terpene region extends for 1000 miles from Yakutat, Alaska to Queets, Washington. Within this area there is a cline for increasing vigour from north to south. Similarly within the main Skeena/Bulkley River region there is a cline for increasing continentality and lower rainfall moving from the coast into the interior. This variation is evident in the forest type and was commented on by Wood (1955), while Aldhous (1976) suggested that this region should be divided into three sub-regions. Without more detailed investigation, Forrest (1980) was content with one rather variable terpene region, but on the basis of several silvicultural and morphological characteristics it seems appropriate to use two sub-regions in this Paper. Within the Southern Interior of British Columbia, Forrest again showed a fairly wide range in variation between individual seed origins. His Central Interior terpene type comes much further south into the (7118) region than had been thought previously. As with the North Coastal region, here again there is an increasing cline for vigour of seed origins from north to south which makes a latitudinal split convenient. A large area in the southern part of the range is not well represented in the experiments that are the subject of this Paper. So few seedlots came from the large Rocky Mountain and Sierra Nevada terpene regions that they have been excluded from Table 1. These seed origins do not appear to have much practical use in British forestry.

The object of this Paper is not to investigate the taxonomic position of lodgepole pine, so that in broad discussion the four sub-species defined by Critchfield (1957, 1980b) are used. All seed origins are treated as separate identities, grouped by seed regions for convenience and to allow more detailed examination in statistical tests.

Table 1. Comparison of seed zonation used in this Paper with earlier zonation schemes

	Major and minor seed regions used in this Paper	BCFTS zone or NWFTS region	Forestry Commission regions from 1957	Terpene regions of Forrest (1980)	Key (see Fig.2d)	Numbers of seedlots in seed origin experiments	Remarks
1.	NORTH COASTAL						
	Alaska						
	Outer Islands	–	7986	North Coastal	NC	12	Includes home collections originally from Hollis
	Inner Islands, Mainland	–	7987	North Coastal		16	Largely from sites with lower rainfall
	Coast British Columbia						
	Queen Charlotte Islands	1110	7111	North Coastal		7	Includes home collections originally from QCI
	North Coast	1100 & 1120	7112	North Coastal		7	
	North and West of Vancouver Island	1010	7116	North Coastal		4	Includes Queets (Chapter 12)
	South and East of Vancouver Island	1020	7116	Vancouver	V	13	
	South Coast	1030 & 1040	7117	Vancouver		5	Excludes Lulu Island and Langley
	Lower Fraser River	1050	7117	Vancouver		12	Excludes Lulu Island and Langley
2.	SOUTH COASTAL						
	Washington						
	Pacific Coast	030	7971 & 7972	Parts of North Coastal & South Coastal	SC	12	Only Queets (Chapter 12) shown to be North Coastal
	Puget Sound	231	7973 & 7975	Puget Sound	P	9	Most seedlots from the dry part of this region
	Oregon						
	Coast	051, 053, 061, 062	7971 & 7952	South Coastal (part), Oregon/California Coastal (part)	OC	17	Some seedlots are from plantations, but probably originate in this region
	California						
	Coast	–	794	Oregon/California Coastal (part) ssp. *bolanderi* (part)	B	4	Progeny from ssp. *bolanderi* behave similarly to those from the coast
3.	YUKON & NORTH INTERIOR BC	8000, 6090, 6100	7121 & 7115 (part)	Yukon and North BC	YU	3	
4.	SKEENA/BULKLEY RIVER						
	Lower Skeena River	1140	7114	Skeena and Bulkley Rivers	SB	19	Includes Nass River
	Upper Skeena/Bulkley River	1150 & 5080	7114	Skeena and Bulkley Rivers		12	Includes part of BCFTS Central Dry Region
5.	CENTRAL INTERIOR BC	5000 & 6020	7113, 7115 (part)	Central Interior BC (part) Introgression zone with Jack pine (part)	CI	31	Trees from the introgression zone behave similarly to those outside it
6.	SOUTHERN INTERIOR BC						
	Southern Dry	2000	7118	Central Interior BC (part) Southern Interior BC (part)	SI	15	) See discussion on p.12 for) separation on these
	Interior Wet	3000	7118	Southern Interior BC (part) Rocky Mountains (part)		26	) regions
7.	ALBERTA & SASKATCHEWAN	–	7123 & 7124	North Alberta, Rocky Mountains	NA	6	Seedlots all from Rocky Mountains
8.	USA NORTH INTERIOR	–	796, 7977, 786	Rocky Mountains	RM	5	Includes East Washington, Idaho and Montana
9.	CASCADES						
	Washington	641, 651, 652	7976	Cascades	C	2	) See pp.11-12 for separation of these
	Oregon	681, 682	7956	Cascades		7	) seed regions
						total 244	

Chapter 4

Introduction and use in Great Britain

Lodgepole pine was probably first seen by Europeans in 1778, when Captain Cook stopped for a short time to repair his ships at Friendly Cove in Nootka Sound on the west side of Vancouver Island. A contemporary painting shows scrubby-looking trees (almost certainly lodgepole pine) on the rocky island in this cove. Seed was obtained from this island 190 years later by K. Illingworth, and included in the IUFRO collection. The interior form was seen first by the Lewis and Clarke Expedition in the Rocky Mountains in 1805. The species was not described botanically until 1825, when it was collected by David Douglas. His seed did not survive and the tree was introduced to arboriculture in Britain by Jeffrey in 1853 from seed collected in the Siskiyou Mountains of California at 2285 m (Johnstone, 1939). With hindsight it is clear that this was an inherently slow-growing seed origin, which may explain the lack of interest in the species for specimen tree planting. Later introductions of unrecorded seed origin must have come from the coast region, as the large individuals at Bodnant, North Wales, planted 1888 (34 m tall by 96 cm in diameter in 1984), Bicton, Devon (31 m tall by 109 cm in diameter in 1964) and Westonbirt, planted 1876 (20 m tall by 91 cm in diameter in 1982) are all clearly the sub-species *contorta*. The Bicton tree blew down in 1968. The tallest lodgepole pine in Britain of the sub-species *latifolia* is at Culcreuch Castle, Stirling – 29.5 m tall by 69 cm in diameter, measured in 1984.

The first plantation was established in 1912 at the Ruttle Wood, Beaufort Estate near Inverness using seed from J. Rafn. From the appearance of the trees they are clearly from the coast of Washington or Oregon. Terpene testing on their progeny has confirmed that they originated either from South Coastal or Vancouver groups. The pattern of terpenes is rather similar to trees from North Bend, Oregon. This stand grew much faster than surrounding crops of other species, with a mean height of 13.4 m and a diameter of 27.5 cm at 40 years before it blew down in a gale. The next oldest stands were planted in 1922 at Culbin (Experiment 2), Nairn, and Inchnacardoch (Experiment 67), Inverness-shire. These are also of Washington Coast appearance and terpene tests show them to be very similar to collections made at Long Beach, Washington. The Culbin experiment is still standing (despite some windthrow) and has been used as a sample plot since 1946. The Yield Class is 10 and the crowns are still spire-like, whereas on adjacent Scots pines of the same age the crowns are becoming rounded. The Inchnacardoch plot suffered from *Heterobasidion* (Fomes) rot and was windthrown in 1952.

In 1928/29 five experiments (not concerned with seed origin) were planted at Inchnacardoch and at three other sites, using seed collected in 1925 from well-documented seed origins in the Southern Interior of British Columbia. One of these (Inchnacardoch 52 P29) is a 0.4 ha block on poor, deep, acid peat whose later performance was noted by Zehetmayr (1954, p.39 and Photo 23) and Lines (1976a, p.120 and Plate 22). The successful growth of lodgepole pine in this experiment had a major influence on future forest policy, as it established that it was technically possible to grow lodgepole pine to timber size on a rotation of 55 years, even on the worst deep peat soils. The seed origin was Mount Ida, just south of Salmon Arm on Shuswap Lake at an elevation between 800 and 1100 m.

The first large consignment of seed (94 kg) came from Alberta. It was sent by the District Forest Inspector at Calgary and described as 'collected in the Foothills of the Rocky Mountains'. Horton (1956) describes four phytogeographic divisions of the lodgepole pine forests in Alberta. The Low and High Foothills nearest to Calgary range from 900 to 1800 m in elevation, so that it is likely that this seedlot was collected at over 1000 m. Between 1928 and 1933 this seed was used to make small plantations in many forests in Scotland and northern England, and gave many foresters their first experience of what was then an unusual species. It grew at a rate similar to that of Scots pine and its clean form, straight stems and ability to grow well on poor heathlands attracted favourable comment. However, on several sites, dieback and death of individuals was apparent when the trees were 22 years old (Day, 1952). Edwards (1960) concluded that 'certain provenances of lodgepole pine, from high elevations at places far removed from the coast of western North America, are susceptible to dieback in this country, and this tendency is related to frost, which has been found to cause the death of branches, so that more dieback may be expected in frost hollows and damp sites than on exposed knolls'. Some later introductions in the 1930s displayed resin bleeding associated with the fungus *Crumenula* (Hayes, 1973).

Although the Research Division of the Forestry Commission used lodgepole pine widely in experiments, only 1300 ha were planted before 1947 in both Forestry Commission and private woodlands (Lines, 1976a). By contrast, it was widely used in Eire from an early date (Anderson and Taylor, 1967) with 40 000 ha established by 1963, while the total area in British woodlands was only 28 000 ha up to 1960. It is possibly significant that from 1919 to 1952 the Forestry Commission was under the leadership of R. L. Robinson (later Lord Robinson) who had a poor opinion of this species (Macdonald, 1954). However, it was used in North (Scotland) Conservancy by J. Fraser in the 1940s in the rehabilitation of checked Sitka spruce. The number of lodgepole pine plants used each year rose from 137 000 in 1946 to more than 20 million in 1964. Figure 3 shows that the big expansion in use of lodgepole pine came in the late 1950s and early 1960s. This increase in use came about partly

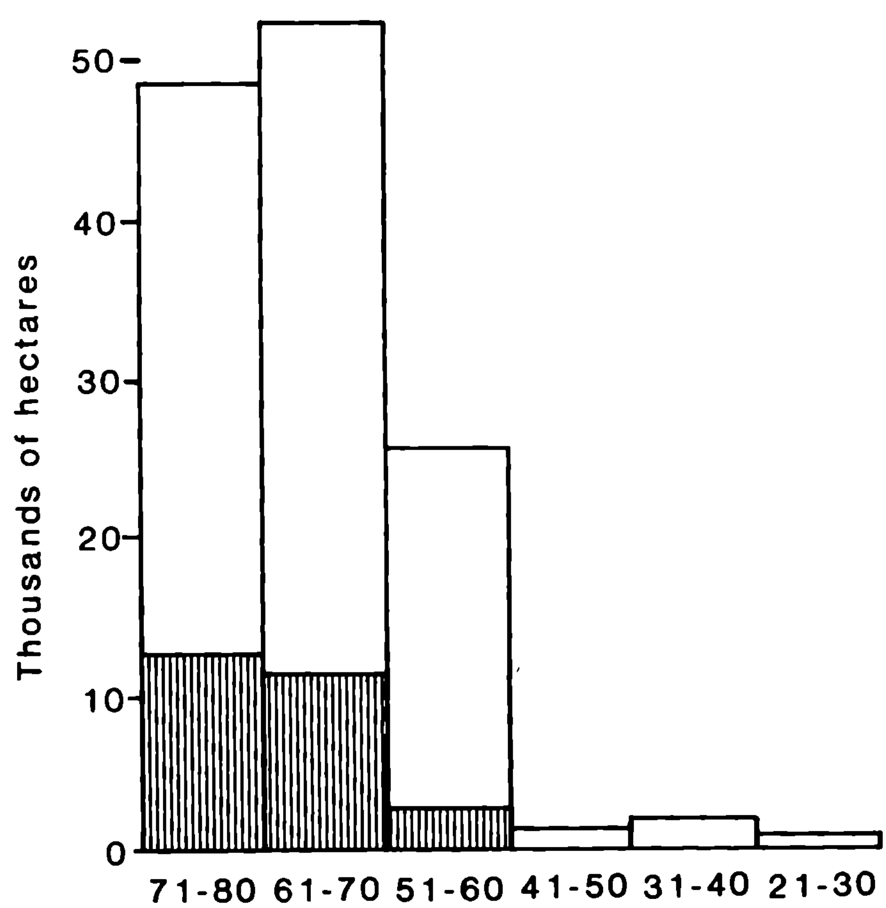

Figure 3. Total area, and area in private woodland (shaded), of lodgepole pine planted in each decade in Great Britain.

because of greater confidence in the species from its success in experiments, partly from a deterioration in the average quality of the ground acquired in later years and partly because much lodgepole pine was used in mixture with Sitka spruce. For example, in South (Scotland) Conservancy these mixtures represented over one-third of the total area of about 20 000 ha planted in 1961–65 (Garforth, 1979). In the late 1960s and 1970s wide-scale use of aerial fertilisation became common, which encouraged greater use of pure Sitka spruce, even when considerable fertiliser input and *Calluna* control with herbicides was required for successful growth. Use of lodgepole pine became confined more and more to the worst blanket peat sites, particularly in Scotland, where it accounted for 93% of all lodgepole pine planted in Britain in 1971–72, nearly all being in North and East Conservancies.

In 1980 there were 101 391 ha of lodgepole pine in Forestry Commission woodlands and 25 677 ha in private woodlands. In Eire there were 80 000 ha of lodgepole pine in pure plantations and 24 000 ha in mixture with Sitka spruce (Carey and Hendrick, 1986). However, in Northern Ireland only about 5000 ha have been planted with this species.

Many of the mixtures of lodgepole pine and Sitka spruce used lodgepole pine seed origins, which are now considered unsuitable, as the pine either had poor resistance to exposure and thus no nursing effect (e.g. Lulu Island origins), or else grew so fast (South Coastal origins) that it suppressed many of the spruce (Lines, 1968). However, experiments planted in the 1960s with Alaskan origins of lodgepole pine and Sitka spruce from the Queen Charlotte Islands showed a clear nursing effect around the time of canopy closure, and growth of spruce in mixture equalled that of heavily fertilised pure spruce plots (McIntosh, 1983). With this new evidence, backed up by more extensive Conservancy stands of these mixtures in north Scotland, mixtures of lodgepole pine and Sitka spruce had become standard silvicultural practice in the 1980s, on infertile sites that would require repeated nitrogen fertilising if planted with pure Sitka spruce, or in frosty hollows where early growth of spruce is repeatedly checked by late spring frosts. It must be stressed that only slow-growing northern origins of lodgepole pine have been shown to achieve this beneficial effect on the growth of spruce (Taylor, 1985).

The locally severe outbreaks of pine beauty moth (*Panolis flammea*) on young stands of lodgepole pine in north Scotland from 1976 onwards (Stoakley, 1977) caused a drastic reappraisal of the position of this species in British forestry. The ecological and silvicultural implications of this pest are now becoming better understood. Fortunately, it shows a lower preference for, and develops less actively on, Alaskan seed origins compared with those from southern coastal areas (Leather, 1985). Severe outbreaks of pine beauty moth seem to be restricted to poor, deep peat sites and most were initiated in stands of southern coastal origins, which are no longer used in Britain. The current position is described in Forestry Commission Bulletin 67 (Leather *et al.*, 1987).

Defoliation by the sawfly *Neodiprion sertifer* frequently caused concern. Techniques of application of the natural polyhedral virus were evolved and these proved an effective control. Defoliation by *Zeiraphera diniana*, which attacks the current shoots, especially when in combination with *Neodiprion*, which attacks mainly older needles, also severely retarded growth on occasions in thicket stands. There are clear differences in the degree of attack by *Zeiraphera* on different seed origins (Day *et al.*, 1991).

Table 2 shows the weight of seed purchased by the Forestry Commission over four periods. This shows how seed origin choice has varied as more information on performance has accumulated and as lodgepole pine has been used in different silvicultural roles. It should also be remembered that a high proportion of the seed used by the Private Woodlands sector was bought from the Forestry Commission.

Table 2. Weight of seed in kilos purchased over four periods with percentage for each seed origin group

Seed origin group	1920–1945	%	1946–1955	%	1956–1964	%	1965–1980	%	Total	Overall %
Alaskan	–	–	<1	<1	9	<1	99	3	108	1
North Coast of BC	2	<1	–	–	32	<1	16	1	50	<1
Lower Fraser River & SE Vancouver Island	14*	2	1309*	66	832†	22	–	–	2155	23
South Coastal (USA)	163	28	174	9	1946	52	620	21	2903	31
Skeena River BC	37	6	–	–	3	<1	892	30	932	10
Central Interior BC	74	13	12	<1	711	19	210	7	1007	11
South Interior BC	155	26	332	17	225	6	1076	36	1788	19
Washington & Oregon Cascade Mountains	49	8	160	8	5	<1	96	3	310	3
Alberta & Rocky Mountains	93	16	–	–	–	–	–	–	93	1
Total	587		1987		3763		3009		9269	

* Mainly from Lulu Island
† Mainly from Sooke, Vancouver Island

From this table it will be seen that large quantities of seed came from the Lower Fraser River (mainly Lulu Island) and South East Vancouver Island (mainly Sooke), while Alaskan seed was first obtained in 1952 and was only imported in any quantity after 1965.

South coastal origins, at first often from the Long Beach area of Washington, but with large imports from the Oregon coast in the 1950s, accounted for only about one-tenth of the total up to 1954, then rose to over half in the third period (a response to its vigorous growth and exposure resistance), falling to 21% in the recent period up to 1980. No seed has been purchased from this area for many years.

Bulk supplies from the Skeena River were hard to obtain before the mid 1960s, but as their good properties became apparent from experimental results, imports rose in the fourth period. Seedlots from the Central Interior of British Columbia comprised about one-third of the seed from British Columbia and were intended largely for drier eastern heathlands. Early imports were mainly from Prince George and Quesnel, with later imports from the more westerly Fort Fraser area.

The Southern Interior of British Columbia was the most important seed source for general use until 1939, with large quantities from Shuswap Lake and Vavenby. The importance of obtaining seed from higher elevation stands in the 'Interior Wet Belt' sector of this large region was not realised in the early years. In the latest period this group accounts for the largest amount of seed purchased.

Only small quantities of seed were purchased from east of the Rocky Mountains, the Washington and Oregon Cascades or the Californian Sierras. No commercial seedlots were purchased from the Yukon or the coast of California, though these areas are represented in experiments to complete the cover of the range.

Throughout the period up to the early 1960s, the Forestry Commission bought seed from merchants in British Columbia and the USA, but until 1965 had never sent an inspector to check collection sites and there was no assurance that bulk collections came from stands with the desired characteristics.

When difficulties arose with seed supplies in some regions of North America, strenuous efforts were made to obtain seed from stands in Britain. This applied particularly to Alaskan seed origins and to those from the North Coastal area of British Columbia. In the native stands, which are often on muskegs or other very poor sites, few cones are borne per tree, which makes commercial collection extremely expensive, whereas under British conditions individual trees of these origins may have 20 to 50 times as many cones. Seventy-six hectares of 'seed plantations', whose primary purpose is to supply seed of origins that are difficult or costly to obtain in bulk, have been established. The trees were planted on sites where early and prolific coning can be predicted, and where cross-fertilisation with undesirable seed origins is unlikely. Home seed sources have become increasingly important, with 750 kg collected during the period 1973–83. About half of this seed was of the scarce North Coastal and Alaskan provenances, the rest mainly of Skeena River provenance.

Chapter 5

Seed origin experiments with lodgepole pine in Britain and abroad

British experiments

The Canadian Government, which was a major supplier of North American seed to the Forestry Commission in the 1920s, sent seven seedlots of lodgepole pine in 1925 and 1928 from the Sicamous–Kamloops–Ashcroft area of British Columbia. These were accompanied by detailed site descriptions made by A.C. Thrupp, the Regional Forester. All were in the valleys of the Thompson River and ranged in elevation from 488 m to 1524 m. These sites cover the transition from the very dry area around Kamloops to the 'Interior Wet Belt' on the upper slopes of Mount Ida. The same area was described after a visit by Ilvessalo (1929), who had been impressed by the growth of some of the oldest plots of lodgepole pine in Europe at the Mustila Forest Garden in Finland. Two of the seedlots sent in 1928 duplicated those in the 1925 collection, so that five different sites are represented. Seed from the 1928 collection was also sent to Finland (Weissenberg, 1972) and other countries in Europe. The plants from the 1925 seed were planted at seven sites and those from the 1928 seed at four sites in Britain. Results from these experiments did not show very large differences, though they indicated that seed from low elevations in the Southern Interior of British Columbia produces taller trees at low elevation sites, but shorter trees on high and exposed sites in Britain.

In 1930, three seedlots from the east side of Vancouver Island were planted at Beddgelert, North Wales, in unreplicated plots on a fairly exposed site at 300 m. Differences between these lots in height and appearance were small, though they were distinct from the interior British Columbia lots planted here earlier. Stem form was good and basal sweep absent. Further minor experiments on three sites in 1934–36 tested seven seedlots (see Edwards and Pinchin, 1953, for the results at Clocaenog, Clwyd). These experiments included the first seed from the Central Interior of British Columbia (Prince George) and the first home collected seed.

In 1933 W. H. Guillebaud, then Chief Research Officer of the Forestry Commission, visited Eire to study plantations of lodgepole pine. His unpublished report shows how impressed he was by the rapid growth and resistance to exposure of the southern coastal origins that he saw there. As a result of this visit, arrangements were made to obtain seed for new experiments testing origins from many parts of the range. The 30 seedlots obtained were sown in 1935 and subsequent years, but not in replicated nursery experiments, with the result that differences between seed origins due to local variations in soil fertility, nursery treatment, etc., could not be ascertained. Experiments were then planted in 1937 to 1939 at eight forests, covering a range of sites from the Yorkshire Moors to Wester Ross. Details of the four main sites are shown in Table 3. Most of the experiments contain a replicated section of small (30–36 plant) plots, together with unreplicated single plots of 150–1000 plants. The experiment at Wykeham, North Yorks is unique for experiments established at this time anywhere in the world, in having three replicates of plots large enough (240 plants) to give reliable long-term volume data. In addition, unreplicated plots (each of 1150 plants) were included for nine of the 16 seed origins. Some of these large plots have since been used as Permanent Sample Plots and the replicated plots have provided sample trees for timber testing. Not all 30 seedlots were available for planting at the same time, so that, apart from Wykeham, the other experiments in this series have sub-experiments testing smaller numbers of origins in successive years. The main demerit of this series of experiments is that details of origins are sparse and the effective life of the replicated sections of the experiments is restricted by interaction between plots, except at Wykeham. Further details are given by Lines (1976b) and the overall conclusions from this series have been summarised (Lines, 1966).

During the postwar period from 1952 to 1968, the main emphasis at first was on assessments

Map reference	NH020480	SE950875	NH661620	NJ473325
Elevation (m)	40	183	145	358
Relative elevation	Valley floor, 25 m, half mile north. Mountainous ridge to 610 m 2 miles to south-west.	Plateau rising to 210 m 1 mile to north-west. Valley floor 135 m quarter mile to west.	Plateau rising to 245 m 2 miles to south-west. Sea 2½ miles to north.	On east to west ridge rising to 380 m quarter mile to north-west and falling to 260 m half mile to south.
Exposure	Moderate.	Moderate.	Severe.	Severe except to north.
Aspect	West-north-west.	South-south-east	North-west.	South to south-west.
Slope	Steep to moderate.	Gentle, even.	Gentle, even.	Moderate.
Topography	Undulating with knolls and steep sided gullies.	Nearly flat.	Nearly flat.	Fairly even slope.
Geology	Moine-Gneiss with consider-able glacial drift.	Lower calcareous grit of Middle Oolite series.	Old Red Sandstone.	Macduff slates of the Highland schists.
Soil	Varying depth of peat over-lying peaty podzolic morainic drift.	Strongly developed podzol with indurated pan at 25 cm over an orange-brown sandy loam.	Two centimetres of peat over a strongly leached pebbly morainic drift. Very compact below 30 cm.	Podsolised silty loam with 5-10 cm of raw humus overlying compact olive grey silt loam with broken slate.
Fertiliser	56 g ground mineral phosphate per tree.	28 g of basic slag per tree.	None.	None.
Rainfall per annum (mm)	2032	950	830	1100
Vegetation before planting	*Trichophorum*/*Calluna* with some *Molinia* and *Myrica* in flushes. *Cladonia* present on knolls.	*Calluna* dominant with occasional *Erica tetralix*, E. *cinerea* and *Nardus*.	Poor *Calluna*/*Trichophorum* with *E. tetralix* and *Cladonia*.	Strong *Calluna* with *E. cinerea*, *Empetrum* and *Arctostaphylos*.

in the 1937–39 series, which were now beginning to yield information on seed origin variation over a range-wide basis for the first time (Macdonald, 1954). These included not only data on height but also on morphology, needle colour and retention, vegetation suppression and stem straightness. Many of the 30 new experiments planted in this period were intended mainly to evaluate seedlots that were imported for widespread commercial use (a few of these clearly showed that the origin stated by the supplier was incorrect), or to investigate parts of the range that were not sampled by the 1937–39 series. For example, the recommended seed source in the early 1950s was 'coastal' origins, based on 12-year results in the 1937–39 experiments with Washington coast sources and on excellent results with these in Eire (Lines, 1957a) and in young afforestation experiments on difficult sites in north Scotland. 'Coastal' seed was available cheaply and in large amounts from the Lower Fraser River, where the firm of Roche had a seed extractory on Lulu Island. At the time it was not known that seed from this area would perform very differently from the Washington coast sources.

Several experiments soon confirmed early forest experience that in both growth rate and resistance to winter blasting damage, the Lulu Island seedlots were greatly inferior to those from the Washington coast (Lines and Aldhous, 1957). On sheltered sites of moderate fertility this 'Lulu Island' type from the mouth of the Fraser River was capable of growing with straight stems and its height growth was about the same as Scots pine. However, even on sheltered sites, basal area production was poor, probably because so much of the biomass was diverted to excessive precocious flower production. Between 1949 and 1953, nearly 1000 kg of 'Lulu Island' seed was purchased. Unfortunately, even after Research staff had begun to appreciate the shortcomings of the 'Lulu Island' origin, a further 272 kg was purchased in 1954/55.

Another series of experiments in 1954 included two seedlots from Alaska, the first time these origins had been imported. They proved exceptionally hardy on exposed northern sites and were outstanding in Orkney and other northern trial plantations, which always included a range of seed origins of lodgepole pine and thus contributed information in addition to that from seed origin experiments proper.

Further seed origin experiments were planted every year from 1957 to 1968, mostly testing the large range of commercial seedlots that became available every year on a much wider range of sites (from Cornwall to Sutherland), than had been covered by earlier experiments. Also included were small plots of 11 origins from the extensive range sampled by Critchfield (1957), including seedlots from an elevation of 2680 m in Colorado, and for the first time seedlots from California and the Yukon.

In addition, North (Scotland) Conservancy formed large-scale trial plantations at Naver, Rumster and Shin Forests. Whole compartments were planted with pure lodgepole pine of different origins each year over several years. These formed a very useful set of reference plots and some were later used for seed collection.

During this period, changes in planting stock production, ground preparation and fertiliser application altered management practice so greatly that it was necessary to re-test seed origins whose performance was by now quite well known from older experiments established using primitive techniques. Particularly affected were seed origins from the coast of Washington and Oregon, whose inherent tendency to develop early basal sweep was greatly increased by deep ploughing and higher rates of phosphate application, compared with planting on individual turves or direct notching, with minimal or no fertiliser in the pre-war experiments. The use of very young seedlings of these South Coastal origins, planted in polystyrene tubes, was one of several attempts to reduce the incidence of basal sweep by cultural means (Low, 1975). Several seed origin experiments included many provenances from selected stands in Eire and from British stands of origins that were difficult to obtain commercially, e.g. the Queen Charlotte Islands. It was noteworthy that the progeny from these collections proved overwhelmingly true to type, suggesting that inter-provenance hybrids occurred rarely, perhaps due to differences in flower phenology under open pollination conditions, as controlled provenance crosses proved easy to make.

By 1964 it was apparent that the existing experiments were unsatisfactory in many respects. No comprehensive set of seed origins covering the whole range existed. Lodgepole pine stands in North America had not been studied by British foresters, except in one or two localities by Wood

(1955). Opportunities for future commercial collections from those areas that looked promising in experiments required further investigation on site. Accordingly an extensive tour was made in 1965 by H.A. Maxwell and J.R. Aldhous (1967). A much longer internal report (Aldhous and Maxwell, 1966) gives a most comprehensive description of the native stands and of stands planted by the Soil Conservation Service on the Oregon dunes. Part of this information was summarised by Aldhous (1976).

One of the objects of this tour was to arrange collections for a new series of seed origin experiments. Over 80 seed origins were obtained in 1965, the majority through commercial collections, but with great attention given to locality and elevation. Though a small proportion of aberrant individuals has emerged, there is no reason to doubt the authenticity of any seedlot. The 13 experiments planted in Scotland and northern England contain 28 to 81 seed origins, while those in Wales, south-west and east England each have 72 seed origins (see Table 4 for site data). Lodgepole pine was the second species selected by the International Union of Forest Research Organizations (IUFRO) to form the basis of a world-wide series of seed origin experiments. One hundred and forty six seedlots were obtained in 1966-68 by a special IUFRO collecting team led by L. Feilberg, with additional seedlots provided by K. Illingworth in British Columbia (Lines, 1971). Because the 1965 collection of Maxwell/Aldhous was so comprehensive, only 24 of the IUFRO seedlots were selected for testing in Britain, mainly to fill gaps in the northern part of the coastal range. Six experiments cover the main range of site types, principally in Scotland (see Table 5).

Over the years, over 300 seedlots have been included in British experiments (not all representing different seed origins, as some are from the same place in different years). These have been planted in over 80 experiments, which cover most of the main site types on which this species has been planted in Britain (Table 6). A recent development has been the extent to which these trials have been used by other researchers, particularly from the Universities and the Institute of Terrestrial Ecology of the Natural Environment Research Council (e.g. Cannell, 1974; Thompson, 1974).

Table 4. Distribution and layout of experiments, 1970/71 series

Experiment	Location	Site type	Number of seed origins	Number of replicates	Number of plants per plot	Notes
Mabie 10 P70	Dumfriesshire	Lowland deep peat	81	5	30	Very uniform site
Shin 25 P70	Sutherland	Northern blanket peat	36	3	144	Typical of huge area
Rumster 8 P71	Caithness	Caithness flats, blanket peat	49	4	36	Includes SP and SS. Close to Expt 4 P69
Glengarry 16 P70	Inverness-shire	Central Moine unflushed bog	36	5	36	Close to Expt 14 P69
Rosarie 3 P70	Banffshire	NE *Calluna* heathland	49	4	36	Includes SP and SS
Glentrool 25 P70	Kirkcudbrightshire	Galloway deep blanket peat	28	3	144	Typical of huge area
Broxa 115 P70	Yorkshire	N Yorks Moors *Calluna* heathland	49	4	36	Includes SS, SP and CP
Beddgelert 24 P70	Caernarvonshire	Exposed infertile wet moorland	72	3+2	25+196	Includes three origins of SS
Brendon 21 P70	Somerset	Infertile, drier moorland	72	3+2	25+196	Includes CP (near its limit?)
Thetford 142 P70	Norfolk	Dry breckland heath	72	3	25	Includes CP
Tywi 16 P70	Cardiganshire	Upland blanket peat	72	3+2	25+196	Includes three origins of SS
Shin 17 P68-71	Sutherland	Northern blanket peat	50	1	120	Demonstration plots
Honiton 4 P70	Devon	Upland infertile sand	69	1	144	Demonstration plots

SP, Scots pine; SS, Sitka spruce; CP, Corsican pine

Table 5. Site data for the IUFRO experiments planted in 1972

Experiment	**Rumster 10**	**Shin 36**	**Farigaig 21**	**Fiunary 5**	**Arecleoch 5**	**Broxa 126**
Region	Highland	Highland	Highland	Highland	Dumfries & Galloway	North Yorkshire
Map reference	ND083467	NC327043	NH478106	NM632498	NX219795	SE949943
Elevation (m)	122	200	250	350	167	210
Exposure	Severe	Moderate	High	Severe	Moderate	Sheltered
Aspect	South. Nearly flat	South-east	North-west	South-west	Flat	Almost flat
Geology	Caithness flags	Moine	Moine	Basalt	Ordovician	Jurassic grit
Soil	Unflushed bog	Unflushed bog	Deep hill peat	Hill peat 2 m	Unflushed bog 2 m	Ironpan
Precipitation (mm)	1000	1400	1140	1778	1270	864
Notes	Most northern site. No topographic shelter. Some early animal damage. Links with P70 experiment.	Climate intermediate between West Coast and and Interior. Links with P70 experiments.	Climate less maritime. Links to P70 experiments at Glengarry.	Very maritime. Possibly suffers from salt spray. Tatter flag on a nearby lower site = 10.84 cm per day.	Infertile peat. Links with Glentrool P70 experiment.	Deep complete ploughing and shelter from older crops enhance this site. Most southern site. Links with P70 experiment.

Table 6. List of experiments with site details

Experiment	National grid reference	Elevation (m)	Rainfall (mm)	Aspect (degrees)	Soil type	Dominant vegetation
Achnashellach 24 P37-41	NH020480	40	2032	360	4, 6	*Calluna*
Achnashellach 28 P52-53	NH020480	84	2032	315	6	*Calluna*
Achnashellach 29 P57	NH021482	80	2032	360	6	*Calluna*
Achnashellach 31 P65	NH018482	84	2032	315	4, 6	*Calluna*
Aeron 1 P59	SN366490	282	1350	225	7	*Ulex*
Arecleoch 5 P72	NX219795	167	1270	flat	10B	*Calluna*
Beddgelert 2 P28	SN559504	300	2800	135	4B	*Calluna*
Beddgelert 18 P30	SH560502	300	2800	135	9	*Calluna*
Beddgelert 24 P70	SH550590	333	1905	270	6	*Calluna*
Borgie 9 P59	NC665548	137	890	270	6	*Trichophorum*
Brendon 11 P65	SS973401	360	1500	250	4	*Calluna*
Brendon 21 P70	SS972402	350	1500	flat	3	*Calluna*
Broxa 115 P70	SE951942	210	864	180	4	*Calluna*
Broxa 126 P72	SE949943	210	864	180	4	*Calluna*
Ceiriog 1 P57	SJ146383	442	1350	67	6	*Calluna*
Ceiriog 2 P57	SJ146383	442	1350	67	6	*Calluna*
Clashindarroch 15 P34-41	NJ473325	358	1100	202	4, 6Z	*Calluna*
Clocaenog 16 P34-38	SJ009536	430	1016	flat	6	*Calluna*
Clocaenog 54 P65	SH954560	415	1270	flat	11C	*Calluna*
Clwyd 6 P64	SJ214584	375	900	135	4	*Calluna*
Clwyd 7 P66	SJ164627	420	900	180	4B	*Calluna*
Croft Pascoe 22 P58	SW725195	91	1100	180	3	*Calluna*
Culbin 13 P31	NH994608	10	584	flat	15I	*Juncus*
Deer 2 P59-60	NJ891572	91	825	flat	11B	*Calluna*
Deer 4 P63	NJ983583	137	825	315	4Z	*Erica*
Devilla 17 P61	NS959872	61	700	360	3	*Calluna*
Dyfi 5 P69	SH830182	610	2160	270	11D	*Eriophorum*
Eddleston 4 P66	NT233548	274	765	90	10B	*Calluna*
Eddleston 7 P67-77	NT234540	282	975	flat	10	*Calluna*
Elchies 1 P57-58	NJ204455	268	890	90	11B	*Calluna*
Elibank 6 P63	NT346354	454	1125	315	4Z	*Calluna*
Farigaig 21 P72	NH478106	350	1140	315	11C	*Trichophorum*
Farigaig 47 P77	NH460117	300	1250	90	11	*Calluna*
Fiunary 5 P72	NM532498	360	1778	225	11C	*Trichophorum*
Glencoe 3 P61	NN311512	305	2032	135	9E	*Calluna*
Glengarry 14 P69	NH194013	91	1905	90	10B	*Trichophorum*
Glengarry 16 P70	NH196009	91	1905	90	10B	*Trichophorum*
Glentrool 17 P59	NX306828	168	1524	flat	11C	*Trichophorum*
Glentrool 25 P70	NX324787	137	1270	157	10B	*Trichophorum*
Harwood Dale 22 P38-39	SE968980	195	950	90	4	*Calluna*
Inchnacardoch 141 P52-53	NH330064	145	1525	135	9B	*Calluna*
Inchnacardoch 149 P58-59	NH333067	170	1270	135	9B	*Calluna*
Inchnacardoch 161 P63-82	NH364087	30	1270	flat	1	*Calluna*
Kielder 71 P54	NY761903	198	1207	flat	9D	*Calluna*
Kirroughtree 1 P39-41	NX446665	120	1270	315	6	*Molinia*
Langdale 100 P65	SE894967	283	890	135	4	*Calluna*
Mabie 10 P70-72	NY042715	12	1016	flat	10A	*Calluna*
Millbuie 1 P38-42	NH661620	160	830	315	7Z	*Calluna*
Millbuie 14 P58	NH665625	145	762	360	7	*Calluna*
New Forest 25 P64	SU365078	15	850	225	6	*Calluna*
Newborough 7 P64	SH391641	10	900	225	15D	*Ammophila*
Rosarie 3 P70	NJ322487	318	890	135	4Z	*Calluna*
Roseisle 2 P30	NJ128668	10	610	flat	1Z	*Ammophila*
Rumster 4 P69	ND167500	91	1080	flat	10B	*Calluna*
Rumster 8 P71	ND083467	122	952	180	11C	*Trichophorum*
Rumster 10 P72	ND083467	122	952	180	11C	*Trichophorum*
South Kintyre 1 P67	NR723324	236	1778	158	11C	*Trichophorum*
South Laggan 7 P28	NN304957	387	2200	23	4B	*Grasses*
Selm Muir 1 P61	NS973581	348	1125	270	11D	*Eriophorum*
Shin 12 P67	NC555005	244	1080	360	9E	*Trichophorum*
Shin 17 P68-71	NC595138	180	1016	flat	9E	*Eriophorum*
Shin 25 P70	NC536224	205	1185	270	9D	*Molinia*
Shin 36 P72	NC327043	205	1395	135	9E	*Trichophorum*
Shin 72 P77	NC528216	190	1387	flat	11C	*Trichophorum*
Strathardle 4 P69	NO143565	244	1120	270	1U	*Calluna*
Taliesin 12 P58	SN737906	457	1900	135	1U	*Vaccinium*

Table 6 (contd)

Experiment	National grid reference	Elevation (m)	Rainfall (mm)	Aspect (degrees)	Soil type	Dominant vegetation
Taliesin 13 P58	SN725887	335	1900	180	1U	*Ulex*
Tarenig 3 P58	SN839789	434	2000	180	9D	*Molinia*
Tarenig 10 P65	SN857794	533	2050	315	11C	*Trichophorum*
Teindland 44 P31	NJ286545	220	890	360	7Z	*Calluna*
Teindland 51 P34-37	NJ288544	230	800	45	4	*Calluna*
Thetford 142 P70	TL818833	38	600	flat	1Z	*Pteridium*
Tywi 16 P70	SN734544	396	1800	flat	6, 9D	*Molinia*
Wareham 125 P58	SY919901	32	950	90	1A	*Erica*
Wark 6 P61	NY654803	427	1206	135	11B	*Calluna*
Wark 37 P77	NY800797	183	1116	160	6	*Calluna*
Watten 5 P52-53	ND220505	91	990	360	11C	*Calluna*
Watten 9 P54	ND220505	91	1016	360	11C	*Calluna*
Wilsey Down 13 P58	SX186881	270	1400	225	3	*Calluna*
Wykeham 55 P38	SE950875	183	950	202	4	*Calluna*
Wykeham 2A P28	SE945888	185	950	202	4	*Calluna*

National soil types are described fully in Forestry Commission Forest Record Number 69, by D. G. Pyatt.

In brief, 1 = Brown earth, 3 = Podzol, 4 = Ironpan, 6 = Peaty gley, 7 = Surface-water gley, 9 = *Molinia* bog, 10 = Unflushed bog, 11 = Unflushed hill peat, 15 = Littoral sand.

Experiments in other countries

Early seed origin experiments with lodgepole pine overseas were described by Edwards (1954, 1955). The oldest were in Finland, where interest in this species continues (Weissenberg, 1972, 1980) though for reasons of forest policy its use is restricted there. In Sweden it is also policy to restrict large-scale planting of lodgepole pine to the northern half of the country, where there are now more than 200 000 ha of plantations. However, experiments were planted throughout the country, e.g. Hagner and Fahlroth (1974), and Persson (1978) for the southern series of IUFRO experiments and Lindgren (1983) for the northern IUFRO experiments. In the far south of Sweden some coastal origins can be grown, but in north Sweden only the sub-species *latifolia* succeeds, especially origins from the Yukon and northern British Columbia (Persson, 1980). In Estonia, 19 of the IUFRO seedlots are being tested (Etverk, 1980).

Seed origin trials in Norway lie mainly in east Norway, where only interior sources had high survival (Skroppa and Dietrichson, 1978; Dietrichson, 1982). However, in west Norway some origins of sub-species *contorta* grow fast, retain their needles well and are more healthy, though they have poorer stem form than those from interior British Columbia (Magnesen, 1980).

Løfting (1966) described older experiments in Denmark and results from these were brought up to date by Larsen (1980). Forty-eight of the IUFRO seedlots planted in 1972 show large differences in survival and growth (Larsen and Neilson, 1982). In Iceland, Bjarnason (1978) reported that Alaskan and Skeena River origins survived best and grow well.

Seed origin trials date from 1890 in Germany, and results from unreplicated older experiments are given by Stephan (1982). Fast growing origins were from the coasts of Washington and British Columbia and from the Southern Interior of British Columbia. The IUFRO collection of 140 seedlots was planted on six sites. *Rhyacionia* is a serious pest on some sites (Stephan, 1980). This insect also makes it impossible to grow lodgepole pine with good stem form in the Netherlands (Kranenborg and Kriek, 1980). The 1973 IUFRO trials with 75 seed origins in the Netherlands are expected to have a short life because of *Rhyacionia* (Kriek, 1980).

In France, the IUFRO collection has been planted both by the Forest Service (Birot, 1978; Giovanini and Roman-Amat, 1986) and by the private owners' Association Forêt-Cellulose (Le Cam, 1984). *Rhyacionia* again restricts wide-scale planting. Early results in Czechoslovakia (Kantor, 1980) with a small range of the IUFRO seedlots, showed southern coastal origins as most promising, whereas northern sub-species *latifolia* origins proved unsuitable. In north and central Poland, only the sub-species *latifolia* was included in the trials described by Bellon (1980). In Turkey, trials with the IUFRO collection on five forest sites show that Southern Coastal sources were outstandingly vigorous (Simsek *et al.*, 1978).

In Northern Ireland, Savill (1976) described four trial series, involving 25 experiments planted from 1964 to 1971. Southern Coastal sources were most vigorous, though stem form of these was poor. Those from the Oregon Cascades grew very poorly. Results were similar in Eire, where three series of trials were planted in the 1960s. The IUFRO collection of 30–60 seedlots was planted in 1972 on five sites (O'Driscoll, 1980).

Lodgepole pine was also an important species for seed origin testing in British Columbia (e.g. Illingworth, 1971, 1975, 1976a, 1980; Ying *et al.*, 1985). Because of the large variations in site conditions, genotype-environment interactions are of special importance. In the USA, seed origin experiments covering a wide part of the range are less common than experiments investigating variation within a region, e.g. Perry and Lotan (1978) and Rehfeldt (1985). There is a basic assumption that local populations are best adapted to local site conditions so that it is safest to use these over the long period of a rotation.

In Australia, 17 of the IUFRO lots were planted at two sites in Victoria (about 37° S) in 1972/73 (Pederick, 1980). After 5 years in the forest, Southern Coastal origins were much taller than inland sources, especially those from the Northern Interior and those of the sub-species *murrayana*. Lodgepole pine grows even faster in the New Zealand climate, though not as fast as *P. radiata*, so that its use became confined to poorer soils, high elevation or frosty sites. As in Victoria there were significant differences in growth vigour, with Southern Coastal sources the best (including home collected seedlots, which were outstanding) (Miller, 1969; Hignett, 1971; Shelbourne and Miller, 1976).

From these experiments it can be seen that in countries whose latitudes are below about 58° N, particularly those with a maritime climate, the most vigorous growth was shown by seed origins from the coasts of Washington and Oregon, while in countries even closer to the Equator, such as New Zealand, Californian coastal seed origins grew best. Even in the Faroe Islands at 62° N, Washington coastal origins can grow well in the extreme oceanic conditions (Lines, 1987a). In Scandinavia, as latitude and continentality increase, the coastal sources are eliminated and interior seed origins from the most northerly part of its range in northern British Columbia and the Yukon showed the highest rates of survival and excellent growth rates. *Rhyacionia* attacks were so severe on lowland sites below 55° N in continental climates that they would prevent commercial use of lodgepole pine, but in the wetter, cooler summers of Ireland, and even to some extent Brittany, attacks were of lesser importance. In Ireland, seed origins from dry continental climates suffered from needle diseases and grew poorly.

Chapter 6

Seed characteristics

Differences in seed characteristics such as seed dimensions, seed weight, cotyledon number, etc., vary with seed origin. These early sources of variation can be correlated with later growth in the nursery (see Chapter 7) and any carry-over effect into the early forest stages. They give an early insight into geographical groupings of relevance to any correlation between seed zones in the country of origin and provenance regions in Great Britain. They also give the first indication of whether a commercial seed-lot is from the correct region. For example, any Skeena River seedlot with a seed weight above 3.00 g per 1000 pure seed would arouse suspicion.

