BULLETIN 127

Forest Research

Choice of Sitka Spruce Seed Origins for Use in British Forests

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Foreword

Since its introduction in 1831, Sitka spruce has become the most widely planted and important commercial tree species in Great Britain.

Studies of the adaptive variation of species introduced into Great Britain have been a fundamental area of research since the establishment of the Forestry Commission. The establishment of seed origin trials and the interpretation of their results has spanned most of the careers of the authors of this Bulletin. Between them, they bring together unrivalled knowledge of Sitka spruce throughout its natural range in the Pacific Northwest, of experimental procedures in evaluating this variation under British conditions, and of analysis and interpretation of field data.

The Bulletin summarises seed origin research in Sitka spruce over a period of 70 years. It provides a background to the ecology of the species, its introduction to Britain and the development and refinement of seed origin evaluation techniques. Phenological variation, particularly in relation to the potential for frost damage is described, height growth and basal area production are dealt with in depth, and current knowledge of variation in timber quality at the seed origin level is reviewed.

The growth and production data are brought together in a new series of suitability maps of Great Britain with guidance to forest managers on their interpretation. Seed origin choice is considered with respect to the increasing availability of improved material from resulting from breeding work. Conclusions and recommendations are provided throughout the text.

The Bulletin is an excellent résumé of a major area of research by the Forestry Commission.

Tim Rollinson
Director General
Forestry Commission

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Summary

Since its introduction by David Douglas in 1831, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) has become the most important commercial species in upland forestry in Great Britain and in 2004 accounted for 36% of the total forest. The natural range of the species extends over 3000 km as a narrow maritime belt along the Pacific coast of North America from Alaska to California.

This extensive latitudinal range gives rise to variation in the climatic conditions under which Sitka spruce has evolved and it is therefore essential to determine by means of provenance experiments the most suitable seed origins for use in Great Britain. Two main series of experiments were established in 1960/61 and 1974/75. The latter was the most comprehensive based on the International Union of Forest Research Organisations (IUFRO) 1968/70 collections with 62 seed origins represented. Results from these experiments, both from the nursery and field stages, have shown the adaptability of several of the seed origins for a range of site types.

Variation in date of flushing between origins is small and therefore cannot be used as a defining factor in selecting seed sources which might avoid spring frost damage. However, variation in date of growth cessation and therefore susceptibility to damage by unseasonal autumn frosts is much greater and has to be considered during the nursery and early forest stages. The southerly origins, in which growth cessation is late in the year, are very susceptible to autumn frosts and also produce the greatest number of lammas shoots.