Seed dimensions and cotyledon number are both associated rather closely with seed weight, i.e. larger seeds tend to be heavier and have more cotyledons; seed weight is the character that has been given most attention in studies of seed origin variation. Most lodgepole pine seed is very small, about half the size of Scots pine seed, though there is a wide range among different seed origins. The data on seed weight given for 140 origins in the IUFRO circulars number 2 and 3 by Barner (1968) does not allow for the percentage of empty seeds, but Birot (1978) estimated seed weight using a method that separates out the empty seed, and thus generally gives a slightly higher figure. The two data sets had a high correlation: r = 0.988. Maschning (1971) used the seed weights in Barner's list for his study of 35 seedlots. Both Maschning and Birot show that seed weight usually increases from north to south. Birot also notes a decrease in weight with increase in elevation within two of the three sub-species. By far the heaviest seed was found in the Californian Sierras, where seed weight was not correlated with elevation. Critchfield (1980b) suggested that the steep north–south gradient within the Cascades/Sierra group reflected adaptation to the summer-dry climate of California. An exception to the north–south gradient was the very light seed (2.79 g per 1000 seeds) of the *bolanderi* sub-species from the Mendocino White Plains in California (IUFRO Number 2107). This anomaly may be partly due to the very stunted growth of the White Plains trees, as the soils on this site are extremely acid and compact. Progeny from this area, when grown on normal forest soils in Britain, have seeds (at 3.53 g per 1000 seeds) that are closer to the average of the South Coastal group. As noted in Chapter 4, Alaskan seed sources often grow on muskegs or other poor sites, which may account in part for the low mean seed weight (3.3 g per 1000 pure seeds, see Table 7), whereas seed plantations of Alaskan provenance in Britain, on much better sites, produced seed averaging 3.8 g per 1000 pure seeds (Samuel, personal communication).

Table 7 shows the weights of the same 140 seedlots (using Barner's data) grouped into seed origin regions for comparison with 71 origins from the 1965 Maxwell/Aldhous collection in Britain. It will be seen that they follow a very similar pattern. Within a region individual seedlots with low seed weight were often found to be from very poor sites or at higher elevations than the rest, for example IUFRO Number 2107 as noted above, or 2004, Auke Mountain, Juneau, with a seed weight of 2.18 g, which was collected at 400 m, whereas nearly all the other Alaskan lots were from below 70 m. In the South Coastal group, the seedlots from the more drought-prone Puget Sound were markedly lighter than those from the much wetter Pacific coast. The effects of these seed differences are considered in Chapter 7.

Table 7. Weight of 1000 pure seed (g) of 71 origins in the 1965 collection and 140 origins in the IUFRO collection

	1965 Collection		IUFRO Collection	
Region	**Mean**	**Range**	**Mean**	**Range**
North Coastal (Alaska–Vancouver Island)	3.09	2.44–3.74	2.98	2.01–3.92
South Coastal (Washington–California)	3.38	2.91–4.34	4.03	2.79–5.50
Yukon	–	–	2.49	2.46–2.63
Skeena/Bulkley River	2.50	2.27–2.73	2.43	2.23–2.71
North and Central Interior BC and Alberta (above 52° N)	2.60	2.38–2.92	2.84	2.33–3.98
Southern Interior BC and Alberta (below 52° N)	3.15	2.95–3.76	3.18	2.46–4.39
Northern Cascades and Rocky Mountains	–	–	4.04	3.58–5.02
Southern Cascades and Sierra	5.18	4.96–5.55	5.90	3.64–9.91

Chapter 7

Nursery performance

Although some information came from earlier nursery experiments with lodgepole pine, e.g. Lines (1957b), Wood and Lines (1959), the most comprehensive set of experiments showing clear trends in performance were those sown at Newton, Morayshire in 1967 with 26 seedlots from the 1965 (Maxwell/Aldhous) collection, four experiments sown in 1968 with up to 86 seedlots of this collection, and another at Bush, Midlothian, with 20 of the same origins in 1970. These four 1968 experiments were at Inchnacardoch, Inverness-shire; Fleet, Galloway; Kennington, Oxford and Wareham, Dorset. The Kennington plants were lined out in 1969 at Alice Holt, Hampshire. Also in 1970 24 seedlots from the IUFRO collection were sown at Newton. In all these experiments, standard seed origin trial procedures (Lines, 1967) were used. These included cold wet stratification and sowing the same number (1300) of viable seeds per square metre for each seedlot.

Performance in the nursery can give an early indication of future performance in the forest, although care must be taken to interpret early results. For example, if a seed origin has a very high mean seed weight, this very likely results in large seedlings and this effect may then carry on into the transplant and early forest stages. The length of the growing season in the first year varies greatly between seed origins. This has an important effect on later growth, which is discussed more fully in Chapter 9. Some seed origins have an inherent tendency to produce much lammas growth during their second growing season, while others more or less cease shoot growth by midsummer. The amount of lammas growth produced may be the most important factor influencing transplant height. Needle colour of different seed origins shows marked variation, particularly during the first winter and this may give the first indication that a seedlot has been supplied with incorrect details of origin.

Speed of germination

Differences in speed of germination were assessed only in the Inchnacardoch experiment. The cold spring of 1968 delayed germination and there were highly significant differences in the speed of germination between seed origins. Those from the Southern Interior of British Columbia were markedly earlier than those from the Central Interior of British Columbia and the Skeena/Bulkley River region. All coastal origins were slow to germinate, with those from Petersburg, Alaska and Tofino, Vancouver Island, particularly tardy. Speed of germination was calculated by comparing the number of seedlings that had germinated on 30 May 1968 with the number on 19 September 1968, all lots being given the same pretreatment. Data from the replicated plots are shown in Table 8. It will be seen that there were large and significant differences, both between and among the groups of seed origins, with South Interior of BC earliest and coastal sources late to germinate.

It is unlikely that pretreatment requirements of the latter were not satisfied by stratification. These results confirm earlier studies by Critchfield (1957) and Roche (1962), and throw more light on variation across the range of seed origins. If data from the unreplicated plots are also considered, it is interesting to note that seed of the *murrayana* sub-species from Klamath, Oregon and the Californian Sierras was very slow to germinate, whereas the Skagway, Alaskan origin germinated quicker than other Alaskan seedlots. Later studies by Illingworth (1976b) have shown highly significant correlations between germination speed and both latitude and elevation.

Table 8. Nursery results at Inchnacarnoch 5/68 at seedling and transplant stages

Identity number	Origin	Germination speed transformed (%)	Height as 1+0 seedling (cm)	Needle colour transformed score	Height as 1+1 transplant (cm)	% of trees with lammas
Alaska						
(7987) 100	Glacier Bay	47.7	5.31	2.24	11.3	13
(7986) 1	Sitka	35.5	5.05	2.24	10.1	15
(7987) 3	Petersburg	0.04	6.73	2.24	12.4	8
(4113) 500	Watten ex Hollis	33.5	5.08	2.18	10.5	5
(7987) 5	Annette Island	30.7	5.16	2.12	9.2	13
North Coast						
(7111) 1	Masset, QCI	36.0	5.87	2.06	11.9	17
(7116) 7	Coombs, Vancouver Is	27.8	6.91	1.41	11.8	62
(7116) 6	Tofino, Vancouver Is	4.9	4.52	1.86	10.1	50
Washington Coast						
(7972) 1	Long Beach	28.9	6.48	1.41	12.5	47
(7975) 2A	Rainier	14.1	7.70	1.31	14.9	74
Oregon Coast						
(7951) 5H	Tillamook	35.1	6.63	1.41	11.7	26
(7951) 1	Waldport	27.5	5.92	1.49	12.5	65
(7952) 5	Bandon	27.6	5.72	1.10	11.2	44
(9317) 100	ex New Zealand	27.7	7.11	1.28	12.8	56
Skeena River						
(7114) 1	Terrace	19.5	5.11	2.18	10.5	26
(7114) 2	Telkwa	32.7	5.46	2.24	10.6	26
(7114) 4	Moricetown	29.9	5.16	2.06	10.9	33
(7114) 7	Kitwanga	33.6	5.46	2.06	11.7	27
(7114) 8	Kispiox, 305 m	26.8	5.00	2.18	9.6	30
(7114) 8A	Kispiox, 460 m	43.2	5.38	2.12	10.5	27
(7114) 10	Carnaby	41.2	5.59	2.12	11.0	27
(7114) 13	Smithers	36.7	5.69	1.91	10.0	21
(7114) 15	Bulkley Canyon	30.0	5.00	2.18	10.9	14
Central Interior BC						
(7113) 11	Germansen Lake	33.2	4.98	2.24	9.5	17
(7113) 9	Wistaria	47.7	5.23	2.18	10.0	14
(7113) 10	Burns Lake, 762 m	40.6	4.67	2.24	9.7	21
(7113) 10A	Burns Lake, 914 m	36.1	5.08	2.24	11.0	20
(7113) 15	Tschesinkut	39.3	5.44	2.12	9.8	37
(7113) 18	Rose Lake	48.5	5.44	2.24	10.5	32
South Interior BC						
(7118) 1A	Chase Creek	55.7	7.39	1.93	12.1	16
(7118) 4	Mount Ida	63.6	7.62	2.00	13.0	33
(7118) 4A	Salmon Arm	56.9	6.60	1.92	11.7	26
(7118) 5A	Falkland	52.3	6.81	1.72	12.3	16
(7118) 5B	Charcoal Creek 914 m	64.0	6.20	2.06	13.4	22
(7118) 5C	Charcoal Creek 1067 m	63.7	7.32	1.86	13.4	28
(7118) 6	Clearwater	45.2	7.98	1.93	13.5	22
(7118) 9A	Steavens Meadow	65.8	6.02	1.93	10.9	15
(7118) 102	Terrace Creek	33.3	5.69	1.80	11.3	14
Washington Cascades						
(7976) 6	Bird Creek	54.4	6.50	1.72	11.0	15
East of Rocky Mountains						
(7123) 100	Crowsnest, Alberta	31.8	4.42	2.24	8.2	8
Standard error ±		3.64	0.23	0.06	0.7	7.96
Difference significant at		***	***	***	***	***

Needle colour

Significant differences in needle colour of seedlings were noted in a nursery experiment at Tulliallan, Fife in October 1955 (Lines, 1957b). In the Newton 1967 experiment needle colour was assessed on three occasions: mid October and November 1967 and mid January 1968. Analyses indicated that the October data showed the highest discrimination between origins (see Table 9). Colour varied from dark blue-green with purpling in the northern lots to bright green on the most southerly coastal sources. The Vancouver Island origin from Coombs was similar in colour to the Washington seed origins.

At Inchnacardoch needle colour of seedlings showed very highly significant differences

Table 9. Results in the nursery experiment Newton 6/67

Identity number	Seed origin	Mean height as 1+0 (cm)	Number of seedlings per plot †	Mean needle colour score ‡	Mean height as 1+1 (cm)	% of plants with lammas
Alaska						
(7986) 1	Sitka, Alaska	4.70	132	4.00	9.68	2.3
(7987) 1	Juneau, Alaska	5.13	210	5.00	10.13	0.0
(7987) 2	Skagway, Alaska	3.38	202	5.00	7.87	6.7
(7987) 3	Petersburg, Alaska	5.16	188	5.00	10.34	1.3
(7987) 4	Ketchikan, Alaska	4.72	179	3.50	9.19	2.0
(4113) 500	Watten ex Hollis, Alaska	4.62	165	3.75	9.12	0.0
Region mean		4.62		4.38	9.40	2.05
Vancouver Island						
(7116) 7	Coombs, Vancouver Island	6.07	186	1.75	14.35	53.3
Region mean		6.07		1.75	14.35	53.3
South Coastal						
(7972) 1	Long Beach, Wash	5.79	183	1.75	12.55	43.3
(7973) 2	Shelton, Wash	6.17	178	1.50	15.06	57.3
(7951) 5	Tillamook, Oregon	6.43	217	1.25	12.78	50.0
(7951) 1	Waldport, Oregon	5.99	217	1.50	14.15	56.3
(7955) 5	Bandon, Oregon	5.74	225	1.50	12.73	55.3
Region mean		6.02		1.50	13.50	52.4
Skeena/Bulkley River						
(7114) 1	Terrace, Skeena	4.11	154	3.50	10.70	41.0
(7114) 3	Hazelton, Skeena	4.19	143	3.75	11.10	36.7
(7114) 10	Carnaby, Skeena	4.55	168	3.25	11.40	35.7
(7114) 7	Kitwanga, Skeena	4.24	182	3.50	9.80	33.0
(7114) 8	Kispiox, Skeena	4.27	127	3.50	10.40	35.7
(7114) 9	Cedarvale, Skeena	4.34	146	3.50	10.60	41.7
(7114) 15	Bulkley Canyon, Bulkley	4.67	142	4.00	10.30	34.3
(7114) 4	Moricetown, Bulkley	4.01	122	3.75	10.30	34.3
(7114) 13	Smithers, Bulkley	4.34	140	3.75	8.90	31.0
(7114) 2A	Telkwa, Bulkley	4.27	139	4.00	8.60	28.3
Region mean		4.30		3.65	10.20	35.2
Central Interior BC						
(7113) 10	Burns Lake	3.68	138	4.00	9.20	15.7
(7113) 2B	Quesnel	4.04	146	4.00	10.10	33.3
Region mean		3.86		4.00	9.60	24.5
South Interior BC						
(7118) 4	Mount Ida	5.92	156	2.75	12.20	33.3
(7118) 5A	Falkland	5.61	172	2.50	11.70	29.0
Region mean		5.76		2.62	11.90	31.2
Standard error±		0.18	8.81	0.20	0.58	6.1
Difference significant at		***	***	***	***	***

† Multiply by 4.3 to give numbers per m^2.
‡ Score 1 bright green to 5 dark blue green with purpling.

between origins, when assessed on 13 November 1968 (Table 8). The results were similar to those from Newton, with Alaskan seed origins having the darkest foliage and South Coastal ones the lightest. The Albertan high elevation source was as dark as the Alaskan ones, whereas those at similar latitudes but lower elevations on the west side of the Rocky Mountains in the Southern Interior of BC were much lighter, as was the Washington Cascades origin. Seed shortages meant that some origins were sown in unreplicated plots. Seedlings from the Oregon Cascades in one of these were even lighter, as were others from high elevations in the Californian Sierras and from near sea level on the Californian coast at Mendocino.

In the IUFRO experiment at Newton (see Table 10), seedling colour differed very highly significantly between origins, with the lightest origins from the coasts of southern Oregon and California and the darkest blue–green ones from

Table 10. Results in the IUFRO nursery experiment Newton 2/70

IUFRO No	Seed origin	1+0 seedlings		1+1 transplants		
		Mean height (cm)	Needle colour mean score †	Mean height (cm)	Mean length of lammas shoots (cm)	% of plants with lammas shoots ‡
Alaska						
2001	Yakutat	3.30	2.12	8.33	1.73	56.3
2007	Sitka	3.60	2.12	9.40	2.10	65.7
2010	Klawack River	3.02	2.12	9.87	2.80	76.2
2011	Gravina Island	2.70	1.95	9.00	2.43	66.6
Region mean		3.16	2.08	9.15	2.26	66.2
North Coast of BC						
2044	Porcher Island	2.33	2.12	8.33	2.30	66.7
2048	Masset Road	3.34	1.87	9.80	2.67	72.0
2050	Mayer Lake	3.00	2.03	9.47	3.03	72.0
2056	Campbell Island	2.87	1.95	9.27	2.67	71.0
2145	Port Hardy	3.87	1.67	10.13	3.13	68.5
2149	Friendly Cove	3.28	1.77	8.70	2.97	72.9
2152	Tofino	3.21	1.87	9.93	3.23	72.0
2083	Queets	4.64	1.77	13.20	3.90	82.3
Region mean		3.32	1.88	9.85	2.99	72.2
Vancouver						
2146	Lund	3.97	1.57	10.83	3.60	74.6
2147	Sayward	3.85	1.85	10.13	3.90	72.6
2148	Garibaldi	2.37	1.77	9.57	2.80	68.3
2067	Gold River	3.61	1.57	9.87	3.47	68.0
2071	Mesachie Lake	4.27	1.95	13.10	4.80	76.7
2072	Sooke	3.36	1.77	10.13	3.43	69.2
Region mean		3.57	1.75	10.60	3.67	71.6
Puget Sound						
2084	John's Prairie	4.43	1.67	12.83	5.17	78.5
2086	Vail	5.54	1.77	15.87	6.73	86.2
Region mean		4.99	1.72	14.35	5.95	82.4
South Coastal						
2092	Pacific City	3.67	2.19	11.30	4.20	73.9
2100	Pistol River	5.08	1.33	12.80	5.67	75.1
Region mean		4.38	1.76	12.05	4.94	74.5
North California Coast						
2105	Samoa	5.14	1.33	14.93	6.00	87.3
Region mean		5.14	1.33	14.93	6.00	87.3
Yukon						
2014	Ethel Lake	1.57	2.02	4.53	0.83	38.4
2016	Frances Lake	1.09	2.34	5.20	1.57	52.8
Region mean		1.33	2.18	4.86	1.20	45.6
Experiment mean		3.48	1.86	10.26	3.40	70.5
Standard error ±		0.197	0.087	0.65	0.99	3.71
Significance level		***	***	***	***	***

† Score transformed by square roots.
‡ Percentage transformed by angles.

Alaska and Frances Lake, Yukon. The other Yukon origin, Ethel Lake, was significantly less dark. A Duncan's range test (Figure 4) shows the significance of the differences between origins and the strong relationship with latitude. A regression of colour on latitude proved highly significant, with a correlation of 0.854, accounting for 71.6% of the variation. For this analysis, one seed origin, IUFRO number 2092, Pacific City, Oregon was omitted. The seedling colour of this origin was so aberrant for its latitude that further enquiries were made about its authenticity. It transpired that the stand at Pacific City was of plantation origin and no record existed of its true seed origin. Later terpene tests (Forrest, 1980) established that it could not have come from the coast of Oregon and that it was almost certainly from the 'North Coastal' terpene region.

		Ranked means and range tests			
Seed origin	**IUFRO number**	**Mean score**	**5%**	**1%**	**Latitude °N**
Pistol River	2100	1.329			42.25
Samoa	2105	1.329			40.78
Lund	2146	1.573			50.02
Gold River	2067	1.573			49.77
Port Hardy	2145	1.671			50.67
John's Prairie	2084	1.671			47.23
Garibaldi	2148	1.768			49.90
Friendly Cove	2149	1.768			49.58
Sooke	2072	1.768			48.47
Queets	2083	1.768			47.52
Vail	2086	1.768			46.87
Sayward	2147	1.852			49.98
Masset	2048	1.866			53.82
Tofino	2152	1.866			49.17
Gravina Island	2011	1.950			55.36
Campbell Island	2056	1.950			52.13
Mesachie Lake	2071	1.950			48.82
Ethel Lake	2014	2.025			63.30
Mayer Lake	2050	2.034			53.65
Yakutat	2001	2.118			59.50
Sitka	2007	2.118			57.07
Klawack	2010	2.118			55.57
Porcher Island	2044	2.118			54.03
Pacific City	2092	2.193			(45.23)
Frances Lake	2016	2.343			61.36

Note: Means not joined by the same vertical line are significantly different at the stated level.

Figure 4. Duncan's range test for needle colour of one-year seedlings. Mean scores transformed by square roots, showing strong relationship with latitude.

Seedling height

Seedling height showed a rather constant pattern of variation between seed origins in all the experiments (for full results, see Tables 8, 9, 10, 11 and 12). A summary by eight seed regions (Table 13) shows that rank order of height across sites was similar, even with differential representation of individual seed origins.

Table 11. Nursery results at Fleet 3/68 at seedling and transplant stages

Identity number	Seed origin	Height as 1+0 seedling (cm)	Height as 1+1 transplant (cm)	% of trees with lammas	
				%	transformed
Alaska					
(7987) 3	Petersburg	4.67	12.9	2.00	6.10
(7987) 4	Ketchikan	3.94	9.8	2.00	4.99
(7987) 5	Annette Island	3.07	10.6	4.00	11.88
North Coast					
(7111) 1	Masset	4.52	12.7	5.00	6.46
Washington Coast					
(7973) 2	Shelton	5.13	17.1	15.00	21.27
(7972) 1	Long Beach	6.43	16.8	34.00	35.18
Oregon and California Coast					
(7951) 4	Warrenton	6.22	15.8	42.00	40.36
(7951) 1H	Newport	6.81	15.3	24.00	28.19
(7952) 5	Bandon	5.23	16.3	28.00	31.72
(7948) 100	Mendocino	6.22	19.5	64.00	53.41
Skeena River					
(7114) 1	Terrace	3.23	11.3	3.00	6.28
(7114) 5	Skeena Crossing	3.58	12.7	4.00	7.91
(7114) 9	Cedarvale	3.73	10.9	4.00	8.15
(7114) 12	Babine	3.83	11.9	2.00	6.41
(7114) 13	Smithers, 610 m	3.23	11.5	3.00	7.55
(7114) 13A	Smithers, 762 m	3.96	11.6	2.00	6.11
(7114) 13B	Smithers, 914 m	4.11	11.2	2.00	5.72
(7114) 13C	Smithers, 1067 m	3.86	11.2	2.00	5.77
Central Interior BC					
(7113) 11	Germansen Lake	3.23	9.7	1.00	4.32
(7113) 6	Pendleton Bay	3.28	11.3	0.25	1.43
(7113) 12	Topley	3.43	11.1	3.00	5.80
(7113) 17	Takysie	3.91	10.9	1.00	2.87
(7113) 1	Fort Fraser	2.97	9.5	3.00	9.31
(7113) 1A	Fraser Lake	3.28	10.9	0.25	1.43
(7113) 4B	Prince George	4.06	12.8	8.00	15.94
(7113) 5	Vanderhoof	4.19	12.1	3.00	6.99
(7113) 3	Anahim Lake	2.69	9.2	4.00	10.53
South Interior BC					
(7118) 1D	Harper Lake	5.23	12.8	1.00	2.88
(7118) 4	Mount Ida	5.00	13.8	4.00	9.49
(7118) 3	Tunkwa Lake	4.78	11.2	1.00	2.88
(7118) 6	Clearwater	4.98	15.4	4.00	11.41
(7118) 8	100 Mile House	5.59	13.6	1.00	2.49
(7118) 100	Esperon Lake	2.72	9.7	0.25	1.43
(7118) 101	Bald Range Creek	4.57	14.8	3.00	6.60
(7118) 102	Terrace Creek	3.81	12.9	2.00	6.04
Washington Cascades					
(7976)	Peterson Prairie	5.44	12.1	0.25	1.43
East of Rocky Mountains					
(7124) 100	Cypress Hills, Saskatchewan	4.42	11.4	0.25	1.43
Standard error ±		0.51	0.71	–	3.21
Differences significant at		***	***	–	***

Table 12. Nursery results at Alice Holt 174 and Wareham 120 combined. Also weight in grams of 1000 pure seeds

Identity number	Origin	Height as 1+0 seedlings (cm)	Height as 1+1 transplants (cm)	Weight of 1000 pure seed (g)
Alaska				
(7987) 4	Ketchikan	4.22	12.42	3.39
(7987) 5	Annette Island	4.24	11.63	2.96
(7986) 1	Sitka	4.70	12.50	3.47
(7987) 1	Juneau	4.93	12.09	3.54
(7987) 3	Petersburg	4.83	14.70	3.89
(7987) 2	Skagway	3.68	9.02	2.60
(7987) 100	Glacier Bay	4.32	11.43	–
(7986) 103	Hollis	4.60	13.72	–
(7986) 102	Thorne River	5.03	14.02	–
North Coast				
(7111) 1	Masset	4.72	14.53	3.45
(7116) 7	Coombs	5.66	19.58	3.05
(7116) 6	Tofino	3.61	12.60	2.44
Washington Coast				
(7972) 1	Long Beach	5.49	17.91	3.44
(7973) 2	Shelton	6.30	18.26	3.01
(7975) 2A	Rainier	6.17	24.49	–
Oregon Coast				
(7951) 1	Waldport	5.49	16.56	3.19
(7951) 4	Warrenton	5.33	15.75	3.35
(7951) 5	Tillamook	5.51	18.75	4.08
(7952) 5	Bandon	5.51	19.08	3.91
Skeena River				
(7114) 3	Hazelton	4.34	14.53	–
(7114) 7	Kitwanga	4.67	12.95	2.27
(7114) 8	Kispiox, 305 m	4.67	14.07	2.47
(7114) 8A	Kispiox, 460 m	4.75	14.00	2.51
(7114) 9	Cedarvale	4.09	13.36	2.54
(7114) 10	Carnaby	4.57	15.11	2.39
(7114) 2	Telkwa	4.47	12.85	2.38
(7114) 13	Smithers, 610 m	4.22	13.21	2.73
(7114) 13A	Smithers, 762 m	4.90	12.95	2.70
(7114) 13B	Smithers, 914 m	4.42	13.08	2.63
(7114) 13C	Smithers, 1067 m	4.75	12.88	2.55
(7114) 14	Doughty	4.09	12.83	2.56
(7114) 15	Bulkley Canyon	4.95	14.43	2.50
Central Interior BC				
(7114) 12	Babine	4.22	13.54	2.58
(7113) 11	Germansen Lake	4.37	11.20	2.73
(7113) 6	Pendleton Bay	4.78	12.16	2.50
(7113) 9	Wistaria	4.22	11.40	2.40
(7113) 10	Burns Lake, 762 m	4.34	11.76	2.43
(7113) 10A	Burns Lake, 914 m	4.17	12.06	2.42
(7113) 12	Topley	4.67	12.52	2.65
(7113) 15	Tchesinkut Lake	3.94	11.38	2.52

Table 12 (contd)

Identity number	Origin	Height as 1+0 seedlings (cm)	Height as 1+1 transplants (cm)	Weight of 1000 pure seed (g)
(7113) 17	Takysie	4.06	11.66	2.58
(7113) 18	Rose Lake	4.22	12.14	2.50
(7113) 1	Fort Fraser	4.52	12.65	2.70
(7113) 1A	Fraser Lake	4.01	12.52	2.60
(7113) 5	Vanderhoof	4.62	13.94	2.96
(7113) 2A	Quesnel	5.26	13.77	2.92
(7113) 3	Anahim Lake	3.63	10.11	2.43
(7115) 101	Wonowon	3.63	10.16	–
<u>South Interior BC</u>				
(7118) 4	Mount Ida	5.44	15.21	3.05
(7118) 4A	Salmon Arm	5.13	15.32	2.96
(7118) 1A	Chase Creek	5.53	14.94	3.07
(7118) 1B	SE of Chase	6.25	16.10	3.04
(7118)1D	Harper Lake	5.21	13.21	3.02
(7118) 5A	Falkland, 823 m	4.65	14.17	3.06
(7118) 5	Falkland, 975 m	6.12	14.12	2.99
(7118) 5B	Charcoal Creek, 914 m	5.74	14.86	3.00
(7118) 5C	Charcoal Creek, 1067 m	5.05	14.20	3.03
(7118) 3	Tunkwa Lake	5.41	12.95	3.83
(7118) 9A	Steavens Meadow	4.93	12.95	2.88
(7118) 6	Clearwater	6.15	16.36	3.55
(7118) 8	100-Mile House	5.46	13.77	3.34
(7118) 100	Esperon Lake	3.45	11.40	–
(7118) 102	Terrace Creek	5.18	13.16	–
(7118) 103	Cape Horne Creek	5.11	15.06	–
<u>Cascades</u>				
(7976) 5	Petersen Prairie	5.92	12.60	4.90
(7976) 6	Bird Creek	5.46	12.42	5.04
(7957)	Klamath County	4.83	11.89	5.55
<u>California</u>				
(7947) 100	Del Norte	4.93	19.25	–
(7948) 100	Mendocino	5.74	19.20	–
(7943) 100	Eldorado	4.01	9.47	–
<u>East of Rocky Mountains</u>				
(7123) 100	Crowsnest	3.38	8.97	3.63
(7124) 100	Cypress Hills	4.34	11.00	–
Standard error±		0.29	0.64	
Differences significant at		***	***	

Table 13. Seedling height (cm) and rank (in brackets) at four* sites

Seed region	Newton	Inchnacardoch	Fleet	Alice Holt/Wareham
Alaska	4.6 (4)	5.5 (5)	3.9 (6)	4.5 (5=)
Coast BC	6.1 (1)	5.8 (4)	4.5 (4)	4.7 (4)
South Coastal	6.0 (2)	6.6 (2)	6.0 (1)	5.6 (1)
Skeena/Bulkley River	4.3 (5)	5.3 (6)	3.7 (7)	4.5 (5=)
Central Interior BC	3.9 (6)	5.1 (7)	3.4 (8)	4.3 (7)
Southern Interior BC	5.8 (3)	6.9 (1)	4.6 (3)	5.3 (3)
Alberta/Saskatchewan	–	4.4 (8)	4.4 (5)	3.9 (8)
Cascades	–	6.5 (3)	5.4 (2)	5.4 (2)

*Data were combined for the two southern sites, Alice Holt and Wareham.

At Newton, where the Coast BC region ranked first, it was represented by only one seed origin (Coombs, southern Vancouver Island), which grew as fast as the South Coastal origins in the experiments at Inchnacardoch and Alice Holt. In the latter, however, the regional mean for the coast of BC was depressed by the poorer growth of seed origins from the Queen Charlotte Islands and the north of Vancouver Island, which were no taller than Alaskan origins. Coombs was not present at Fleet. At Inchnacardoch, the South Coastal origins were out-grown by those from the Southern Interior of BC. This somewhat unexpected result is probably due to the significantly quicker germination of the latter group that effectively gave them a longer growing season.

In all experiments there were highly significant regressions of seedling height on seed weight. For example, at Newton the correlation coefficient between seedling height and seed weight was 0.63, and when these data were plotted graphically, distinct seed origin groupings were evident (Figure 5). Seed weights

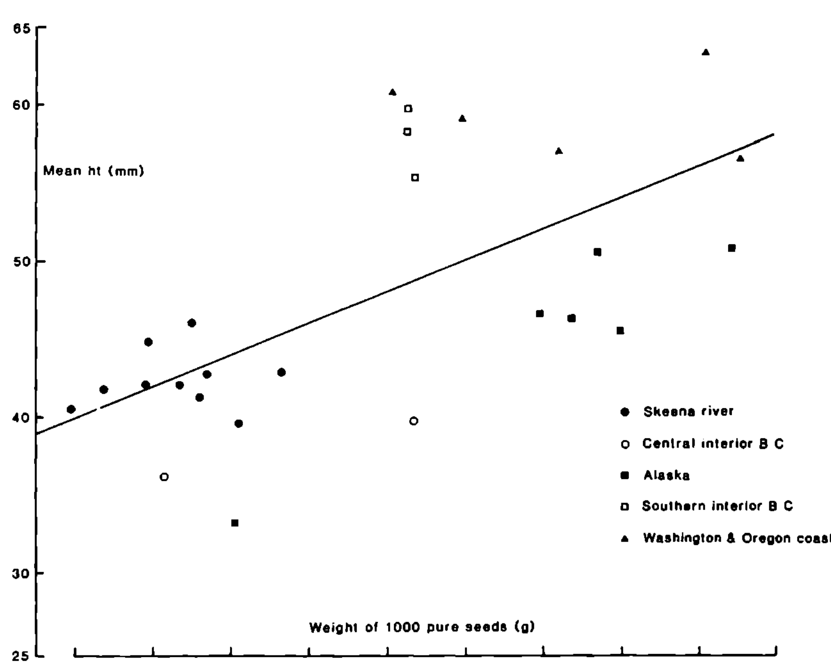

Figure 5. Regression of mean height as one-year seedlings and seed weight at Newton nursery, 6/67.

are shown in Table 12. Skagway, Alaska had very low seed weight compared with the other Alaskan lots and it also had the poorest height growth of any origin. The Skeena/Bulkley River seed origins form a homogeneous group in Figure 5 with both low seed weight and poor seedling height.

Table 12 shows that the seed weight of the Cascades seed origins was by far the largest of any region. This probably explains the rather high ranking of this region for seedling height, though fast germination (see Table 8) may have added to this effect. Conversely, origins from the Skeena/Bulkley River region and those from the Central Interior of BC all had low seed weight and this appears to have reduced their seedling height.

The IUFRO experiment sown at Newton in 1970 has such a different set of seed origins that it could not readily be included in Table 12. Highly significant differences were found in seedling height, the tallest being from the Oregon and California coast, while those from the Yukon were the shortest (Table 10). Multiple regressions of seedling height on seed weight, latitude and elevation showed that each factor when considered singly had a significant linear relation with height and together these accounted for 70% of the variation. Latitude alone accounted for 63%.

Transplant height and lammas growth

A similar regular pattern was found across sites with transplant height (see Tables 8, 9, 10, 11, and 12). A summary table below (Table 14) shows much similarity with the seedling heights, but also some changes in rank that are worth closer examination.

Lammas growth has such an important effect on the height reached by a transplant at the end of the season that it is best to consider both these characters together. Incidence of lammas growth was recorded in the 1967 experiment at Newton as the percentage of plants showing lammas when the height was assessed at the end of the second growing season. This varied from 0 to 57% (Table 9). At Inchnacardoch the percentage of trees with lammas varied from 5 to 74% (Table 8), while at Fleet there was much less lammas growth, with only five seed origins having more than 15% of the plants with lammas (Table 11). These were all from the South Coastal region, with the Californian origin from Mendocino outstanding at 64%.

By contrast, in the 1970 IUFRO experiment at Newton (Table 10), the percentage of plants with lammas growth was very high. Only three of the 25 origins had less than 84% of the trees with some lammas growth. These exceptions were two Yukon seed origins and the most

Table 14. Transplant height (cm) and rank (in brackets) at four sites

Seed region	Newton	Inchnacardoch	Fleet	Alice Holt/Wareham
Alaska	9.4 (6)	10.7 (5)	11.1 (7)	12.4 (5)
Coast BC	14.4 (1)	11.3 (3)	12.7 (3)	15.7 (2)
South Coastal	13.5 (2)	12.6 (1)	16.8 (1)	18.8 (1)
Skeena/Bulkley River	10.2 (4)	10.6 (6)	11.5 (5)	13.6 (4)
Central Interior BC	9.6 (5)	10.1 (7)	10.8 (8)	12.0 (7)
Southern Interior BC	11.9 (3)	12.4 (2)	13.0 (2)	14.2 (3)
Alberta/Saskatchewan	–	8.2 (8)	11.4 (6)	10.0 (8)
Cascades	–	11.0 (4)	12.1 (4)	12.3 (6)

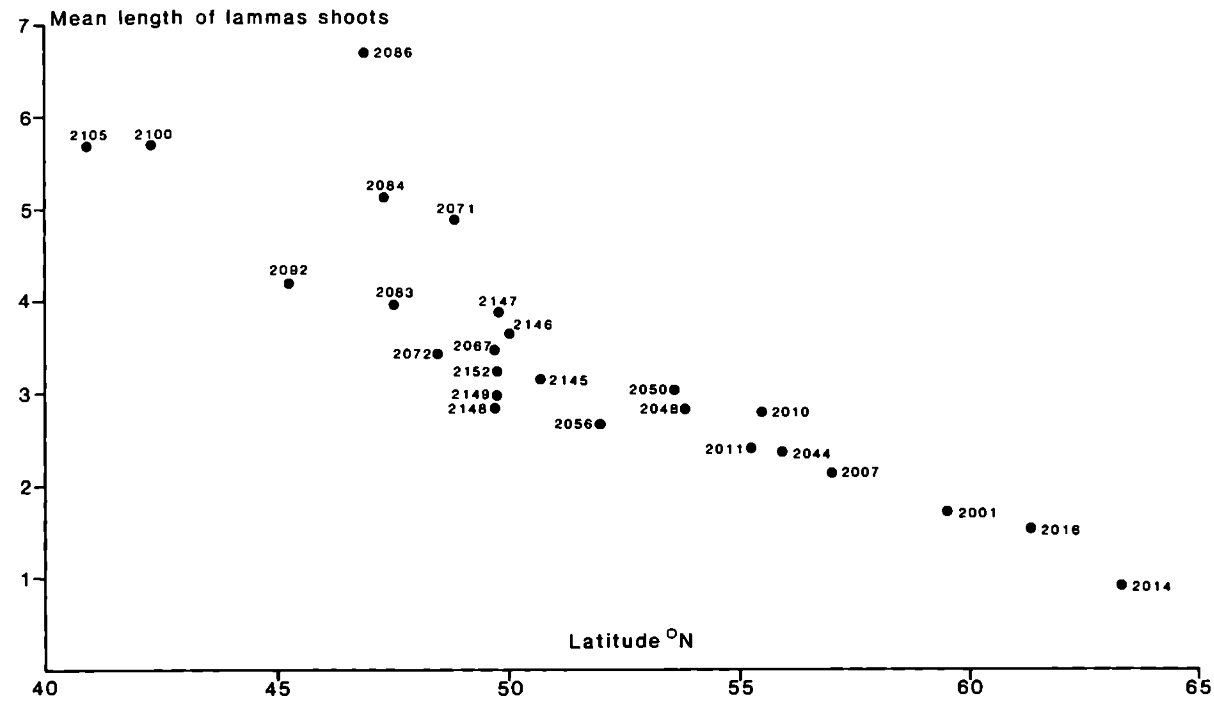

Figure 6. Relationship between mean length of lammas shoots and latitude of origin at Newton nursery, 2/70

northerly Alaskan seedlot from Yakutat. As it was clear that mere incidence of lammas would give no clear distinction between seed origins, the length of lammas shoots was measured to show their relative contribution to final tree height. The mean length varied from 0.83 cm (Ethel Lake, Yukon number 2014) to 6.73 cm for Vail, Washington (number 2086). The latter represents 42% of the transplant height at the end of the season. A regression of lammas growth on latitude (Figure 6) proved very highly significant (correlation coefficient 0.878). It is obvious from this figure that transplant height is heavily influenced by the amount of lammas growth, particularly in nurseries or seasons when the inherent potential for lammas growth is given full expression. For example, at Inchnacardoch the Cascades origin from Bird Creek ranked 12th for seedling height. It had only 15% of the trees with lammas and fell to 21st place for transplant height. The South Coastal origin from Waldport, Oregon was 16th for seedling height but with 65% lammas growth it rose to seventh place for transplant height.

Autumn frost damage on southern seed origins of Sitka spruce, which have much lammas growth, is a well recognised serious hazard. With lodgepole pine, some frost damage at the seedling stage to the most southerly origins has been noted occasionally and in Fleet Nursery a few seedlings of the Mendocino, California origin were damaged. However, despite frosts there in November and December 1969, no damage occurred to the lammas shoots of transplants, even on the Mendocino origin, which had the greatest height as a transplant of any origin.

Transplant height is thus influenced by:

1. seedling height (which itself is affected by seed weight, germination speed and length of the growing season); and

2. growth physiology during the second growing season, which may lead to early growth cessation, as on some far northern origins, or a second flush of growth (lammas).

Comparing the seedling and transplant data (Tables 13 and 14) shows downward changes in rank order for the Alaskan and Cascades seed regions, while upward changes occurred in the Coast BC and Skeena/Bulkley River regions. The first would appear to be falling in rank because of a combination of factors. They had either relatively high or very high seed weights and low potential for lammas growth. Within the coast BC region, Coombs had a high value for lammas, which accounts for its upward movement in rank, but Masset, Queen Charlotte Islands, also grew well though with little lammas. Origins from the Skeena/Bulkley River region started as small seedlings (associated with low seed weight) but developed much lammas growth. Even at Fleet, where the percentage of lammas was slight, their transplant heights showed a marked relative improvement on their seedling height. The South Coastal region origins extended their lead above other regions at the transplant stage largely due to high incidence of lammas growth, such as that already noted above for Waldport at Inchnacardoch.

Transplant height of individual seed origins will give a more reliable guide to future performance if it is based on results from many nurseries. The northern Inchnacardoch and Fleet experiments were designed as a combined experiment, as were the southern Alice Holt/Wareham experiments. Sixty-six seed origins are common to these experiments and adjusted mean heights for North, South and the overall mean are given in Table 15.

The data were adjusted as follows:

1. An analysis of the transplant heights of the 12 seed origins common to Inchnacardoch and Fleet showed a non-significant site x seed origin interaction. It was therefore concluded that heights of all origins at Fleet could be adjusted by the proportion by which the mean heights of the 12 seed origins there exceeded their height at Inchnacardoch, i.e.:

$$\times \frac{22.69}{26.07}$$

2. On a similar basis, the data from the southern series was adjusted by the ratio of its overall mean height (13.72 cm) with the overall mean height in the northern series (11.05 cm), i.e.:

$$\times \frac{11.05}{13.72}$$

3. Similarly, the data from Newton 6/67 were adjusted to allow comparison with the overall mean using the mean heights of those origins in both series, i.e.:

$$\times \frac{11.52}{11.04}$$

Discussion and conclusions

Some clear trends emerge from these results.

1. Within the *contorta* sub-species there is a broad latitudinal cline, with vigour increasing as latitude decreases. As there is little variation in elevation between seed origins of this sub-species, this factor cannot explain differences in this group of origins. The cline has marked discontinuities, with sharp changes in vigour around the latitude of about 49–50° N. These seem to be associated with a genetic difference shown by the boundaries between the terpene regions of Forrest (1980). Thus Masset, Queen Charlotte Islands and Tofino on the west coast of Vancouver Island fall into the 'North Coastal' terpene region and were not much faster-growing than the better Alaskan origins. Coombs, on the south-east coast of Vancouver Island is in the 'Vancouver' terpene region and was as vigorous as seed origins 5° of latitude further south. Within the South Coastal region there is little evidence for a latitudinal cline, as the Washington origins were just as vigorous as those from Oregon. In the Northern series of experiments, the Californian origin from Mendocino (to be strictly accurate, the sub-species *bolanderi*) was outstanding for height, while in the Southern series, the Puget Sound origin, Rainier, was equally outstanding. Differences in vigour within this region are less strongly associated with the terpene regions than those to the north of the 49° parallel.

2. Within the *latifolia* sub-species, any latitudinal cline for vigour is confounded by wide elevational differences within and between regions. Thus the Skeena/Bulkley River origins come mainly from higher latitudes than those in the Central Interior of BC, while the latter are generally from higher elevations. The Skeena/Bulkley River origins were nearly always taller than those from the Central Interior of BC. Origins from the Southern Interior BC cover a range in elevation from 460 m to over 1500 m. There was a significant decrease in transplant vigour with increase in elevation within this seed region, irrespective of latitudinal differences. The Alberta/Saskatchewan seed origins were significantly poorest in vigour, although both came from high elevation sites, which would account for some of their poor performance. The Yukon origins belong to this sub-species, but cannot be compared statistically with other origins because they occurred only in Newton 2/70 experiment. They grow even more slowly than those from Alberta.

Table 15. Comparison of adjusted transplant height as 1+1 across 5 nursery sites (cm)

Seed region and identity number	Origin	Inchnacardoch and Fleet	Alice Holt and Wareham	Overall mean	Newton
Alaska					
65(7987) 2	Skagway	9.0	7.2	8.1	8.2
65(7987) 100	Gustavus	11.3	9.1	10.2	–
65(7986) 1	Sitka	10.1	10.0	10.0	10.1
66(7987) 3	Petersburg	11.8	11.8	11.8	10.8
65(7986) 102	Thorne River	11.6	11.2	11.4	–
65(7986) 103	Cat Island	11.4	11.0	11.2	–
65(7987) 4	Ketchikan	8.5	10.0	9.2	9.6
65(7987) 5	Annette Island	9.2	9.3	9.2	–
Region mean				10.1	
Coast of British Columbia					
66(7111) 1	Masset	11.5	11.6	11.6	–
65(7116) 7	Coombs	11.8	15.7	13.8	15.0
65(7116) 6	Tofino	10.1	10.1	10.1	–
Region mean				11.8	
South Coastal					
65(7973) 2	Shelton	14.8	14.7	14.8	15.7
65(7975) 2A	Rainier	14.9	19.7	17.3	–
65(7972) 1	Long Beach	13.6	14.4	14.0	13.1
65(7951) 4	Warrenton	13.7	12.7	13.2	–
65(7951) 5	Tillamook	11.7	15.1	13.4	13.3
65(7951) 1	Waldport	12.5	13.3	12.9	14.8
65(7952) 5	Bandon	12.7	15.3	14.0	13.3
65(7947) 100	Del Norte Co	14.7	15.4	15.0	–
65(7948) 100	Mendocino	17.0	15.4	16.2	–
Region mean				14.5	
Southern Interior BC					
65(7118) 8	100 Mile House	11.8	11.1	11.4	–
65(7118) 6	Clearwater	13.5	13.2	13.4	–
65(7118) 1A	Chase Creek	12.1	12.0	12.0	–
65(7118) 4A	Salmon Arm	11.7	12.3	12.0	–
65(7118) 4	Mount Ida	12.5	12.2	12.4	12.7
65(7118) 1D	Harper Lake	11.2	10.6	10.9	–
65(7118) 5B	Charcoal Creek, 900 m	13.4	12.0	12.7	–
65(7118) 5C	Charcoal Creek, 1050 m	13.4	11.4	12.4	–
65(7118) 9A	Steavens Meadow	10.9	10.4	10.6	–
65(7118) 3	Tunkwa Lake	9.8	10.4	10.1	–
65(7118) 5A	Falkland	12.3	11.4	11.8	12.2
65(7118) 100	Esperon Lake	8.5	9.1	8.8	–
65(7118) 102	Terrace Creek	11.3	10.6	11.0	–
65(7118) 103	Cape Horne Creek	12.6	12.1	12.4	–
Region mean				11.6	
Skeena/Bulkley River					
65(7114) 8	Kispiox, 300 m	9.6	11.3	10.4	10.8
65(7114) 8A	Kispiox, 450 m	10.5	11.2	10.8	–
65(7114) 10	Carnaby	11.0	12.1	11.6	11.9
65(7114) 7	Kitwanga	11.7	10.4	11.0	10.3
65(7114) 9	Cedarvale	9.5	10.8	10.2	11.1
65(7114) 12	Babine	10.4	10.8	10.6	–
65(7114) 15	Bulkley Cangon	10.9	11.6	11.2	10.7
65(7114) 14	Doughty	14.0	10.3	12.2	–
65(7114) 13	Smithers, 600 m	10.0	10.6	10.3	9.3
65(7114) 13A	Smithers, 750 m	10.1	10.4	10.2	–
65(7114) 13B	Smithers, 900 m	9.7	10.5	10.1	–
65(7114) 13C	Smithers, 1050 m	9.8	10.4	10.1	–
65(7114) 2	Telkwa	10.6	10.3	10.4	9.0
Region mean				10.7	

Table 15 (contd)

Seed region and identity number	Origin	Inchnacardoch and Fleet	Alice Holt and Wareham	Overall mean	Newton
Central Interior of BC					
65(7115) 101	Wonowon	10.3	8.2	9.2	–
65(7113) 11	Germansen Lake	9.0	9.0	9.0	–
65(7113) 6	Pendleton Bay	9.8	9.8	9.8	–
65(7113) 12	Topley	9.6	10.0	9.8	–
65(7113) 1	Fort St James	8.3	10.1	9.2	–
65(7113) 10	Burns Lake, 750 m	9.7	9.5	9.6	9.6
65(7113) 10A	Burns Lake, 900 m	9.4	10.0	9.7	–
65(7113) 15	Tschesinkut	9.8	9.1	9.4	–
65(7113) 1A	Fraser Lake	9.4	10.0	9.7	–
65(7113) 5	Vanderhoof	10.5	11.2	10.8	–
65(7113) 9	Wisteria	10.0	9.1	9.6	–
65(7113) 17	Takysie	9.5	9.4	9.4	–
65(7113) 3	Anahim Lake	8.0	8.1	8.0	–
65(7113) 2A	Barkerville Road	10.9	11.1	11.0	10.5
Region mean				9.6	
Alberta/Saskatchewan					
65(7123) 100	Crowsnest, Alberta	8.2	7.2	7.7	–
65(7124) 100	Cypress Hills, Saskatchewan	9.9	8.8	9.4	–
Region mean				8.6	
Cascades					
65(7976) 6	Bird Creek, Washington	11.0	10.1	10.6	–
65(7976) 5	Peterson prairie, Washington	10.6	10.0	10.3	–
63(7957)	Klamath Co, Oregon	11.6	9.5	10.6	–
Region mean				10.5	

3. Within the *murrayana* sub-species the same elevational effect should have caused growth depression, as all were from high elevations. However, as already noted above, the effect of high seed weight continued to exert a large influence on transplant height, so that they were only marginally less tall than the Skeena/Bulkley River seed origins.

4. It is well known that height of a tree at the transplant stage will influence its early growth in the forest. This 'carry-over' effect must be taken into consideration when examining early results from forest stage experiments.

Chapter 8

Studies on root:shoot ratios in relation to early instability

Problems of early instability leading to basal sweep have long been a factor influencing the use of different seed origins of lodgepole pine. The history of British attempts to control the problem has been described by Lines (1980c). Instability was believed to be caused partly by a poor root:shoot ratio, resulting in 'top heavy' plants, particularly the heavy-crowned south coastal origins. Martinsson (1986) showed significant differences in root:shoot ratios among seed origins of the northern sub-species *latifolia* in Sweden, where tree toppling from wind and snow can be a serious problem with lodgepole pine.

This chapter deals only with the variation in root:shoot ratios and their influence on early instability. The wider problem of instability in the forest is covered in Chapter 11. Preliminary assessments of the dry weight root:shoot ratios for seedlings of five seed origins in Inchnacardoch 5/68 showed significant differences, with the highest ratio (0.48) on an Alaskan source and much lower ratios on those from the Oregon coast (0.22) and South Interior BC (0.20) (see Figure 9). The assessment was based on 30 seedlings in each of two replicates. The following year, 18 seed origins were sampled as 1+1 transplants. The results are shown in Table 16. There were highly significant differences between origins, with Alaska, Queen Charlotte Islands and Washington Cascades having high ratios, while those with the lowest ratios were Long Beach, Washington, Mount Ida, South Interior British Columbia and Coombs, Vancouver Island.

To provide more material for these studies of root:shoot ratios, an experiment was sown at Bush, Midlothian (2/70) with two replications of 20 seedlots of the 1965 collection, including 16 of the same lots already sampled in Inchnacardoch 5/68. It was hoped that this would provide more information about seed origin differences in root:shoot ratio at the seedling stage, as only five seedlots had been used in the earlier experiment as seedlings. The results are also shown in Table 16. There was a highly significant correlation (r = 0.678) between the seedling root:shoot ratios at Bush and the transplant ratios at Inchnacardoch (see Figure 7). Due to a high interaction between seed origins and replicates the differences were not significant. The following year, the transplants at Bush were also assessed for root-shoot ratio and a very similar pattern of ratios emerged (Table 16). The factors that most influence the ratios are latitude and elevation of the seed origin, as shown in Figure 8 (based on the data given above and first published by Cannell and Willett, 1976).

The distribution of dry matter between root and shoot for several seed origins of lodgepole pine was also investigated on a seasonal basis by Cannell and Willett (1976) and Thompson (1974). Both found considerable changes in the ratio of root to shoot during the growing season and the first authors concluded that there were no lasting differences in allometry between seed origins of lodgepole pine. Thus the end of season differences may merely reflect the extent to which the origins are phenologically adapted to the length of the growing season in which they are grown. From the practical forester's point of view, however, they do acknowledge that these end of season differences are important for wind stability during the winter period (when gales are most frequent), particularly if accompanied by differences in crown or 'sail' area. The differences in the nursery between seed origins in root:shoot ratios persist at least up to the fourth year (Roberts and Wareing, 1975) and up to 8 years in the forest (Danby, 1973), based on excavation of over 500 trees in five experiments. As with other species, the proportion of root to shoot in lodgepole pine reduces with age, at least up to 12 years (Eis, 1970). Unsuccessful attempts were made to control shoot growth by omitting initial fertilising and modifying size of planting turf and planting position (see Chapter 11).

Table 16. Dry weight root:shoot ratios at Inchnacardoch 5/68 and Bush 2/70

Identity number	Seed origin	Inchnacardoch 1+0	Inchnacardoch 1+1	Bush 1+0	Bush 1+1
Alaska					
(7987) 100	Glacier Bay	0.483	0.490	0.66	0.532
(7987) 3	Petersburg		0.439	0.55	0.491
North Coast					
(7111) 1	Masset, QCI		0.425	0.58	0.513
(7116) 6	Tofino, Vancouver Island		0.328	0.50	0.400
(7116) 7	Coombs, Vancouver Island		0.390	0.47	0.381
Washington Coast					
(7972) 1	Long Beach		0.287	–	–
(7973) 2	Shelton		–	0.53	0.381
(7975) 2A	Rainier		0.334	0.49	0.292
Oregon Coast					
(7951) 5H	Tillamook	0.215	0.340	0.38	0.332
(7948) 100	Mendocino		–	0.41	0.214
Skeena River					
(7114) 8	Kispiox		0.413	0.43	0.518
(7114) 7	Kitwanga	0.365	0.347	0.51	0.534
(7114) 2	Telkwa		0.435	0.54	0.430
Central Interior BC					
(7113) 10	Burns Lake	0.350	0.408	0.63	0.393
(7113) 2A	Quesnel		0.402	–	–
(7113) 5	Vanderhoof		–	0.64	0.427
South Interior BC					
(7118) 6	Clearwater		0.357	0.55	0.360
(7118) 4	Mount Ida	0.199	0.301	0.49	0.394
(7118) 5B	Charcoal Creek		0.357	0.55	0.435
Washington Cascades					
(7976) 6	Bird Creek		0.459	0.62	0.474
East of Rocky Mountains					
(7123) 100	Crowsnest, Alberta		0.472	0.66	0.445
Standard error ±		0.032	0.032	–	–
Differences significant at		*	**	n.s.	n.s.

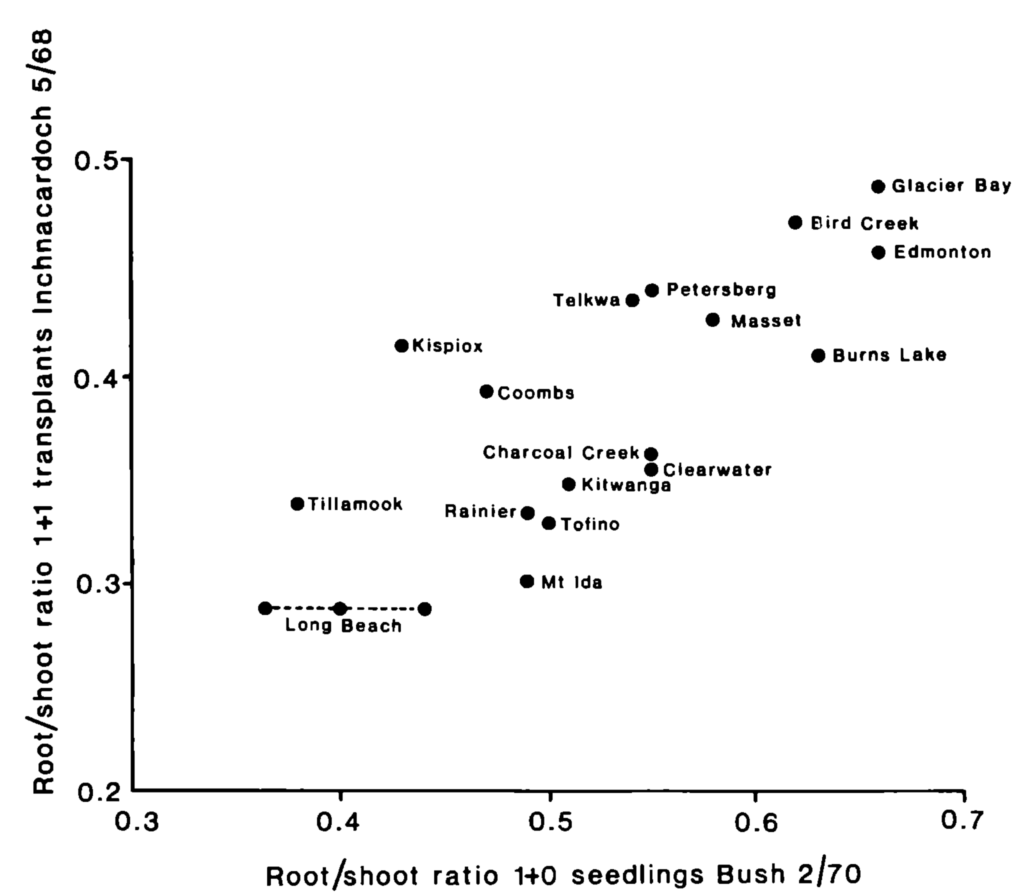

Figure 7. Comparison of root:shoot ratios of seedlings and transplants at Bush and Inchnacardoch nurseries.

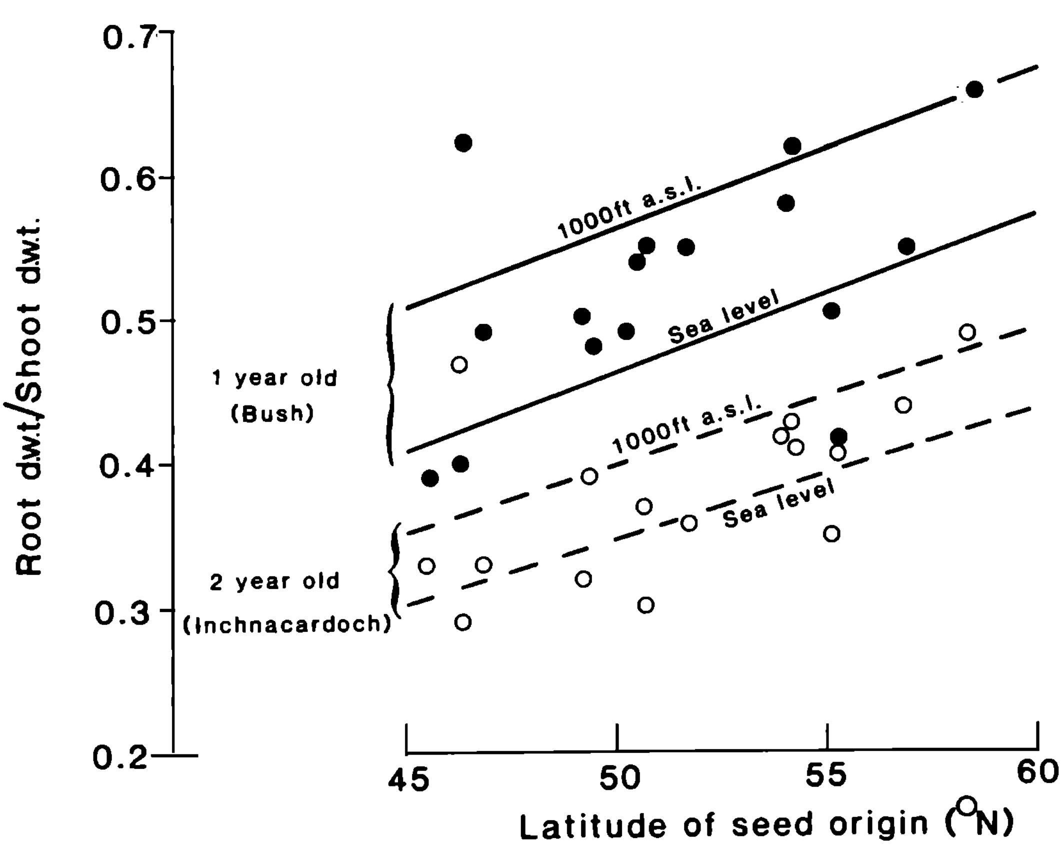

Figure 8. Relationships between root:shoot ratios of 16 seed origins and their latitudes and elevations.

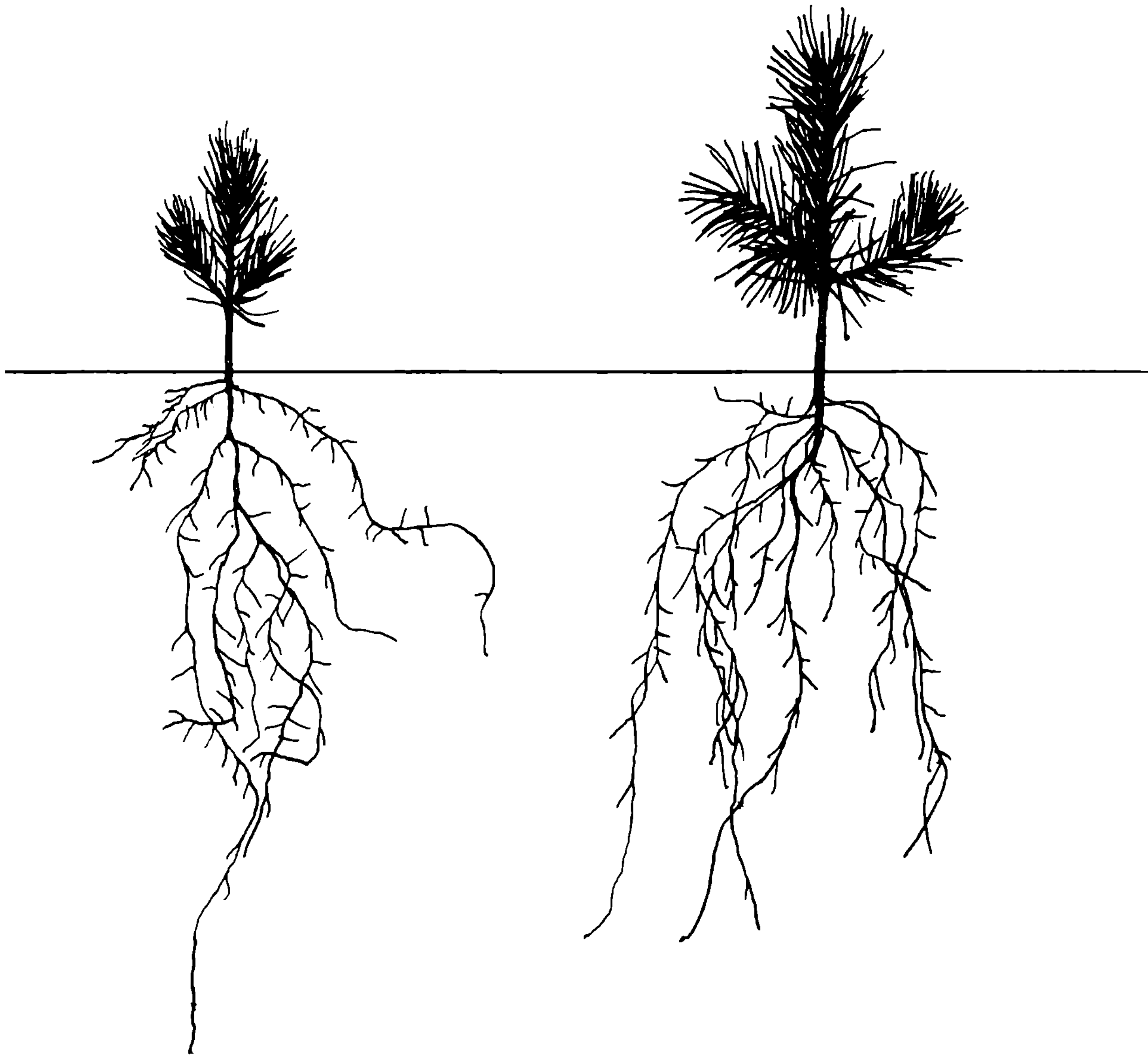

Figure 9. Left. Seedling at Inchnacardoch nursery from Glacier Bay, Alaska (root:shoot ratio 0.48).
Right. Seedling from Tillamook, Oregon (root:shoot ratio 0.22).

Chapter 9

Phenology and length of growing season

Differences in the length of the growing season for first-year seedlings were shown to be highly significant by Critchfield (1957), varying from 81 days for a Yukon origin to 214 days for one from the Mendocino White Plains, when grown in California. These differences were also noted in Forestry Commission nursery experiments, though unfortunately not assessed, except in terms of the associated colour changes in the needles. The length of the growing season is greatly influenced by the location of the nursery and there is a very strong interaction between seed origin and nursery climate, especially day length (which is related to latitude) and the onset of cool temperatures at the end of the growing season. Illingworth (1976b) noted that in a nursery with a mild climate on Vancouver Island (49^{o} N), Californian and Oregon coastal origins did not set buds in their first year at all. They just stopped growing and in February resumed growth for about a month, then they set buds for a short time, before these buds extended subsequently. In a nursery with a harsh interior climate at Prince George (54^{o} N) some of the same seed origins were killed by frost, though seedlings from the coast of British Columbia survived. In Sweden, at latitudes north of 63^{o} the summer daylength is longer than in the Yukon, these seed origins have a longer growing season than in their native land, and are considered the best choice. This is in contrast to their very short growing season in Britain, where the optimum daylength for Yukon origins is never reached and growth is poorer than with any other origin. Later experiments with 15 of the same or very similar origins to those in the 1968 and 1970 Forestry Commission experiments were carried out by Thompson in north-east Scotland. He assessed the presence or absence of developing buds at approximately weekly intervals on the first-year seedlings and thus obtained the dates on which 85% of the trees had set their buds. Seed origins varied by 55 days and this characteristic was later shown to be very highly correlated with mean height after 6 years' growth in the forest. The correlation was stronger for bud set than for the amount of lammas growth on 1+1 transplants and 6-year height for 25 of the IUFRO seed origins (Cannell *et al.*, 1981).

Flushing

Because even the earliest flushing origins are very rarely damaged by late spring frosts in Britain (unlike Sitka spruce), little attention was given to phenological differences between origins until the 1970s. Studies by Dietrichson (1964) and Hagner (1970), suggested that growth rhythms should be investigated in more detail. Winter cold is a major factor affecting tree survival in Scandinavia (Lindgren *et al.*, 1976) and the interior of north-west America (Rehfeldt, 1980) with large variation due to seed origin. Fortunately in Britain only the far southern origins are affected.

The first assessment of flushing was carried out during 1971 in an experiment at Deer (4 P63), Aberdeenshire, which showed highly significant differences among origins. Origins from the Central Interior and South Interior of British Columbia were earliest and coastal sources were late flushers, with the Washington coast origin last of all (see Table 17). In 1973, flushing was assessed by scoring (on a scale of 1 = unflushed to 5 = fully flushed) on six occasions between 7 May and 11 June on 78 seed origins in an unreplicated demonstration at Inchnacardoch, Inverness-shire. This assessment was repeated in 1974 with very similar results. In 1975, 35 origins were assessed for flushing in Broxa 115 P70 and the adjacent experiment Broxa 126 P72, Yorkshire on three occasions. The results were highly significant at all three dates and the data shown in Table 17 refer to the midpoint of flushing on 21 April. By far the earliest to flush was a Yukon seed origin from Ethel Lake and this origin has been noticed as outstandingly early in several other experiments. Seed origins from Central and South Interior of British Columbia flushed at about the same time as those from a high elevation stand in Alberta and one from the Washington

Table 17. Flushing scores as a percentage of the experiment mean at four sites

	Deer 4 P63	Inchnacardoch 161 P70		Broxa 115/126	Mabie 10
Site and assessment date:	1971	1973	1974	1975	1975
Seed origin region					
Alaska	99	97	88	96	70
North Coast BC	92	93	85	79	79
Vancouver Island	82	93	95	88	60
Washington Coast	53	91	97	75	71
Oregon/Californian Coast	–	91	90	107	77
Yukon	–	–	–	132	–
Skeena River	106	107	109	108	118
Central Interior BC	116	112	112	115	118
South Interior BC	119	109	110	113	124
East of Rockies	–	112	113	113	124
Cascades	–	95	101	113	109

Cascades, while those from Vail and Queets, on the Washington Coast, were very late. There were highly significant differences within the Vancouver Island region, with Coombs much earlier than Port Hardy.

At Mabie (10 P70), Dumfriesshire, flushing was also assessed three times on 23 seed origins in 1975. The midpoint of flushing is shown in Table 17, and seed origin differences were very highly significant. The earliest groups were from the South Interior of British Columbia and Skeena River regions were not much later. The coastal sources were significantly later in flushing, with Vancouver Island the last to flush.

Although these comparisons have different numbers of individual seed origins within the groups at different sites, all show a rather similar rank order, even though the assessments cover 3 years and widely different sites, while the Broxa data include not only origins from the 1965 collection but also 14 of the IUFRO collection. Relative flushing times are apparently strongly inherited, whereas there seems to be little interaction with site or age of tree.

Shoot extension during the growing season

Flushing denotes the start of shoot extension, but differences in this factor are probably less important for practical forestry than the pattern of shoot extension through the growing season, since there is evidence that low density 'springwood' is laid down during the period of rapid shoot extension, whereas higher density 'summer-wood' is laid down after the period of rapid shoot extension ceases. Shoot extension was assessed on the 1965 collection at Broxa 115 P70 and Rosarie 3 P70, Morayshire in 1973, mainly at weekly intervals, measuring 16 plants (four plants from each of four replicates) on each of 14 seed origins at Broxa and 20 origins at Rosarie.

At Broxa, measurements were made of leading shoot length at weekly intervals from 5 April to 12 July and then fortnightly until 6 September. The data on shoot length were expressed as a percentage of the total growth attained on 6 September, by which time growth had ceased. The weekly or fortnightly means for each seed origin were found and growth curves plotted using a graph plotter. The resulting curves were compared visually by overlaying them on a light table and it was clear that they could be grouped into sets with similar properties, without reference to their seed origins but that nevertheless grouped together origins by recognisable seed regions.

The sets were found to be as follows:

I. Alaskan
(7987)3 Petersburg
(7987)5 Annette Island

II. North Coastal
(7111)1 Masset, Queen Charlotte Islands
(7116)7 Coombs, Vancouver Island

III. South Coastal
(7972)1 Long Beach, Washington
(7951)1H Newport, Oregon
(7948)100 Mendocino, California

IV. Interior BC
(7113)4B Prince George
(7114)1 Terrace
(7118)4 Mount Ida
(7118)8 100 Mile House

V. Miscellaneous
(7113)1A Fraser Lake
(7123)100 Crowsnest, Alberta
(7976)5 Peterson Prairie, Washington

Figure 10 shows curves typical of each of these sets, which may be compared in relation to their starting sizes (which may reflect differences in bud length or possibly early growth before assessment began) and their patterns of growth in the three parts of the season, early, mid and late (Table 18). Similar patterns were found by Hagner and Fahlroth (1974), Thompson (1976) and Rehfeldt and Wykoff (1981).

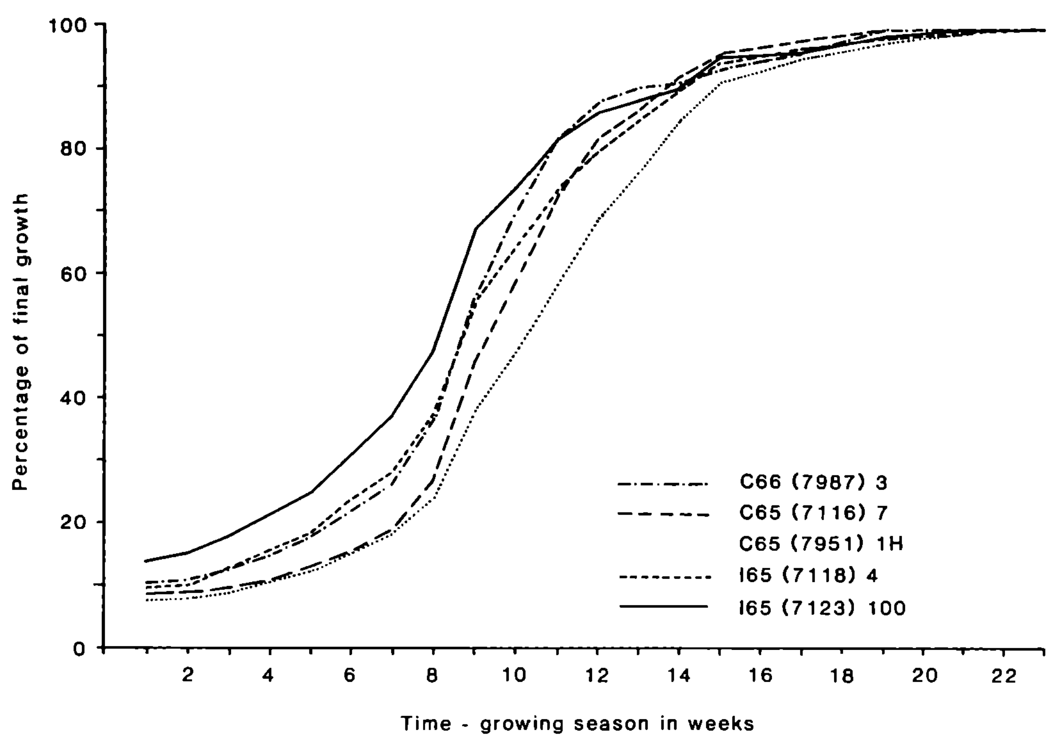

Figure 10. Growth curves of five typical sets of seed origins at Broxa 115 P70.

Table 18. Pattern of shoot growth in early, mid and late season

Set number	Origin	Starting size as % of annual growth	Early growth	Mid season growth	Late growth
I	Alaskan	10	moderate	very fast	early cessation, lammas growth
II	North Coastal	9–10	slow	fast	fairly early cessation
III	South Coastal	7–8	very slow	moderate	much late growth
IV	Interior BC	10–15	fairly fast	steady	continuing steady
V	Miscellaneous	12–15	very fast	steady	very early cessation followed by lammas growth

In order to examine the variation in growth within seed origins, three were selected – Petersburg from the Alaskan region, Mendocino, South Coastal and Mount Ida from Interior BC. The curves for the 16 individual trees were drawn, with one replicate (i.e. four trees) per graph (not reproduced).

The Petersburg trees started at between 8% and 13% of final shoot length. After some variation in the early weeks they all increased at about the same rate during mid season. All showed lammas growth, though there was considerable variation in the date of the first cessation of growth and the length of the pause, before growth restarted.

The Mendocino trees were extremely uniform in performance. Starting small at between 4% and 10%, they were very slow to start growth, virtually nothing appearing before 4 May. Mid season growth was slow, but continued steadily right up to 28 August. Although Mendocino fits best in Set III it is quite distinct from the two other South Coastal origins because of its extremely late start. Mount Ida was much more variable. At the start the trees ranged from 5% to 16% of the final shoot length. The general pattern was rather similar to Petersburg, though lammas growth was less marked.

These data were also subjected to analysis of variance for a number of factors, e.g. maximum weekly growth, total shoot length, the week in which maximum growth took place, the period over which 80% of shoot growth took place in weeks, the total number of needles on the shoot, the mean internode length between needles (also known as stem unit length), and these are shown in Table 19. A correlation matrix analysis shows the relationship between these growth factors and site characters at the place of origin (Table 20).

The results from the parallel experiment at Rosarie, using the same graph-plotting technique, were very similar for the Alaskan, North and South Coastal groups. However, in the group from the Interior of BC there were some minor differences and four seed origins from different elevations at Smithers on the Bulkley River formed a compact group with very similar curves, which were rather different from that of Terrace, which might fit better in the North Coastal group at Rosarie. Salmon Arm on Shuswap Lake (which was not present at Broxa) had a unique pattern, quite unlike that of the nearby Mount Ida origin, with a long growing season and the most rapid growth between weeks 3 and 9. The Salmon Arm seedlot was collected at about 670 m, while the Mount Ida one came from about 840 m. Whether this difference in elevation and the associated climatic factors in this transition zone to the 'Interior Wet Belt' could account for the different growth pattern must be speculative.

It can be concluded that there are inherent differences in shoot extension growth patterns between seed origins and if these can be shown to be related to wood properties, they may be of economic significance. The influence of seed origin on shoot growth patterns has also been studied in Britain by Thompson (1976), Cannell and Willett (1976) and Cannell *et al.* (1976). Cannell *et al.* (1981) have shown that seed origins that had a long growing season before setting buds as nursery seedlings, were the tallest after 6 years growth in the forest. The underlying reason for their superior growth was considered to be the prolonged period of late summer and early autumn apical meristematic activity, leading to large apical domes in the overwintering bud. Although these patterns are inherited, it is possible that selective hybridisation of geno-types that have a rapid start to growth with others having a later start but an extended growth period, might produce a combination of both characteristics that would be well adapted to the long potential growing season in many parts of Britain.

Table 19. Shoot growth data in 1973 at Broxa 115 P70

Identity number	Origin	Set number	Maximum weekly shoot growth (cm)	Total shoot length (cm)	Period over which 80% of growth occurred, weeks	Total number of needles on shoot	Mean internode length between needles (stem units) (mm)
Alaska							
(7987) 3	Petersburg	I	4.452	29.13	7.00	246	1.090
(7987) 5	Annette Island	I	4.762	31.23	6.50	308	0.980
North Coastal							
(7111) 1	Masset, QCI	II	4.625	31.22	6.25	292	0.974
(7116) 7	Coombs, Vancouver Is	II	6.642	44.32	5.50	414	1.025
South Coastal							
(7972) 1	Long Beach, Washington	III	6.835	58.85	7.50	462	1.191
(7951) 1H	Newport, Oregon	III	7.270	63.28	7.00	486	1.158
(7948) 100	Mendocino, California	III	7.460	60.63	7.00	529	1.115
Skeena River							
(7114) 1	Terrace	IV	4.887	38.03	7.00	363	1.088
Central Interior BC							
(7113) 1A	Fraser Lake	V	4.482	36.00	8.75	280	1.110
(7113) 4B	Prince George	IV	4.762	38.60	7.50	346	1.167
South Interior BC							
(7118) 8	100 Mile House	IV	5.852	43.13	7.75	316	1.241
(7118) 4	Mount Ida	IV	5.877	47.47	8.00	338	1.189
East of Rockies							
(7123) 100	Crowsnest, Alberta	V	3.602	28.63	8.25	262	1.140
Washington Cascades							
(7976) 5	Peterson Prairie	V	5.067	40.47	9.50	300	1.252
Standard error ±			0.296	1.90	0.44	22.1	0.048
Differences significant at			***	***	***	***	**

Tables 20. Multiple regression of shoot growth factors at Broxa 115 P70 and characteristics of the place of origin

Maximum weekly shoot growth	1								Differences for significance
Total shoot length	2	0.903	2						* 0.273
Period over which 80% of growth occurred	3	−0.282	−0.029	3					** 0.354
Number of needles	4	0.798	0.850	−0.255	4				*** 0.443
Internode length	5	0.263	0.348	0.351	−0.069	5			
Latitude	6	−0.770	−0.849	0.116	−0.754	−0.287	6		
Longitude	7	−0.451	−0.570	−0.392	−0.342	−0.572	0.579	7	
Elevation	8	−0.237	−0.163	0.539	−0.359	0.460	0.070	−0.669	

Patterns of diameter increment within the growing season

Little information is currently available on patterns of diameter increment on older trees of different seed origin. One study in the 1938 Wykeham 55 experiment, showed a rather similar pattern for diameter to the shoot growth studies at Broxa and Rosarie (Figure 11). The early start of the Prince George and Smithers origins is similar to that in the Set IV or V at Broxa, while Sonora Island resembles the North Coastal Set II. Shuswap Lake at Wykeham followed a course intermediate between Set IV and Set II, while the Shelton, Washington and southwest Lincoln County, Oregon curve resembled that of Newport in Set III at Broxa. These patterns may be related to seed origin differences in specific gravity of the timber (Brazier, 1980).

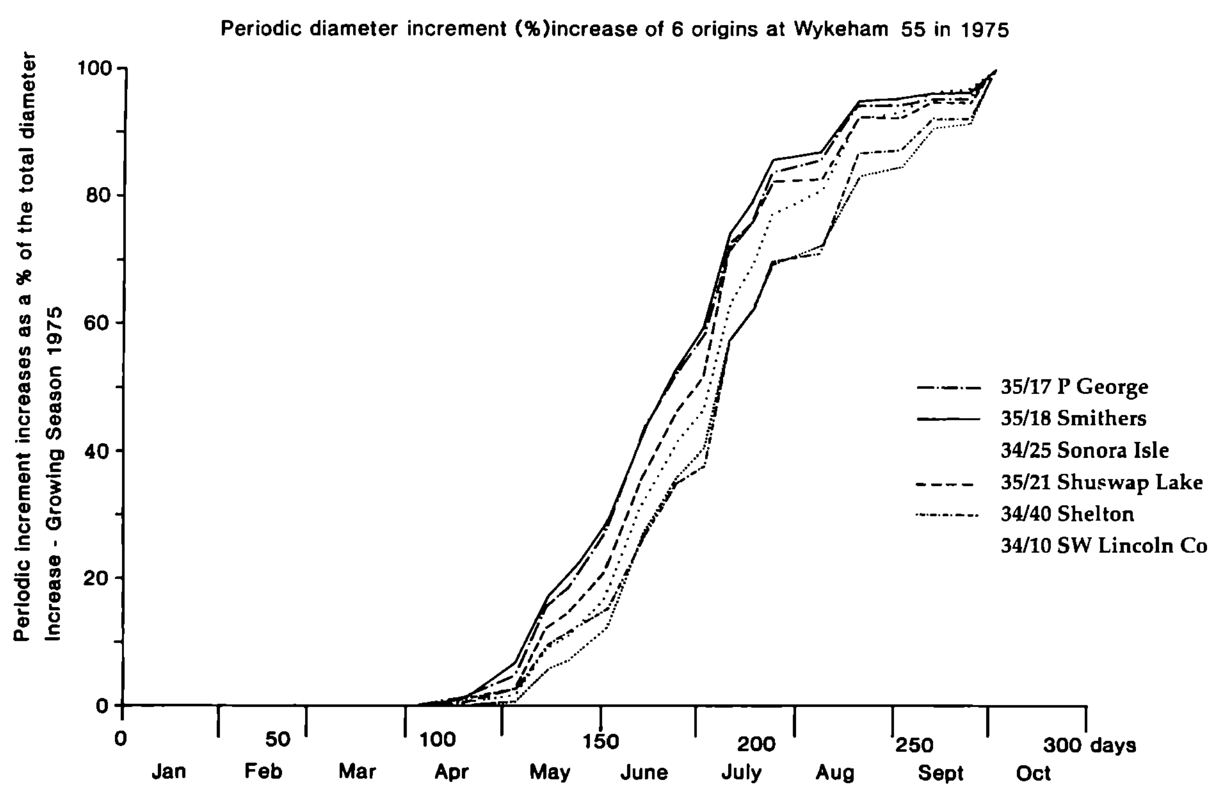

Figure 11. Periodic diameter increment of six origins at Wykeham 55 in 1975.

Chapter 10

Growth rate in the forest: 1937-1942 experiments

Introduction

The growth characteristic that is most important in the long term is *volume* growth per hectare in so far as it does not adversely affect timber quality. Information on this comes mainly from the 1937–42 series of experiments that are the subject of the following chapter. The post-war experiments have all been assessed for height, and in some cases diameter or basal area; these will give a provisional indication of the General Yield Class to be expected, based on top height extrapolated from mean height using the information in Forestry Commission Booklet 41 (Everard, 1974). Even if these extrapolated Yield Classes are not exact, they show the relative yield to be expected from different seed origins. The 1965 seed collection was planted on many sites and these experiments provide information on mean height and diameter. The data have been analysed to show the variation between seed origins and also across sites to show origin x site interaction, using the method of Finlay and Wilkinson (1963). The same technique was applied to the IUFRO series.

1937–42 experiments

As noted in Chapter 5, about 30 seedlots were sown in the period 1935–39 and planted on eight sites, in some cases only as unreplicated demonstration plots. The four main sites are: Achnashellach (24 P37-41) Wester Ross, Millbuie (1 P38-42) Easter Ross, Clashindarroch (15 P38-41) Aberdeenshire and Wykeham (55 P38) North Yorkshire (see Table 3). Achnashellach has a mild west coast climate with heavy rainfall and rather uneven topography, with knolls covered by shallow *Trichophorum* peat grading into hollows with deeper but more fertile peat with *Molinia*. Millbuie and Clashindarroch are on *Calluna*-covered drier heathlands with cooler winters and at the time of planting they were much more exposed. The Clashindarroch site is at an elevation of 360 m and was considered then to be above the normal planting limit. Wykeham lies on the bleak eastern plateau of the North Yorks Moors at 183 m in a low rainfall (900 mm) area. It has a somewhat indurated ironpan soil on Lower Calcareous Grit. The Millbuie soil is a strong ironpan developed over strongly indurated Old Red Sandstone till. At Clashindarroch the soil is a podzol with 10 cm of raw humus on a silty loam over slate bedrock. Ground preparation at Clashindarroch was screefed patches and at Achnashellach hand turfing with drains at 6.4 m spacing. At Wykeham the site had been double-furrow shallow ploughed 5 years before planting, and the *Calluna*, which had reinvaded, required screefing before planting. At Millbuie the shallow single-furrow ploughing barely touched the ironpan and did not penetrate the deep indurated layer.

The plants were grown at three nurseries and were planted mainly as 2+1 transplants. At Wykeham, they varied in size from a minimum of 15 cm to a maximum of 50 cm, the smallest being 35/59 from Klamath, Oregon Cascades and the largest 35/21 Salmon Arm, Southern Interior BC. It is possible that the use of such large plants may have contributed to early instability, which was minimal on seed origins with smaller initial sizes. At Millbuie, the tallest plants were from Shuswap Lake (30 cm tall), which later developed more basal sweep than any other interior origin, though South Coastal origins, which were smaller at planting, later had higher numbers of trees with basal sweep.

Results up to 18 years

Early growth in these experiments was measured only at Wykeham (see Table 21), due to wartime staff shortages.

As this is the only comprehensive experiment where height growth can be followed through to near rotation age, it is interesting to compare changes in rank with age (see Table 22). This subject will be discussed more fully later. Meanwhile it is worth noting that seed origin

Table 21. Mean height at 2, 5 and 9 years in Wykeham 55 P38

Region	Identity number	Seed origin	Height in cm		
			2 years	5 years	9 years
Coast BC	34/25	Sonora Island and New Westminster	42.7	91	189
South Coastal	34/40	Olympic Peninsula	45.2	104	238
	34/10	SW Lincoln County	50.3	119	287
Skeena/Bulkley River	35/18	Smithers	33.3	88	204
	35/22	Hazelton	39.1	104	229
Central Interior BC	34/24	Prince George	38.6	98	207
	35/17	Prince George	31.0	81	186
	35/19	Williams Lake	34.5	94	210
Southern Interior BC	35/20	Vavenby	36.1	98	204
	34/23	Shuswap Lake	45.7	110	247
	35/21	Salmon Arm	49.3	112	259
Northern Interior USA	34/69	Priest River	35.6	85	189
	35/53	East Washington	45.7	110	241
	34/68	West Yellowstone	25.9	73	162
Cascades	35/59	Klamath	29.5	76	162
	35/54	Oregon	17.0	46	116

Table 22. Rank for height at ages from 2 years to 44 years in Wykeham 55 P38

Region	Identity number	Seed origin	Rank on height at age (years)					
			2	5	9	13	17	44
Coast BC	34/25	Sonora Island and New Westminster	6	10	11	11	13	11
South Coastal	34/40	Olympic Peninsula	5	5	5	3	2	1
	34/10	SW Lincoln County	1	2	1	1	1	3
Skeena/Bulkley River	35/18	Smithers	12	11	9=	8	7=	8
	35/22	Hazelton	7	6	6	6	7=	10
Central Interior BC	34/24	Prince George	8	7	8	9	9=	5=
	35/17	Prince George	13	13	13	13	12	13
	35/19	Williams Lake	11	9	7	7	6	12
Southern Interior BC	35/20	Vavenby	9	8	9=	9	11	4
	34/23	Shuswap Lake	3=	4	3	5	4=	5=
	35/21	Salmon Arm	2	1	2	2	3	2
Northern Interior USA	34/69	Priest River	10	12	11=	11	9=	7
	35/53	East Washington	3=	3	4	4	4=	9
	34/68	West Yellowstone	15	15	14=	15	15	16
Cascades	35/59	Klamath	14	14	14=	14	14	14
	35/54	Oregon	16	16	16	16	16	16

Table 23. Mean height (metres) at age 16 to 18 years and height % at Millbuie 1, Wykeham 55, Achnashellach 24, Clashindarroch 15

Region	Seed origin	Identity number	Millbuie 1 P38–42 Mean height	Millbuie 1 Height (%)	Wykeham 55 P38 Mean height	Wykeham 55 Height (%)	Achnashellach 24 P37–41 Mean height	Achnashellach 24 Height (%)	Clashindarroch 15 P38–41 Mean height	Clashindarroch 15 Height (%)	Overall mean height (%)	Region mean height (%)
			Age 17 years		Age 17 years		Age 18 years		Age 17 years			
Coast BC	Sonora Island and New Westminster	34/25	6.36	97	6.28	94	6.74	115	–	–	102	102
South Coastal	Coast USA	34/39	7.13	108	–	–	7.44	127	–	–	(117)	
	Olympic Peninsula, Washington	34/40	7.13	108	7.47	112	5.39	92	–	–	104	115
	SW Lincoln County, Oregon	34/10	–	–	7.86	118	7.62	130	–	–	(124)	
Skeena/Bulkley River	Smithers	35/18	6.37	97	6.89	103	4.48†	77	3.84	97	(94)	94
	Hazelton	35/22	6.52	99	6.86	103	4.55†	78	4.02	101	(95)	
Central Interior, BC	Prince George	34/24	6.67	101	6.68	100	5.61	96	–	–	99	
	Prince George	35/17	6.40	97	6.46	97	5.00†	85	3.90	98	94	97
	Williams Lake, Quesnel	35/19	6.64	101	6.92	104	4.71†	80	4.11	104	97	
Southern Interior, BC	Vavenby, Clearwater	35/20	6.34	96	6.58	99	5.73	98	–	–	98	
	Shuswap Lake	34/23	7.06	107	7.25	109	5.85	100	–	–	105	105
	Salmon Arm, Shuswap Lake	35/21	6.89	105	7.50	112	7.04	120	–	–	112	
Northern Interior, USA	Priest River, Idaho	34/69	6.71	102	6.68	100	5.64	96	–	–	99	
	East Washington	35/53	6.58	100	7.25	109	6.22	106	–	–	105	95
	West Yellowstone, Montana	34/68	–	–	5.42	81	–	–	–	–	(81)	
Cascades	Williamson River, Oregon	35/59	5.27	80	5.67	85	5.79	99	–	–	88	81
	'Oregon'	35/54	–	–	4.94	74	–	–	–	–	(74)	
	Standard error ±		0.15		0.13		0.66		0.13			
	Differences significant at		***		***		n.s.		n.s.			
			Age 16 years				Age 16 years		Age 16 years			
Coast BC	Queen Charlotte Islands	36/42	5.42	92	–	–	3.54	83	3.78	97		91
South Coastal	Auchterawe S135	36/505	6.34	107	–	–	4.79	113	4.60	118	113	105
	Inchnacardoch 16	36/506	6.28	106	–	–	3.69	87	–	–	(97)	
Skeena/Bulkley River	Terrace	36/40	5.85	99	–	–	4.69	111	3.75	96	102	101
	Hazelton	36/43	5.73	97	–	–	4.63	109	4.05	104	104	
	Smithers	36/41	5.85	99	–	–	4.15	98	3.60	92	96	
CI,BC	Prince George	36/22	5.85	99	–	–	4.24	100	3.57	92	97	97
	Standard error ±		0.13				0.18		0.18			
	Differences significant at		n.s.				***		n.s.			

† Assessed at 17 years and adjusted x $\frac{18}{17}$

differences quickly became apparent, and after 5 years changes in rank were rather slight. Shoot length was also assessed at 5 and 9 years. Mean shoot length varied from 11cm to 25 cm at 5 years and from 20 cm to 55 cm at 9 years. The maximum shoot length on any individual tree was just under 1 m for the South Coastal source from south west Lincoln County, Oregon.

Table 23 shows the mean heights at 16–18 years in the replicated smaller plots (mainly of 30 plants) at Millbuie, Wykeham, Achnashellach and Clashindarroch. Heights are also expressed as a percentage of the experiment mean at that site. This facilitates comparisons across sites that differ in fertility and age of assessment. The data have been abstracted from an unpublished internal report (Shelbourne, 1974). Results from these experiments have been reported by Macdonald (1954), Lines (1966, 1968, 1976b), Moss (1971) and Lines and Booth (1972).

Discussion

Seed origin differences in height were very highly significant at Millbuie and Wykeham (Table 23). Due to ground variability at Achnashellach only the two most uniform of the five replicates were assessed and even then the results were not significant except in the younger section. At Clashindarroch the range of seed origins represented is poor and growth was depressed by the difficult site conditions, so that the lack of statistical significance was not unexpected.

The overall pattern of results is nevertheless quite clear. Seed origin performance on each site tended to follow a similar pattern, with large differences between the regional means for height over all experiments. The South Coastal region seed origins were outstanding for vigour. Next came those from the Southern Interior of BC. Skeena River origins grew better in the younger experiments than in the older ones. The Cascades origins were by far the poorest. Each region is now considered in more detail.

The two North Coastal origins are 36/42 from the Queen Charlotte Islands and 34/25, which was a mixture of seed from Sonora Island, lying between Vancouver Island and the mainland at 50^{o} 25′ N, and New Westminster, which is now a suburb of Vancouver City at 49^{o} 12′ N. This mixed origin grew at an average rate (and above average at Achnashellach) while the Queen Charlotte Island lot was significantly slower growing. Some of the New Westminster seed will have been very similar to that from Lulu Island, which grew poorly on exposed sites in the 1950s (see Chapter 4). Individuals bearing abundant flowers, which are characteristic of this ecotype, could be recognised easily when the experiments were young, though their poorer vigour and spindly growth habit have caused them to be largely eliminated by later selective thinning, or by natural suppression from the more heavily crowned Sonora Island trees.

The Oregon coastal source from south west Lincoln County (collected near the town of Waldport) was outstanding for vigour at both Wykeham and Achnashellach. Another seedlot direct from the Pacific coast, 34/39 (which on appearance and terpene type is identical with later imports from Long Beach, Washington) was only slightly less vigorous. The two home collected provenances 36/505 and 36/506 (known to be of South Coastal origin) grew at about the same rate as 34/39 at Millbuie, but at Achnashellach 36/506 was unexpectedly poor, perhaps due to site irregularity there. The remaining origin from this South Coastal group, 34/40, which came from the Olympic Peninsula (and was most likely from near Shelton in the rain shadow of the Olympic Mountains), grew well on the drier sites at Wykeham and Millbuie, though less well at Achnashellach, where the annual rainfall is more than twice as high – 2030 mm (see Table 3).

In the 16-year-old experiments in this series the Skeena River origins from Terrace and Hazelton grew quite fast and usually were taller than the seedlot from further inland at Smithers on the Bulkley River (see Table 23). In the 17–18-year-old experiments, the Skeena origins were below average in growth rate.

The origins from the Central Interior of BC all grew at an average rate, the tallest one at the well-replicated experiments at Wykeham and Millbuie being the most southerly origin from Williams Lake, 35/19.

The most vigorous inland origin, 35/21 from Salmon Arm, Shuswap Lake, South Interior of BC, was not significantly shorter than the South Coastal origins, though its appearance was entirely different. The nearby seedlot 34/23 from a higher elevation in the hills above Shuswap Lake also grew well, surpassing 35/21 at Millbuie, whereas the Vavenby (Clearwater) origin 35/20, which comes from a much drier climate (500 mm annual rainfall) outside the 'Interior Wet Belt', was much less vigorous.

The Northern Interior USA region brings together a number of somewhat disparate seed origins, and it could be argued that the Montana origin should not be included in this region. There was not a significant difference in height between the origin vaguely described as 'East Washington' 35/53 and seedlot 34/69, which came from the Priest River Research Station in northern Idaho. This part of Idaho is in ecological terms a southern extension of the 'Interior Wet Belt' of BC. From terpene testing (Forrest, 1980) it is clear that both these origins have affinities with this Southern Interior of British Columbia group and therefore 35/53 most likely came from the Colville National Forest. Both gave an average performance for height growth, with the Idaho origin tallest at Millbuie and the East Washington one being tallest at Wykeham and Achnashellach. The West Yellowstone, Montana origin, 34/68 was from a very high elevation (2050 m) on the east side of the Rocky Mountains. This is the main explanation for its poor growth at Wykeham, the rest being attributable to its transfer from an extremely continental climate to the British maritime climate. Despite the large climatic mismatch between Britain and Montana, a later import of seed from western Montana grew quite well, e.g. in a cultivation experiment at Teindland, Morayshire (Wilson and Pyatt, 1984).

The Cascades Oregon seedlots are both of the sub-species *murrayana*, with 35/59 Williamson River, Klamath known to be from a fairly high elevation (1300 m) and 35/54 merely described as 'Oregon', but very likely also from a high elevation stand. Its seed weight was recorded as 'exceptionally high'; from Table 7 this would suggest it came from the Cascade Mountains. Terpenes also show it to be from the Cascades region. Height growth of these was significantly poorer than the mean.

Volume estimates

Height serves as one measure for distinguishing growth rate of different seed origins. These experiments were also assessed at the same time for breast height girth. If these data are used to compute the mean tree volume, assuming each tree is a cone and using the formula: volume = $1/3\ \pi r^2 h$, then seed origin differences become even greater than with height (Table 24). The main changes are that the South Coastal origins become even more outstanding, though less dramatically with the Olympic Peninsula origin 34/40, because of aberrant results at Achnashellach. There was a similar large relative increase in the North Coastal origin, while those from the Skeena River and Central Interior groups show relatively lesser volume production. The pattern of volume growth of the Southern Interior sources (including those from Idaho and East Washington) was similar to that for height alone. It is interesting that the southern Cascades origins appear to be poorer for volume than for height, even though the girth:height ratios for these were by far the highest. The average ratio for the whole experiment was 0.572 and those for 35/59 Klamath and 35/54 'Oregon' were 0.628 and 0.750 respectively. The only other seed origin with a comparably high ratio (0.635) was the Queen Charlotte Islands seedlot 36/42, which was not included in these volume calculations as it was planted a year later. Salmon Arm 35/21 had the lowest ratio of 0.505, reflecting the tall spindly appearance of these trees. The East Washington origin 35/53 also had a low ratio of 0.522.

Later measurements of height and volume

Growth in the Wykeham experiment was measured at regular intervals (see Table II in Lines and Booth, 1972), the most recent height assessment being at 44 years (Table 25). This was for top height, i.e. the mean height of the 100 trees of largest diameter per hectare. By this age, windthrow had virtually eliminated the plots from south west Lincoln County, Oregon (which stood clear above the slow-growing origins and thus faced greater danger from wind). Wind probably also removed some of the tallest trees in the Shelton, Washington and Salmon Arm, BC plots. A gale in January 1976 caused the destruction of several of the unreplicated large plots in this experiment. These plots were being used as Permanent Sample Plots and had been thinned shortly before the gale struck, whereas the replicated section with smaller plots had not been thinned for several years and was relatively undamaged, apart from the plots from south-west Lincoln County, Oregon.

If ranking is compared between the 44-year top-height data and that for mean height at 17 years (shown in Table 22), it will be seen that the later heights are in general well correlated with the earlier ones. The main differences are that

Table 24. Mean tree volume in dm^3 and volumes as a percentage of the experiment mean at Millbuie, Wykeham and Achnashellach at 17–18 years and % of experiment mean

Identity number	Seed origin	Millbuie 1 P38		Wykeham 55 P38 17 years		Achnashellach 24 P37 18 years		Overall (%)
		Volume	Volume (%)	Volume	Volume (%)	Volume	Volume (%)	
North Coastal								
34/25	Sonora Island and New Westminster	14.67	94	18.72	97	19.17	178	123
South Coastal								
34/39	Coast USA	21.95	141	–	–	24.24	225	(183)
34/40	Olympic Peninsula	19.68	126	22.63	118	8.52	79	108
34/10	SW Lincoln County, Oregon	–	–	32.48	169	20.90	194	(182)
Skeena River								
35/18	Smithers	14.44	93	19.43	96	3.65†	34	74
35/22	Hazelton	15.26	98	19.57	102	4.14†	38	79
Central Interior BC								
34/24	Prince George	16.42	105	19.03	99	7.11	66	90
35/17	Prince George	14.75	95	17.02	88	4.68†	43	75
35/19	Williams Lake	14.50	93	20.95	109	3.95†	37	80
South Interior BC								
35/20	Vavenby	12.66	81	17.87	93	9.43	88	87
34/23	Shuswap Lake	17.41	112	21.63	112	9.23	86	103
35/21	Salmon Arm	17.53	112	21.38	111	13.02	121	115

Table 25. Analysis of variance of top height (m) at 44 years and Duncan's multiple range test, Wykeham 55 P38

Source	Sums of squares	Degrees of freedom	Mean square	*F* ratio
Blocks	1.878952	2	0.939476	4.22*
Origins	22.824664	13	1.755743	7.88***
Breakdown of sum of squares within				
Skeena River	0.024067	1	0.024067	0.11 n.s.
Central Interior BC	0.289089	2	0.144544	0.65 n.s
South Interior BC	0.394467	2	0.197233	0.89 n.s.
North Interior USA	0.018150	1	0.018150	0.08 n.s.
Cascades	0.244482	1	0.244482	1.10 n.s.
Between groups	21.400719	5	4.280144	19.21***
Error	5.570147	25	0.222806	
Total	30.273762	41		

Group	Number of origins	Rank	Mean height (m)	Within-group standard error in analysis of variance
North Coastal	1	5	17.977	0.273
South Coastal	1	1	19.280	0.273
Skeena River	2	4	18.050	0.193
Central Interior BC	3	6	17.938	0.157
South Interior BC	3	2	18.467	0.157
North Interior USA	2	3	18.112	0.193
Cascades	2	7	16.425	0.193

Duncan's multiple range test

Standard error of an origin mean = 0.2725

Mean	Name	5%			1%		
19.280	34/40 Shelton	│			│		
18.690	35/21 Salmon Arm	│	│		│	│	
18.523	35/20 Vavenby	│	│		│	│	
18.190	34/24 Prince George		│		│	│	
18.187	34/23 Shuswap Lake		│		│	│	
18.167	34/69 Priest River, Idaho		│		│	│	
18.113	35/18 Smithers		│		│	│	
18.057	35/53 East Washington		│			│	
17.987	35/22 Hazelton		│			│	
17.977	34/25 Sonora Island		│			│	
17.833	35/17 Prince George		│			│	
17.790	35/19 Williams Lake		│			│	
16.627	35/59 Klamath County			│			│
16.223	35/54 Oregon			│			│

Origin means which have no line in common are significantly different at the given probability level.
Origin means which have a common line are not significantly different at the given probability level.

Table 26. Millbuie 1 P38–40. Comparison of heights (m) at 20 years in the replicated and large single plots, and total volume in large plots at 47 years

Identity	Seed origin	Height at 20 years in replicated plots		Top height at 20 years in large single plots		Total volume (m^3 ha) for single plots adjusted to 47 years		Regional mean volume as a % of overall mean
		Height	Rank	Height	Rank	Volume	Rank	
North Coastal								
34/25	Sonora Island and New Westminster	8.28	11=	9.14	5=	526	5	108
36/42	Queen Charlotte Islands	7.42	19	7.92	18=	493	7=	
South Coastal								
34/39	Coast USA (Long Beach?)	8.86	3=	9.45	3=	510	6	
34/40	Olympic Peninsula	9.22	1	9.75	1=	580	2	
36/505	Coast USA, ex Auchterawe	8.76	5	9.14	5=	527	4	114
37/55	Olympic Peninsula	7.74	18	8.23	14=	453	12	
37/56	Grays Harbor	8.61	7	9.75	1=	618	1	
Skeena River								
35/18	Smithers	8.38	9	8.23	14=	436	14	
36/40	Terrace	8.28	11=	7.92	18=	460	11	99
36/41	Smithers	8.12	15	8.23	14=	484	10	
36/43	Hazelton	7.97	16=	8.23	14=	493	7=	
Central Interior BC								
34/24	Prince George	8.33	10	8.53	9=	417	15	
35/17	Prince George	8.55	8	8.53	9=	443	13	94
36/22	Prince George	7.97	16=	8.84	8	492	9	
35/19	Williams Lake	8.86	3=	8.53	9=	413	17	
South Interior								
35/20	Vavenby, BC	8.28	11=	8.53	9=	323	20	
34/23	Shuswap Lake, BC	8.71	6	8.53	9=	391	19	80
35/21	Salmon Arm, BC	8.28	11=	9.14	5=	415	16	
Northern Interior USA								
34/69	Priest River, Idaho	8.97	2	9.45	3=	554	3	117
Cascades								
35/59	Klamath	7.16	20	6.71	20	398	18	84

Table 27. Actual production and adjusted production to 47 years ago ($m^3 ha^{-1}$) at Millbuie 1 P38-40

Region and seed origin	Identity number	P year/age		Number/ha	Top height (m)	Mean diameter (cm)	Standing volume	Volume thinned	Total production	CAI	MAI	Volume adjusted to 47 years	Regional mean volumes to 47 years
North Coastal													
Sonora Island and New Westminster	34/25	38	47	767	20.0	23.5	310.7	215.7	526.4	16.1	11.2	526.4	509.8
Queen Charlotte Islands	36/42	39	46	857	17.9	20.0	224.5	251.4	475.9	17.4	10.3	493.3	
South Coastal													
Coast USA (Long Beach?)	34/39	38	47	766	19.8	24.5	280.0	230.2	510.2	9.6	10.9	510.2	
Olympic Peninsula, Washington	34/40	38	47	922	21.5	24.0	385.7	194.7	580.4	17.0	12.3	580.4[†]	
Coast USA, ex Auchterawe	36/505	39	47	732	18.9	22.5	257.8	269.4	527.2	12.6	11.2	527.2	538.5
Olympic Peninsula, Washington	37/55	40	45	722	16.9	21.5	208.5	223.1	431.6	10.7	9.6	453.0	
Grays Harbor, Washington	37/56	40	45	934	20.4	24.0	397.9	182.2	580.1	19.1	12.9	618.3	
Coast USA (Long Beach?)	38/14	40	45	948	18.5	22.0	326.8	182.9	509.7	16.0	11.3	541.7[†]	
Skeena River													
Smithers	35/18	38	47	822	18.2	21.0	230.0	205.5	435.5	8.9	9.3	435.5	
Terrace	36/40	39	46	977	17.9	20.5	254.0	195.9	449.5	11.0	9.8	460.5	468.3
Smithers	36/41	39	46	1064	17.8	19.5	268.0	199.6	467.6	16.6	10.2	484.2	
Hazelton	36/43	39	46	769	18.5	20.0	202.6	276.1	478.7	14.2	10.4	492.9	
Central Interior BC													
Prince George	34/24	38	47	745	18.3	21.0	220.1	197.1	417.2	11.5	8.9	417.2	
Prince George	35/17	38	47	1063	19.0	21.0	288.8	154.5	443.3	10.4	9.4	443.3[†]	441.3
Prince George	36/22	39	46	888	19.5	21.0	276.6	196.8	473.4	18.3	10.3	491.7	
Williams Lake	35/19	38	47	804	18.4	20.5	210.0	203.1	413.1	10.3	8.8	413.1	
South Interior													
Vavenby	35/20	38	47	618	17.6	22.5	194.1	129.5	323.6	6.7	6.9	323.6	
Shuswap Lake	34/23	39	47	720	18.6	22.5	245.5	145.9	391.4	10.2	8.3	391.4	376.8
Salmon Arm, Shuswap Lake	35/21	38	47	871	17.6	22.0	248.1	167.3	415.3	4.7	8.8	415.3	
Northern Interior USA													
Priest River, Idaho	34/69	38	47	782	19.0	23.0	286.5	267.2	553.7	10.7	11.8	553.7	553.7
Cascades													
Klamath	35/59	38	47	1042	17.2	20.0	259.1	138.8	397.9	11.1	8.5	397.9	397.9

[†] Plots 8, 9 and 22 were volume Sample Plots last measured in 1980. They were omitted from the 1985 thinning and assessments following windthrow in 1982. The figures for these plots include estimated values for the growth from 1980 to 1985.

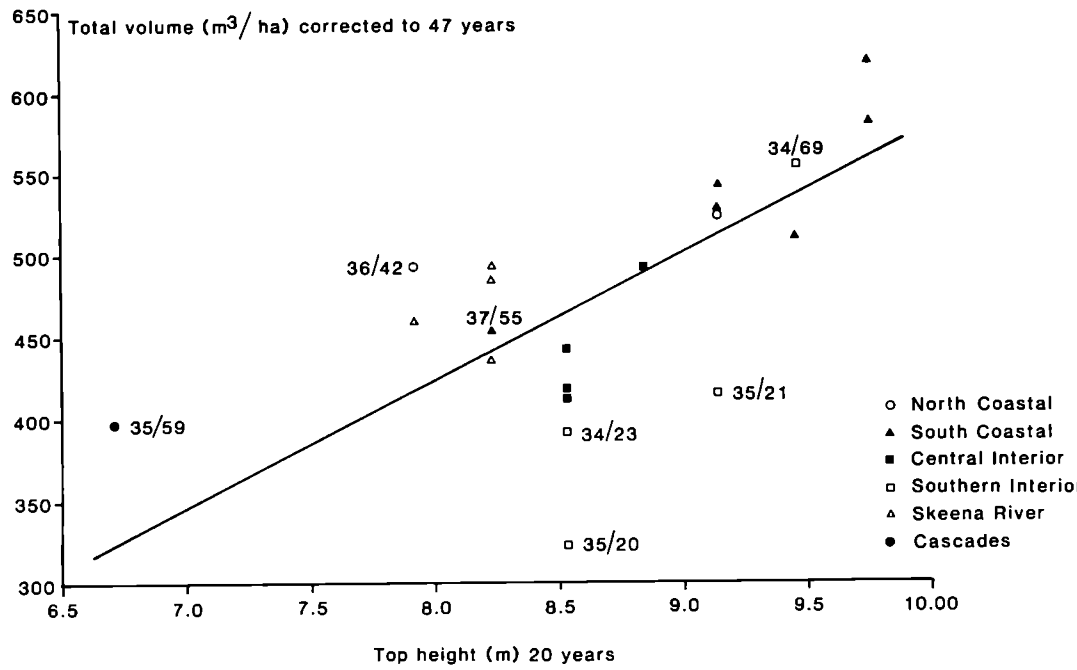

Figure 12. Total volume production, corrected to 47 years, against top height at 20 years in large plots at Millbuie 1 P38-40.

Vavenby rose from 11th to 4th place, while Williams Lake slipped from 6th to 12th place.

In the Millbuie experiment a series of unreplicated larger plots (0.02–0.13 ha) were planted adjacent to the replicated section with 30 plant plots. It is possible to compare the top height in these larger plots at age 20 years with the mean height at 20 years in the replicated smaller plots. The sections planted in 1939 and 1940 were measured 1 and 2 years later respectively to give the heights at a common age. Table 26 shows the heights and the rank order to facilitate comparison. Regular assessments were carried out in the larger plots and all production, either from thinning or windthrow was recorded up to 47 years of age. Table 27 shows the actual production, with the final column giving total volume either actual or adjusted to the predicted total at 47 years for different ages of planting. Figure 12 shows a fairly close relationship between top height at 20 years and total volume production at 47 years. As expected, the South Coastal origins were outstanding for height at 20 years and for total production, with the exception of 37/55, Olympic Peninsula, Washington. There is no obvious reason why this particular seedlot should be so much poorer than the seedlot 34/40 from the same general area. The two North Coastal seed origins both had good productivity in relation to their height at 20 years, especially the bushy 'muskeg' type from the Queen Charlotte Islands 36/42. Although considerably heavier-branched than the inland origins when in the thicket stage, this origin does not now appear unacceptably coarse-branched. By contrast, the South Interior of BC origins were all poor for volume production, with 35/21 Salmon Arm particularly disappointing in ranking only 17th for total production, when it had been fifth equal for top height at 20 years. Vavenby, 35/20, from this region was poorest of all for volume production, even the inherently slow growing sub-species *murrayana* seedlot from Klamath, Oregon being more productive. On the ground it is obvious that those origins with poor volume production have much lighter crowns than the productive ones, though the Priest River, Idaho plot is known from the pre-planting survey to be on a more fertile site than the rest of the experiment. Unfortunately, the whole experiment was destroyed in the catastrophic gale of February 1989, when gusts of 120 knots were recorded not far away.

Small differences in either height, diameter or volume growth are relatively unimportant compared with long-term wind stability and stem form. These aspects will be discussed in a later chapter.

Chapter 11

Growth rate in the forest: 1952–1967 experiments

In the experiments planted between 1952 and 1967 there was at first a tacit assumption that the main patterns of variation among seed origins from the natural range had been discovered and it was merely necessary to fill in the gaps in our knowledge and to test new commercial seed supplies as they became available. Thus the first experiments planted in 1952–53 at Achnashellach and Inchnacardoch tested seed from Lulu Island supplied by three different seed merchants against seedlots from Salmon Arm, Shuswap Lake (by this time a well-established origin) and western Montana. On both sites the early growth of the Lulu Island lots was superior to that from western Montana (Wood and Lines, 1959), but by 15 years trees from western Montana equalled them in height. The Salmon Arm origin was the tallest at all stages. All of these origins produced very spindly trees with poor foliage retention on both sites.

In 1954 the first seed from Alaska was obtained. This came from Hollis, Prince of Wales Island and Haines near Skagway, at the head of the Lynn Canal. At Hollis the annual precipitation is over 2000 mm, whereas at Haines it is only about half as much and the climate is more continental (see Aldhous, 1976, p14). These two origins were planted at Watten, Caithness and Kielder, Northumberland, together with seedlots from Lulu Island and a Scottish provenance, originally from the Washington coast. At Watten the experiment was planted on 4-year-old ploughing. At this date, the risk of basal sweep damage due to over-rapid early growth was already apparent, and in an attempt to control this, no fertiliser was applied at planting. This merely had the effect of reducing growth to such an extent that at 6 years the mean heights at Watten were all less than 0.5 m, even though 43 g of rock phosphate per tree was applied after the third growing season (Lines and Mitchell, 1966). The Kielder site is less infertile, but here the tallest origin (Lulu Island) at 6 years was only 1 m tall, partly as a result of repeated grouse and blackgame damage. Results after 21–25 years are shown in Table 28. Note that the Hollis origin was relatively poor for height, but second to the South Coastal provenance for basal area and volume, calculated from diameter and height assuming the tree as a cone.

Table 28. Height, basal area and calculated volume at Watten 9 P54 and Kielder 71 P54

Region and identity number	Seed origin	Watten at 25 years		Kielder at 21 years		
		Top height (m)	Basal area (m^3 ha^{-1})	Height (m)	Diameter (cm)	Volume (dm^3)
Alaska						
51/212	Haines, Alaska	6.73	35.4	6.11	8.92	128
52/211	Hollis, Alaska	6.70	45.7	6.69	9.76	168
Coast BC						
51/347	Lulu Island, BC	6.99	33.0	7.31	8.56	144
South Coastal						
52/207	South Coastal ex Inchnacardoch	7.85	53.7	7.91	10.68	243
Standard error ±		0.09	2.2	0.17	–	14
Differences significant at		***	***	**	–	**

These results illustrate the differences to be expected within the Alaskan group of seed origins and the inferior basal area production of the light-foliaged Lulu Island strain. At Kielder windthrow of some trees in the heavy-branched South Coastal origin accentuated by heavy snow damage in the winter of 1978–79, was becoming apparent by 27 years, whereas the Hollis trees were continuing to grow steadily, with healthy dense foliage.

1957 experiments

Three experiments were planted in 1957, mainly with provenances collected in Scotland or Eire (see Table 29). The Irish stands were described by Lines (1957a). The plants were raised at Tulliallan heathland nursery in 1955, where they already showed large differences in height, seedling colour and growth cessation as 1 year seedlings (Lines, 1957b). They were planted at Achnashellach, Wester Ross; Elchies, Moray and Ceiriog, Denbigh. Results after 3 years (Lines and Aldhous, 1962) showed the considerable superiority in height of the South Coastal provenances over both the North Coastal one from the Queen Charlotte Islands and those from the Central Interior of British Columbia. At this stage, the one direct from Fort Fraser was poorest on all three sites. The Ceiriog experiment was not assessed after the 15th year, when the results were roughly the same as at Elchies for rank order of height at 15 years, though the overall experiment mean height on this site was only two-thirds that at Elchies. The latest assessments of top height and basal area for Achnashellach and Elchies are shown in Table 29. The Elchies experiment suffered severe damage from heavy wet snow and gale-force winds in the winter of 1976/77. Damage was highly selective and restricted to the South Coastal provenances, except where edge trees of these plots blew into adjacent plots of inland or Queen Charlotte Islands origin. Despite the heavy crowns of the Queen Charlotte Islands trees, they proved highly resistant to snow and wind damage. Even with this damage, the ranking for top height at 20 years was almost identical with that for mean height at 15 years. At both sites the significance of differences between seed origins for basal area was considerably greater than for top height, although there is little indication of a provenance x site interaction.

The Queen Charlotte Islands provenance grew poorly in height, but its basal area production was appreciably better and this, combined with superior stability and resistance to snow damage would suggest it as a safe choice. Poor resistance to damage from wind and snow unfortunately rules out all the vigorous South Coastal group, of which the poorest was 55/228. This seed was collected from the small number of surviving trees in the Ruttle Wood (see Chapter 4), after most had been windthrown. These individuals may have been inherently less vigorous or there could have been a degree of inbreeding. Of the two Skeena River provenances, Smithers proved more consistent in basal area production. They both had above average stem form and continued to look healthy. Both Central Interior BC seedlots were poor in height and basal area on these sites, with a very maritime climate at Achnashellach and Elchies on a deep peat bog. Seed origins from this region often grow relatively better on dry eastern heathlands with mineral soils, such as Millbuie and Clashindarroch. The provenance that originated at Shuswap Lake was the tallest inland seedlot, though its basal area was lower than the shorter Skeena River provenances. The Albertan provenance, which derived from the early bulk import (very likely from quite a high elevation in the eastern Rockies) was particularly poor on these sites and just as bad at Elchies at 15 years.

1958 and 1959 experiments

In 1958, two demonstrations were planted at Inchnacardoch and Millbuie using seed origins from the collection made by Dr W.B. Critchfield (1957). These covered a much wider range of seed origins than ever before, including seedlots from the Yukon, California and from a very high elevation site at 2680 m in Colorado.

Also in 1958, experiments were planted at Wareham, Dorset; Wilsey Down in Cornwall; Aeron and Taliesin in Cardigan; and Tarenig, Montgomery (Wood and Lines, 1959). These tested a range of South Coastal seed origins (thought at this stage to be the first choice for many poor exposed sites) against three from the Vancouver area and two from the Cascade Mountains of Oregon. The following year (1959) approximately the same set of origins was planted at three sites in Scotland (Borgie, Sutherland; Deer, Aberdeenshire; and Glentrool, Kirkcudbrightshire). Brief notes on the nursery stage of these experiments were given by Wood, Lines and Aldhous (1960). By 6 years the South Coastal lots had established a clear superiority over the more northerly coastal ones. There was not often a significant

Table 29. Top height and basal area at Achnashellach 29 (25 years) and at Elchies 1 (20 years)

Identity number	Seed origin	Provenance	Achnashellach 29 P57				Elchies 1 P57				Overall basal area (%)
			Top height (m)	Height (%)	Mean basal area per plot (m^2)	BA (%)	Top height (m)	Height (%)	Mean basal area per plot (m^2)	BA (%)	
North Coastal											
55/227	QCI	Kirroughtree 1	10.16	94	0.317	94	8.53	97	0.322	92	93
South Coastal											
54/143	Washington coast	Forth Forest, Eire	11.46	106	0.443	132	9.26	106	0.424	122	127
54/145	Washington coast	Kilworth Forest, Eire	11.10	102	0.387	115	8.84	101	0.385	110	112
55/228	Washington coast	Ruttle Wood, Inverness	10.72	99	0.306	91	9.20	105	0.316	91	91
55/229	Washington coast	Inchnacardoch 16	11.78	109	0.467	139	9.42	108	0.422	121	130
55/682	Long Beach	Long Beach, Wash	11.20	103	0.380	113	9.34	107	0.419	120	116
Skeena River											
55/226	Smithers	Kirroughtree 1	10.72	99	0.320	95	8.73	100	0.363	104	100
55/247	Terrace	Millbuie 1	10.76	99	0.363	108	8.08	92	0.319	91	100
Central Interior BC											
55/253	Prince George	Harwood Dale, Yorkshire	9.42	87	0.243	72	8.27	94	0.292	84	78
55/681	Fort Fraser	Fort Fraser	11.04	102	0.271	81	8.10	92	0.323	93	87
South Interior BC											
55/258	Shuswap Lake	Roseisle, Moray	11.32	104	0.296	88	8.77	100	0.340	97	92
East of Rocky Mountains											
55/249	Alberta	Montreathmont, Angus	10.58	97	0.237	71	8.55	98	0.260	75	73
Standard error ±			0.39		0.018		0.25		0.016		
Differences significant at			*		***		**		***		

difference among the South Coastal group (Lines *et al.*, 1967). Results at the latest assessment are shown in Table 30 for the combined 1958/59 experiments. It will be seen that decreasing interest in this species in southern Britain, partly caused by the realisation that the pine shoot moth, *Rhyacionia*, might seriously damage the leading shoots, led to the early closure of the experiments in south-west England and Wales. The Glentrool 17 experiment differed from the other Scottish experiments in having two replicates of large (400 plant) plots as well as five replicates of small (36 plant) plots. By 27 years there was so much interaction between the small plots that measurements were restricted to the large plots, which can provide realistic data on basal area per hectare for many more years.

At Borgie, all of the South Coastal origins had very heavy branches and poor stem form, though stem lean was more apparent than basal sweep, probably because rapid early height growth was restricted by blackgame damage. At 22 years some windthrow had started, affecting up to 15% of the trees in the worst origin (North Bend), but even the shorter and lightly crowned seedlot from Hat Creek had 5% windthrown stems. The Ladysmith, Vancouver Island origin was only slightly shorter than the South Coastal lots and had much more slender stems and correspondingly lower basal area. The Cascades origins were both poor in height and basal area. It was discovered after these experiments were established that due to a misunderstanding over the seed region numbering system, 56/657, originally thought to be from Cascadia on the west side of the Cascades, was in fact collected in the Sisters/La Pine area (zone 681) on the east side of the Cascades. The basal area data show a much greater variation between seed origins than for height. The Inchnacardoch provenance was the most productive for basal area as well as the tallest, while Tidewater was surprisingly poor in view of its good overall performance in other experiments. The low basal area was not due to windthrow in this case.

At Glentrool, early growth was faster than at Borgie and incidence of basal sweep was just as bad. The trees exhausted their small initial dose of rock phosphate (28 g per plant) by the sixth year. After serious infestations by pine sawfly (*Neodiprion sertifer*) in 1966 and 1967 they were in poor condition, and required top dressing in summer 1967 with 60 kg of P and 100 kg of K per ha and spraying with Didimac (DDT). A sample of trees was felled in each seed origin in December 1968 and shoot length measured for each of the years 1965–1968. Shoot length generally fell in 1966 and 1967, then made a spectacular increase in 1968 in response to topdressing. This response was much greater on the South Coastal origins than on the inland ones. The position at 27 years was that Long Beach was tallest and had the greatest basal area, while differences among the other South Coastal origins were not significant, though all were significantly superior to the three inland origins.

The 'dominant' heights at Deer were assessed by splitting each 36 tree plot into six subplots and measuring the tallest tree in each of these. As at Borgie, the Inchnacardoch provenance was tallest, with the other South Coastal ones not significantly poorer, except for Keyport, which was not significantly taller than the one from Ladysmith. Sisters/La Pine, from the Oregon Cascades, was by far the poorest. Two unreplicated plots from Shuswap Lake and Lulu Island were below the experiment mean for height and both looked poor in needle retention and general health. As at Glentrool, there were heavy *Neodiprion* attacks in 1966 and 1967. Infestation in 1968 started at a high level, but was quickly controlled by a natural virus. It was noted that Ladysmith was particularly badly affected by sawfly, partly because it already had poor needle retention, due to continued winter blasting of its foliage.

Although the southern experiments were assessed over a much shorter period, the pattern of height growth was similar to that in the Scottish experiments, even at the most southerly experiments at Wareham and Wilsey Down. The general conclusion from these experiments is that the incidence of early basal sweep and later instability makes the South Coastal group of origins too risky for normal use, while those from the North Coastal group were unsatisfactory because of poor resistance to winter blasting before canopy closure (Ladysmith), or poor growth and excessive flower production (Langley and Lulu Island). On these sites, none of the inland origins was satisfactory either, thus indicating the need for origins that combine long-term wind stability with good health and vigour. It is unfortunate that these experiments have no Skeena River origins or the better North Coastal ones, such as Queen Charlotte Islands and Sonora Island, which grew well in the 1938/39 experiments.

Table 30. Height at eight sites and basal area at two sites in the 1958/59 series of experiments

Identity number	Seed origin	Borgie 9 P59 Top height (m)	Borgie 9 P59 Height (%)	Borgie 9 P59 Mean basal area per plot (m^2)	Borgie 9 P59 BA (%)	Glentrool 17 P59 Top height (m)	Glentrool 17 P59 Height (%)	Glentrool 17 P59 Mean basal area per plot ($m^2 ha^{-1}$)	Glentrool 17 P59 BA (%)	Deer 2 P59 Dominant height (m)	Deer 2 P59 Height (%)	Aeron 1 P59 Mean height (m)	Aeron 1 P59 Height (%)	Taliesin 12 P58 Mean height (m)	Taliesin 12 P58 Height (%)	Tarenig 3 P58 Mean height (m)	Tarenig 3 P58 Height (%)	Wareham 125 P58 Mean height (m)	Wareham 125 P58 Height (%)	Wilsey Down 13 P58 Mean height (m)	Wilsey Down 13 P58 Height (%)	Overall height %
<u>Age/years</u>		22		22		27		27		15		6		8		6		21		9		
<u>North Coastal</u>																						
56/658	Ladysmith Vancouver Is	8.74	103	0.506	94	12.65	102	42.90	109	6.32	100	2.08	85	1.30	82	1.82	106	4.62	96	3.23	99	96.6
53/627	Langley, Lower Fraser River	-	-	-		-		-		–		1.69	69	1.43	90	1.65	96	3.62	75	2.85	88	(83.6)
52/343	Lulu Island, Lower Fraser River	-	-	-		-		-		(5.90)	(93)	1.51	62	1.47	92	1.68	98	3.17	66	3.03	93	(84.0)
<u>South Coastal</u>																						
56/656	Keyport, Puget Sound, Washington	8.71	102	0.561	105	12.25	99	41.34	105	6.45	102	2.81	115	1.36	85	1.86	109	5.32	111	3.61	110	104.1
56/654	Long Beach, Washington	9.09	107	0.624	116	14.20	115	45.35	116	6.81	107	2.85	117	1.69	106	2.01	117	5.62	117	3.85	118	113.0
56(4118)501	Inchnacardoch 16, ex Washington	9.12	107	0.661	123	13.35	108	44.18	113	6.82	107	-	-	-	-	-	-	-	-	-	-	(107.3)
56/655b	Newport, Oregon	8.89	105	0.578	108	12.70	103	41.62	106	6.57	104	3.29	135	2.04	128	2.03	118	6.30	131	3.83	118	117.8
56/655c	Tidewater, Oregon	8.94	105	0.533	99	13.40	109	42.46	108	6.66	105	3.27	134	2.22	139	1.94	113	6.40	133	3.93	121	119.9
56/655d	Florence, Oregon	8.75	103	0.642	120	12.55	102	40.54	103	6.62	104	3.08	126	2.16	136	2.08	121	5.72	119	4.21	129	117.5
56/655a	North Bend, Oregon	9.01	106	0.635	118	13.55	110	40.66	104	6.69	105	3.14	128	1.87	117	1.97	115	6.07	126	4.04	124	116.4
<u>South Interior, BC</u>																						
56(4118)500	Inchnacardoch, ex Hat Creek	7.26	85	0.406	76	10.60	86	32.91	84	6.03	95	-	-	-	-	-	-	-	-	-	-	(88.7)
51/315	Shuswap Lake	-	-	-	-	-	-	-	-	(6.30)	(99)	2.04	83	1.15	72	1.25	73	4.02	84	2.10	65	(79.3)
<u>Oregon Cascades</u>																						
56/651	Oakridge	7.64	90	0.350	65	10.75	87	31.64	81	5.68	89	1.90	78	1.26	79	1.12	65	3.37	70	2.23	69	78.4
56/657	Sisters/La Pine	7.26	88	0.405	76	9.85	80	27.96	71	5.18	82	1.67	68	1.15	72	1.16	68	3.47	72	2.11	65	74.4
Standard error ±		0.30	-	0.023	-	0.38	-	1.53	-	0.08	-	-										
Differences significant at		**		***		***		***		***												

1961 Experiments

In 1961 three further experiments, using mainly the same origins as in 1958/59, were planted with the objectives of improving the range of site types covered (and thus giving local forest managers more reliable information on seed origin choice) and evaluating some newly acquired seedlots. The latter included one from Skagway, Alaska (to see whether it performed like those from nearby Haines in the 1954 experiments), one from Fort Fraser, about 80 miles west of Prince George, one from the Cypress Hills, Saskatchewan, the most easterly part of the range in Canada and one said to be from Bella Coola at the end of a long fjord (the Burke Channel). It was believed that trees from this area might have some intermediate characteristics between coastal and inland populations. Seed was obtained in 1958 and 1960 stated by the seed merchant to be from Bella Coola and although early performance was that of an inland type, it was several years before it was discovered that both lots had in fact been collected from near Anahim Lake, a place that is well beyond the crest of the Coast Range in the Central Interior Plateau at an elevation of 1220 m. The climate at Anahim Lake is much more continental, with less than 1000 mm annual precipitation, much of it as snow. Terpene analysis later confirmed that these seedlots were of the Central Interior of BC type.

The experiments were planted at Wark, Northumberland, on a *Calluna/Eriophorum* peat at 427 m above sea level; at Selm Muir, Midlothian, on a deep *Eriophorum* peat at 350 m; and on Rannoch Moor (Glencoe Forest) on deep *Calluna/Trichophorum* peat at 305 m. Results up to 6 years were reported by Lines and Mitchell (1968). They showed that height growth was fastest on the South Coastal group of seed origins, and while the home-collected provenance originally from the Queen Charlotte Islands was significantly taller than the one from Skagway, it was significantly shorter than the other North Coastal origin from Ladysmith. The Anahim Lake origin grew at about the same rate as the other Central Interior BC source from Fort Fraser.

Height growth at 10 years is shown in Table 31, with results similar to those at 6 years. There is little evidence of a large seed origin x site interaction. Growth in the Glencoe experiment was much faster than at the other sites, even allowing for the fact that the trees were one year older when assessed. Basal area per plot was also assessed at 11 years (data not shown). Seed origin differences were very highly significant and followed the same order as for height, except that Skagway was poorest for basal area, while the Oregon Cascades seedlot from Sisters/La Pine was poorest for height. A similar result was found in the Wark experiment at 23 years, where the Sisters/La Pine origin was poorest for height, but had a larger diameter than five other seedlots. As noted earlier, it is a characteristic of the sub-species *murrayana* that it has a relatively large diameter for its height. At Selm Muir the rank order for top height at 21 years was fairly close to that at Wark at 23 years. Apart from Skagway, all the coastal seed origins were taller than all the inland ones. Keyport, from the Puget Sound of Washington, was second tallest at 21 years, after being only fifth at 6 years. This origin had poor needle retention before canopy closure and probably benefited from mutual shelter after the tenth year. This experiment suffered considerable snow damage in January 1977. As this was worst on the most heavily crowned South Coastal origins, with up to 75% of the trees affected by either basal sweep, or heavy wet snow damage in some plots, it may have distorted the results from the surviving trees. The Glencoe experiment was also heavily damaged by wet snow in the winter of 1973/74. Long Beach, Newport and North Bend were the worst affected and this caused the experiment to be closed. Fort Fraser and Sisters/La Pine had negligible snow damage. The Wark experiment was severely damaged by snow and wind during the winter of 1978/79, this was again worst on the South Coastal origins (see Chapter 15), with the Oregon ones having greater damage than those from Washington. The North Coastal origins from Ladysmith and the Queen Charlotte Islands were not significantly damaged, while the inland origins (and Skagway) escaped damage, apart from occasional trees.

The general conclusions from this series of experiments are that although the South Coastal origins are outstandingly fast-growing and appear the most healthy and exposure resistant, their poor stem form and susceptibility to windthrow and damage by wet snow make them unacceptable for forest use. Ladysmith grew rather better in this series of experiments than in the 1958–59 series, though it is clearly not a good choice for exposed sites. The home-collected seedlot from the Queen Charlotte Islands grew rather slowly, but its straight stem

Table 31. Height and diameter in 1961 experiments at Glencoe 3, Selm Muir 1 and Wark 6

Identity number	Seed origin	10 year height (m)						Top height (m)				Mean diameter (cm)	
		Glencoe†		Selm Muir		Wark		Selm Muir		Wark		Wark	
		Actual	%	Actual	%	Actual	%	21 years	Height (%)	23 years	Height (%)	23 years	Diameter (%)
58(7987)2	Skagway, Alaska	2.66	89	1.42	73	1.30	85	6.06	91	5.70	91	8.44	86
55/227	QCI, ex Kirroughtree	2.65	88	1.85	94	1.30	85	6.86	103	6.04	96	8.78	89
56/658	Ladysmith, Vancouver Island	2.93	98	2.10	107	1.47	96	7.05	106	5.97	95	9.66	98
56/654	Long Beach, Washington	3.49	116	2.41	123	1.89	123	7.14	107	6.98	112	10.78	109
56/655b	Newport, Oregon	3.27	109	2.40	123	1.81	118	7.14	107	6.86	110	12.07	122
56/655a	North Bend, Oregon	3.45	115	2.54	130	1.98	129	7.43	111	6.70	107	12.72	129
56/655c	Tidewater, Oregon	–	–	2.41	123	1.92	125	7.28	109	6.71	107	11.61	118
56/656	Keyport, Washington	–	–	2.25	115	1.69	110	7.39	111	6.75	108	10.63	108
57(7113)1	Fort Fraser	2.99	100	1.68	86	1.39	90	6.24	93	6.21	99	8.58	87
58(7113)3	Anahim Lake	3.01	100	1.66	85	1.42	92	6.28	94	6.19	99	9.61	97
57(7124)	Cypress Hills, Saskatchewan	–	–	1.61	82	1.36	88	5.70	85	5.85	93	7.88	80
56/651	Oakridge, Oregon	–	–	1.79	91	1.39	90	6.60	99	5.72	91	8.65	88
56/657	Sisters/La Pine, Oregon	2.53	84	1.56	80	1.27	83	5.60	84	5.69	91	8.90	90
Standard error ±		0.12		0.06		0.05		0.17		0.20		0.45	
Differences significant at		***		***		***		***		***		***	

† Height at Glencoe measured at 11 years

form and excellent health on rather testing sites suggest that it would be a safe choice. None of the inland origins was particularly promising in terms of growth vigour or ability to retain a healthy crown; in fact by 23 years of age the Cypress Hills origin at Wark had become moribund, with severe needle browning and crown dieback, similar to that noted on the Albertan seedlot 26/58 at Kielder.

1963/1967 experiments

Further experiments in 1963–66 extended the range of sites on which the main groups of lodgepole pine were tested. They also tested the progeny from British stands that had grown well and included new origins not previously tested. The sites were mainly selected for their rigorous climatic or soil conditions, although the Achnashellach site was chosen so that performance of the new seed origins could be linked with three older experiments on adjacent ground. Langdale represented one of the most exposed areas on the plateau top of the North York Moors, at an elevation of 283 m. Lodgepole pine near to this experiment showed severe winter desiccation at the time of site selection. No phosphate was applied at planting, following local practice, but as early growth rate was very slow (the experiment mean height was only 0.36 m at 3 years) it was given rock phosphate at 42 g per plant after two seasons. Since there was little response to phosphate, it seems likely that the main cause of the initial slow growth was that the trees were planted by notching into the uncultivated moorland surface and not into the plough furrow or ridge. This local practice had developed with the aim of reducing basal sweep. This experiment also suffered heavily from *Neodiprion* attack during the fifth year. Because of continued slow growth, it was top dressed with NPK fertiliser (Shellstar Number 2 at 800 kg ha^{-1}) in 1971. In that year a heavy attack of *Zeiraphera* budmoth further restricted leader growth on many trees and rapid height growth did not start until canopy closed at about 10 years of age.

The Eddleston site is a deep basin peat (depth 2 m+) at 282 m, chosen mainly as a demonstration area close to the Northern Research Station and replicated only twice. It is moderately exposed. Early growth on this site was quite rapid, with consequent basal sweep developing on susceptible seed origins on this type of soft peat.

At Elibank in the Tweed Valley, the site chosen was at the upper planting limit at 454 m and thus severely exposed. The soil is very stony and some plants were injured at the root collar by rocking in strong winds. The exposure resistance of different seed origins was thoroughly tested on this site.

The Achnashellach site has been described in the section on the 1937–42 series. For the new experiment a single mouldboard tine plough was used, with hand turfing in wet patches. Phosphate was applied at 42 g per plant. This site enjoys a mild wet climate (2032 mm of rainfall) and is sheltered by surrounding hills. Early growth was quite rapid.

The site at Deer, Aberdeenshire, was again chosen for its testing nature, having been classed as 'unplantable' for normal afforestation. It lies at an elevation of 137 m on the northern side of Mormond Hill, an isolated quartzite mass projecting above the Buchan plain, with a thin impoverished soil full of quartz boulders, which made tine ploughing to a depth of 30 cm difficult. Exposure to the sea 6 miles away to the north is severe. Early growth was very slow due to the soil and climatic exposure, not helped by damage from grouse, hares and sheep.

Several of the seed origins included were already being tested in other experiments. The new origins were from Sooke at the southern tip of Vancouver Island; Nass River, which lies to the north of the Skeena River; Penticton, a very dry area at the south end of Okanagan Lake, BC; and Glacier, which lies at 300 m on the north side of Mount Baker, Washington.

Results shown in Table 32 include heights at 10 to 20 years, with actual heights used to calculate the percentage heights from each experiment mean. It will be seen that, as in earlier experiments, the South Coastal group were outstanding in height growth, while the North Coastal group were very erratic in performance. The home-collected provenance originally from the Queen Charlotte Islands was well above average in all four experiments, contrasting with the poor growth of the Langley and Sooke origins. Growth of trees from Sooke has been restricted on the exposed sites in this series of experiments due to winter-blast injury, whereas on more sheltered sites, growth rates have been fair. It is unfortunate that between 1956 and

Table 32. Height at 10–20 years at Langdale, Eddleston, Elibank, Achnashellach and Deer

Identity number	Seed origin	Langdale 100 P65			Eddleston 4 P66			Elibank 6 P63			Achnashellach 31 P64/65			Deer 4 P63			Overall height (%)
		Mean height 10 yrs	Mean height 16 yrs	Height (%) 16 yrs	Mean height 10 yrs	Mean diameter cm 20 yrs	Height (%) 10 yrs	Mean height 10 yrs	Mean height 15 yrs	Height (%) 15 yrs	Mean height 10 yrs	Mean height 15 yrs	Height (%) 15 yrs	Mean height 10 yrs	Mean height 20 yrs	Height (%) 20 yrs	
North Coastal																	
58(7987)2	Skagway	–	–	–	2.73	11.00	88	1.05	2.51	105	2.11	4.64	87	1.16	3.64	125	101
60(4138) 500	Kirroughtree ex QCI	1.78	3.80	110	–	–	–	0.94	2.51	105	2.66	5.66	106	1.02	3.18	109	108
53/627†	Langley, BC	1.53	3.17	91	3.07	10.24	98	0.74	1.92	80	2.55	5.24	98	0.80	2.47	85	90
58(7116)3	Sooke, Vancouver Is	1.58	3.34	96	3.07	10.74	98	0.71	1.91	80	2.19	4.44	83	0.85	2.76	95	90
South Coastal																	
57(7972)1	Long Beach, Washington	2.23	4.51	130	3.64	13.22	117	1.26	3.22	135	3.65	7.05	132	1.38	4.22	145	132
57(7951)	Newport, Oregon	2.71	5.18	149	3.57	12.96	114	–	–	–	–	–	–	–	–	–	(132)
Skeena River																	
62(7119)	Nass River, BC	1.59	3.35	97	3.26	12.27	104	–	–	–	2.40	–	–	–	–	–	(100)
60(4127)500	Loch Ard ex Hazelton	1.55	3.39	98	2.98	12.46	96	0.97	2.42	101	2.40	5.17	97	0.93	2.64	91	97
62(7114)1	Terrace, BC	1.57	3.44	99	3.23	12.37	104	–	–	–	2.53	–	–	–	–	–	(102)
Central Interior BC																	
60(4265)500	Wykeham ex 'North BC'	1.66	3.64	105	–	–	–	1.00	2.55	107	2.43	5.14	96	1.04	3.01	103	103
58(7113)3	Anahim Lake	1.56	3.43	99	2.72	12.22	87	0.92	2.42	101	2.24	4.87	91	1.00	3.06	105	97
59(7113)2	Quesnel	1.47	3.25	94	2.94	12.27	94	1.02	2.54	106	2.39	5.19	97	0.91	2.81	96	97
South Interior, BC																	
59(7118)2	Penticton	1.61	3.43	99	–	–	–	0.95	2.44	102	2.60	5.34	100	0.96	2.44	84	96
Washington Cascades																	
59(7974)1	Glacier	1.41	2.90	84	–	–	–	0.81	2.07	87	2.64	5.54	104	0.74	2.21	76	88
Standard error ±		0.11	0.20		n.a.	n.a.		0.06	0.11		0.10	0.20		0.05	0.14		
Differences significant at		***	***					***	***		***	***		***	***		

† At Langdale and Eddleston seedlot 55/694 from the same dealer was used.

n.a. = not analysed

1959, 829 kg of seed was bought from the Sooke area. The Skagway origin showed the reverse trend, with its best relative growth on the very exposed sites at Deer and Elibank and poorer percentage growth on the more sheltered Eddleston and Achnashellach sites. The Skeena origins showed average growth rates, with the Nass River seedlot having similar performance to those from the main Skeena River basin. In the Central Interior of BC group, the seedlot imported as 'North BC' was at first suspected as being from the Skeena River, until terpene analysis clearly showed its similarity to others from the Central Interior. Its performance in these experiments was above average, whereas Anahim Lake (mentioned above as a seedlot originally bought in the belief that it was from the coast) was slightly below the overall mean. This is another origin bought in bulk (372 kg in 1958 and 1960). The Southern Interior seedlot from Penticton is not from the Interior Wet Belt, recommended by Aldhous (1976), but from a hot, almost semi-desert climate and its performance in these experiments shows that it is ill-adapted to the harsh climate of upland Britain. The Glacier origin is from an area of Washington where lodgepole pine occurs only adventitiously as a coloniser of landslips, fire-sites, etc. Its terpene pattern is of the Puget Sound type (Forrest, 1980) and its poor performance, except at the relatively sheltered Achnashellach site, does not encourage wider use.

By the mid 1960s the success under very testing conditions of such Alaskan seed origins as Hollis and Skagway led to further experiments with seed origins from this region on two sites selected for their exposure and poor quality peat soils. These were at Shin, Sutherland and South Kintyre, Argyll. Table 33 shows the seed origins included and their performance. The replicated experiments included seven origins, while three others were present in unreplicated demonstration plots. The Alaskan seedlots comprise two from the outer islands (Sitka and the home-collected Hollis) and two from the mainland and inner islands (Juneau and Petersburg). The same Queen Charlotte Islands seedlot used in the 1963-66 experiments was also included. Two seedlots from Port Alberni, Vancouver Island, and Hope, about 80 miles up the Fraser River, were intended to test the performance of trees from these areas, about which little was known. Long Beach, Washington was at this time the 'standard' for this type of poor exposed site and acted as a control. The Irish seedlot from a good stand at Ballynoe was originally from the coast of Washington or Oregon. The Terrace seedlot was included in the hope that it would show better stem form than the more heavily branched coastal sources, although there was evidence that inland seed origins did not grow well on these kind of sites.

As will be seen from Table 33, growth in the first 6 years was rather poor on both sites, except for the South Coastal origins. At the South Kintyre site, animal damage from sheep and blackgame was an additional deleterious

Table 33. Height at 6–15 years at Shin 12 P67 and South Kintyre 1 P67

Seed origin	Identity number	6 year height (m)		15 year height (m)	10 year height (m)	Height % at 10 and 15 years	
		Shin	South Kintyre	Shin	South Kintyre	Shin	South Kintyre
Sitka, Alaska	63(7986)1	1.01	0.76	3.47	1.58	77	87
Juneau, Alaska	63(7987)1	(1.11)	(0.66)[†]	(4.02)	(1.58)	(89)	(87)
Petersburg, Alaska	63(7987)3	1.12	0.60	3.74	1.45	83	80
Hollis, Alaska ex Watten	63(4113)500	0.92	0.70	3.73	1.53	83	84
QCI ex Kirroughtree	60(4138)500	1.06	0.79	4.90	1.87	109	103
Port Alberni, Vancouver Island	62(7116)1	(1.13)	(1.00)	(3.78)	(2.14)	(84)	(118)
Hope, BC	63(7117)2	1.23	0.73	4.55	1.82	101	100
Long Beach, Washington	63(7972)1	1.69	1.26	6.27	2.50	139	138
Ballynoe, Eire	63(417)500	(1.89)	(1.08)	(6.02)	(2.50)	(134)	(138)
Terrace, Skeena River	62(7114)1	1.35	0.80	4.85	1.95	108	107
Standard error ±		0.06	0.04	0.21	0.09		
Differences significant at		***	***	***	***		

[†] Figures in parentheses from unreplicated large plots

factor to winter-browning of foliage, which affected all seed origins more or less equally. Adjacent Sitka spruce were more resistant to both forms of damage. After canopy closure, shoot growth improved markedly at both sites and, although a full 15-year assessment was not made at South Kintyre, the average heights there ranged from 3 m for Juneau to 4.5 m for Long Beach. There was little seed origin x site interaction.

The main results were that all the Alaskan seed origins grew at approximately the same rate and were also similar in appearance. Basal sweep was negligible and stem form was good, apart from rather heavy branch nodes. The Queen Charlotte Islands seedlot was significantly faster growing, but otherwise morphologically similar to the Alaskan lots. The 'Port Alberni' seedlot turned out to be untrue to name (as shown by terpene analysis) and consisted of a mixture of South Coastal and Interior BC seed with only a minority of trees of Vancouver Island type. The seedlot from Hope grew at about the average rate in each experiment and morphologically it was very similar to Lulu Island and Langley in older experiments. It had profuse male flowers and its terpene pattern (Forrest, 1980) was typical of the Vancouver group. The performance of the Long Beach origin was much as expected. It was by far the most vigorous, and the trees had dense crowns and dark green foliage. Because of relatively slow early growth, the amount of basal sweep was very low at South Kintyre. At Shin stem lean was more common than basal sweep, but by the 18th year wind and snow damage were beginning in one of the Long Beach plots and are likely to get worse. To date, the unreplicated Ballynoe plot has no windthrow or snow damage. The Terrace origin grew rather well on both sites, after looking rather thin in the crown before canopy closure, and its foliage was lighter green than the coastal origins. It had a little windsway, but in general its performance on height was very satisfactory and its stem form good. Bark fraying by deer was worst on this origin, probably due to the combination of thin bark and light branching (see Chapter 17).

These experiments both suffered severe winter-browning injury before canopy closure, but subsequently the degree of winter injury became minimal. This suggests that conditions can be so much improved after canopy closure that this kind of early damage (associated with water stress) is not critical in seed origin choice, except for those that are particularly susceptible, e.g. Lulu Island.

Chapter 12

Experiments with the Aldhous/Maxwell collection in 1969 and 1970/71

1969 experiments

The seed collection that resulted from the visit to north-west America by J.R. Aldhous and H.A. Maxwell in 1965 was not all available for sowing in 1967 (see Newton 6/67 in Chapter 7). Twenty-four seedlots were selected for this nursery trial to form the first phase of a much more comprehensive series of forest experiments. The main objectives were:

1. to extend the range of Alaskan seed origins;

2. to investigate differences within the Skeena/Bulkley River area; and

3. to test a new collection from the Mount Ida source, which had grown well in older trials.

Other origins from Vancouver Island, the South Coastal region and the Central and South Interior of British Columbia were also included.

Three contrasting sites were chosen; Rumster is a deep (6 m) poor quality peat with *Calluna/ Eriophorum/Trichophorum* vegetation on the exposed Caithness flats. Until the 1970s this site would have been considered unplantable. Glengarry is also a non-flushed oligotrophic deep (2 m) peat site with *Trichophorum/ Sphagnum* vegetation. It is at 91 m and fairly well sheltered by surrounding hills. Strathardle, at 244 m, is much more exposed, particularly to the north. The soil is an upland Brown Earth with dominant *Calluna* and a long history of moor-burning. The site is fertile enough for Sitka spruce, but in this area, spruce is prone to severe heather check. Adequate control by herbicides is difficult to achieve, as is shown in the adjacent stand of Sitka spruce, which at 15 years even after herbicide treatment was still appreciably shorter than the slowest-growing seed origins of lodgepole pine in this experiment.

Results

Survival averaged over 95% at all sites in the first year, but early growth rate was reduced by animal browsing during the first 2 years at Glengarry, by blackgame clipping of buds at Strathardle (55% of the plants damaged) and by blasting winds at Rumster. The plants that grew away most rapidly (the South Coastal group) suffered less browsing and consequent development of double stems, than the inherently slower-growing Alaskan sources, which remained susceptible to damage for a longer period. At Rumster the experiment was established on ground ploughed nearly 2 years earlier and the plants soon began to show nutrient deficiencies, which were corrected by a PK top-dressing in 1972. The severe exposure to blasting winds on this site affected the seed origins differentially (Lines, 1975). Those worst affected were Coombs, Vancouver Island and Shelton on the Puget Sound of Washington, while Bandon, the most southerly of the coastal Oregon sources, also suffered shoot dieback and foliage browning. By 15 years of age survival of the Coombs seedlot was down to 68%, with the survivors showing poor form. However, the experiment mean survival was still 93%, with only Bandon at 75% and Shelton at 82% significantly below average survival among the other origins.

The experiments were assessed for height at 3, 6, 10 and 15 years. The heights at 3 years (Lines *et al.*, 1972) may give a slightly misleading impression due to animal damage. At 15 years mean height was measured on all of the 30 trees per plot at Rumster and Glengarry; at Strathardle only the two trees of largest diameter per plot were measured for height, thus inflating the mean height for the site. To achieve greater uniformity when comparing results across all three sites, the 10-year mean height data were used (see Table 34). The seed origins have been grouped using the seven

Table 34. Mean height (m) at 10 years at Rumster 4, Glengarry 14 and Strathardle 4 with origins arranged by terpene regions

Identity number	Seed origin	Rumster	Glengarry	Strathardle	Overall mean
North Coastal					
65(7986) 1	Sitka, Alaska	2.5	3.0	2.5	2.7
65(7987) 1	Juneau, Alaska	2.6	2.9	2.4	2.6
66(7987) 3	Petersburg, Alaska	2.5	3.2	2.5	2.7
65(7987) 4	Ketchikan, Alaska	2.6	3.2	2.6	2.8
67(4113) 500	Hollis, Alaska ex Watten	2.7	3.2	2.8	2.9
65(7116) 6	Tofino, Vancouver Island	2.8	4.1	(3.6)	3.5
Region means		2.6	3.3	2.7	2.9
Vancouver area					
65(7116) 7	Coombs, Vancouver Island	2.4	4.5	4.1	3.7
Puget Sound					
65(7973) 2	Shelton, Washington	2.8	4.3	3.9	3.7
South Coastal					
65(7972) 1	Long Beach, Washington	3.2	4.7	4.5	4.1
65(7951) 5H	Tillamook, Oregon	3.2	4.5	4.3	4.0
65(7951) 1	Waldport, Oregon	3.5	4.7	4.5	4.2
65(7952) 5	Bandon, Oregon	3.0	4.5	4.0	3.8
Region means		3.2	4.6	4.3	4.0
Skeena/Bulkley					
65(7114) 1	Terrace, Skeena River	3.0	4.0	3.8	3.6
65(7114) 3	Hazelton, Skeena River	2.8	3.6	3.7	3.4
65(7114) 7	Kitwanga, Skeena River	3.0	3.7	3.8	3.5
65(7114) 8	Kispiox, Skeena River	3.1	3.5	3.6	3.4
65(7114) 9	Cedarvale, Skeena River	3.2	3.8	3.6	3.5
65(7114) 15	Bulkley Canyon, Bulkley River	2.9	3.9	3.7	3.5
65(7114) 4	Moricetown, Bulkley River	2.7	3.8	3.6	3.4
65(7114) 13	Smithers, Bulkley River	3.0	3.7	3.6	3.4
Region means		3.0	3.8	3.7	3.5
Central Interior BC					
65(7113) 2B	Quesnel	3.0	3.5	3.4	3.3
65(7113) 10	Burns Lake	2.8	3.4	3.6	3.2
Region means		2.9	3.4	3.5	3.3
Souther Interior BC					
65(7118) 5A	Falkland	2.9	4.0	3.9	3.6
65(7118) 4	Mount Ida	3.0	3.8	3.7	3.5
Region means		3.0	3.9	3.8	3.6
Site mean		2.9	3.8	3.6	3.4

	Standard error of mean	Least significant difference at 5%	1%	0.1%
Origins	0.06	0.16	0.22	0.27
Sites	0.02	0.06	0.08	0.10

terpene regions of Forrest (1980) as this produces a biologically meaningful division in terms of their forest performance. The Tofino seed origin was not included in the Strathardle experiment because of plant shortages, and missing data were calculated by standard statistical methods.

Each experiment was first analysed individually; for all sites, at all ages from 3 to 15 years the seed origin differences were very highly significant (***). A combined analysis across the three sites at 10 years gave the following results:

1. variation between:

   - seed origins;
   - sites;
   - origin x site interaction;
   - replicates within sites;
   - seed origin regions;

   were all very highly significant (***);

2. only the North Coastal region showed significant (*) differences among origins within regions;

3. by far the largest amount of variation was accounted for by differences between the seed regions.

The performance of origins from the different seed regions was very similar at Glengarry and Strathardle, with identical rank order, but this contrasted with the very different results at Rumster. At the latter site the Coombs, Vancouver region origin grew so poorly that it was surpassed by the Alaskan group and ranked only seventh, whereas it was second in rank at Glengarry and Strathardle. The Alaskan origins grew relatively fast at Rumster, achieving 90% of the experiment mean height, while they were only 84% and 72% of the experiment means at Glengarry and Strathardle. Even though the South Coastal region had the greatest height at 10 years at all sites, it was only slightly better than most other groups of origins at Rumster and this was shown even more clearly during the establishment phase. At the sixth-year assessment, the South Coastal group regional mean was only 104% of the mean at Rumster, compared with 129% and 122% of the means at Glengarry and Strathardle. The Shelton, Puget Sound origin also grew much more slowly at Rumster than at the other sites. Conversely, the Southern Interior region ranked second at Rumster and fourth at the other sites, while the Skeena River group also performed relatively better at Rumster. Seed origin x site interaction is considered in more detail later in this chapter.

As noted above, the amount of variation between individual seed origins within a regional group was not significant, except for the Tofino seedlot in the North Coastal region, whose performance was outstanding at both Rumster and Glengarry. Tofino lies more than 6° of latitude further south than the Alaskan origins. Among the South Coastal origins, Bandon was consistently poor in height. The Skeena/Bulkley River origins were rather uniform in performance, with Terrace, which is closest to oceanic influence, the tallest.

Diameter growth at 15 years in the Strathardle experiment was highly correlated with height growth and gave even higher levels of statistical significance. The home collected provenance, originally from Hollis, Alaska, had a significantly higher mean diameter than the other Alaskan origins, while in the South Coastal group, Long Beach was poorest for diameter, though the tallest for height. Diameter variation within all other groups was non-significant.

The practical conclusions to be drawn from these results are that although the South Coastal origins were outstanding for vigour, their susceptibility to damage by snow and wind are so suspect from results in older experiments that it would be unwise to use them, except in exceptional circumstances. Snow damage had already started in these origins at Strathardle by 13 years and an assessment in November 1982 showed that it was confined to this group. No damage occurred in the fast-growing, but less heavily crowned, Shelton or Coombs origins. In the other experiments all trees were still standing at 15 years, though some basal sweep or lean affected many trees in the South Coastal group. There was enough winter-cold damage in the early years to act as a warning against using the Oregon coastal sources on exposed far northern sites, such as the Caithness moorlands, even if the problems of windfirmness were ignored. This applied even more strongly to the Coombs and Shelton origins, which were severely damaged over-winter at Rumster, but which grew well on the Glengarry and Strathardle sites. The best origins from the Skeena/Bulkley region grew at about average rate or above on all three sites and combined good stem form with adequate foliage retention, even on the severe Rumster site. Those from the Central Interior of BC were the slowest-growing of the inland regions, though stem form was good. The South Interior of BC origins grew quite fast and, rather surprisingly, ranked second for height on the exposed Rumster site at both 10 and 15 years, in view of the fact that their crowns tended to be less dense than the best Skeena River ones. Most of the Alaskan origins in the North Coastal group grew too slowly to be of practical value as pure plantations, though this inherently slow growth rate is a positive advantage in intimate mixtures with Sitka spruce. However, the Tofino seedlot grew significantly faster than the mean of this group, and could certainly be considered as a safe choice for a wide range of poor sites; its height at Glengarry exceeded that of any inland origin.

1970/71 experiments

As noted in Chapter 7, origins from the 1965 seed collection were grown as 1+1 transplants at two nurseries in England and two in Scotland. The planning of the forest stage was carefully designed to cover a wide range of site types throughout Britain, so that any seed origin x environment interaction would be revealed and any seed origins that were insufficiently hardy for wide-scale use would be eliminated.

Thirteen sites were selected (Table 4). An additional aspect was that on seven sites the design incorporated species comparisons with either Sitka spruce or Scots and Corsican pines randomised into the design.

In Scotland and northern England the numbers of plants available varied so much that it was decided to allocate the seed origins selectively, so that on the drier heathland sites the interior origins were more fully represented, while on the wetter northern peats a higher proportion of coastal origins were included, while still keeping a range of seed origins common to all sites. In Wales, south-west England and east England the same 72 origins were used in three replicates of small plots and two replicates of larger ones, except at Thetford where only small plots were used.

Table 4 shows that these experiments cover a wide range of latitudes from 58° 15′ N at Rumster to 51° N at Brendon, and a range of elevation from 12 m at Mabie to 396 m at Tywi. Rainfall varies from 600 mm per annum at Thetford to 1905 mm at Glengarry and Beddgelert.

Various experimental designs were used, including randomised blocks, balanced lattices and partially balanced incomplete blocks. In most cases, little gain in precision was found from using the more complex designs (several of which were compromised by incorrect layout) and for the most part the data were analysed using simple randomised blocks.

The 86 seed origins involved include those already used in the 1969 series, but the larger numbers permit more intensive scrutiny of variation within a seed origin region. For example, instead of only two seed origins in the South Interior of BC group in the 1969 experiments, in the Mabie experiment 18 seedlots can be compared from this region. Although most of the collections were made through commercial seed merchants, no cases have been found where the stated origin is incorrect. Terpene patterns determined for 70 of these seedlots (Forrest, 1980) provided further evidence for their authenticity.

Results

The establishment of this series of experiments was generally very successful, with survival exceeding 95% in most experiments. On some sites, the Mendocino, California, origin, which was tallest at planting, had the poorest survival. This was particularly low at the northern experiment Shin 25. Early foliage browning was also noted on the Coombs, Vancouver Island seedlot and animal browsing had a slight effect in a few experiments. The South Coastal group of origins grew poorly for the first 3 years at Rumster, just as these had a poor start in the 1969 experiment at this forest. Results for the Shin and Rosarie experiments at 3 years were published by Lines (1976a) and a general summary of height growth at 6 years by seed regions for 13 sites (including the 1969 series) was also reported (Lines, 1977). Height growth at 10 years for the regional groups of origins on 12 sites showed that regional means varied from 80% of the overall mean for origins from the Washington Cascades, to 116% for those from the South Coastal region (Lines, 1985). These last two reports bring together sets of seed origins that differ between sites, and the 6-year data were analysed using a programme in which a great many missing values had to be calculated. The expanding evidence of far greater variation between regional groups than within groups provides some justification for using such a method to examine the pattern of growth between the different regions. However, in an analysis across sites that is looking specifically at seed origin x site interaction, it is preferable to adopt a more conservative method using a smaller number of seed origins, which are well represented across a smaller number of sites to give more reliable results.

Mean heights were assessed at 6 and 10 years in most experiments. However, at 15 years due to the pressure of work on field staff, the experiments at Glengarry and Beddgelert were assessed at 16 and 14 years respectively. Also, while the majority of experiments were given 100% height assessment at 15 years, those at Broxa and Glentrool were assessed on a smaller sample of the trees of largest diameter per plot. As a result, although the relative differences between the seed origins in these experiments remain perfectly valid, for the purposes of statistical comparison across sites in this Paper it was preferable to restrict consideration to the 10-year height assessment. Nine experiments contain the 58 seed origins selected, with only a small number of missing values. Table 35 shows the mean heights in these experiments, which cover the whole of the latitudinal range in Britain. The seed origins have been arranged in the same terpene regional groups as for the 1969 experiments (Table 34).

The analysis of variance across sites (Table 36) shows that height differences between origins, sites, origin x site interaction, replications within sites and seed region means were all very highly significant (***).

Analysis of height responses

The height data are examined first as they are presented in Tables 35 and 37 and origin x site interactions discussed later.

As expected, the South Coastal group were oustanding for height on all sites, and while the most southerly one from Bandon was poorest on seven out of the nine sites, it was not significantly shorter than the others from this region. Coombs was the sole representative from the Vancouver region. It ranked second and its performance was very similar to those from the Puget Sound. The two Puget Sound origins differed at the 5% level of significance, with Shelton poorer than Rainier on seven sites. The South Interior of BC region ranked fourth. There were highly significant differences within this group, the tallest being from Mount Ida and the nearby Charcoal Creek. The shortest were Esperon Lake and Steavens Meadow (both from high elevation sites), and 100 Mile House from the Caribou Parklands, a much drier region. These results confirm the opinion of Aldhous (1976) that it is best to choose origins from the relatively restricted 'Interior Wet Belt' within this large region. The seed origin from Clearwater, which was the tallest from this group at the nursery stage and still second tallest at 6 years, had fallen to seventh place by the tenth year and ranked eighth at 15 years.

The Skeena region came fifth for overall height and proved to be very uniform in performance. The difference between the tallest seedlot (Terrace) and the shortest (Smithers – high elevation) was not statistically significant.

The Mendocino, California, origin performed very erratically (see below) with an overall mean height far lower than the most southerly Oregon Coastal origin. It ranked second at 6 years, sixth at 10 years and seventh at 15 years. Its nursery height as a 1+1 transplant was outstanding (see Table 11), exceeding the next tallest seed origin by a clear 2 cm, thus showing how dangerous it would be to make decisions on suitability of origins for wide-scale use too early.

The Central Interior of BC group had a mean height slightly below the experiment mean and showed little variation in vigour between the 13 origins. The tallest was from Vanderhoof on the Nechako River and the shortest from Germansen Lake, the most northerly origin in this region included for group analysis.

The North Coastal group share very similar terpene patterns, though the Alaskan origins formed a uniform group with slow growth rate, while the Masset, Queen Charlotte Islands origin was very significantly taller.

The two Washington Cascades origins grew slower than any Alaskan origin and with no significant difference between them, while the two from East of the Rocky Mountains showed large differences. The Cypress Hills seedlot was significantly taller than that from Crowsnest in the Alberta Rocky Mountain foothills. The latter was from the highest elevation (1635 m) of any seedlot in this series, which perhaps explains its exceedingly slow growth.

Table 35. Mean height (m) 10 years after planting of 58 origins at nine sites

	Mabi	Shin	Rums	GlGa	Rosa	GlTr	Brox	Bren	Tywi	Mean
North Coastal										
1 Gustavus	3.5	2.6	2.7	3.6	3.4	3.6	3.1	2.1	2.6	3.1
2 Sitka	3.1	2.4	2.3	3.6	3.2	3.4	3.0	1.9	3.0	2.9
3 Petersburg	3.7	2.4	3.0	3.7	3.0	3.6	2.7	2.1	3.2	3.1
4 Ketchikan	3.5	2.3	2.9	3.5	3.4	3.6	3.1	1.8	2.9	3.0
5 Annette Island	3.2	2.6	2.7	3.6	3.1	3.5	2.6	1.8	3.0	2.9
6 Masset	4.2	2.9	3.0	3.7	3.5	4.1	3.2	2.0	3.5	3.4
Region means	3.5	2.5	2.8	3.6	3.3	3.6	3.0	2.0	3.0	3.1
Vancouver Area										
7 Coombs	5.0	3.0	2.5	4.2	4.4	4.5	4.0	2.4	4.0	3.9
Region means	5.0	3.0	2.5	4.2	4.4	4.5	4.0	2.4	4.0	3.9
Puget Sound										
8 Shelton	4.6	2.9	2.7	4.0	4.0	4.5	3.7	2.9	3.7	3.7
9 Rainier	4.9	3.0	2.6	4.9	4.4	4.7	4.1	2.8	3.9	4.0
Region means	4.8	2.9	2.7	4.4	4.2	4.6	3.9	2.9	3.8	3.9
South Coastal										
10 Long Beach	5.3	3.5	3.3	4.3	4.6	5.1	4.6	3.3	4.2	4.3
11 Warrenton	5.3	3.9	3.3	4.6	4.5	5.1	4.3	3.3	4.4	4.3
12 Newport, Waldport	5.1	4.1	3.3	4.6	4.5	5.1	4.2	3.4	3.9	4.3
13 Newport	5.2	4.0	3.2	4.7	4.6	4.9	4.5	3.4	4.5	4.4
14 Bandon	5.1	3.3	3.0	4.3	4.4	5.0	4.1	3.1	4.5	4.1
Region means	5.2	3.8	3.2	4.5	4.5	5.0	4.3	3.3	4.3	4.3
California										
15 Mendocino	4.6	1.5	2.9	2.8	3.9	4.1	4.4	3.2	3.5	3.5
Region means	4.6	1.5	2.9	2.8	3.9	4.1	4.4	3.2	3.5	3.5
Skeena/Bulkley										
16 Kispiox 305 m	4.3	3.2	2.8	3.9	3.6	4.1	3.4	2.4	3.5	3.5
17 Kispiox 460 m	4.4	3.1	3.0	4.3	3.7	4.2	3.4	2.4	3.5	3.6
18 Skeena Crossing	4.4	3.2	2.8	4.0	3.8	4.2	3.5	2.5	3.6	3.6
19 Kitwanga	4.3	3.1	2.9	4.0	4.0	4.2	3.5	2.2	3.7	3.6
20 Cedarvale	4.4	3.1	3.2	4.0	3.8	4.3	3.5	2.4	3.6	3.6
21 Terrace	4.4	3.4	2.9	3.8	3.8	4.4	3.7	2.6	3.6	3.7
22 Babine	4.2	3.1	3.3	4.0	3.7	4.6	3.4	2.3	3.6	3.6
23 Bulkley Canyon	4.2	3.1	3.0	4.0	4.0	4.2	3.5	2.4	3.6	3.6
24 Smithers 610 m	4.3	3.1	3.1	4.0	3.8	4.2	3.7	2.4	3.6	3.6
25 Smithers 760 m	4.2	3.0	3.1	3.9	3.7	4.2	3.4	2.2	3.6	3.5
26 Smithers 915 m	4.2	2.2	2.9	3.9	3.6	3.9	3.5	2.4	3.5	3.5
27 Smithers 1065 m	4.1	2.9	3.0	3.8	3.6	3.8	3.5	2.3	3.3	3.4
28 Telkwa	4.2	3.3	2.9	3.9	3.9	4.2	3.5	2.3	3.5	3.6
Region means	4.3	3.1	3.0	4.0	3.8	4.2	3.5	2.4	3.6	3.6
Central Interior										
29 Germansen Lake	3.7	2.9	3.1	3.7	3.5	3.6	3.3	1.9	3.2	3.3
30 Pendleton Bay	4.0	2.8	3.0	3.8	3.6	4.0	3.3	2.0	3.4	3.4
31 Topley	3.9	2.8	2.9	3.8	3.7	4.0	3.4	2.3	3.2	3.4
32 Fort St James	4.2	2.9	3.0	3.9	3.8	4.2	3.4	2.2	3.4	3.5
33 Burns Lake 760 m	3.9	2.7	2.7	3.7	3.4	3.9	3.5	2.3	3.4	3.3
34 Burns Lake 915 m	3.7	2.7	2.7	3.9	3.3	3.8	3.5	2.3	3.1	3.3
35 Fraser Lake	4.0	2.9	2.9	3.8	3.8	4.1	3.2	2.6	3.4	3.5
36 Vanderhoof	4.2	3.5	2.8	4.0	4.0	4.1	3.5	2.4	3.4	3.6
37 Wistaria	3.9	3.3	2.8	3.8	3.7	4.0	3.5	2.1	3.4	3.4
38 Takysie	4.0	2.8	3.0	3.8	3.6	4.0	3.4	2.2	3.3	3.4
39 Anahim Lake	3.9	2.7	2.8	3.9	3.5	3.8	3.3	2.2	3.0	3.3
40 Pr George 915 m	4.1	3.3	3.0	3.9	3.9	4.1	3.6	2.4	3.5	3.6
41 Barkerville Road	4.2	3.3	2.9	3.5	3.8	4.2	3.6	2.6	3.6	3.5
Region means	4.0	3.0	2.9	3.8	3.7	4.0	3.4	2.3	3.3	3.4

Table 35 (contd)

	Mabi	Shin	Rums	GlGa	Rosa	GlTr	Brox	Bren	Tywi	Mean
South Interior										
42 100 Mile House	4.3	3.2	2.7	4.0	4.0	4.2	3.7	2.2	3.4	3.6
43 Clearwater	4.5	2.6	2.9	4.2	4.1	4.3	3.9	2.5	3.9	3.7
44 Chase Creek	4.3	3.6	3.0	4.0	4.2	4.4	3.9	2.3	3.8	3.8
45 Salmon Arm	4.3	3.2	3.1	4.1	4.3	4.1	3.8	2.2	3.7	3.7
46 Mount Ida	4.5	3.3	2.8	4.4	4.3	4.6	3.8	2.7	3.7	3.8
47 Harper Lake	4.3	3.2	3.2	4.1	4.0	4.3	3.9	2.2	3.5	3.7
48 Charcoal Cr. 915 m	4.4	3.3	3.1	4.3	4.0	4.4	3.8	2.6	3.6	3.8
49 Charcoal Cr. 1220 m	4.5	3.2	3.2	4.1	4.3	4.5	3.9	2.5	3.6	3.8
50 Steavens Meadow	3.9	3.0	2.9	4.0	4.1	4.1	3.6	2.2	3.3	3.5
51 Tunkwa	4.4	3.2	3.3	4.1	3.8	4.2	3.7	2.6	3.5	3.7
52 Falkland 760–915 m	4.3	3.5	3.2	4.2	4.0	4.5	4.0	2.4	3.9	3.8
53 Esperon	3.8	2.7	3.1	3.7	3.6	3.8	3.2	2.0	3.1	3.3
54 Terrace Creek	4.2	3.2	3.0	4.1	3.9	4.3	3.8	2.5	3.4	3.7
Region means	4.3	3.2	3.0	4.1	4.0	4.3	3.8	2.4	3.6	3.7
East of Rockies										
55 Crowsnest	3.1	1.9	2.1	3.1	3.1	3.0	2.7	1.6	2.5	2.6
56 Cypress Hills	3.3	2.3	2.7	3.4	3.2	3.4	2.9	2.2	2.7	2.9
Region means	3.2	2.1	2.4	3.2	3.2	3.2	2.8	1.9	2.6	2.8
Washington Cascades										
57 Bird Creek	3.5	2.5	2.2	3.1	3.1	3.3	2.8	1.8	2.7	2.8
58 Peterson Prairie	3.3	2.0	2.6	2.9	3.2	3.3	2.9	2.0	2.8	2.8
Region means	3.4	2.3	2.4	3.0	3.1	3.3	2.9	1.9	2.8	2.8
Overall mean	4.2	3.0	2.9	3.9	3.8	4.1	3.6	2.4	3.5	3.5

Key to sites: Mabi = Mabie, Shin = Shin, Rums = Rumster, GlGa = Glengarry
Rosa = Rosarie, GlTr = Glentrool, Brox = Broxa, Bren = Brendon
Tywi = Tywi

Table 36. Analysis of variance across nine sites

Source	Degrees of freedom	Mean square	Differences significant at:
Seed origins	57	4.5324	***
Sites	8	75.2192	***
Origin x site interaction	335	0.2317	***
Replicates within sites	24	0.7310	***
Replicates x origins within sites	1048	0.0562	
Total for plot means	1472		

The breakdown of the differences within regions is shown in Table 37.

Table 37. Regional mean heights (m) and significance of differences within regions

Seed region	Mean height	Number of origins	Standard error±	Rank	Differences among origins within regions significant at:
North Coastal	3.08	6	0.017	8	***
Vancouver	3.86	1	0.041	2	n.s.
Puget Sound	3.86	2	0.029	3	*
South Coastal	4.29	5	0.018	1	n.s.
California Coast	3.50	1	0.041	6	n.s.
Skeena/Bulkley	3.57	13	0.114	5	n.s.
Central Interior BC	3.41	13	0.114	7	*
South Interior BC	3.68	13	0.114	4	**
East of Rocky Mts	2.77	2	0.029	10	**
Washington Cascades	2.83	2	0.029	9	n.s.
Overall	3.49	58			

Analysis of origin x site interactions

A regression analysis used in this series of experiments was similar to that developed by Finlay and Wilkinson (1963). The method uses the mean height of all seed origins at a site as an index of the total environmental conditions at that site. The regression of individual origin performance on this site index across all sites is then used to show the overall response to site potential and the consistency of each origin. The object of the analysis is to provide three aspects of the performance of each seed origin in relation to its growth on a range of different sites. These are:

1. its overall *mean height;*
2. its *response* to an increasing trend in site conditions, e.g. higher fertility, a longer growing season, or greater shelter; and
3. its *consistency* in growth performance (note that in mathematical terminology, 'stability' is a better expression than 'consistency', but the latter term is used here to avoid confusion with its mechanical stability against wind or snow).

Response

The regression analysis shows the overall mean height (already given in Table 35) and the regression coefficient or response. The results are shown in Table 38. Origins that had an average response were rated 1.0, those with a higher or lower response being rated above or below this figure. Those with a higher response show better relative growth on the higher quality sites, while those with a lower response show their best relative growth on the poorer sites. All the regression coefficients were very highly significant (***), except that for Mendocino, which was not significant. The general conclusion was that the highly significant differences among the regression slopes do explain origin x site interaction, but that significant deviations about the regression lines remain. Figure 13 illustrates the regression slopes for three origins. Coombs has a high regression coefficient (1.526) or response. Its performance contrasts with that of Smithers, 65(7114)13, which has a near average response (regression coefficient 0.996). Note that on the better sites Coombs was much taller than Smithers, whereas on the three poorest sites, Coombs was shorter than Smithers. The regression line for Mendocino was non-significant and its wide scatter of points will be discussed below.

If the overall origin mean heights at 10 years are plotted against the regression coefficients (Figure 14) a clear pattern emerges of the relationship between mean height of the different origins and their interaction with site quality. In general, the origins formed a natural grouping into the seed origin regions and their performance will now be discussed region by region.

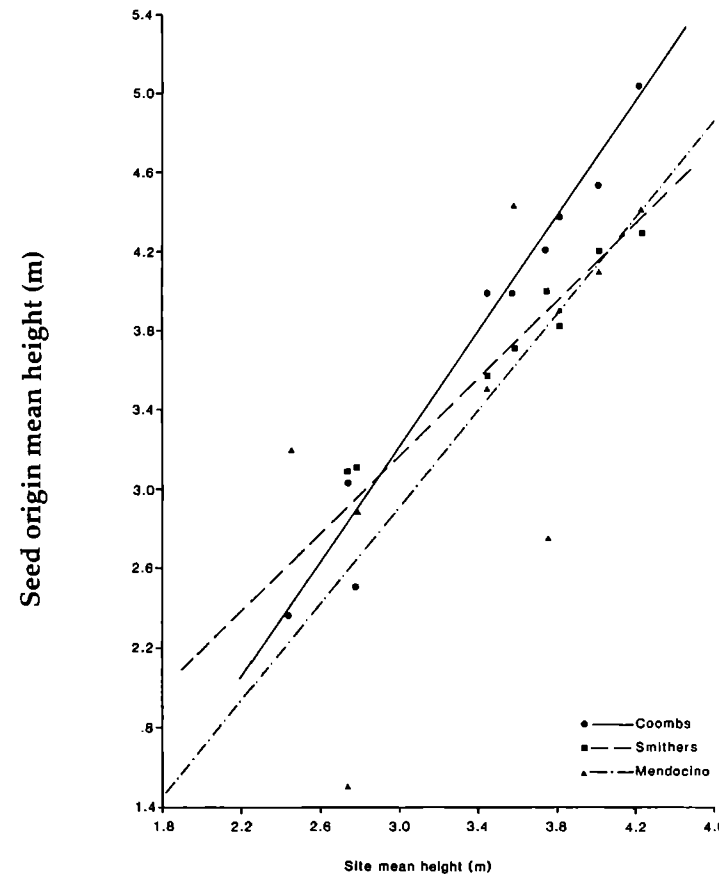

Figure 13. Regression of seed origin height on site mean height for Coombs, Smithers and Medocino at 10 years.

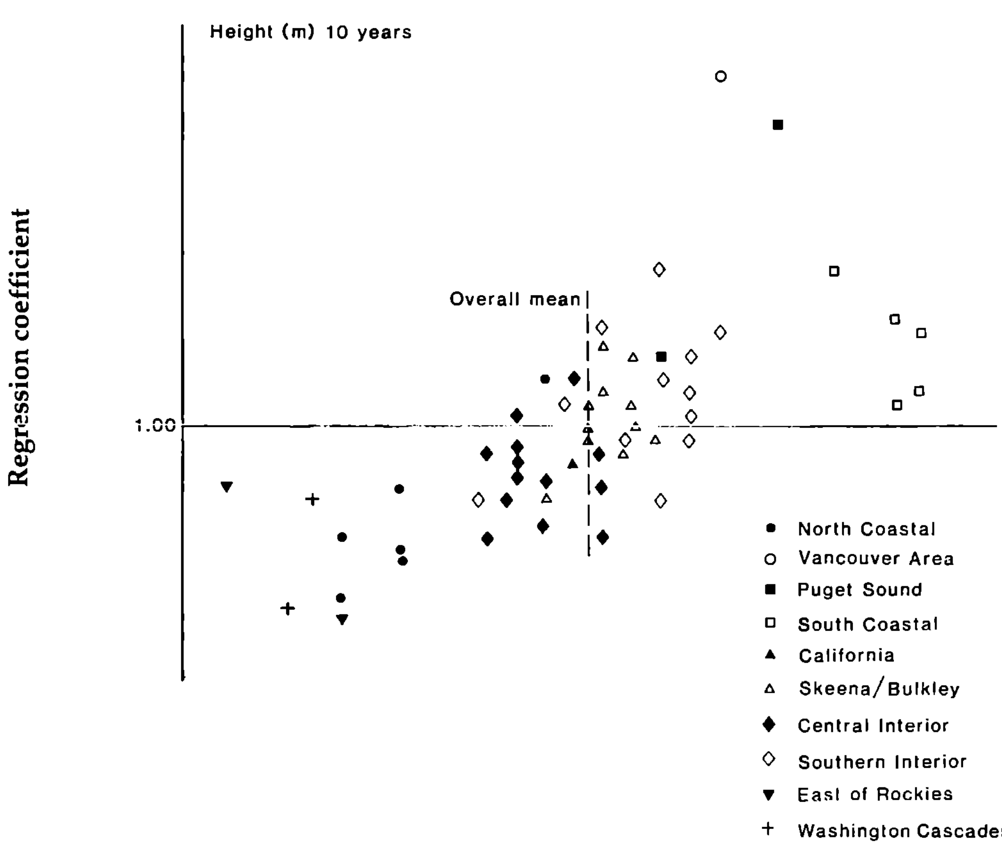

Figure 14. Scatter diagram relating overall origin mean height at 10 years and regression coefficient.

Table 38. Response and consistency of 58 seed origins from analysis across sites at 10 years

Identity number	Origin	Response Regression coefficient	Consistency Residual
North Coastal			
(7987) 100	Glacier Bay	0.816	0.130*
(7986) 1	Sitka	0.833	0.160**
(7987) 3	Petersburg	0.804	0.320***
(7987) 4	Ketchikan	0.908	0.189**
(7987) 5	Annette Island	0.754	0.244***
(7111) 1	Masset	1.076	0.109
Vancouver			
(7116) 7	Coombs	1.526	0.242***
Puget Sound			
(7973) 2	Shelton	1.111	0.231***
(7975) 2A	Rainier	1.454	0.360***
South Coastal			
(7972) 1	Long Beach	1.157	0.282***
(7951) 4	Warrenton	1.142	0.177**
(7951) 1	Waldport	1.029	0.240***
(7951) 1H	Newport	1.064	0.269***
(7952) 5	Bandon	1.244	0.305***
California Coast			
(7948) 100	Mendocino	0.941	2.515***
Skeena/Bulkley			
(7114) 8	Kispiox, 305 m	0.993	0.067
(7114) 8A	Kispiox, 457 m	1.112	0.116*
(7114) 5	Skeena Crossing	1.060	0.053
(7114) 7	Kitwanga	1.128	0.038
(7114) 9	Cedarvale	1.041	0.050
(7114) 1	Terrace	0.981	0.098
(7114) 12	Babine	0.992	0.162**
(7114) 15	Bulkley Canyon	0.987	0.022
(7114) 13	Smithers, 610 m	0.996	0.020
(7114) 13A	Smithers, 762 m	1.034	0.064
(7114) 13B	Smithers, 914 m	0.974	0.034
(7114) 13C	Smithers, 1067 m	0.890	0.050
(7114) 2	Telkwa	0.968	0.047
Central Interior of BC			
(7113) 11	Germansen Lake	0.833	0.148*
(7113) 6	Pendleton Bay	1.024	0.067
(7113) 12	Topley	0.935	0.023
(7113) 1	Fort Fraser	1.077	0.025
(7113) 10	Burns Lake, 762 m	0.938	0.040
(7113) 10A	Burns Lake, 914 m	0.894	0.146*
(7113) 1A	Fraser Lake	0.847	0.080
(7113) 5	Vanderhoof	0.970	0.166**
(7113) 9	Wistaria	0.917	0.106
(7113) 17	Takysie	0.956	0.026
(7113) 3	Anahim Lake	0.956	0.077
(7113) 4B	Prince George	0.908	0.030
(7113) 2A	Barkerville Road	0.840	0.102
South Interior of BC			
(7118) 8	100 Mile House	1.139	0.062
(7118) 6	Clearwater	1.231	0.167**
(7118) 1A	Chase Creek	1.063	0.167**
(7118) 4A	Salmon Arm	1.079	0.134*
(7118) 4	Mount Ida	1.152	0.135*
(7118) 1D	Harper Lake	1.065	0.081
(7118) 5B	Charcoal Creek, 914 m	1.026	0.034
(7118) 5C	Charcoal Creek, 1067 m	1.113	0.042
(7118) 9A	Steavens Meadow	1.040	0.108
(7118) 3	Tunkwa Lake	0.885	0.045
(7118) 5A	Falkland	0.981	0.094
(7118) 100	Esperon Lake	0.896	0.103
(7118) 102	Terrace Creek	0.980	0.045
East of Rocky Mountains			
(7123) 100	Crowsnest	0.905	0.106
(7124) 100	Cypress Hills	0.715	0.097
Washington Cascades			
(7976) 6	Bird Creek	0.899	0.037
(7976) 5	Petersen Prairie	0.720	0.146*

Overall there is a broad pattern of response (regression coefficient) increasing with tree height. This was also true for the regression analysis for height at 6 and 15 years and has been observed for both Sitka spruce (Lines, 1987b) and for Douglas fir (Lines and Samuel, 1987). What is perhaps unusual for lodgepole pine is that origins in the South Coastal region had a relatively low response for their height (only Bandon was greater than 1.157), i.e. they were able to grow fast on both poor and good sites. By contrast, in the Puget Sound regional group, Rainier had an exceptionally high response (1.454) and was not far behind the South Coastal group in mean height, whereas Shelton had a markedly lower response (1.111) and its mean height was only marginally better than the mean of the South Interior of BC group. Rainier grew poorly on the testing northern sites at Shin and Rumster, particularly the latter, where it was well below the experiment mean, whereas on the more sheltered Glengarry site it achieved 129% of the experiment mean height. Coombs in the Vancouver region had the highest response of all (1.526) and behaved in a similar manner to Rainier. Its performance across the range of sites is shown in Figure 13. It is typical of other seed origins from this area, which are very responsive to good sites and perform badly on poor quality exposed sites. The South Interior of BC region is represented by 13 origins, forming a fairly compact group that follow the broad pattern of increasing response with greater mean height. However, they show important differences in response within the region. Thus, Clearwater had the highest response (1.231) while Tunkwa Lake was well below average (0.885) in response, yet both had very similar mean height overall. At the testing Shin and Rumster sites, Clearwater was only 81% and 94% of the regional mean, whereas Tunkwa Lake was taller than Clearwater at Rumster. It was not present at Shin and did not grow so fast as Clearwater on the better sites at Mabie and Glentrool. There was a tendency for low elevation origins to have a high response, whereas the two highest elevation sources had a low response.

The Skeena/Bulkley river region also has 13 origins, which form an even more compact group in the scatter diagram than the South Interior of BC group. Their response varied only between 1.128 for Kitwanga and 0.890 for the highest elevation Smithers origin. The scatter diagrams for height at 6 years and 15 years (not included) also show a similar compact grouping.

The Mendocino origin appears in Figure 14 about halfway between the South Coastal and North Coastal groups. As noted above, its regression coefficient was the only non-significant one out of 58 origins, probably because of the wide scatter. This origin is unique in not only growing poorly on the northern site at Shin (it is absent from Rumster), but also having such poor survival there as to make the mean height of doubtful reliability. This contrasts with its much better growth on the poor fertility site at Brendon. On this southern site with a rather mild winter climate it was taller than the experiment mean.

The Central Interior of BC group formed a similar compact group to that from the Skeena River, though with both poorer height and lower response; only two origins had above average response (Fort Fraser and Pendleton Bay). Within this group there was no overall trend of higher response with greater mean height. It is interesting to note that Prince George was the tallest origin from this region, as it corresponds closely with 35/17 in the 1937–42 series of experiments, except that the latter seed was collected at an elevation about 300 m lower.

The pattern shown by the North Coastal group again brings out very clearly the similarity between the Alaskan origins, which form a compact group, and the other North Coastal seedlot from Masset, Queen Charlotte Islands, which was both significantly taller and more responsive to better site conditions. Annette Island, Alaska had the poorest response in this group.

The Washington Cascades origins were very similar in height, though widely separated in response; Bird Creek, from a higher elevation, being significantly more responsive than Petersen Prairie from a lower elevation. Similarly, in the East of Rocky Mountains group, the very high elevation Crowsnest origin was significantly more responsive than Cypress Hills. This contrasts with the response of origins in the South Interior of BC region.

Consistency

For the forest manager who is planning to plant a chosen seed origin on the basis of its response, hoping thereby to exploit its adaptability to specific site types, he must have confidence in the reliability of the response indicated by the regression slope. The regression analysis provides an estimate of consistency of the response, which is shown by the size of any residual deviation (see Table 38). The most consistent origins are those with the lowest values, while high values indicate extreme inconsistency. An example of this can be seen in Figure 13, if the erratic behaviour of the origin from Mendocino (which has such a wide scatter of points that it is difficult to fit a regression slope), is compared with Smithers, where the deviation of individual values from the regression is very small. Coombs also has a highly significant deviation from the regression, mainly due to its poor performance at the exposed northern sites at Shin and Rumster.

In general the coastal populations, from Alaska to California, had the highest degree of inconsistency. Masset was the only origin that was not significantly inconsistent at 10 years. However, at 6 years Sitka and Annette Island were consistent, and at 15 years Glacier Bay, Ketchikan and Shelton proved consistent. Among the inland seed regions significant inconsistency was absent from the East of Rocky Mountains group and occurred only on two origins in the Skeena River group, on three origins in the Central Interior of BC group and on four origins in the Southern Interior BC group. There is no obvious reason why coastal sources should be so much less consistent than inland origins.

Diameter growth

Diameter was measured at 15 years in four experiments (Mabie, Shin, Broxa and Glentrool) and at 16 years at Tywi. At Glentrool, the 64 plant assessment plots were quartered and the largest tree in each quarter measured to give a 'top diameter'. At the other sites, mean diameter was recorded. The same set of 58 seed origins was selected and, where necessary, missing values calculated. At Tywi, snow and wind damage had affected some plots of the South Coastal origins so badly that missing values had again to be calculated in one replicate. It should also be noted that height was not assessed at 16 years at Tywi, so that no comparison can be made between height and diameter there. Also note that the set of experiments assessed for diameter are not identical with those used for height at 15 years.

Table 39 shows that the data for diameter with the regional means. The overall rank order follows that for height fairly closely, except for the Californian Mendocino origin. This ranked first at Mabie, Broxa and Tywi, but failed at Shin (where a missing value was calculated). It was not present at Glentrool, where another missing value was inserted. The poor survival of this origin gave it more growing space and so increased its mean diameter. For these reasons it is best to regard results for this origin as not comparable with the others. It is interesting to note that the two Washington Cascades origins had a large diameter for their height, thus following the same pattern of a high diameter:height ratio, similar to that of the Oregon Cascades seed origins in the 1937–42 series.

An analysis across sites similar to that for height at 10 years was carried out and very highly significant differences (***) found between seed origins, sites, the interaction between origins x sites, replicates within sites and between regional means. The variation between the latter accounted for a high degree of the variation. For the comparison of origins within regions, the only group showing significant differences was the North Coastal one, due entirely to the Masset origin, which had a much higher diameter than any of the Alaskan ones in this group.

Using the same method of regression analysis as for height, certain seed origins are revealed as being highly significantly different in diameter response. Shelton, from the Puget Sound region showed the greatest response, with higher diameter at Tywi and Glentrool, whereas at Shin it was only 92% of the experiment mean. The other Puget Sound origin from Rainier also had a high response and Coombs behaved slightly less responsively. Clearwater had a high response, but a poor mean diameter, i.e. it grew best on the better sites, but so poorly at Shin that its overall diameter was reduced to only 71% of the experiment mean value. Petersen Prairie from the Washington Cascades, behaved similarly in that it was 105% of the experiment mean at Tywi, but only 66% of the experiment mean at Shin.

So far as consistency in diameter growth is concerned, those with the highest response in general also had significantly high levels of inconsistency, particularly Petersen Prairie and Clearwater. Newport in the South Coastal group was very erratic. However, among those origins with high ranking for diameter: Long Beach, Terrace, Prince George, Mount Ida and Charcoal Creek, all were relatively consistent. In general the seed origins noted earlier as being susceptible to foliage browning and crown

Table 39. Mean diameter (cm) 15 years after planting of 58 origins at five sites

		Mabi	Shin	Brox	GlTr	Tywi	Mean
North Coastal							
1	Gustavus	8.9	7.7	8.7	12.1	8.6	9.2
2	Sitka	8.1	7.1	8.2	11.4	8.7	8.6
3	Petersburg	8.7	7.1	7.4	11.3	8.5	8.6
4	Ketchikan	9.2	6.9	8.5	11.4	8.6	9.0
5	Annette Island	8.6	7.8	7.8	10.4	8.5	8.6
6	Masset	10.5	8.5	9.0	12.7	9.4	10.0
	Region means	9.0	7.5	8.3	11.6	8.7	9.0
Vancouver area							
7	Coombs	11.6	8.6	10.2	14.3	10.6	11.1
	Region means	11.6	8.6	10.2	14.3	10.6	11.1
Puget Sound							
8	Shelton	11.2	7.6	10.1	14.5	11.1	10.9
9	Rainier	11.6	8.2	9.7	14.0	10.4	10.8
	Region means	11.4	7.9	9.9	14.2	10.8	10.9
South Coastal							
10	Long Beach	11.3	9.7	10.9	13.7	4.6	10.6
11	Warrenton	11.5	6.8	9.3	14.6	5.1	10.0
12	Newport, Waldport	11.7	10.6	9.9	13.8	4.8	10.7
13	Newport	11.6	10.7	11.2	15.6	12.8	12.2
14	Bandon	12.2	9.9	10.1	14.6	4.5	10.8
	Region means	11.7	9.5	10.3	14.5	6.4	10.8
California							
15	Mendocino	11.8	9.1	11.1	14.0	5.7	10.8
	Region means	11.8	9.1	11.1	14.0	5.7	10.8
Skeena/Bulkley							
16	Kispiox 305 m	9.7	8.6	9.1	12.9	9.5	9.9
17	Kispiox 460 m	10.2	8.1	8.8	12.9	9.7	9.9
18	Skeena Crossing	10.5	8.6	9.3	13.4	9.5	10.3
19	Kitwanga	10.0	8.0	8.8	12.9	10.0	9.9
20	Cedarvale	10.7	8.7	9.6	13.4	9.5	10.4
21	Terrace	10.6	9.2	9.6	13.0	9.9	10.5
22	Babine	10.2	8.1	9.0	13.1	9.5	10.0
23	Bulkley Canyon	9.8	8.0	9.2	12.9	9.7	9.9
24	Smithers 610 m	10.2	8.3	9.7	12.7	9.7	10.1
25	Smithers 760 m	10.4	8.6	9.5	13.2	10.4	10.4
26	Smithers 915 m	10.4	8.4	9.9	12.5	9.8	10.2
27	Smithers 1065 m	10.1	8.3	9.7	13.0	9.2	10.1
28	Telkwa	10.3	9.1	9.3	13.5	9.9	10.4
	Region means	10.2	8.5	9.3	13.0	9.7	10.1

Table 39. (contd)

		Mabi	Shin	Brox	GlTr	Tywi	Mean
Central Interior of BC							
29	Germansen Lake	9.4	7.6	8.8	11.9	9.0	9.3
30	Pendleton Bay	10.0	8.0	9.2	12.5	9.5	9.8
31	Topley	9.7	8.3	9.5	13.8	9.5	10.1
32	Fort St James	10.1	8.2	9.2	13.4	9.1	10.0
33	Burns Lake 760 m	10.2	8.2	9.4	13.1	9.2	10.0
34	Burns Lake 915 m	9.5	7.9	9.5	12.7	9.1	9.7
35	Fraser Lake	9.6	8.0	9.0	13.4	9.5	9.8
36	Vanderhoof	10.0	9.3	9.6	14.1	9.1	10.4
37	Wistaria	9.7	8.9	9.5	13.2	9.6	10.1
38	Takysie	10.1	8.2	9.2	13.2	9.2	10.0
39	Anahim Lake	9.6	8.1	9.7	13.0	9.4	10.0
40	Pr George 915 m	10.4	8.7	9.4	13.2	9.5	10.3
41	Barkerville Road	10.0	8.1	9.5	13.2	10.0	10.1
	Region means	9.9	8.3	9.3	13.1	9.4	10.0
South Interior of BC							
42	100 Mile House	10.1	8.3	9.7	13.2	9.4	10.1
43	Clearwater	10.1	5.9	9.8	12.8	9.9	9.7
44	Chase Creek	10.1	8.8	9.6	13.3	9.5	10.2
45	Salmon Arm	9.9	8.4	9.8	13.4	9.5	10.2
46	Mount Ida	10.5	8.3	9.6	13.7	9.3	10.3
47	Harper Lake	10.4	8.8	10.2	13.8	9.1	10.5
48	Charcoal Cr. 915 m	10.6	8.8	9.9	13.7	9.8	10.6
49	Charcoal Cr. 1220 m	10.6	8.1	10.1	13.6	10.0	10.5
50	Steavens Meadow	9.5	8.0	9.6	12.9	9.5	9.9
51	Tunkwa	10.7	8.4	9.3	12.5	10.0	10.2
52	Falkland 760–915 m	10.1	8.8	10.2	13.5	9.7	10.5
53	Esperon	9.9	8.0	9.5	12.8	8.5	9.8
54	Terrace Creek	10.0	8.2	9.7	13.2	9.4	10.1
	Region means	10.2	8.2	9.8	13.3	9.5	10.2
East of Rockies							
55	Crowsnest	8.6	6.4	7.9	11.3	7.9	8.4
56	Cypress Hills	8.7	6.6	8.1	11.4	8.0	8.6
	Region means	8.7	6.5	8.0	11.3	8.0	8.5
Washington Cascades							
57	Bird Creek	10.1	7.6	9.0	12.8	9.7	9.8
58	Peterson Prairie	9.9	5.5	8.9	12.3	10.2	9.3
	Region means	10.0	6.5	8.9	12.6	9.9	9.6
Overall mean		10.2	8.2	9.4	13.1	9.1	10.0

Key to sites: Mabi = Mabie, Shin = Shin, Brox = Broxa, GlTr = Glentrool, Tywi = Tywi damage on exposed sites are those that have shown the highest response in this analysis.

Conclusions

Bearing in mind the data on mean height and diameter, and the response and consistency of these characters of growth, the following conclusions can be drawn, taking the groups of origins in decreasing order of vigour:

1. Just as in the 1969 series, the South Coastal origins were outstanding for vigour on all sites, but already the basal sweep that accompanies this fast growth, together with their heavy crowns, had produced a significant amount of wind and snow damage by 15 years. Even where this has not yet occurred, the evidence from older experiments is so strong that these origins must be considered too risky. Large knots and compression wood on leaning trees also result in poorer timber quality. These origins should be used only in special circumstances, e.g. for shelterbelts on extremely poor sites, where only trees of greatest vigour can grow at all.

2. With only one origin from the Vancouver region, firm conclusions cannot be drawn. This origin ranked second for height, first for response in height and third in diameter, suggesting that it had a place on the higher quality sites, though it should clearly not be used on northern exposed sites. It is on the latter kind of site that its growth becomes erratic, resulting in high inconsistency. Although the terpene patterns of the Puget Sound and Vancouver groups are appreciably different, the silvicultural behaviour of these two groups is similar.

3. So far, little or no damage from snow or wind has occurred in the two origins from the Puget Sound. They also tend to have less basal sweep and lighter crowns, which accumulate less snow. On the other hand, their poorer resistance to extreme exposure, especially on sites in the far north of Scotland would suggest a limited role. Perhaps their main use might be inter-origin hybridisation, where their vigour (rank third overall) and lesser incidence of basal sweep might be of value. Their response at both 10 and 15 years was high, though unfortunately accompanied by erratic behaviour on the poorer sites.

4. The Southern Interior of BC region exhibited a broad range of vigour, response and consistency. It was encouraging to find that Mount Ida, which had grown well in some of the oldest seed origin trials, was the tallest in this group of 13 origins, with a high response and it was acceptably consistent (a low value of 0.135). Other good all round performers from this region were from Charcoal Creek and Falkland. However, this region also contains undesirable origins, such as the slow-growing Esperon Lake and Steavens Meadow, while Clearwater, which, as previously noted, grew well on some sites, but poorly at Rumster, thus showing its inconsistency of growth responses.

5. The Skeena/Bulkley region origins were characterised by their uniformity in growth rate, which was 3% above the overall mean, their uniformity in response, averaging 1.01 and their growth rate across sites was very consistent, with only two of the 13 origins showing significant inconsistency. This behaviour suggests that they can be used safely on a wide range of sites. Although the differences in growth between individual origins from this region were not significant in the across sites analysis, at Rosarie and Glentrool there were highly significant differences within this group. Thus it would be worth while to ensure that seed is obtained from the better origins: e.g. Terrace, Cedarvale and the Smithers seedlot collected at 610 m. The evidence from the collections at four different elevations in the Smithers area is that growth rate decreases evenly with increasing elevation. These origins have good stem form and suffered very little snow and wind damage though on very exposed sites some foliage browning occurred.

6. Little need be said about the Californian coastal origin from Mendocino. Although showing the largest diameter of any group and being fifth tallest out of 72 origins at the most southerly site at Brendon (where another origin of this group from Del Norte was second tallest), its survival on northern sites was low and its behaviour was so

erratic and its winter frost resistance so marginal that it has no use in British forest practice.

7. The Central Interior of BC origins were below average for height, diameter and response, but had high consistency, except for the tallest one from Vanderhoof. The Prince George origin (well known from the older experiments) combined above average vigour with high consistency in growth response, and the fact that it had a low response indicates that it is best suited to poorer quality sites. These origins showed rather greater differences in vigour among them than the Skeena ones; at this slower rate of growth it is particularly important to avoid the least vigorous. These were from Germansen Lake, the most northerly origin in this region, the higher elevation seedlot from Burns Lake and Anahim Lake, which was from an even higher elevation (1220 m).

8. Differences in vigour within the North Coastal group have already been discussed; from their overall performance the Masset origin stands out as being superior in height, diameter, response and consistency in growth response. There were no significant differences in vigour among the Alaskan origins, which all had a low response, i.e. they grew relatively better on the poorer sites and (apart from Glacier Bay) their performance was inconsistent. Undoubtedly the main use for Alaskan origins is in mixture with Sitka spruce (see Chapter 14).

9. The Washington Cascades group were second poorest in vigour, low in response and fairly consistent across sites. On this evidence, there seems no reason why these origins should find any place in British forestry.

10. The East of Rocky Mountains group grew even more slowly and do not merit further consideration as possible origins for use in Britain.

Species comparisons in the 1970 experiment series

The species comparisons built into the design of these experiments are best examined from the results when the trees were 10 years old (Table 40). One of the main aspects of interest is the use of lodgepole pine as a nurse for Sitka spruce. For this reason the data shown are the regional means for the groups that are most likely to be used in these mixtures, i.e. from the Skeena River and Alaska; the faster-growing North Coastal origins from the Queen Charlotte Islands and Vancouver Island have been excluded. Results at Thetford cannot be used as the experiment had been devastated by *Rhyacionia* before 10 years, though at 6 years the regional mean heights of the lodgepole pine ranged from 2.75 m for the South Coastal group to 1.30 m for that from East of the Rocky Mountains, while the Corsican pine (ex Corsica) was only 0.84 m. At Beddgelert the 10-year height assessment was omitted and the results shown are from the assessment at 14 years.

Table 40. Comparison of mean height (m) at 10 years for regions of lodgepole pine and other species

Experiment	Lodgepole pine		Sitka spruce			Scots pine	Corsican pine
	Skeena River	Alaska	Alaska	QCI	Washington		
Rumster 8	2.98	2.81	–	2.92	–	2.63	–
Rosarie 3	3.78	3.09	–	3.21	–	3.33	–
Broxa 115	3.50	2.68	–	3.56	–	3.16	2.12
Beddgelert 24*	5.08	4.57	4.70	5.25	5.91	–	–
Brendon 21	2.33	1.95	–	–	–	–	1.66
Tywi 16	3.56	2.97	2.83	3.46	3.64	–	–

* At 14 years

This table shows that in every experiment where lodgepole pine and Sitka spruce can be compared, the Queen Charlotte Islands seed origin of Sitka spruce has grown faster than the Alaskan origins of lodgepole pine. However, the Skeena River origins were taller than the Queen Charlotte Islands Sitka spruce on three of the five sites. The height data at 6 years show that only at Tywi was the Queen Charlotte Islands Sitka spruce marginally taller than lodgepole pine from the Skeena region. Scots pine grew best on the heathland sites and was always poorer than Skeena River lodgepole pine, which has advantages in nursing terms. Corsican pine is always a slow-starting species and was far slower than even the poorest lodgepole pine origin. Even at 15 years it was only just catching up with the slowest Alaskan origin at the Broxa experiment. The implications of these differences in growth are discussed in Chapter 14.

Chapter 13

The IUFRO 1972 experiments

The background to the IUFRO collection of 146 seedlots has been described in detail (Lines, 1971). In brief, the intention of the 27 collaborators in the IUFRO Working Party was to sample the whole range and to set up a large number of experiments (up to 100) in many countries. In Britain, because the 1969–70 series of experiments was already in train, it was decided to select origins only from those parts of the natural range that were poorly represented in the 1965 collection, though believed to offer good potential for British conditions. Two Yukon seed origins were included to allow comparison with IUFRO experiments in Scandinavia, rather than because they were expected to grow well in Britain. The exact location of each seed origin was known, together with unusually full data on climatic and site factors. It was also beneficial to be able to compare results in the British experiments with those in countries with a similar climate, such as Northern Ireland, Eire, Norway, France and The Netherlands. The nursery stage (Newton 2/70) has been described in Chapter 7. Twenty-four IUFRO seedlots were sown, together with one from Tofino, BC, which although not collected by the IUFRO team, came from the identical site. Due to variable germination, the number of IUFRO plants was insufficient in some seedlots to supply all sites, so three of the 1965 collection seed origins were included to give uniform designs at all six sites. Of the two Yukon seed origins that had poor nursery germination, the Frances Lake origin had to be excluded from the later analyses across sites. The sites were chosen mainly to link with the 1970 experiments, except for Fiunary, which is a severely exposed site near the limit of afforestation, in a part of Scotland not previously represented by a lodgepole pine seed origin experiment (see Table 5).

Results

First year survival was excellent, averaging over 90% at all sites. Except at the very exposed Fiunary site, where at 6 years overall survival was 61%, later survival remained high, ranging from 100% for the North Coastal origin from Gravina Island down to 25% for the origins from Samoa, California and Ethel Lake, Yukon. Climatic foliage browning occurred on most seed origins each winter at Fiunary with only the Alaskan origins, together with those from Mayer Lake and Campbell Island, BC showing minimal brown foliage. It is possible that some of the damage was caused by salt spray carried by Atlantic gales.

Results after 3 years (Table 41) showed wide variation between seed origins and sites (Lines, 1976c) with a highly significant origin x site interaction. The Broxa site was omitted from the combined analysis because both mean height and experimental error were much higher than at the other sites. The tallest regional groups were from the coasts of Oregon and California, while the next ones from the Puget Sound and Vancouver regions were similar in height. Next were North Coast BC, while the Alaskan group was twice the height of the Yukon origins. There were highly significant differences within the Alaskan group and within the groups from the North Coast of BC and Vancouver region, but no significant differences between origins within the Yukon, Puget Sound or Oregon and California groups. By far the largest amount of variation was accounted for by differences between seed regions.

At 6 years, height and diameter at the centre of the fourth internode from the apex were measured, taking care to exclude internodal branch whorls on trees with this bicyclic habit. Results (Lines, 1980b) showed a similar pattern to that at 3 years, though the Yukon origins were excluded from the 3-year analysis.

These later analyses have been made using the same terpene type grouping as in the 1970 series. In this case, so many of the origins in the North Coastal group were from British Columbia (compared with the sole Masset

Table 41. Mean height at 3 years. Data combined across five sites for IUFRO series

IUFRO number	Seed origin	Mean height at 3 years (cm). Combined analysis						Mean height (cm)
		Shin	Rumster	Farigaig	Fiunary	Arecleoch	Mean	Broxa
2014	Ethel Lake	(22.89)	21.90	28.67	15.49	(21.89)	22.17	28.97
2016	Frances Lake	(27.11)	28.33	(35.28)	(14.65)	26.53	26.38	–
2001	Yakutat	44.30	42.40	50.65	34.55	40.80	42.54	65.40
2007	Sitka	49.70	54.78	60.96	41.67	49.53	51.33	67.37
2010	Klawack River	52.00	55.35	62.36	50.09	49.47	53.85	72.30
2011	Gravina Island	(55.71)	54.45	62.32	48.27	54.17	54.98	73.60
2044	Porcher Island	48.70	51.78	(59.72)	41.17	52.73	50.82	80.33
2048	Masset Road	57.30	64.15	63.52	52.12	54.40	58.30	86.70
2050	Mayer Lake	61.00	62.38	65.77	49.43	60.30	59.78	80.70
2056	Campbell Island	51.30	53.28	57.76	37.33	49.33	49.80	77.00
2145	Port Hardy	55.00	59.40	66.67	43.81	59.87	56.95	86.43
2146	Lund	69.30	68.05	79.70	46.32	63.80	65.43	89.97
2147	Sayward	63.30	57.45	70.69	36.73	59.67	57.57	87.90
2148	Garibaldi	61.30	62.58	72.82	42.33	62.50	60.31	99.53
2067	Gold River	64.70	57.80	(67.97)	47.46	57.73	59.07	94.03
2149	Friendly Cove	53.30	57.88	65.15	43.66	55.03	55.00	67.53
(2152)	Tofino	55.00	57.63	61.98	46.33	50.47	54.28	73.63
2071	Mesachie Lake	61.70	69.25	70.98	52.39	70.90	65.04	85.37
2072	Sooke	63.30	67.45	80.47	49.93	67.20	65.67	94.43
2083	Queets	60.00	63.35	68.94	(48.37)	(59.82)	60.09	85.90
2084	John's Prairie	(60.23)	62.78	66.81	52.35	55.37	59.51	98.47
2086	Vail	65.30	68.55	77.80	41.13	65.37	63.63	102.80
65(797)	Shelton/Long Beach	70.00	(64.66)	64.14	(50.54)	(61.99)	62.27	–
2092	Pacific City	70.30	68.80	74..48	59.60	66.27	67.89	91.40
2100	Pistol River	72.70	(72.50)	90.04	50.24	65.03	70.10	–
2105	Samoa	57.30	70.50	82.93	41.68	69.33	64.35	99.33
65(7114) 3	Hazelton	53.30	54.50	5.063	41.60	49.03	49.81	73.33
65(7113) 4B	Prince George	42.30	(42.80)	37.13	39.65	40.13	40.40	–
65(7118)	Mount Ida	51.00	(53.54)	(60.03)	(39.41)	51.70	51.14	70.53
Site mean		55.84	57.52	64.01	43.39	54.84	55.12	81.32
Standard error ±		3.49	3.06	2.07	2.87	2.84	2.10	6.96
Significance level		***	***	***	***	***	***	***

Note: figures in parentheses are calculated missing values

origin in the 1970 series) that this terpene group has been split into Alaskan and North Coastal BC regions. The origin Queets, from a peat bog on the west side of the Olympic Peninsula of Washington, is also known to be of the North Coastal terpene type (Forrest, 1980) and is therefore included in this group. Shelbourne and Miller (1976) independently came to the same conclusion on the basis of its growth in New Zealand trials.

There is doubt about the proper allocation of 2092, Pacific City. As already discussed in Chapter 7, this seed was from a plantation of unknown origin and its performance in the nursery suggested a North Coastal origin. Its terpenes put it firmly in the North Coastal group (Forrest, 1980), though its later behaviour strongly suggest a South Coastal origin, as its vigour was outstanding at 6 and 10 years and its overall appearance very similar to the other South Coastal origins. Its overall rate of height growth can be matched most closely with Lund in the Vancouver group. The growth of Pacific City on the very testing Fiunary site was so much better, at 153% of the site mean, compared with Lund at 98% and a mean for the Vancouver group of 97% of the site mean at Fiunary, that it seems doubtful whether Pacific City should be placed in the Vancouver group merely because of its similar growth to Lund overall.

Three analyses were made using the regression technique described above for the 1970 series. Table 42 shows the overall mean values for the

6-year height and diameter measurements. The full data have not been presented as they fall midway between the 3- and 10-year data that are shown in Table 43. For height, there were very highly significant differences (***) for origins, sites, origin x site interaction, between origins within a region (except for the Puget Sound and South Coastal regions) and between regional means. The latter accounted for by far the largest part of the origin variation. The South Coastal region was the tallest group, with the Vancouver group and Samoa equal second. The Puget Sound origins were not much shorter, while the North Coastal BC group were significantly shorter. The Washington seed origin from Queets was shorter than the two Queen Charlotte Islands origins within this group. The Alaskan origins ranked sixth, while Ethel Lake (Yukon) was only half the height of the mean of the Alaskan origins.

Table 42. Overall mean height (m), diameter (mm) and height/diameter ratio at 6 years

IUFRO number	Seed origin	Height (m)	Diameter (mm)	Height: diameter ratio
Alaska				
2001	Yakutat	1.13	29.16	3.87
2007	Sitka	1.31	29.51	4.45
2010	Klawack River	1.40	30.89	4.54
2011	Gravina Island	1.35	30.41	4.42
	Region mean	1.30	29.99	4.32
North Coast of BC				
2044	Porcher Island	1.31	30.28	4.33
2048	Masset Road	1.51	33.58	4.49
2050	Mayer Lake	1.57	34.61	4.54
2056	Campbell Island	1.29	30.47	4.22
2145	Port Hardy	1.48	32.31	4.61
2149	Friendly Cove	1.45	34.08	4.25
2152	Tofino	1.46	33.27	4.38
2083	Queets	1.51	35.48	4.23
	Region mean	1.45	33.01	4.38
Vancouver				
2146	Lund	2.00	37.89	5.26
2147	Sayward	1.64	35.79	4.58
2148	Garibaldi	1.81	38.11	4.74
2067	Gold River	1.68	35.78	4.70
2071	Mesachie Lake	1.86	37.84	4.92
2072	Sooke	1.89	40.32	4.69
	Region mean	1.81	37.62	4.82
Puget Sound				
2084	John's Prairie	1.74	36.54	4.74
2086	Vail	1.72	34.49	5.12
	Region mean	1.73	35.52	4.93
South Coastal				
2092	Pacific City	2.00	41.71	4.80
2100	Pistol River	1.93	45.01	4.27
	Region mean	1.96	43.36	4.54
South Oregon/North California Coast				
2105	Samoa	1.81	41.49	4.35
	Region mean	1.81	41.49	4.35
Yukon				
2014	Ethel Lake	0.62	16.37	3.82
	Region mean	0.62	16.37	3.82
Overall mean		1.56	34.39	4.45

Table 43. Mean height (m) at 10 years for six sites

IUFRO number	Seed origin	Shin	Rumster	Farigaig	Fiunary	Arecleoch	Broxa	Overall
Alaska								
2001	Yakutat	2.01	2.39	1.98	1.48	2.39	2.15	2.05
2007	Sitka	2.63	2.89	2.45	1.75	2.54	2.31	2.42
2010	Klawack River	2.92	2.85	2.49	1.87	3.03	2.39	2.57
2011	Gravina Island	2.66	2.81	2.38	1.97	2.60	2.44	2.47
Mean		2.55	2.73	2.33	1.77	2.64	2.32	2.38
North Coastal BC								
2044	Porcher Island	2.62	2.67	2.46	1.81	2.67	2.25	2.40
2048	Masset Road	2.93	3.16	2.83	2.15	3.07	2.89	2.82
2050	Mayer Lake	3.22	3.24	2.69	2.09	3.15	3.03	2.88
2056	Campbell Island	2.60	2.67	2.50	1.71	2.58	2.15	2.35
2145	Port Hardy	2.89	3.15	2.79	1.77	2.96	2.62	2.67
2149	Friendly Cove	2.81	3.00	2.88	1.85	2.85	2.74	2.66
2152	Tofino	3.05	3.00	2.57	1.71	2.83	3.07	2.67
2083	Queets	2.98	3.00	2.77	1.65	3.14	3.28	2.76
Mean		2.89	2.98	2.69	1.84	2.91	2.76	2.65
Vancouver								
2146	Lund	3.20	3.75	4.02	1.67	4.06	4.36	3.43
2147	Sayward	3.60	3.19	3.32	1.36	3.38	3.42	2.97
2148	Garibaldi	3.75	3.49	3.50	1.53	3.75	4.15	3.28
2067	Gold River	3.31	3.34	3.23	1.75	3.67	3.59	3.09
2071	Mesachie Lake	3.55	3.65	3.31	1.68	3.83	4.03	3.27
2072	Sooke	3.67	3.45	3.77	1.89	3.89	4.23	3.40
Mean		3.51	3.48	3.52	1.65	3.76	3.96	3.24
Puget Sound								
2084	John's Prairie	3.22	3.33	3.26	1.22	3.55	3.74	2.98
2086	Vail	3.44	3.29	3.30	0.89	3.77	3.61	2.96
Mean		3.33	3.31	3.28	1.06	3.66	3.68	2.97
South Coastal								
2092	Pacific City	4.02	3.92	3.35	2.59	4.26	4.30	3.69
2100	Pistol River	3.54	3.57	3.62	2.02	4.02	3.79	3.36
Mean		3.78	3.75	3.48	2.31	4.14	4.04	3.58
S. Oregon/N. California								
2105	Samoa	3.00	3.45	3.15	1.62	3.39	4.29	3.09
Mean		3.00	3.45	3.15	1.62	3.39	4.29	3.09
Yukon								
2014	Ethel Lake	1.33	1.42	1.51	0.67	1.50	1.39	1.28
Mean		1.33	1.42	1.51	0.67	1.50	1.39	1.28
Overall mean		3.04	3.11	2.92	1.69	3.20	3.18	2.81

The regression analysis for 6-year height showed similarities with that for the 1970 series at 6 years. For example, the IUFRO Puget Sound origins from Vail and John's Prairie had a high response, like Rainier and Shelton in the 1970 experiments. Likewise the six Vancouver region origins combined a high response and well above average mean height, as did the South Coastal origins in both series. Masset in the IUFRO series occupied an almost identical position on the scatter diagrams (not reproduced) for both series, while the Alaskan ones showed poor height and low response. Samoa from northern California represents a terpene region not present in the 1970 experiments. Its performance was similar to Mendocino in that series, although its consistency in growth performance was much greater than Mendocino, having better than average growth on all sites except Fiunary, where it was 98% of the mean.

At 6 years, the regional means for diameter ranked almost identically with those for height. Because the mean height of the trees at Fiunary was only 84 cm, stem diameter at the fourth internode was so small that it would have been difficult to measure accurately and was not assessed. There were highly significant differences between origins, sites and between regions. The origin x site interaction was not significant, nor were there significant differences (greater than the 5% level) within the regions Alaska and Puget Sound, although very highly significant differences were found in the North Coastal BC, Vancouver and South Coastal regions.

Table 42 also shows the height:diameter ratios. Trees from seed origins with a high ratio have a tall and spindly appearance, whereas those with a low ratio are generally squat and bushy. The highest ratios were for Lund in the Vancouver group and Vail in the Puget Sound group. Both these regions had much higher ratios than average. In the absence of terpene information, this character helps to separate the two groups, which both occur on Vancouver Island. Port Hardy was the only origin in the North Coastal group to have a ratio slightly higher than the lowest one in the Vancouver region. In the South Coastal group, Pacific City was not significantly taller than Pistol River, but the latter had a particularly high diameter, associated with a dense bushy crown, giving it a very low ratio. Once again, the plantation source Pacific City showed an anomalous result, which does not clarify its true affiliation. The Yukon origin had a low diameter and an even lower mean height. In the Farigaig experiment it was observed that shoot extension of this origin had almost ceased in early July 1973, at a time when the Pistol River seed origin had not yet fully flushed. This extremely short period of shoot extension, combined with a long season over which diameter growth can continue, accounts for its squat form.

The 10-year height data across six sites (Table 43) showed a very similar pattern to the 6-year heights and ranking of the regional means was almost identical. Analysis showed that variation between origins, sites, origin x site interaction and replicates within sites were all very highly significant (***). The comparison of origins within regions showed very highly significant differences in all except the Puget Sound region, where it was non-significant. By far the largest amount of variation due to origins could be explained by the differences between regional groups.

A regression analysis across sites was carried out using the same method applied in the 1970 series. Figure 15 is a scatter diagram relating overall origin mean height and regression coefficient (response). These origins with outstanding response were those from the Puget Sound region, followed by those from the Vancouver region and Samoa. The origins grow well on good sites, and poorly on the more testing sites such as Fiunary. The South Coastal origins had a regional mean response significantly lower than these three groups and the performance of the Pacific City origin was notably different from the others.

It was observed in the 1970 series (with a larger number of origins) that there was a broad relationship between response and overall mean height. This was again clear at 6 years in the IUFRO series and for most origins at 10 years also. The main exceptions were Vail, with an exceptionally high response for its mean height (i.e. it grew very well on the best sites, and very poorly on the worst sites) and Pacific City, which had an average response, yet its mean height was oustanding. This indicates good growth on all sites. Table 43 shows that it was never less than 115% of the experiment mean on any site and usually 130% of the mean. A comparison of Figures 14 and 15 shows that Pacific City matches up closely in its position from the scatter diagram with Newport and Waldport in the 1970 series.

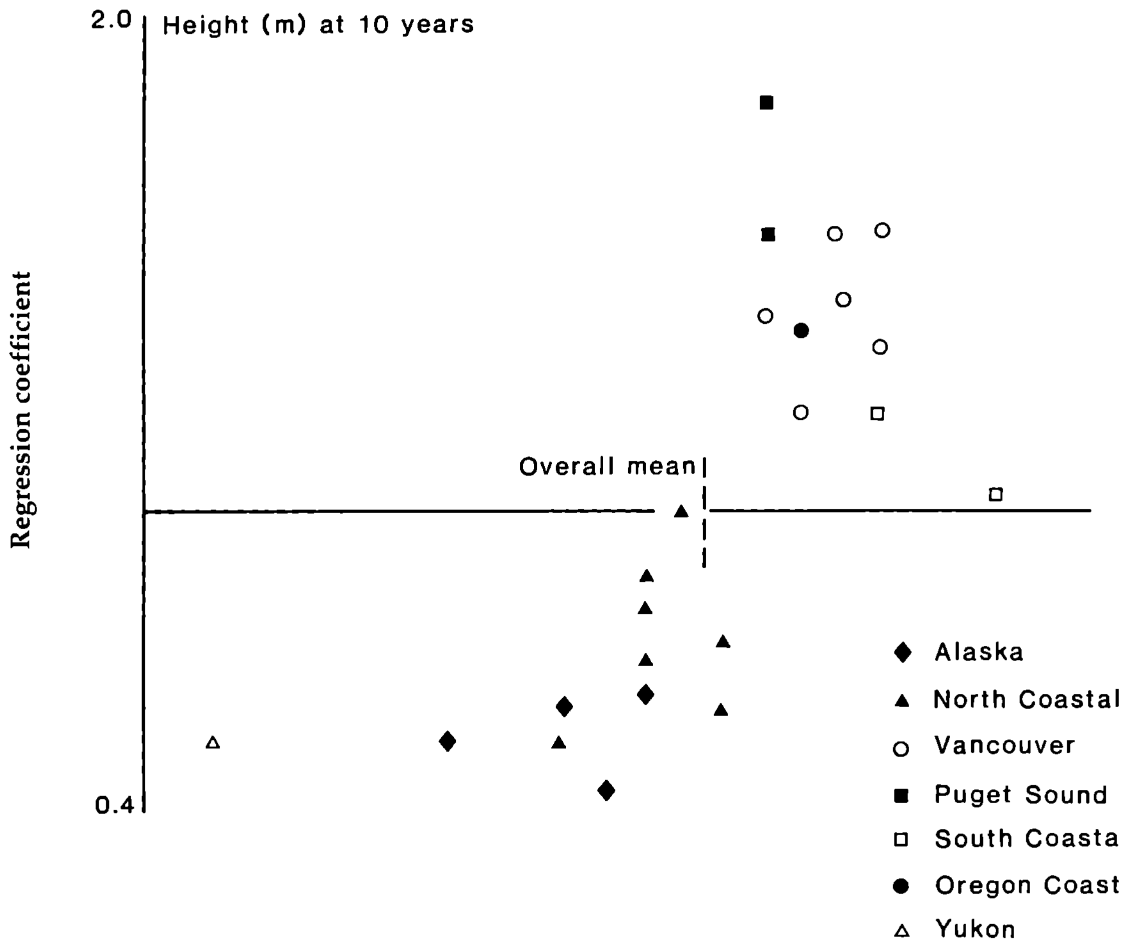

Figure 15. Scatter diagram relating overall origin mean height at 10 years and regression coefficient.

Apart from Campbell Island and Porcher Island, which appear to behave like the Alaskan seed origins, the North Coastal BC lots form a coherent group in Figure 15. The position of the two Queen Charlotte Islands lots indicates a very low response (i.e. they show their best relative growth on the poorer sites) but are still above the overall mean height. If their performance on the most severely exposed site at Fiunary is examined (Table 43) it can be seen that Masset Road was 127% of the experiment mean and Mayer Lake was 123% of the mean there. At Broxa, where the surrounding plantations provided a fair degree of shelter, the respective heights for these seedlots were only 91% and 95% of the experiment mean. These results contrast with the two Puget Sound origins, whose heights were 72% and 53% of the mean at Fiunary, compared with 118% and 114% of the mean at Broxa. It is quite clear that there is a differential response between these groups to the effects of exposure. The Samoa origin behaved rather like the Vancouver group and although its mean height at Fiunary was 95% of the experiment mean, this may be somewhat misleading, in that the more exposure-sensitive individual trees had not survived to the tenth year. All trees had died in the worst replicate and in the other three, survival ranged from 22% to 44%. The Yukon origin had the same overall survival percentage (25%) and its height growth was only 39% of the mean.

Conclusions

To sum up the additional evidence which these IUFRO experiments have provided, they show that:

1. The poorest of the Alaskan origins is from the isolated northern population at Yakutat. The others from this region grew as fast as the less vigorous North Coast BC origins, i.e. Porcher Island and Campbell Island. All would be suitable as nurses in mixture with Sitka spruce. Yakutat grows so slowly that the nursing effect would be delayed.

2. The two Queen Charlotte Islands origins grew faster than the rest of this North Coastal BC group. While they would

also be suitable in mixture with Sitka spruce and not outgrow it, on the most exposed sites they are probably the best choice for use as a pure crop, especially on the kind of site where pure Sitka spruce would need repeated fertiliser input and heather control by herbicides.

3. The Vancouver region contains origins with considerable potential vigour and high response to growth on the better sites. Lund and Sooke performed in a rather similar way to Coombs in the 1970 series. The IUFRO collection from Sooke was from an elevation of 550 m and thus probably different genetically from 58(7116)3 Sooke, which came from below 150 m and proved sensitive to exposure in the 1963–66 experiments. The IUFRO collection from Sooke origin was well above average height at the exposed Fiunary site. Garibaldi came from an elevation of 400–460 m close to the border between the coastal and inland populations. It appears to have some intermediate characteristics and, apart from its poor performance at the extremely oceanic site at Fiunary, it has grown fast on the other five sites. All these origins grow too fast for use in mixture with Sitka spruce and are unsuitable for severely exposed sites. On less exposed sites of moderate fertility their early growth may be so fast as to produce early instability and basal sweep. Snow damage has not yet caused serious damage in these young experiments and, if they behave like Coombs, is unlikely to be severe.

4. The IUFRO Puget Sound origins behaved very similarly to those from Rainier and Shelton in the 1970 series. This further reinforces our knowledge of their high response to better site conditions, particularly a sheltered environment. They are less liable to basal sweep and probably to later snow damage than the South Coastal origins.

5. Of the South Coastal origins, Pistol River behaved like other Oregon coastal seedlots. It comes from a latitude of 42° 15′ N, almost a degree further south than Bandon in the 1970 series, and thus probably too far south to transfer comfortably to northern Britain. Pacific City remains an enigma. Its rate of growth was very high, much more like a South Coastal than a North Coastal origin and yet its terpene pattern is clearly of the latter. As it is known to be from a plantation, one possible explanation for its superior vigour could be an outbreeding effect, similar to that known from plantation sources of this species in New Zealand (Miller, 1969) and France (Giovanini and Roman-Amat, 1986), compared with direct seed imports from stands which may have some inbreeding effects. This vigour has already caused basal sweep on some sites and it has rather coarse branching. Its height: diameter ratio was similar to the Vancouver group, though it is clearly far more resistant to exposure.

6. The Samoa origin shows all the poor features of southern coastal origins, i.e. poor form, heavy branching and frost tenderness. At Arecleoch, several trees suffered leader dieback in the severe winter of 1978–79.

7. The Yukon origins (2016 Frances Lake behaved very much like Ethel Lake) have no practical use in British forestry, because of their inability to adapt to the photoclimate in Britain. It is interesting to note that they are the preferred choice in northern Sweden, when transferred to latitudes even higher than in their native range.

Chapter 14

Use of lodgepole pine in mixtures with Sitka spruce

In pre-war plantations lodgepole pine was often used in mixture, usually with Sitka spruce. A typical stand of Southern Interior of BC lodgepole pine mixed with Sitka spruce was planted in 1937 at Clashindarroch, Aberdeenshire. Unusually its history has been well recorded, and it was described and illustrated by Lines (1968). These older stands were usually planted on better quality land than is now used for mixtures with lodgepole pine. In this stand the spruce grew well and was able to compete successfully, even with a relatively fast-growing seed origin of lodgepole pine during the first 11 years.

Because of its fast early growth, a stand of Yield Class 10 lodgepole pine will have a top height of nearly 4 m at age 10. A stand of 4 m top height will have a mean height of about 2.8 m (see Figure 8 in Everard, 1974) and it is relevant to compare the mean heights shown in Tables 35 and 43. Sitka spruce at the same age would have to grow at a rate equivalent to Yield Class 16 to keep up in height. Zehetmayr (1954) gives examples of successful mixtures of lodgepole pine and Sitka spruce on peatlands when the lodgepole pine was the slow-growing Albertan origin, but warned of the 'delicate balance of these intimate mixtures ...; a slight change of site, a change of provenance and a mixture alters to pure crop'. Similarly, on heathland sites Zehetmayr (1960) devotes a whole chapter to mixtures, stressing the importance of choosing slow-growing seed origins. Macdonald (1954) listed a range of site types where lodgepole pine was suitable for use in mixture with a range of species and was already aware of the need to select the correct seed origin of lodgepole pine in each case.

In the period from 1950 to 1970 lodgepole pine was often planted in intimate mixtures with Sitka spruce, particularly on heather-covered peatland in Scotland, northern England and Wales. In south Scotland these mixtures represented over one-third of the total area of about 20 000 ha planted in 1961–65 (Garforth, 1979). In 1950 the greater potential yield of Sitka spruce over lodgepole pine was known, but the techniques for raising a spruce crop successfully on these moorlands were still uncertain. Only later was it clear that competition from heather must be eliminated either by chemical means (e.g. 2,4-D) or by shading of a tree species and a suitable fertiliser regime of phosphate, potash and (on the poorer sites) nitrogen be applied at the correct time. There was research evidence that in mixed stands lodgepole pine could suppress the heather under certain conditions, whereas pure Sitka spruce went into 'check'.

A survey of 91 mixed stands (Neustein, 1967) was carried out to define the conditions under which nursing benefit occurred. Choice of unsuitable seed origin was one of the main factors for lack of success. Often a very vigorous South Coastal origin had been used, in which case a high proportion of the spruce was suppressed and the resulting widely spaced pine became unstable and were even more heavily branched than when grown pure. During this period (1950–70), particularly in the first half, large quantities of seed came from Lulu Island and other unsatisfactory sources such as Sooke and the Oregon Cascades. With the minimal fertiliser applied at this time, lodgepole pine in these stands soon became very thin in the crown on exposed sites and had little suppressive effect on the heather and thus the spruce went into check. It was impossible to spray the heather with 2,4-D without seriously damaging the pine, and aerial application of fertiliser was less cost effective than on pure spruce stands.

By 1970, research into improved establishment techniques for pure Sitka spruce had overcome most of the difficulties produced by heather check, by using a combination of good ground preparation with fertilisers and herbicides applied at the correct time (e.g. Binns *et al.*, 1970). Forestry Commission policy then swung strongly against mixtures of lodgepole pine with Sitka spruce, as many costly errors had been made by using origins that grew too fast or that were ineffective in heather suppression. In the long term, although the Lulu Island mixtures were almost useless as nurses, they posed no threat to properly fertilised Sitka spruce and many of these stands have now resulted in 'self-thinned' crops, with the spruce at wider spacing than in adjacent pure stands of spruce. Davies (1980, 1982), one of the enthusiastic supporters of high input pure Sitka spruce forestry, gave a forest manager's view of distaste for lodgepole pine, and outlined the maximum intensity of fertiliser input (based on research evidence) required to ensure a Yield Class of 16 for Sitka spruce planted on the poorest peatland. His suggested regime would involve seven aerial applications of fertiliser during the first 18 years, plus one and often two herbicide applications. In practice, these costly intensive prescriptions for Sitka spruce have not been followed, most forest managers tolerating nitrogen deficiency to some degree, with correspondingly lower growth rates. Although economic calculations show that this kind of high input can give a Sitka spruce crop of Yield Class 12 with a Net Present Value at 3% similar to a crop of Yield Class 8 lodgepole pine, the system is rather inflexible and financial stringency or rising fertiliser costs might make the regime impossible to apply. Research on lower input systems using the nursing effect of other conifers on spruce was beginning to yield results by the late 1970s, and this reopened the mixture question (Taylor, 1985). Experiments planted in 1965 using Sitka spruce in mixture with Alaskan lodgepole pine (as well as with Japanese larch and with fertilisers alone) showed that these relatively slow-growing seed origins, with their bushy form, not only had the effect of suppressing heather, but also enhanced the growth of Sitka spruce almost as effectively as direct application of fertilisers, while nitrogen levels in the spruce foliage were the same as in the fertilised plots (McIntosh, 1983).

Seed of Alaskan origins has sometimes been in short supply and in recent years forest managers have been forced to use alternative seed origins. Some choose to use a mixture with fast-growing seed origins of lodgepole pine, using the philosophy of 'insurance' mixtures. Any large moorland area will contain a mosaic of sites, with some relatively fertile patches 'flushed' with minerals in the ground water, as well as deep hollows and knolls with thin impoverished soil. They hoped by planting this mixture over the variable site that the more demanding spruce would thrive on the fertile soils and eventually suppress the pine, whereas on the poorest ground only the less demanding pine would form a crop. On intermediate areas a mixture would form the final crop. Although superficially attractive, in practice this idea has many disadvantages, e.g. costly tending to save the spruce from strong early competition by the pine may be necessary; many 'flushed' sites, where spruce should grow well, are also frost hollows so that the spruce is frosted repeatedly whereas the pine is not; application of fertilisers or herbicides may be essential for the spruce, but difficult or less cost-effective when applied to mixed stands; the market value of an irregular mixed crop at the end of the rotation will be lower than for a single species.

The relative height growth of lodgepole pine and Sitka spruce during the first 10 to 15 years is the key to successful mixtures. The heights at 10 years in six different climate provinces are shown in Table 40 and give some guide to the chance of Sitka spruce being able to complete satisfactorily with lodgepole pine. These are mean heights for several origins in each seed region and the tallest Skeena River origins may offer some threat to Sitka spruce in mixture. At four of these sites, 15-year heights are also available and give some guidance as to the chance of later interaction (Table 44).

Table 44. Comparison of mean height (m) and range of heights at 15 years for two seed regions of lodgepole pine and Sitka spruce from the Queen Charlotte Islands

Experiment	Lodgepole pine region		Sitka spruce
	Skeena River	Alaska	
Rumster 8	5.16 (4.92–5.36)	4.79 (4.62–5.11)	4.59
Rosarie 3	6.63 (6.38–6.98)	5.56 (5.54–5.58)	6.38
Broxa 115	6.89 (6.49–7.14)	5.71 (5.54–5.88)	7.01
Beddgelert 24*	5.08 (4.87–5.29)	4.57 (4.41–4.75)	5.25

*At 14 years

From Table 44 it can be seen that Queen Charlotte Islands Sitka spruce should compete successfully with even the faster-growing Alaskan origins on all sites and at three sites with the fastest-growing Skeena River origin. On sites like Rumster, Sitka spruce is in danger of strong competition and partial suppression by the fastest-growing Skeena River origins. These examples compare the two species grown only in pure plots. The two oldest experiments where Alaskan lodgepole pine can be compared with Sitka spruce grown in intimate mixtures are Inchnacardoch 164 P65 and Strathy 6 P65. At Inchnacardoch, the Sitka spruce in mixture with lodgepole pine from Skagway was always marginally taller than the pine. At 12 years the spruce was 2.86 m and the pine 2.60 m (compared with pure Sitka spruce at 2.28 m). By 18 years the spruce was 6.54 m and the pine 5.32 m. At Strathy, where the same Skagway origin was used, several severe frosts in the 1970s held back the spruce, which up to 6 years had grown much faster than at Inchnacardoch. Nevertheless, by 17 years the spruce was beginning to catch up, with a height of 4.70 m, compared with 5.66 m for the pine, and by 20 years the spruce was 6.39 m and the pine 6.78 m. Thus, it will take many years before the pine is suppressed naturally in these stands and it is likely that the final crop will still contain pine.

The exact mechanism for these nursing effects has not yet been fully explained. It appears to be due to an inherent superior ability of lodgepole pine (and some other species such as Scots pine and Japanese larch) to obtain nitrogen on poor sites, especially in competition with heather. The spruce is then able to obtain its supplies of nitrogen, either via the litter-fall from the pine, or else via mycorrhizal associations. This is currently the subject of detailed investigation by Professor H. Miller at Aberdeen University and M. Carey in Eire (Carey *et al.*, 1988). Nevertheless the nutritional status of the spruce in such mixtures is considerably higher than in a pure stand of spruce and very similar to that of spruce that has had the *Calluna* removed by herbicide and also given additional nitrogen fertiliser.

Provenance experiments provided the database for advice on the right match of lodgepole pine seed origins for different regions and sites that would effectively suppress *Calluna* and not seriously out-perform Sitka spruce in early years. This formed the basis of a change in silvicultural practice on the moorlands of North Scotland in the early 1980s towards mixtures of lodgepole pine and Sitka spruce.

Chapter 15

Susceptibility to wind and snow damage

Because of its pioneer nature, one of the characteristics of lodgepole pine is its capacity for very fast initial growth, unlike the silver firs and some spruce that take much longer to become established on poor sites before they start to grow fast. On a favourable site, South Coastal lodgepole pine may be over 1 m high at 3 years and 2.7 m high at 6 years. Early instability affects many species that show this pattern of growth, e.g. *Pinus radiata* in New Zealand, *P. pinaster* on some sites in France and Britain, and even *P. sylvestris* if large plants are used on fertile sites. Instability can be greatly accentuated by some methods of ground preparation and the position of planting. For example, on indurated heathland soils it was known that early survival was highest if the tree was planted in the bottom of the furrow made by a tine plough. Only later did it emerge that this was the worst position for encouraging or inducing instability (Edwards *et al.*, 1963) and on their recommendation this practice ceased.

Once a young tree has become loosened it tends to rock backwards and forwards in the 'socket' until either the lateral roots become sufficiently stiff to stabilise it, or it progresses to a point where the stem is nearly lying on the ground and then grows upwards again. Most commonly a basal bow develops, which results in the main mass of the tree exerting a vertical force at some distance laterally from the centre of the root system. Thus such trees are very prone to later wind and snow damage, even though the tree is now apparently firm. Each year on windy sites the tree may develop a leader that leans away from the prevailing wind, even if there is little basal sweep. Some origins are very prone to this – particularly the South Coastal ones, while others on the same site grow with little tendency to lean. Even slightly leaning trees may develop compression wood in the same way that this is developed to an excessive degree in the wood associated with the basal bow.

In pre-war experiments early instability did not appear a major problem, as most of the seed origins were from the interior, methods of ground preparation were less intensive and fertiliser applications minimal compared with present day practice. Nevertheless, the first assessments of stem form carried out in 1951 in the 1937–39 experiments did show large differences, mainly concerned with sinuosity and basal sweep. The South Coastal origins had the poorest form. Shelton, from the Puget Sound region had better form and ranked equally with the fast-growing interior origin from Shuswap Lake (Macdonald, 1954).

In the post-war period South Coastal origins of lodgepole pine, largely from the Long Beach area, were used widely in trial plantations that had been ploughed to produce a large turf ridge and fertilised with rock phosphate. At Strathy, Sutherland, the leading shoots of trees in their third growing season were up to 70 cm long, and unstable trees were common after the following winter. When the extent of the problem was realised, the first experiments were established in 1953 to investigate whether delayed fertilisation would eliminate the problem (Lines, 1980c). These experiments failed because it was not then realised that some Northern Coastal seed sources (in particular from Lulu Island) were inherently less fast-growing and light-crowned and thus did not become unstable. The following year, two experiments (including a South Coastal origin) were planted with delayed fertilisation. The result was that the trees failed to grow until they were given phosphate fertiliser 3 years later. Even then growth was slow, and though it eliminated basal bow, more than 4 years increment was lost. The late 1950s saw a return to South Coastal seed origins and in 1958 another fertiliser trial at Naver, Sutherland again showed that without phosphate the trees merely stayed in check, while those given 14 g per tree of rock phosphate grew almost as fast as and suffered similar basal bow to those given the standard rate of 42 g. Other experiments tested minute doses in the form of a slurry into which the roots were dipped before planting. These trees grew slowly and straight, but it appeared that it merely delayed the 'moment of truth', since later topdressing at standard rates could not be avoided and this resulted in heavy crown development and instability.

In 1966 a survey was carried out in Scottish forests to quantify the extent of the problem. This showed that between 1956 and 1965, 8675 ha had been planted with South Coastal origins of lodgepole pine. Of these, about 40–50% of the stands were affected by basal sweep to a severe or moderate extent (Fraser and Neustein, 1967). In the same year three experiments were planted testing 13 treatments that it was hoped would reduce basal sweep on peat sites. The general position at this time was given by Neustein (1969). The treatments included position of planting, various fertiliser treatments and growth reduction by clipping or chemical treatment, as well as use of an Alaskan origin. A clear relationship was found between tree height and basal bow at two sites. Intensive measurement of the trees for many morphological characters and multiple regression of stem straightness (as a measure of basal bow) on these showed that a combination of root collar diameter and minimum root diameter was highly significant in relation to straightness, explaining 57% of the variation, though the exclusion of the Alaskan origin nullified the significance of the relationship.

Since over-rapid early growth and a low root:shoot ratio were indicated as major factors in worsening instability, one known way of achieving slow early growth and a better balanced plant was by direct sowing. Observations had shown that natural regeneration of lodgepole pine in Britain seldom suffered instability. Aldhous (1976) observed that in planted stands on the Pacific coast of Washington almost all trees had some basal bow, whereas natural seedlings were straight. Burdett (1979) has observed the same in British Columbia. Direct sowing has been tried several times but seldom with success in Britain. The Ontario system of planting young seedling trees in small polystyrene tubes was currently being tested in Britain (Low, 1975) and it was hoped that the use of such young seedlings would reduce the instability problem to a great extent. This was found to be generally true and later root excavations demonstrated the superior root form of trees established as tubed seedlings compared with transplants. However, the method was not put into general use for a number of reasons, one of the critical ones for lodgepole pine being that the early instability problem of South Coastal origins was soon added to by a further hazard – damage by wet snow in the thicket and pole-stage.

As the large areas of South Coastal lodgepole pine reached the late thicket and early pole-stages, there were more and more cases of serious damage from a combination of wind and wet snow. The heavy crowns of these origins held such a great weight of snow that they snapped off or fell over in patches throughout whole compartments. The financial loss was worst when this occurred just before the trees had reached the size where they could be utilised for pulpwood or chipwood. Lighter-crowned interior origins suffered very little damage and so far damage in the almost equally heavy-crowned, but slower growing, North Coastal and Alaskan origins has been negligible.

Root:shoot ratios are believed to influence early instability and as noted in Chapter 8 the unstable South Coastal origins had the lowest ratios as seedlings and transplants in the nursery (Table 16). Danby (1973) summarised the results from the excavation of over 500 trees aged between 3 and 8 years and measured for fresh weight of root and shoot. The ratio varied widely between different sites, but differences due to seed origin within sites were consistent. Danby also measured root:shoot ratios in older trees (32–44 years) and in these seed origin appeared less important than site in its influence on the ratio.

Instability has been assessed in many of the British seed origin experiments. Results from the IUFRO experiments of 1972 were reported by Lines (1980b). These consist mainly of counts of the percentage of trees showing basal sweep or lean. Seed origin differences were always highly significant and demonstrate a general relationship between tree height and the incidence of basal bow. Figure 16 shows the results at Farigaig where basal bow was highly correlated with height (r = 0.61, significant at ***). The origins form a pattern where those from the less heavily crowned Vancouver and Puget Sound region are generally below the regression line, i.e. a lower degree of bow for their height, compared with the South Coastal and Californian ones, which have a higher incidence of bow for their height. The anomalous Pacific City origin falls within the latter group. This diagram also

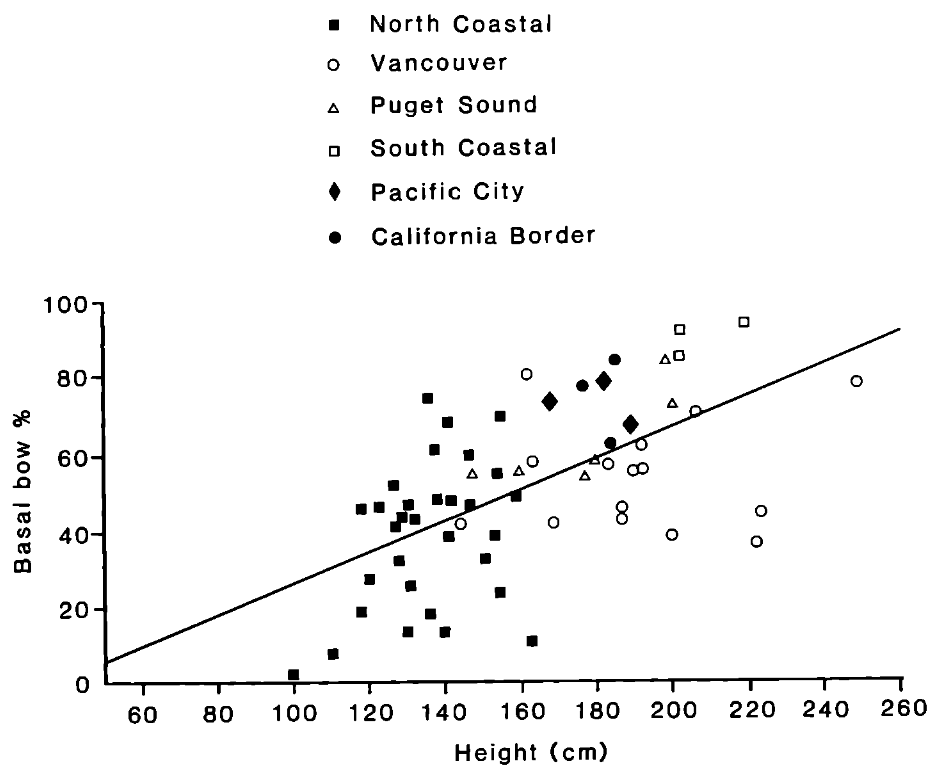

Figure 16. Relation between height at 6 years (cm) and basal bow at Farigaig.

illustrates that there is no sharp line dividing origins affected by basal bow and those that are unaffected.

In the 1970 series, instability was assessed in the Rosarie, Glentrool, Brendon and Broxa experiments. Results were rather similar for the behaviour of different seed regions in all experiments, so that the data from the Rosarie experiment at 10 years are given as an example in Table 45. The South Coastal group were by far the worst at 43%, with the Southern Interior BC group next at less than 5%. The rest had negligible damage. The main points to note were the highly significant differences within the coastal origins, with the Puget Sound origin from Rainier very highly significantly more stable than those from the Pacific Coast; Coombs, in the North Coastal group, which was taller than Mendocino, yet suffered far less damage. Further evidence for the lesser damage sustained by Puget Sound origins comes from Wark 6 P61, which suffered from heavy wet snow damage during the winter of 1978/79. Three Oregon coastal origins were significantly more heavily damaged than one from Long Beach, which in turn had significantly more damage than one from Keyport in the Puget Sound. All others (see Table 31) were not badly damaged.

At Elchies 1 P57 an assessment of basal bow was made at 15 years. This showed highly significant differences between origins. When the experiment was 20 years old, heavy wet snow caused serious damage in those origins that had a high incidence of basal bow 5 years before. The correlation ($r = 0.836$) between the two assessments was highly significant and indicates how the early basal bow data can be used to predict later catastrophic damage from heavy wet snow.

The main conclusions are that rapid-growing origins of lodgepole pine can become unstable under present methods of establishment on some sites. Trees that develop basal bow show that they are potentially at risk from heavy wet snow in the future, especially if they are of the heavy-crowned South Coastal type. Those from the Puget Sound and Vancouver regions (based on terpene type) are less at risk, because their lighter crowns do not trap so much wind or snow. Experiments to limit basal bow have not produced an effective practical treatment, apart from using tubed seedlings or natural regeneration, both of which have only limited application. Seed origins from the Skeena River and North Coastal groups have mostly proved acceptably stable under a wide range of site conditions.

Table 45. Percentage of trees affected by wind or snow at Rosarie 3 at 10 years

Identity number	Seed origin	%	% transformed to angles
Alaska			
(7987) 3	Petersburg	1.39	3.41
(7987) 5	Annette	0.70	2.40
North Coast BC			
(7111) 1	Masset	2.78	6.59
(7116) 7	Coombs	1.39	4.80
South Coastal			
(7975) 2A	Rainier	6.94	14.98
(7972) 1	Long Beach	29.86	32.95
(7951) 1H	Newport	54.86	47.88
(7948) 100	Mendocino	46.53	42.91
Skeena River			
(7114) 8	Kispiox, 300 m	3.47	8.99
(7114) 8A	Kispiox, 460 m	6.25	10.22
(7114) 5	Skeena Crossing	3.47	5.47
(7114) 7	Kitwanga	0.00	0.00
(7114) 9	Cedarvale	4.17	10.00
(7114) 1	Terrace	3.47	7.27
Bulkley River			
(7114) 12	Babine	3.47	7.27
(7114) 15	Bulkley Canyon	1.39	4.80
(7114) 13	Smithers, 600 m	0.70	2.40
(7114) 13A	Smithers, 760 m	0.70	2.40
(7114) 13B	Smithers, 900 m	1.39	3.41
(7114) 13C	Smithers, 1070 m	1.39	4.80
(7114) 2	Telkwa	1.39	3.41
Central Interior BC			
(7113) 11	Germansen Lake	2.09	7.20
(7113) 6	Pendleton Bay	0.70	2.40
(7113) 1	Fort Fraser	2.08	5.81
(7113) 10	Burns Lake, 760 m	5.56	9.43
(7113) 10A	Burns Lake, 900 m	2.78	4.87
Central Interior BC			
(7113) 1A	Fraser Lake	1.39	3.41
(7113) 5	Vanderhoof	6.25	14.19
(7113) 17	Takysie	1.39	4.80
(7113) 3	Anahim Lake	4.86	12.40
(7113) 4B	Prince George	0.00	0.00
South Interior BC			
(7118) 8	100 Mile House	4.86	8.88
(7118) 6	Clearwater	5.55	13.41
(7118) 1A	Chase Creek	4.86	10.67
(7118) 4A	Salmon Arm	3.47	8.99
(7118) 4	Mount Ida	2.08	5.81
(7118) 1D	Harper Lake	3.47	9.21
(7118) 5B	Charcoal Creek, 900 m	8.34	15.69
(7118) 5C	Charcoal Creek, 900–1200 m	8.33	14.35
(7118) 9A	Steavens Meadow	1.39	4.80
(7118) 3	Tunkwa Lake	7.64	11.23
(7113) 5A	Falkland	5.56	10.82
(7118) 100	Esperon Lake	0.70	2.40
(7118) 102	Terrace Creek	5.56	13.07
(7118) 101	Bald Range Creek	5.56	9.43
East of Rockies			
(7123) 100	Crowsnest	0.00	0.00
(7124) 100	Cypress Hills	7.64	14.75
Washington Cascades			
(7976) 6	Bird Creek	2.78	6.59
(7976) 5	Petersen Prairie	1.39	4.80
Standard error ±			3.46
Differences significant at			***

Chapter 16

Stem form, crown morphology and efficiency of suppression of ground vegetation

Stem form

Stem defects of lodgepole pine, i.e. basal bow and stem lean have already been discussed in the previous chapter. Stem sinuosity is less easy to assess, but can also affect some seed origins more than others. It is worst on South Coastal origins though trees of some seed origins from the Southern Interior of BC region, such as Vavenby and Clearwater, are sometimes quite sinuous.

Basal forking can result from browsing by animals or birds, from shoot dieback in winter or from planting too deeply in peat, thus forcing side branches up into the vertical position. It gives rise to two or more main stems when it occurs in the establishment phase. It is necessary to distinguish carefully between multiple stems that arise from browsing or blackgame damage to buds and are therefore probably not directly related to seed origin, and those caused by climatic shoot die-back, which may well result from differential exposure susceptibility of certain seed origins.

In the later stages, a tendency to fork appears to be associated with particular seed origins. This was first noted in the 1938 series of experiments (Lines, 1966). In Mabie 10 P70 all trees that forked low down were singled and at 15 years all trees in the inner three rows x four trees were assessed for height and presence of forks in the upper crown. Tree height averaged 7 m throughout the experiment. Differences in the percentage of forking were very highly significant and by far the largest amount of variation was between the regional groups (in this case shown geographically rather than in terpene groups, see Table 46). The overall mean was 26%, which is surprisingly high.

Table 46. Incidence of upper stem forking in Mabie 10 at 15 years

Region	Number of origins	Mean % of forked trees	Standard error ±	Rank	Height rank at 15 years
Alaska	10	9.6	1.604	11	10
Queen Charlotte Is	1	9.9	5.073	10	6
Vancouver Island	2	16.9	3.587	9	2
South Coastal	10	31.6	1.604	2	1
Skeena River	7	24.2	1.918	6	3
Bulkley River	11	21.6	1.530	7	5
Central Interior BC	17	28.0	1.230	4	7
South Interior BC	18	35.6	1.196	1	4
East of Rocky Mnts	2	30.8	3.587	3	11
Washington Cascades	2	18.7	3.587	8	9
Oregon Cascades	1	26.0	5.073	5	8

There were significant differences within the Vancouver Island group, due to Coombs having nearly seven times as many forked trees as Tofino, and in the Bulkley River group, Matlin Creek had 34% forked trees compared with Smithers (610 m) which had only 12%. There were no significant differences within any of the other regional groups. Although there is some association between forking and height, with the worst forking on some of the tallest origins, height is obviously not the main factor influencing forking. For example, the Vancouver Island group shows remarkably good height growth combined with low incidence of forking while the East of Rocky Mountains group shows the reverse trend. Forking was also assessed at 15 years in the Rosarie 3 P70 experiment with similar results. The general incidence of forking was much less, ranging from 2% for the Alaskan region to 14% for trees from the Southern Interior of BC region.

Crown and branch form

An unusual feature of lodgepole pine is the tendency for some origins to produce internodal branch whorls, the so-called 'bicyclic' habit (Scobie, 1971). This was assessed at Wykeham 55 P38 at the age of 24 years by counting the number of internodal whorls within the first three internodes above the limit of brashing (about 2 m). Thirty trees per plot were assessed and the results are shown in Table 47.

The Oregon coast seedlot had the fewest internodal whorls. The other coastal groups had slightly more, while those from the Skeena River and Central and South Interior of BC had the most. Another Oregon coastal origin in a subsidiary part of this experiment had so few internodal whorls that it was recorded as 'not worth assessing'. The Oregon Cascades origins are the sub-species *murrayana* and these appear to have fewer internodal whorls than the East of Rocky Mountain group (ssp. *latifolia*).

The incidence of bicyclic (multinodal) growth was also assessed after 6 years in the IUFRO experiment Arecleoch 5 P72 on a scoring basis (1 = scarce to 4 = generally present). The score was allocated to the plot as a whole and not to individual trees so that it is not a very precise assessment. Table 48 shows the results.

The Oregon/California coast region was the only one within which there were significant differences. Differences between regions were very highly significant and they followed the same pattern as in the Wykeham experiment.

These forms of branch arrangement are not of purely academic interest, as the possession of additional branch whorls tends to distribute the weight of snow more evenly over the crown. The crowns of South Coastal origins have a tendency to snap at the node because the many heavy branches at each node and the resulting mass of distorted grain produces a point of weakness. The densely crowded branches of trees from the North Coast of BC and Alaska may make the stem less easily accessible to marauding red and sika deer attempting to eat the bark, compared with trees having widely spaced branch whorls. Trees with many whorls of smaller branches will also have a smaller maximum knot size than trees of the same crown mass but fewer large branches. Trees with very large knots produce inferior structural timber.

Other crown characteristics, such as crown spread, needle retention, number of branches per whorl, branch girth, etc., were first assessed in 1951 in the 1937–41 series of experiments. Some results were given by Macdonald (1954). Later, more detailed assessments in these experiments were made and the results in Millbuie 1 P38/39 were published (Lines, 1976a).

Branch length tends to be largely an expression of tree vigour, with wide variation between sites. If the ratio of branch length to tree height is considered, then highly significant differences were found between seed origins at Achnashellach, Wykeham, Millbuie and Clashindarroch. Table 49 gives the overall regional mean ratios at age 16–17 years.

The general conclusion is that the North Coastal origins (Queen Charlotte Islands and Sonora Island/New Westminster) had the longest branches for their height. Those from the Skeena River had longer branches than those from the rest of the interior and the South Coastal ones were intermediate. However, in the South Coastal group the most southerly origin from SW Lincoln County, Oregon had a much higher ratio (0.288) than those from Shelton and Long Beach.

Different seed origins can be readily distinguished by their 'bushiness' of crown. The degree of 'bushiness' results from a combination of characters: number of whorls per unit length

Table 47. Mean number of internodal whorls in three internodes above 2 m at Wykeham 55 P38

Identity number	Seed origin		Mean number of internodal whorls
Coast BC			
34/25	Sonora Island & New Westminster, BC		1.47
Puget Sound			
34/40	Shelton, Washington		1.07
South Coastal			
34/10	SW Lincoln County, Oregon		0.50
Skeena River			
35/18	Smithers		2.37
35/22	Hazelton		2.60
		Mean	2.48
Central Interior BC			
34/24	Prince George		2.23
35/17	Prince George		2.30
35/19	Williams Lake		2.57
		Mean	2.37
Southern Interior BC			
35/20	Clearwater		2.60
34/23	Shuswap Lake		2.47
35/21	Shuswap Lake		2.20
		Mean	2.42
East of Rocky Mountains			
34/69	Priest River, Idaho		2.07
35/53	East Washington		2.38
34/68	West Yellowstone, Montana		2.50
		Mean	2.32
Oregon Cascades			
35/54	'Oregon'		1.03
35/59	Klamath, Williamson R		2.10
		Mean	1.56

Table 48. Score for incidence of bicyclic growth habit at Arecleoch 5 P72

Identity number	Seed origin	Score	Angular transformed score
Alaska			
2001	Yakutat	2.3	0.52
2007	Sitka	3.0	0.60
2010	Klawack River	3.3	0.63
2011	Gravina Island	2.3	0.52
North Coast BC			
2044	Porcher Island	2.3	0.52
2048	Masset Road	3.3	0.63
2050	Mayer Lake	2.7	0.56
2056	Campbell Island	3.0	0.59
South Coast BC			
2145	Port Hardy	2.3	0.52
2146	Lund	2.3	0.52
2147	Sayward	2.3	0.52
2148	Garibaldi	2.3	0.52
2067	Gold River	2.7	0.56
2149	Friendly Cove	2.3	0.52
2152	Tofino	2.7	0.56
2071	Mesachie Lake	1.7	0.42
2072	Sooke	2.3	0.52
Puget Sound			
2084	John's Prairie	2.7	0.56
2086	Vail	3.0	0.59
Oregon/California Coast			
2092	Pacific City	1.0	0.30
2100	Pistol River	1.0	0.30
2105	Samoa	2.3	0.52
Yukon			
2016	Frances Lake	2.7	0.56
Skeena River			
(7114) 3	Hazelton	3.3	0.63
South Interior BC			
(7118) 4	Mount Ida	3.3	0.63
Standard error ±		–	0.04
Differences significant at		–	***

Region	Number	Mean	Rank
Alaska	4	0.57	4
North Coast BC	4	0.58	5=
South Coast BC	9	0.52	2
Puget Sound	2	0.58	5=
Oregon/California Coast	3	0.37	1 least
Yukon	1	0.56	3
Skeena River	1	0.63	7= most
South Interior BC	1	0.63	7= most

Table 49. Regional mean ratios of branch length to tree height at Achnashellach, Wykeham, Millbuie and Clashindarroch

North Coast BC	0.30
South Coastal	0.26
Skeena River	0.26
Central Interior BC	0.24
South Interior BC	0.24
Northern Interior USA	0.24

of stem; number of branches per whorl; number of second and lower order branches; live needle retention; needle number per unit shoot length; and needle length. Cannell (1974) made a detailed analysis of shoot growth on six origins in the Eddleston 4 P66 experiment, when the trees were 6 years old. He measured the total accumulated shoot length per tree and found that the South Coastal origin from Newport had a total length of 89 m compared with one from Skagway, Alaska, which had only 33 m. Thus the former produced nearly three times as much total length of branch, while it was only 35% taller. This technique, which employs destructive sampling to measure total accumulated shoot length, is too cumbersome to apply when many seed origins are to be assessed on a range of sites. A much simpler method to assess 'bushiness' was to count the number of shoots on one well-illuminated side branch on ten trees per plot. Five years' growth was found by counting back the internodes of this branch and then working outwards from this point all live current shoots were counted (see Figure 17). This was done in 1954 on five trees

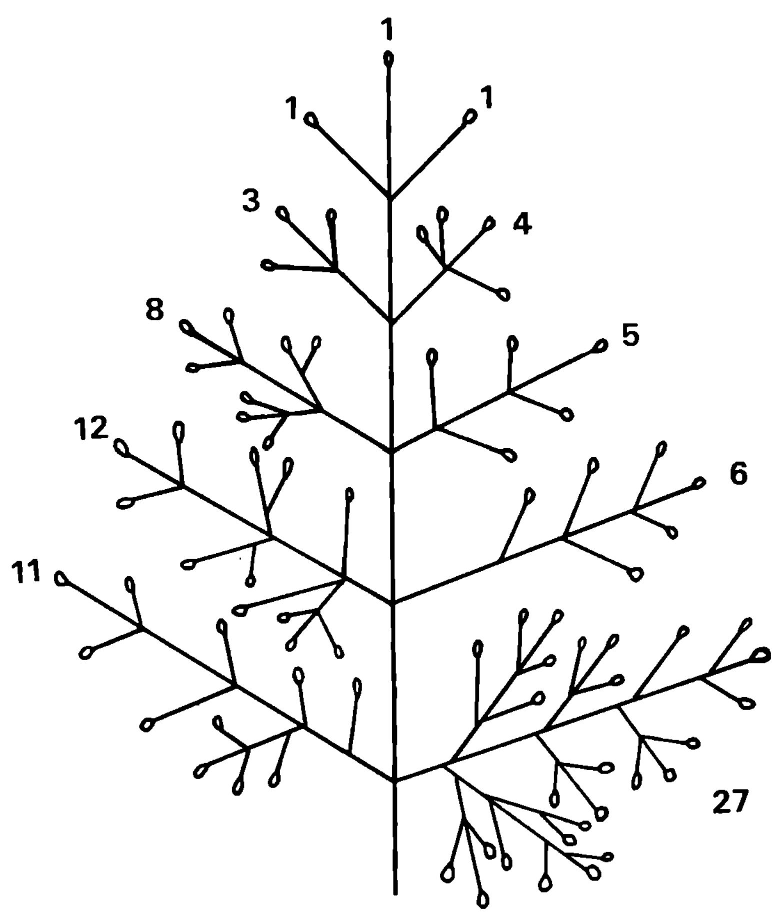

Figure 17. Method of counting number of live shoots on a branch.

Table 50. Regional mean number of shoots per branch at Achnashellach, Wykeham, Millbuie and Clashindarroch

Region	Number of shoots per branch
North Coast BC	22.25
South Coastal	36.33
Skeena River	15.20
Central Interior BC	13.60
South Interior BC	13.28
Northern Interior USA	11.55

per plot in each replicate of the experiments at Achnashellach, Wykeham, Millbuie and Clashindarroch. The mean number of shoots per branch varied from 10.2 for the rather spindly East Washington origin to 54.5 for the very bushy SW Lincoln County, Oregon seedlot in the South Coastal group. The seed origin differences were highly significant at each site and the regional means across all sites are shown in Table 50.

The South Coastal group had by far the largest number of shoots, with the North Coastal origins next. The Queen Charlotte Islands origin had significantly more shoots than the one from Sonora Island and New Westminster in the Millbuie experiment. The Skeena origins generally had more shoots than those from the other inland origins.

Needle characters

Cannell (1974) also calculated the total number of needles per tree, the volume per needle pair and the total volume of needles per tree (Table 51). The data again emphasise the much greater bushiness of the South Coastal origins and show how the Terrace seedlot (Skeena River region) had almost double the foliage volume of the Anahim Lake (Central Interior BC region) origin. Although Sisters/La Pine (which is subspecies *murrayana*) had significantly larger needles, mainly due to their greater width, its total volume of needles per tree was less than that of the shorter Skagway, Alaskan origin.

Needle dimensions have been assessed on many occasions in British experiments (Macdonald, 1954; Jeffers and Black, 1963). Results from these earlier studies at Millbuie were shown by Lines (1976a). When results from the 1938 and 1939 sections are amalgamated (Table 52) they show a clear picture of consistent grouping by seed regions, with the South Coastal region having the shortest needles, followed by the North Coastal region. The Puget Sound origin from Shelton had needles similar in length to those from the Pacific coast of Washington. Origins

Table 51. Needle characteristics of six origins in Eddleston 4 P66 (± standard error) (from Cannell, 1974)

Identity number	Seed region	Seed origin	Total number of needles per tree (x 10^3)	Volume per needle pair (mm^3)	Total volume of needles per tree (dm^3)
(7987) 2	Alaska	Skagway, Alaska	19 ± 2.8	83 ± 6.1	1.5 ± 0.19
(7951)	South Coastal	Newport, Oregon	56 ± 5.3	75 ± 5.5	4.1 ± 0.51
(7116) 3	Vancouver	Sooke, BC	23 ± 2.5	75 ± 5.1	1.6 ± 0.15
(7114) 1	Skeena River	Terrace, BC	22 ± 1.8	92 ± 5.2	2.0 ± 0.16
(7113) 3	Central Interior BC	Anahim Lake, BC	12 ± 1.2	90 ± 8.4	1.1 ± 0.13
56/657	Oregon Cascades	Sisters/La Pine	12 ± 1.4	109 ± 8.6	1.3 ± 0.22
Least significant differences at 5%			8.1	15.0	0.76
Mean			24.9	85.1	1.95

Table 52. Needle length (mm) measured in different years at Millbuie 1 P38-39

Region	Identity number	Seed origin	Year of measurement			Mean	Region mean
			1951	1960	1966		
North Coastal	34/25	Sonora Island & New Westminster	50.9	47.9	52.7	50.50	50.30
	36/42	Queen Charlotte Islands	50.1	52.4	47.8	50.10	
South Coastal	34/39	Coast USA (Long Beach?)	44.1	51.1	48.9	48.03	48.26
	34/40	Shelton, Puget Sound	45.7	50.3	51.4	49.13	
	36/505	Long Beach? ex Auchterawe	46.9	53.4	48.1	49.47	
	36/506	? ex Ruttle Wood	42.6	50.2	–	46.40	
Skeena River	36/40	Terrace	51.8	56.2	53.2	53.73	59.70
	35/22	Hazelton	56.1	62.0	–	59.05	
	36/43	Hazelton	54.3	60.8	58.9	58.00	
	35/18	Smithers	57.5	64.5	63.4	61.87	
	36/41	Smithers	60.1	70.4	67.1	65.87	
Central Interior BC	34/24	Prince George	59.1	72.0	71.9	67.67	67.80
	35/17	Prince George	64.3	73.1	71.0	69.47	
	36/22	Prince George	63.0	73.0	63.1	66.37	
	35/19	Williams Lake	60.9	73.0	69.2	67.70	
South Interior BC	35/20	Vavenby	60.4	66.1	62.0	62.83	64.22
	34/23	Shuswap Lake	58.5	71.5	65.8	65.27	
	35/21	Salmon Arm	61.2	67.2	65.3	64.57	
East Washington/Idaho	35/53	East Washington	58.8	63.9	–	61.35	62.06
	34/69	Priest River, Idaho	61.0	64.5	62.8	62.77	
Oregon Cascades	35/59	Klamath	54.3	65.6	64.6	61.50	61.50
Standard error ±			1.5	1.8	2.5		
Differences significant at			***	***	***		

from the Skeena River were the third shortest, and there was an increase in needle length with increasing distance from the coast, i.e. those from Terrace were shorter than those from Hazelton, which were shorter than those from Smithers. The Smithers seedlots did not differ significantly from those in the South Interior BC, East Washington and Oregon Cascades groups. The Central Interior of BC group had the longest needles. Similar patterns of needle length have been found at several other sites.

Critchfield (1957) studied needle dimensions of trees within the native range and on samples sent from British experiments, while Roche (1962) studied needle dimensions on populations from the coast of British Columbia and assessed needles of Critchfield's collection growing at Placerville. In the juvenile stages the South Coastal origins often have longer needles than interior sources (Critchfield, 1957) and these juvenile effects may last for up to 4 or 5 years from seed. Needles of lodgepole pine continue to extend throughout their first season from an intercalary meristem at the base of the needle and the course of seasonal expansion differs with seed origin (Thompson, 1976). Needle length in any year is greatly affected by nutritional status and weather conditions. Needle length may also be greatly reduced in the year following a heavy sawfly attack.

Needle length in a given year varies significantly between sites. Table 53 shows the variation at three contrasting sites. There was a highly significant (***) correlation between needle length for seed origins at all sites, but the mean needle length at Achnashellach was much the shortest. Analysis across sites showed a much higher variance ratio for sites compared with the ratio for seed origins. These large site effects mean that it is impossible to identify an unknown seed origin with any certainty by needle length alone.

To investigate whether additional needle characteristics would help in identification, a detailed study was carried out at Millbuie

Table 53. Needle length (mm) on three sites in 1960

Identity no. and region	Seed origin	Clashindarroch	Achnashellach	Millbuie	Mean	Region mean
North Coastal						
36/42	Queen Charlotte Islands	47.6	38.5	52.4	46.2	46.2
South Coastal						
36/505	Coast USA ex Auchterawe	52.6	45.7	53.4	50.6	48.8
38/510	Coast USA ex Ruttle Wood	47.8	40.1	53.1	47.0	
Skeena River						
35/18	Smithers	64.1	57.4	64.5	62.0	
35/22	Hazelton	57.7	50.4	62.0	56.7	
36/40	Terrace	55.1	44.1	56.2	51.8	58.1
36/41	Smithers	66.3	56.5	70.4	64.4	
36/43	Hazelton	56.7	49.4	60.8	55.6	
Central Interior BC						
35/17	Prince George	66.7	60.3	73.1	68.7	
36/22	Prince George	67.8	53.5	73.0	64.8	66.7
35/19	Williams Lake	67.4	59.5	73.0	66.6	
South Interior BC						
34/23	Shuswap Lake	71.8	59.2	71.5	67.5	67.5
Site mean		60.1	51.7	63.6		

1 P38 in 1966. Nineteen origins were selected and 500 needles from each measured for length to the nearest 0.5 mm and width to the nearest 0.025 mm. Needle thickness was measured under a microscope to the nearest 0.025 mm on needle transverse sections at the mid point on 100 needles per origin. The number of resin canals in the upper, middle and basal sections of the needles was also counted (see Table 54).

Table 54. Needle characteristics at Millbuie 1 P38-39 assessed in 1966

Region	Identity number	Seed origin	Width (mm)	Thickness (mm)	Ratio of length: thickness	No. of resin canals at tip of 5 needles
North Coastal	34/25	Sonora Island & New Westminster	1.43	0.82	64.9	8.0
	36/42	Queen Charlotte Islands	1.51	0.86	55.2	10.0
Region mean			1.47	0.84	60.0	9.0
South Coastal	34/39	Coast USA (Long Beach?)	1.37	0.83	59.1	1.5
	34/40	Shelton, Puget Sound	1.44	0.85	60.7	2.7
	36/505	Long Beach? ex Auchterawe	1.37	0.80	60.1	2.1
	37/56	Grays Harbor	1.36	0.81	60.7	4.4
Region mean			1.38	0.82	60.2	2.7
Skeena River	36/40	Terrace	1.50	0.84	63.4	5.5
	36/43	Hazelton	1.63	0.91	64.9	4.5
	35/18	Smithers	1.62	0.89	71.1	3.1
	36/41	Smithers	1.62	0.90	74.6	4.7
Region mean			1.59	0.88	68.5	4.5
Central Interior BC	34/24	Prince George	1.63	0.90	79.7	3.6
	35/17	Prince George	1.62	0.89	80.4	4.2
	36/22	Prince George	1.51	0.85	73.8	1.2
	35/19	Williams Lake	1.61	0.88	78.8	2.5
Region mean			1.59	0.88	78.2	2.9
South Interior BC	35/20	Vavenby	1.51	0.82	75.3	3.2
	34/23	Shuswap Lake	1.56	0.86	76.8	2.8
	35/21	Salmon Arm	1.56	0.88	74.5	4.6
Region mean			1.54	0.85	75.5	3.5
Idaho	34/69	Priest River, Idaho	1.59	0.88	71.5	3.9
Oregon Cascades	35/59	Klamath	1.80	0.99	66.7	2.0
Standard error ±			0.04	0.02	2.7	1.1
Differences significant at			***	***	***	***

It will be seen that seed origins varied highly significantly in every character assessed. For width, needles from the two coastal regions were significantly narrower than needles from interior region trees. However, Terrace, in the Skeena River region, was closer to the coastal sources. The sub-species *murrayana* origin from Klamath had such wide needles that it could be separated from all the others merely by the naked eye.

Needle thickness showed rather less variation between seed origins, except for the outstandingly thick Klamath origin. In the absence of terpene testing facilities, the ratio of needle length to thickness offers a good opportunity for discovering the seed region of a stand whose identity is unknown. From Table 54 it can be seen that the two coastal regions could not be distinguished from each other, though these are usually separable on other characters such as growth rate. Similarly, the Central and South Interior BC regions could not be separated, although they should be distinct from the Skeena River origins. The number of resin canals showed the greatest seed origin variation in the upper section, though the general pattern was the same at the middle and base of the needles. The variation in resin canals is more erratic than with the other needle characters, though the North Coastal origins had by far the most resin canals.

These patterns of needle characters are similar to those found in the natural populations by Critchfield (1957). However, he found that elevation of seed origins had a marked influence on needle dimensions, whereas when grown in plantations at relatively low elevations, needle length of inland origins was proportionately greater than that of coastal origins.

Needle retention is also greatly affected by site conditions, the most important factors being nutritional status and exposure. The very poor needle retention of the Vancouver group, particularly origins from the mouth of the Fraser River such as Lulu Island, has already been mentioned in Chapter 5. At Millbuie 1 P38/39, needle retention at 17 years varied from 6.4 years for the Puget Sound origin from Shelton to 4.2 years for the origin from Priest River, Idaho (Lines, 1976a). The North Coastal group had the next best retention, while the Skeena River group retained their needles longer than the other inland groups. Seed origin differences were very highly significant. A similar pattern was observed at Achnashellach 24 in this series (Table 55).

Table 55. Needle retention at 17 years at Millbuie 1 P38/39 and Achnashellach 24 P37/39

Region	Seed origin	Needle retention			
		Millbuie 1 P38		Achnashellach 24 P37/39	
		Years	Mean	Years	Mean
North Coastal	Sonora Island	5.6	5.65	5.9	5.75
	Queen Charlotte Islands	5.7		5.6	
South Coastal	Long Beach	6.3		5.5	
	Shelton	6.4	6.23	5.5	5.50
	Auchterawe	6.0		–	
Skeena River	Smithers	5.2		4.9	
	Hazelton	5.7		5.3	
	Terrace	5.4	5.38	5.2	5.24
	Hazelton	5.4		5.6	
	Smithers	5.2		5.2	
Central Interior BC	Prince George	4.9		4.8	
	Prince George	4.6	4.72	3.6	4.60
	Prince George	4.4		5.4	
	Quesnel	5.0		4.6	
South Interior BC	Vavenby	4.5		4.3	
	Shuswap Lake	4.8	4.83	5.2	4.63
	Salmon Arm	5.2		4.4	
East Washington/Idaho	East Washington	4.8	4.50	4.1	4.00
	Priest River, Idaho	4.2		3.9	
Oregon Cascades	Klamath	4.7	4.70	4.8	4.80
Standard error ±		0.48		0.30	
Differences significant at		***		**	

Neither Millbuie nor Achnashellach is a particularly exposed site and poor needle retention and associated foliage browning has been a major concern of forest managers in the large pine forests planted in north Scotland in the 1960s on sites with much worse topographic exposure. At that time, seed origins that are now known to be much more susceptible to foliage browning than any of those shown in Table 55 were widely used, i.e. those from the Lulu Island area at the mouth of the Fraser River and Sooke on Vancouver Island. Seed origin differences in needle retention are most apparent in the juvenile stage before canopy closes, and in an experiment in which different origins occur randomly mixed with others, those with good needle retention soon begin to shelter those with inherently poor retention. The age factor is also important, as shown in the many trial plantations established on exposed sites in the early 1950s (Lines and Howell, 1963). Most of these used Lulu Island origins, giving trees with very poor needle retention. However, even on these testing sites, when the trees were 15–20 years old, there was a noticeable improvement in needle retention.

Effect of crown variation on suppression of ground vegetation

The speed of suppression of competing vegetation varies widely between different seed origins. In the extreme case of the very slow-growing interior origins, which also have thin crowns, complete suppression may never occur, e.g. in the extensive plot from Klamath (at a high elevation in the Oregon Cascades) at Millbuie 1 P38. Vegetation suppression was assessed in 1954 in the Millbuie 1 P38/39 experiment (Lines, 1976a) when the trees were 16–17 years old. Scores (1 = nil to 5 = complete) were allotted to each of the five replicated plots per origin. Highest scores for suppression were gained by the South Coastal and North Coastal groups, with the Skeena group the best of the interior origins and no significant difference occurred between the other inland groups, apart from Klamath, which was significantly the poorest. Vegetation suppression was correlated better with the 'bushiness' factor (total shoots per plant shown in Table 50) than with mean height.

Heather suppression was assessed using a similar scoring method in the IUFRO experiment at Arecleoch 5 P72 when assessed for height at 10 years. Vegetation suppression will be influenced mainly by canopy density and canopy closure. In this experiment, the spacing and survival were virtually identical for all seed origins, so that canopy closure in terms of branch length and canopy density or bushiness, will be the important factors. Neither was measured directly in this experiment. As already noted in Chapter 15, branch length was broadly related to tree height. Although there was a clear increase in suppression with increasing mean height, the rankings for the two show interesting discrepancies (Table 56).

Table 56. Height (m) and vegetation suppression scores at 10 years in Arecleoch 5 P72

Region	Mean height (m)	Rank (height)	Heather suppression score*	Rank (heather suppression)	Score adjusted for height by covariance	Rank on adjusted score
Alaska	2.64	7	2.58	5	3.46	1
North Coast BC	2.87	6	2.83	4	3.37	2
South Coast BC	3.47	4	3.11	3	2.77	5
Puget Sound	3.66	2	3.33	2	2.71	6
Oregon/California Coast	3.89	1	3.89	1	2.93	4
Yukon	1.85	8	1.00	8	3.03	3
Skeena River	3.19	5	2.33	6	2.40	7
South Interior BC	3.59	3	2.00	7	1.48	8

* Score 1 = No suppression to 5 = Complete suppression

A strong correlation between height and heather suppression indicated that by removing the effect of height by covariance analysis, the adjusted values would show more clearly the inherent ability of the different seed origins to suppress heather. This is shown for individual seed origins in Figure 18. Note how all the bushy-crowned Alaskan and North Coastal origins are below the regression line, whereas the ones above the regression line are the less densely crowned ones from the Interior or South Coast of BC (in the terpene group from Vancouver). The Alaskan origin 2010 from Gravina was particularly effective in suppressing heather, being equally effective as the much taller origin 2071 Mesachie Lake.

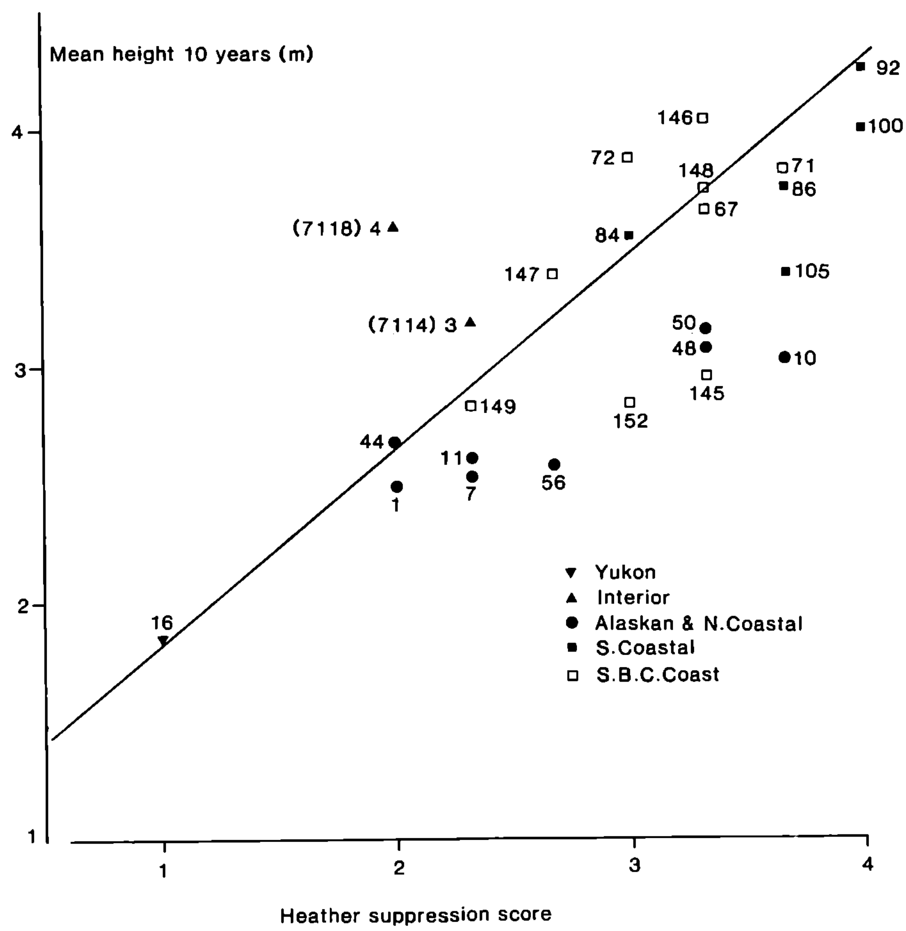

Figure 18. Graph of mean height (m) at 10 years plotted against score for vegetation suppression at Arecleoch 5 P72.

Chapter 17

Bark and cone characteristics

Bark characters

Bark type and thickness show very wide variation in lodgepole pine, both within its native range (Critchfield, 1957; Aldhous, 1976) and in Britain (Lines, 1966). A major study of bark thickness (expressed as bark percentage) in British Columbia was made by Smith and Kozak (1981). They showed that the bark percentage varied from 4.0 in the East Kootenay region to 8.4 in the South West Dry Belt. Coastal stands varied from 6.3 to 6.8. These data confirm observations by Aldhous (1976) of the very thick bark on trees in the Southern Interior Dry Belt, e.g. at Squilax (see his Plate 10), which is 20 miles north west of Salmon Arm. As noted in Chapter 2, these thick-barked ecotypes have developed by the selective action of frequent fires, whereas within a short distance on high elevation sites with a cool, moist climate, most trees have quite thin bark. Data on bark thickness in 1954 at Millbuie 1 P38 (Lines, 1976a) showed very highly significant differences, both between seed regions and within them (Table 57).

The Skeena River, Central Interior of BC and Oregon Cascades regions had the thinnest bark, whereas the South Coastal, Southern Interior BC and USA Interior regions had much thicker bark. Because trees with higher diameter will tend to have thicker bark than trees with lower diameter, bark samples were taken at a standard diameter of 10.5 cm. The mean diameter at breast height of the trees ranged from 8.29 cm (Klamath) to 10.83 cm (Shelton) so that most samples were from below breast height.

Data from measurements made on 1642 trees in British Sample Plots (Christie, personal communication) show a similar pattern (Table 57).

Table 57. Bark thickness (mm) at Millbuie 1 P38 (17 years) and sample plot bark %

	Millbuie 1 P38		Sample plot bark percentage		
Region	**Bark thickness (mm)**	**Number of origins**	**Bark %**	**Standard error ±**	**Number of trees in sample**
North Coast BC	1.50	1	10.9	0.22	108
South Coastal	2.73	2	14.1	0.21	439
Skeena River	1.18	2	11.7	0.22	142
Central Interior BC	1.34	3	10.0	0.13	330
South Interior BC	2.66	3	12.6	0.23	436
Inland USA	2.72	2	12.0	0.23	110
Alberta	–	–	11.3	0.34	77
Oregon Cascades	1.22	1	–	–	–
Standard error ±	0.27				
Differences significant at	***				

Table 58. Bark thickness at 20 years in Glentrool 17 P59 and Borgie 9 P59

Region	Identity number	Seed origin	Bark thickness (mm) at			
			Glentrool	Rank	Borgie	Rank
South Coastal	56/654	Long Beach, Washington	6.6	1	6.9	1
	56/655a	North Bend, Oregon	5.3	2	5.6	4
	56/655b	Newport, Oregon	4.5	6	4.6	6
	56/655c	Tidewater, Oregon	4.6	5	4.1	7=
	56/655d	Florence, Oregon	4.3	7	5.3	5
	56(4118) 501	Washington ex Inchnacardoch	4.8	4	6.0	2
Puget Sound	56/656	Keyport	5.1	3	6.0	2=
Vancouver	56/658	Ladysmith, Vancouver Island	3.2	8	4.1	7=
South Interior BC	56 (4118) 500	Hat Creek ex Inchnacardoch	2.3	9	2.8	10
Cascades	56/657	Sisters/La Pine, Oregon	2.1	10	2.6	11
	56/651	Oakbridge, Oregon	2.0	11	3.0	9

Bark percentage was calculated using the formula:

$$\text{Bark \%} = \frac{\text{Volume over-bark} - \text{volume under-bark} \times 100}{\text{Volume over-bark}}$$

In the experiments planted at Glentrool and Borgie in 1959 bark thickness was assessed in 1979 with the results shown in Table 58.

These confirm the thick bark on seed origins from the South Coastal and Puget Sound regions and the thin bark on those from the Oregon Cascades. It is interesting that the Southern Interior BC trees with thin bark came originally from an elevation of 1500 m and hence from a cool, moist site, whereas the trees from this region in Table 57 with much thicker bark probably came from lower elevation fire-prone sites. There is a good correlation in bark thickness on the two sites, showing that inherent seed origin differences are a major cause of variation.

Bark stripping

Bark stripping of lodgepole pine by red deer in the pre-thicket and thicket stages is a major problem in Galloway and the Highlands of Scotland. McIntyre (1976) found that in some sample areas in Galloway 60% of the lodgepole pine over 10 years of age had bark stripping wounds. It can affect increment, reduce timber quality and increase the risk of fungal infection. Damaged trees may later be more prone to windsnap or snow break. Melville (Internal Reports, Forestry Commission, 1979/80) has shown large differences in damage among a range of seed origins in the Glentrool 17 P59 and Achnashellach 31 P64 experiments. Data from Achnashellach 31 are given as an example in Table 59.

A detailed assessment of bark stripping by red deer was made by Wildlife Research Branch in 1979, each of about 24 trees per plot being scored 1–4 for increasing amounts of damage. The percentage of the total maximum score was then calculated and plotted against bark thickness (see Figure 19). The correlation was significant (r = 0.66*). In this experiment the South Coastal and Puget Sound origins had very much thicker bark than origins from the Central and South Interior of BC and the Skeena River region. In the Vancouver region, Langley had very thin bark, whereas Nanaimo, Vancouver Island had much thicker bark. It is clear that the Long Beach origin suffered much less damage than the three Vancouver region origins, which suffered similar damage, despite wide variation in bark thickness (1.6–3.8 mm). Macdonald (1954) had earlier noted less deer damage on the heavy-branched South Coastal origins than on light branched inland ones. Elliott (1985) noted bark stripping may be attributed to three factors:

1. site factors, such as tree spacing and ground vegetation;

2. morphological factors, such as growth habit, branchiness and degree of bicyclic growth;

3. chemical and physical features of the bark.

Tree spacing will influence speed of canopy closure. Many of the badly damaged Galloway stands were intimate mixtures of lodgepole pine and Sitka spruce. On infertile or frosty sites, the spruce was checked, thus allowing easier deer access. In Figure 19, many of the seed origins below the line of correlation have stronger branching or bicyclic growth, whereas those above the line tend to have weak, spindly branching. The chemical features of the bark were the main subject of Elliott's thesis. He showed that 'when given a choice between bark from different origins, deer are capable of selecting bark with the highest digestability', i.e. those with higher nitrogen and lower fibre levels.

Cone characters

Within the native range nearly all trees in coastal stands open their cones between the end of August and early October. Inland trees vary from almost complete serotiny (i.e. their cones remain closed indefinitely, until fire breaks the resin bond between the scales), to the open-cone condition, where serotinous cones are unknown (Critchfield, 1980a). Serotiny is absent from the sub-species *murrayana* populations in the southern Cascades and Sierra Nevada. Serotinous cones are common in the sub-species *bolanderi* on the Mendocino White Plain and in another isolated population in the Siskyou Mountains of Del Norte County, California. Viereck and Little (1972) noted closed cones in the coastal populations near Skagway, Alaska and suggested these showed the influence of the nearby populations of sub-species *latifolia* in the Yukon. Closed cones had been observed earlier in this area by Aldhous and Harris (Aldhous and Maxwell, 1966). Mature stands in the interior of British Columbia show large variation in the frequency of trees with serotinous cones: high towards the Yukon border and less than 35% in some stands in the Interior Wet Belt of south-east BC (Illingworth, 1970).

The serotinous habit develops as the tree ages. Various authors quoted by Critchfield (1980a) give the critical age for development of serotiny as from 17 to 60 years. In Britain, few stands of known seed origin exceed 60 years, so that although the true serotinous habit has not yet been observed here, the reason could be either our mild maritime climate, or the immaturity of British stands. Lodgepole pine in Britain usually retain their cones for many years and in wet weather the cone scales close, giving the false appearance of serotiny. As rotations for lodgepole pine are unlikely to exceed 60 years here, it can be concluded that cone serotiny will be of merely academic interest in Britain. The lack of serotiny means that where conditions are suitable, natural regeneration is often profuse around British stands over about 20 years old, and where forest nature reserves adjoin commercial plantations, some control of natural regeneration may be necessary.

Table 59. Bark thickness (mm) and deer damage (% of maximum score) at Achnashellach 31 P64

Region	Identity number	Seed origin	Bark thickness	% of maximum damage score
North Coastal	(7987) 2	Skagway, Alaska	3.1	36
	(4138) 500	Queen Charlotte Islands ex Kirroughtree	3.4	31
		Region mean	3.2	34
South Coastal	(7972) 1	Long Beach, Washington	5.9	24
Puget Sound	(7974) 1	Glacier, Washington	6.0	30
Vancouver	53/627	Langley (Lulu Island type) BC	1.6	47
	(7116) 5	Nanaimo, Vancouver Island	3.8	46
	(7116) 3	Sooke, Vancouver Island	2.4	45
		Region mean	2.6	46
Skeena River	(7119)	Nass River	1.3	46
	(4138) 501	Terrace ex Kirroughtree	2.6	33
	(7114) 1	Terrace	1.6	42
	(4127) 500	Hazelton ex Loch Ard	2.7	31
		Region mean	2.0	38
Central Interior BC	58 (7113) 3	Anahim Lake	2.5	47
	60 (7113) 3	Anahim Lake	1.8	38
	(4127) 501	Prince George ex Loch Ard	3.0	31
	(7113) 2	Quesnel	2.5	40
	(4265) 500	North BC ex Wykeham	2.2	45
		Region mean	2.4	40
South Interior BC	(7118) 2	Penticton	1.8	38

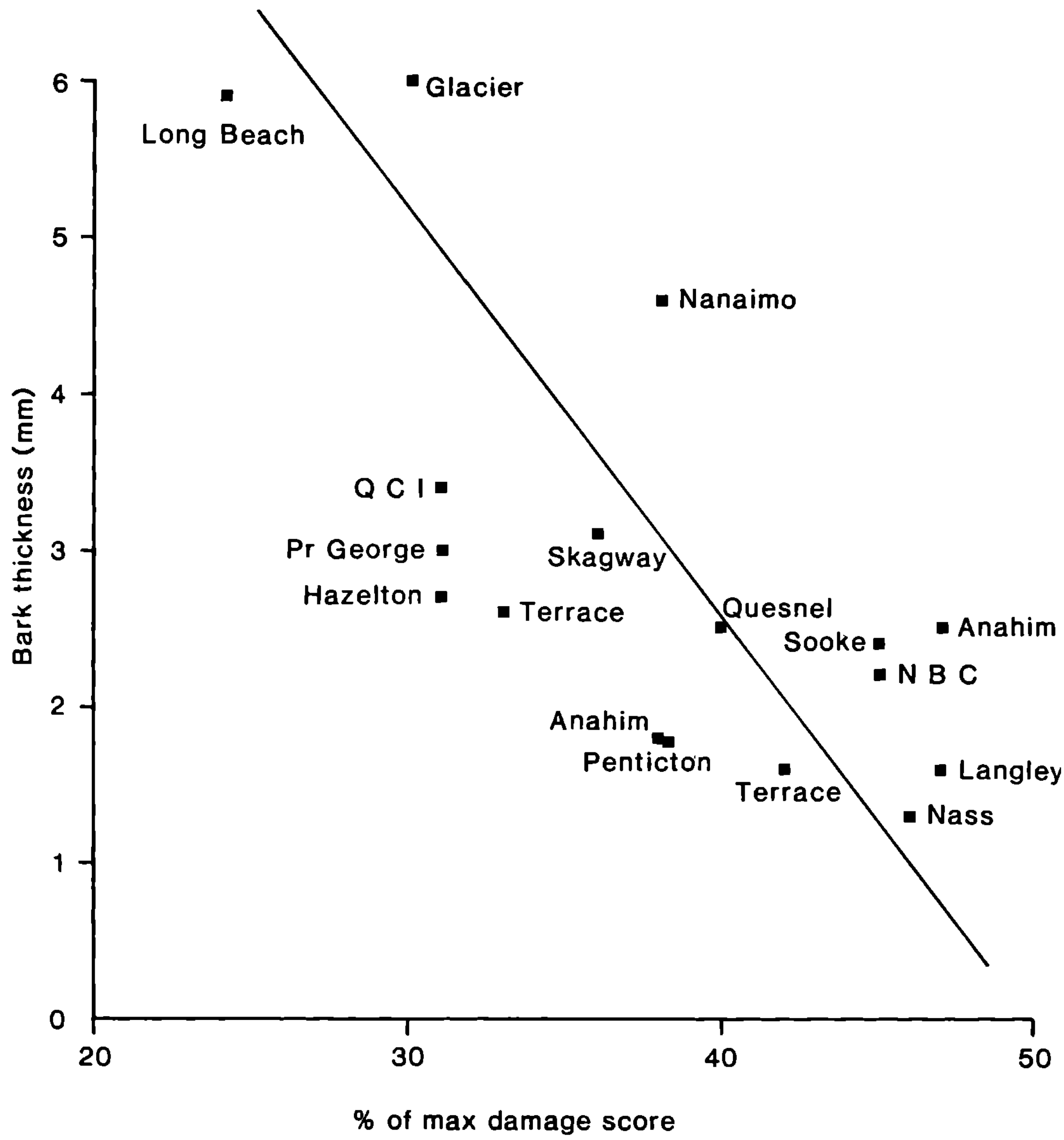

Figure 19. Relationship between percentage of deer damage and bark thickness.

Chapter 18

Discussion on choice of seed origins

General uses

From what has already been discussed, lodgepole pine is likely to have two major roles in British silviculture within the foreseeable future: firstly as a nurse to Sitka spruce or other possible nutritionally demanding species (e.g. artifically produced hybrids between Sitka spruce and either *Picea glauca* or *Picea engelmannii*); and secondly as a pure plantation crop on sites where either spruces or Corsican pine are liable to climatic stress or very likely to go into check unless given repeated herbicide and fertiliser application. The third possibility of the insurance mixture has disadvantages that were discussed in Chapter 14.

Nursing mixtures

For use in mixture with spruce, the characteristics that are of greatest importance are a bushy form of tree that can grow reliably on a range of exposed sites and retain its needles for at least 3–4 years, even where the site is poor nutritionally. Its growth rate, at least of the lower branches, should be fast enough to cover the ground vegetation before the beneficial effects of ground preparation and initial fertilisation begin to wane. On the other hand it must not grow so fast that it competes with the spruce to such an extent that the leading shoot of the spruce is damaged by coarse branches of a taller pine waving in the wind. Both observation of existing mixed stands and comparison of relative growth rates in experiments show that most South Coastal origins grow too fast and by 10–15 years will have already partially suppressed the spruce. At the other extreme, slow-growing interior sources are almost as bad, as they take much longer to form broad crowns and suppress the ground vegetation. While much less of a threat to the spruce, they will also give a much reduced nursing effect. The best origins are undoubtedly from Alaska and Queen Charlotte Islands, which combine effective heather suppression with relatively slow height growth, e.g. Klawack River, Alaska; Masset Road and Mayer Lake, Queen Charlotte Islands were very effective at Arecleoch (as shown in Figure 18). By comparison, the faster-growing Mount Ida origin was much less effective in suppressing heather in this experiment due to its more open crown. The Skeena River origin from Hazelton grew at the same rate as the Queen Charlotte Islands seedlots so would not have offered a threat to spruce on this site. However, its ability to suppress heather was considerably less and the potential nursing effect thus probably reduced. If Alaskan or Queen Charlotte Islands origins are not available, then the preferred substitutes are those from the North and West Coast of Vancouver Island, such as Port Hardy or Tofino. Sonora Island or Campbell Island are other suitable alternatives. Origins from the Puget Sound and Vancouver regions either grow too fast on good sites, with a tendency to suppress the spruce, or on severely exposed sites (see Fiunary, Chapter 13) are likely to have such poor foliage retention that vegetation suppression would be long delayed. Origins from the Central Interior of BC would eventually suppress competing vegetation and most grow slowly enough to enable a high proportion of spruce to reach the final crop stage, though Alaskan origins are more efficient nurses.

Lodgepole pine as a pure plantation

If pure plantations are to be established then the forest manager should realise that it is virtually impossible to obtain simultaneously: fast height growth, high volume production, good stem form, good consistency (in the sense of good growth over a range of different sites), low susceptibility to wind and snow damage, good resistance to climatic damage on exposed sites and resistance to bark stripping. There is an option of placing most emphasis on good stem form, relatively slow growth and the prospect of higher quality timber, or even the possibility on some sites of high value transmission poles. An alternative option is for faster-growing origins for bulk production of small roundwood on a short rotation. The choice will be constrained by local site conditions; if these are very variable the manager may be forced to use more than one seed origin or to select one which is very tolerant of poor conditions, yet not capable of growing fast on the better sites.

Use on poor sites

The main use for lodgepole pine is on the poorest end of the range of sites, whether these are very infertile peatlands, heathlands of more quartzitic type, exposed upland moorlands with heather, basins subject to repeated frost, low status sites too rocky and steep to plough, or sites in areas of industrial pollution. In its native range lodgepole pine is adapted to growing on muskegs (wet peat swamps) that are waterlogged for much of the year. The Macaulay Institute, Aberdeen was the first to show the greater flooding tolerance of lodgepole pine compared with Sitka spruce on deep peat sites, where the water-table was controlled at a range of depths below the surface (Boggie and Miller, 1976). Coutts and Philipson (1978) have demonstrated the anatomical and physiological features that make lodgepole pine superior to Sitka spruce as a pioneer on wet sites. Its ability to root into partially anaerobic lower layers of the soil enables it to dry out wet peat sites appreciably quicker than spruce, though this facility is less evident on gleyed moist mineral soils. These special features are not exclusive to the origins that grow naturally on muskegs, so that Skeena River or Interior BC origins also possess this ability to adapt to a certain degree of soil waterlogging.

From the growth of pioneer crops of lodgepole pine on some of the poorest deep sites in Sutherland or Caithness there is now increasing evidence that these sites have been so much improved that spruce may be used in the second rotation. The devastating attack of pine beauty moth (*Panolis flammea*) on 18-year-old plantations at Rimsdale in 1976/77 (Stoakley, 1977; Leather *et al.*, 1987) resulted in the death of 360 ha of forest. This has been replanted largely with Sitka spruce, which is growing very well, even though the first rotation was only one-third of the normal length. No one would suggest growing a 'sacrificial' pioneer crop of lodgepole pine to prepare the site for Sitka spruce. However, the severe attacks of pine beauty moth nearly all began in stands of South Coastal origin. This is no longer used and Leather *et al.* (1987) have shown that some alternative origins are significantly less attractive to this insect. Nevertheless, pure lodgepole pine plantations on poor deep peat in this area are more risky than mixtures of Alaskan lodgepole pine and Sitka spruce.

Lodgepole pine also has a place on sites where Corsican pine is at risk from *Brunchorstia* dieback, caused by *Gremmeniella abietina*. These are upland sites with higher rainfall and cooler summers than on the optimum sites for this Mediterranean pine. There are large areas in the uplands of Yorkshire and the central Pennines where Corsican pine fails at elevations above 200 m and where different origins of lodgepole pine have grown well (Lines, 1984). The latest results from the 1977 experiment in the Pennines shows that the tallest of eight seed origins was from the Queen Charlotte Islands, nearly twice the height of one from Alaska and outgrowing one from the South Coastal region. In the North Yorkshire Moors, Corsican pine is again poised on a knife edge of being able to outgrow Scots pine easily at lower elevations and on south facing slopes, while on the plateau top it may fail from dieback. The Wykeham (55 P38) and Broxa (115 P70 and 126 P72) experiments show that lodgepole pine from the better South Interior BC and Skeena River groups grew at about General Yield Class 12 while adjacent Corsican pine was GYC 10 or less.

Silvicultural characteristics of the main groups of seed origins

The growth rate and other silvicultural characteristics of the main groups of lodgepole pine are summarised in Table 60. These will now be discussed region by region.

Alaskan region

These origins are characterised by slow growth, very bushy form and a high tolerance of exposure and poor soil conditions. There is little variation between seedlots within this region, except for the notably slower growth of the most northerly outlier (Yakutat) and less bushy form in those from the Skagway area. The 1954 experiments (Chapter 11) showed significantly lower basal area on the seedlot from Haines, which lies in the rainshadow area at the northern end of Lynn Canal. Skagway is 15 miles further inland and although trees in British experiments are clearly the sub-species *contorta*, their seed weight (Table 12) was close to that of the Yukon origins (Table 7). Skagway has been the main source of seed for Icelandic forests of this species (Sigurgeirsson, 1988) and the stands there are much less bushy and more inland in appearance than British stands of Skagway origin (Lines, 1990). The Icelandic seed was

Table 60. Characteristics shown by progeny of a range of lodgepole pine seed origins

Origin	Code	Growth rate	Crown density	Consistency	Stem form	Exposure tolerance	Tolerance of poor soils	Notes
Coastal Alaska	ALP (798)	4	1	1	1	1	2	Grow best in north Scotland. Ideal for mixture with Sitka spruce.
North Coastal (including QCI and north and west Vancouver Island)	(7111) (7112) (7116) part NLP	3	1	1	1	2	2	Hardy general purpose sources, second choice for mixture with Sitka spruce.
Vancouver (south and east Island and adjacent mainland)	(7116) part	2	2	4	3	4	3	Not recommended for exposed sites and avoid seed from delta of Fraser River (e.g. Lulu Island).
Puget Sound (rain shadow of Olympic Mountains)	(7973) SLP	2	2	4	3	4	3	Not recommended for exposed sites. Best in low rainfall areas.
Pacific Coast of Washington	(7971) (7972)	1	1	5	4	1	1	Useful for quick shelter on exposed infertile sites where stem form unimportant.
Oregon Coast	(7951) (7952)	1	1	5	5	1	1	Generally unsuitable, especially in north Scotland.
Inland Yukon	– (7121)	5	5	1	1	2	5	Unsuitable for use in Britain.
Skeena River	(7114) West KLP	2	3	2	2	3	3	General purpose sources for less exposed sites and mineral soils. May grow too fast for use in mixture with Sitka spruce.
Bulkley River	(7114) East	3	4	2	1	3	3	Second choice to Skeena. Stem form on some sources may be superior.
Central Interior of British Columbia	CLP (7113)	4	4	1	1	2	4	Hardy, well proven.
Southern Interior British Columba (includes NE Washington and Idaho)	ILP (7118)	2	4	3	3	3	4	Variable performance within this group. Forking can be serious. Best ones grow well on many sites.
East of Rockies (Alberta, Saskatchewan, Montana)	– (7123)	5	4	1	1	3	4	In general should be avoided.
Cascade Mountains of south Washington and Oregon	– (7957)	5	4	1	1	3	4	Good form, low production

Scoring: Very high = 1 to very low = 5 for each character probably collected further inland and closer to the Yukon populations only a few miles further north over the tree-less Chilkoot Pass. The true coastal origins are well suited for nursing mixtures with Sitka spruce as they quickly suppress competing *Calluna.*

Coast of British Columbia region

These show considerably more variation than Alaskan origins and, although six sub-divisions of this seed region can be distinguished on the basis of their silvicultural behaviour, they fall into two major types that are separated by their terpene type (see Table 1).

North Coastal terpene type

As noted in Chapters 12 and 13, origins from the North Coastal sub-region behave similarly to Alaskan origins, where those from the Queen Charlotte Islands are similar in bushiness, but appreciably faster growing. The latter are suitable both as nurses to Sitka spruce and as a pure plantation on some of the poorest sites, where Sitka spruce would require repeated nitrogen input. Table 27 shows that the total volume production of the oldest Queen Charlotte Islands origin (36/42) was much higher than might have been expected from its moderate rate of height growth (Table 27). Their stem form and resistance to wind and snow damage are high, though their dense crowns tend to produce rather knotty stems.

Vancouver terpene type

These origins are highly variable and include the fast-growing South-East Vancouver Island origins from Coombs and very similar IUFRO origins from Mesachie Lake and Sooke (see Table 43). Lund on the adjacent mainland was equally vigorous. However, this terpene type also includes origins from Lulu Island and Langley, which performed so badly in the 1950s and seedlots from Sooke planted in the 1960s, which were little better. The better origins from this area are particularly responsive to site quality and on less exposed sites of moderate fertility (for this species) they have produced vigorous stands of good form with little incidence of basal sweep. So far these origins have not been severely damaged by wind or snow in experiments up to 15 years of age. However, as they were not included in the replicated pre-war experiments and the Vancouver Island origins used in the 1950s and 1960s have not grown so fast as the later ones from this region, they should be used with caution even on the less exposed sites. The British Columbian seed zonation is a useful guide (see Table 1) and in particular seed from zone 1050 (Lower Fraser River) should not be used.

South Coastal region

This main seed region is divided into three sub-regions (see Table 1) of decreasing latitude along the Pacific Coast and a fourth, the Puget Sound, which experiences lower rainfall and a less oceanic climate. There is some variation between individual seedlots in growth vigour and bushiness along the Pacific Coast and the most southerly origins are sensitive to frost and perform poorly at high elevation in exposure. South Coastal origins for many years posed a serious dilemma. On the one hand, all the evidence from many experiments demonstrates the outstanding growth rate and foliage retention of these origins, and this led to this region being recommended for seed imports at first. Chapter 15 describes the considerable research efforts devoted to finding a technique that would reduce basal sweep and increase root:shoot ratios. The lack of a successful solution (apart perhaps from use of tubed seedlings) would have led to further research. However it now became apparent that the major problem with these origins was damage in the thicket and pole-stage from wind and wet snow associated with the very heavy crowns of these origins. A possible solution crossing these vigorous origins with a wind-firm less heavily crowned origin is currently under test. In the mean time use of these origins will be very restricted. There are some sites where conditions are so difficult, e.g. very infertile soils such as serpentines and quartzites, or extreme maritime exposure, e.g. the Faroe or Falkland Islands (Low, 1986; Lines, 1987a) that the only hope of getting trees to form a closed woodland is to use the most vigorous South Coastal origins. These would be essentially pioneer shelterbelts, whose main purpose was to provide shelter to help in establishing more tender species. For most sites this group of seed origins has no practical use due to its liability to wind and snow damage.

Origins from the Puget South sub-region show less variation between origins than those from the adjacent Vancouver area. However they share several characteristics with origins from that region, e.g. high response and rather poor relative growth on the most exposed sites. Basal sweep is common on susceptible sites, though less than on origins from the Pacific coast of Washington and Oregon. Wind and snow damage in the later stages is known from older experiments, though significantly less than in those from the Pacific coast region. The overall judgement on these seed origins is to give them low priority and to use them only with caution on less exposed sites and in areas where heavy wet snow is uncommon. Table 27 shows that the Olympic peninsula (Shelton) origin 34/40 at Millbuie had the second highest volume production at 47 years. This origin also had the second highest volume production in the Wykeham experiment.

Yukon region

These origins need not be considered further, as they are so ill-adapted to British conditions that their growth rate is impossibly slow.

Skeena and Bulkley River region

In the 1937–39 series of experiments, height growth and volume production of trees from this region was usually at or below average. In the 1970 series, the fastest growing origins are not far behind the better ones from the South Interior of BC group and on some poorer sites they were superior. There are appreciable differences between the extremes in this group due to elevation and distance from the coast. In general, vigour decreases as elevation increases and with greater distance from the coast. A number of other characteristics also shows similar variation within this region. The Terrace origin in particular shows a number of anatomical, morphological and nutritional characteristics that indicate its intermediate position between the broad coastal and inland groups. For example, its needle length was shorter than the rest of this group (see Table 52), but longer than that of coastal origins. The pattern of major nutrients in the needles of the Terrace origin was intermediate between the coastal and inland groups (Lines and Mitchell, 1970).

It is, however, convenient to consider the Skeena and Bulkley groups together as they generally perform in a broadly similar manner. Their response to improved site conditions is only slightly above average. This implies that they are not site specific. Their consistency of response was high (shown as low values in Table 38). Thus they can be regarded as moderately fast-growing general purpose origins for use on a broad range of sites. They are more likely to show phosphate and potash deficiencies on oligotrophic peats than North or South Coastal origins and on very exposed sites their foliage retention may be poor until canopy closure, thus delaying heather suppression. Stem form is usually good and they have less forking than trees of the South Interior of BC group.

Central Interior of BC region

Growth rates of origins from this area are generally significantly poorer than in the Skeena and South Interior BC groups. Stem form is generally good, though forking is more prevalent than on trees from the Skeena region. These origins are rather uniform in their behaviour, though origins from the north of the region or from high elevations (above 1000 m) grow significantly more slowly. These origins are relatively unresponsive to improved site quality, suggesting that they will perform relatively better on the poorer sites. The best individual origins are from the Upper Fraser River around Prince George and Vanderhoof in the North West Lakes area. These origins show nutrient deficiencies by their yellow foliage on poor peats within 6 years of planting and on such sites require top-dressing with phosphate and potash earlier than coastal sources. As the climate in their native range approximates to that of Moscow, they are not affected by severe cold. They grow well on drier eastern heathland soils where experiments have shown them to be a good alternative to Scots pine. They are less suitable for wet peat sites in maritime climates.

South Interior of BC region

Origins from this region include some that are inherently very fast-growing and of good form. The tallest origin from this area at 15 years in Mabie 10 P70 experiment was from Celista on the north shore of Shuswap Lake. This had a mean height of 8.4 m (equivalent to Yield Class 16) (exceeding the mean of the South Coastal group) but is unfortunately represented only at the Mabie site, due to the small amount of seed obtained. The shortest origin from this region at Mabie was the high elevation seedlot Esperon Lake 5.7 m tall (equivalent to Yield Class 10). Because they have been used in seed origin experiments over such a long period, the performance of origins from this region is well known. Their pattern of mean height and response to site quality was rather variable (Figure 14).

The Clearwater origin had the highest response but its relative growth rate over a range of eight sites has deteriorated as it became older, from being first in this regional group at the nursery stage to eighth out of 13 by 15 years. Table 27 shows that the volume production at Millbuie of seed origins from this group was in the poor end of the range, with 35/20 Clearwater, the least of all. Clearwater in the 1970 series had the lowest diameter among seed origins of this region at 15 years, though the mean value for diameter of this region at 15 years was higher than that for the Skeena River and Central Interior of BC regions.

Plotting height at 15 years on a map of this region (not reproduced) shows that the tallest origins all clump together close to the town of Salmon Arm, with poorer growth on peripheral sites, especially those from above 1000 m. There is a sharp transition to a much drier climate between the west end of Shuswap Lake and the town of Kamloops. In the period between 1930 and 1960, much seed was collected near Squilax, an Indian settlement just to the west of Shuswap Lake (Aldhous, 1976). This seed was imported under the name 'Shuswap Lake'. This is a low elevation, dry area, where frequent ground fires have swept through the forest. Conditions are very different in the forests on the moister north facing side of Mount Ida at 750-1000 m. It is strongly recommended that seed should in future be collected from well-grown trees on the latter type of site rather than from dry sites in the valley floor.

Alberta and Saskatchewan region

Trees from this region grow straight and normally do not suffer from wind or snow damage. That is about all that can be said in their favour, as their rate of growth is very slow and they tend to have thin crowns, which are not very resistant to winter blasting. In the long term they are likely to suffer resin-bleeding and dieback of the type noted in Chapter 4.

North Interior USA region

This region covers a wide area from East Washington to Montana and is represented by only five seedlots, some from unknown elevations. The best origins can grow fast in height, e.g. Priest River, Idaho at Millbuie (see Table 26) though their crowns tend to be spindly and they are not immune from basal sweep. Coming from a region whose climate differs greatly from that of Britain there is no justification for using these seed origins here.

Cascade Mountains of Washington and Oregon region

None of the origins from this area has grown sufficiently fast to encourage more wide-spread use and their delayed vegetation suppression, compared with the almost equally slow-growing Alaskan origins, does not suggest that they would be suitable in a nursing role. Stem form is good and there is some evidence that their basal area production is comparatively high for their height. This alone would not encourage widescale use.

Chapter 19

Conclusions and main recommendations

1. This Paper attempts to summarise and review the results from over 90 experiments covering a period of over 50 years of investigations into the suitability of different origins of lodgepole pine for various site types and silvicultural purposes.

2. The very wide geographical range of lodgepole pine and its ability to succeed on sites varying from deep acid bogs at sea-level in Alaska, through near perma-frost areas in the Yukon to semi-desert conditions in Colorado or tree-line forests at Yosemite emphasises its wide ecological tolerance. Over a long period, in each locality the population has become adapted to the particular site conditions and its characteristics genetically fixed. This adaptation to site and differentiation of behaviour persists when seeds are transferred to quite different conditions in Britain. This explains the extreme variation in growth performance in Britain of progeny from different parts of its native range. No other species shows such a wide range of behaviour in Britain. Seed origin experiments in overseas countries have further emphasised both its growth potential (particularly in northern Scandinavia) and the very strong seed origin x site interactions.

3. Although introduced into British arboriculture in 1853, and first tried in forest research from 1928, widespread use of lodgepole pine in forest practice began only about 40 years ago. Because different seed origins perform almost as though they are different species, much disappointment was caused among forest managers from the lack of reliable information about the characteristics of the seed origins available at the time plantations were established, or to guide seed purchasers about their specification.

4. As the research work proceeded, the complexity of the genetic variation within lodgepole pine became more apparent and the unsatisfactory nature of some of the older trials was realised. For example, seedlots were often purchased from commercial sources with vague details as to location and hence the performance to be expected of the particular origin. It costs the same to establish, maintain and assess a seed origin experiment with randomly selected, poorly documented origins as one with well-documented and carefully selected origins (such as the IUFRO series). With hindsight, much research effort would have been saved if a well-organised seed collection had been carried out much earlier in the course of these investigations.

5. Changes in establishment practice have had a marked effect on seed origin choice. For example, during the phase when planting pure Sitka spruce was general practice, then Alaskan lodgepole pine had hardly any place in British silviculture. When experiments showed that mixtures of Sitka spruce and Alaskan seed origins of lodgepole pine were very beneficial, it resulted in a vastly increased demand for Alaskan lodgepole pine seed, and the need to know what alternative origins might be used as substitutes when Alaskan seed was insufficient to meet requirements.

6. Research described in this Paper has been predominantly of a practical nature, so that results can be quickly used to advise on seed purchase and expected crop performance for certain purposes in different regions. However, by using these experiments and by close co-operation with the Research Division of the Forestry Commission, valuable contributions have been made by forest scientists investigating more fundamental aspects of seed origin variation and these have led to a better understanding of behaviour of different genotypes, e.g. the morphological/physiological studies by Cannell and his colleagues at the Institute of Terrestrial Ecology of the

Natural Environment Research Council, described in Chapters 8 and 9. The shoot terpene studies carried out within the Forestry Commission by Forrest (1980, 1981) were a major breakthrough in clarifying the regional pattern of genetic variation, which enabled the boundaries between regions to be based on independent biochemical evidence, rather than on speculative geographical or political boundaries. Nevertheless, there are wide variations in growth performance within some of the terpene regions, especially the Vancouver region (as noted above).

7. Patterns of flushing time, growth cessation, lammas growth and relative growth rates during the growing season have been shown to be strongly related to seed origin and may influence patterns of wood formation. Apart from the most southerly coastal origins, frost damage is very unusual in lodgepole pine under British conditions, though lack of frost hardiness is a major factor restricting the use of coastal origins in parts of Scandinavia. Daylength has a strong influence on flushing time and growth cessation, with far northern seed origins showing much earlier flushing and an extremely short period of shoot extension in Britain. Thus such seed origins are not able to utilise our very long growing season, a feature of the British climate that is exploited so effectively by Sitka spruce.

8. One of the main uses of lodgepole pine, now and in the immediate future is as a nurse to Sitka spruce on sites where pure Sitka spruce is liable to heather check. For reasons that are more fully explained in Chapter 14, it is wise to use a seed origin of lodgepole pine that is relatively slow-growing in height, and with a squat bushy form that effectively suppresses competing *Calluna*. The mechanism by which lodgepole pine in intimate mixture is able to act as a nurse has not yet been fully explained. Because the curves for height growth of young lodgepole pine are fundamentally different from those of Sitka spruce (Everard, 1974) a stand of lodgepole pine growing at Yield Class 10 is the same height at 10 years as a Sitka spruce stand of Yield Class 16. Thus, if a fast-growing origin of lodgepole pine is used, it may not act as a nurse but may tend to suppress or damage the spruce. Ideally the mixture should be self-thinning with a high proportion of the pine shaded out by the end of a fairly short rotation.

9. Susceptibility to damage by wind and snow is one of the main demerits of the faster-growing seed origins of lodgepole pine. The problem assumed major significance in the 1950s with the development of more intensive cultivation and heavier fertiliser applications, further accentuated by planting in the furrow bottom on mineral soils or on the top of high ridges on peatlands. South Coastal origins proved liable to develop a high proportion of trees with basal sweep and other fast-growing origins were affected to a lesser degree. No reliable silvicultural technique could be found to reduce this damage to an acceptable level and, although most stands later became temporarily stabilised in the thicket stage, this was merely a prelude to catastrophic damage from a combination of wind and wet snow in the later thicket or early pole-stage. Assessments showed that damage was highly selective and that most Interior sources and Northern Coastal ones suffered little damage at this later stage (see Chapter 15 for more detailed discussion of susceptible and resistant origins).

10. Although most attention has been given to studies of growth in height, diameter or volume, the form of different seed origins shows important differences, especially in forking of the main stem, the different patterns of crown and branch form, needle dimensions and bark type. The highest incidence of forking was found in origins from the South Interior of BC, where in one experiment 35% of the trees were affected. Observations in older experiments and in stands within the native range confirm that this tendency to fork is genetic and not caused by accidental damage, insect attack, etc. By comparison Northern Coastal origins had less than 10% of forked trees.

    The incidence of trees that produce more than one whorl of branches per annum varies considerably between seed origins. Very few multi-nodal trees occur in the South Coastal region and even fewer in the South Oregon and Californian coast. Multinodal trees are frequent in the Skeena River, South Interior of BC and some North Coastal origins. Crown density varies very widely between seed origins and has important silvicultural effects on the speed of suppression of ground vegetation in the establishment phase and on potential basal area production at a later stage. Although the rate of vegetation suppression was influenced by tree height, seed origins with the most bushy crowns killed the vegetation much faster than those of equal height with thin crowns. North Coastal seedlots were very efficient in this respect.

Bark type and thickness are strongly inherited with large differences between seed regions. Although interior seed origins have generally thinner bark than coastal sources, some North Coastal origins have thin bark, while trees from, e.g. Squilax near Shuswap Lake, BC tend to have thick bark, probably as a result of natural selection of fire-resistant individuals (Aldhous, 1976). The amount of bark stripping by red deer was significantly correlated with bark thickness, thick barked origins having least damage.

11. The growth patterns of origins from the main seed regions are now becoming reasonably well known and one of the striking results has been the finding that differences in height, diameter or volume were nearly always highly significant between the regional means, whereas differences within a region were much smaller and frequently non-significant. The implication is that prescriptions can be based mainly on these regional groups, rather than having to specify a particular locality, from which seed may not be available on a regular basis. However, it should be remembered that within several seed regions there are areas that would be important to avoid. For example, within the South Interior of BC region the dry valley-bottom sites to the west of Shuswap Lake and high elevation sites (above 1 200 m) should both be avoided. Similarly, within the Vancouver region Mesachie Lake would be quite acceptable, whereas Lulu Island and Langley would not. A coherent overall pattern of differences in growth rate between the seed regions runs through the whole series of experiments. This gives greater confidence in extrapolating results from those at 10 or 15 years in the younger experiments by using the 1937–41 series as a model for long-term growth rate.

It is necessary to continue assessments in some of the younger experiments that have large plots so as to detect changes in performance as the trees become older. The Clearwater origin in the 1970 series mentioned in Chapter 13 is just one rather obvious example. The main changes that are likely to occur are in those origins that show very fast early growth, but have spindly crowns that are likely to result in lower volume production, compared with those with slow early height growth and dense crowns that may well show the reverse pattern. There is already a suggestion that the Alaskan origins, which had such long lower branches during the early thicket stage, develop an appreciably narrower crown in the early pole-stage.

12. The main characteristics of interest to the forest manager for each seed region are outlined in Table 60 and their performance is discussed in Chapter 18.

13. Long-term susceptibility to snow and wind damage can only be determined by keeping a proportion of these experiments under observation for many years. Damage susceptibility is a vitally important aspect of seed origin choice and it would not be costly to make periodic inspections and assessments where necessary.

14. Timber quality has been mentioned briefly in this Paper in relation to compression wood of trees with lean or basal sweep. Brazier (1980) summarised the existing information in timber properties of different seed origins sampled at about 25 years of age in these experiments and concluded that in practical terms differences were often small, 'no provenance can be rated as unsuitable on the grounds of its timber characteristics, though differences in yield between them could well be appreciable. Provenance selection and stand management to favour a good stem form could be the most significant aspect in ensuring an adequate timber quality in lodgepole pine'.

Doubts remained about the timber properties of more mature timber. Accordingly, Marshall (1989) studied timber properties of seven seed origins in the Wykeham 55 P38 experiment when the trees where 48 years old and thus approaching rotation age. She found that bark thickness and percentage late wood were the only parameters that differed significantly between seed origins. Her results broadly confirm those of earlier investigators working in the same experiments when the trees were much younger. Marshall emphasises the much larger variation in wood characteristics between individuals within a seed origin compared with that between seed origins, suggesting that tree improvement by individual tree selection offers scope for higher density combined with increased tracheid length independent of growth rate.

Many stands of lodgepole pine exist for which records may have been lost, and in some cases the origin may be too vague (e.g. 'British Columbia') to allow the forest manager to make decisions on its future management or growth potential. To clarify identity the first step is to look at the general appearance of the trees in relation to the particular site factors. Foliage colour, crown and stem form can often indicate whether the stand is Inland or Coastal and growth rate (taking account of the particular site factors) will tend to separate northern from southern seedlots. If the trees have abundant male flowers (or gaps in the leafy shoots where these have been shed) then there is a strong indication that they are of the 'Lulu Island' type. Chapters 16 and 17 provide several other indicators of origin in terms of forking, number of inter-nodal whorls, crown spread, needle retention, 'bushiness', needle characteristics, bark and cone type. However, it must be stressed that site differences affect most of these characters and the only character that is completely unaffected by site is the terpene type. Unfortunately this requires specialised equipment to determine the terpene pattern, so that it is too expensive a method to use on a routine basis.

16. The future for lodgepole pine in British Silviculture will depend partly on national and regional forest policy and in particular on the quality of land released for forest use. Lodgepole pine is essentially a pioneer tree that can grow well on poor sites with minimal fertiliser input, and it is physiologically better adapted than the spruces for growth on deep peat bogs. It can be a substitute for Scots pine on poor heaths (where it can give higher production and, with certain origins, supply transmission poles). The seed origin experiments described in this Paper have given a sound foundation for current seed origin choice. However a programme of tree improvement at the individual tree level and using inter-provenance hybrids has been running for more than 20 years. The long-term future probably lies with the products of this breeding programme, which should provide trees with a combination of improved form, greater stability against wind and snow and enhanced resistance to diseases and insect pests.

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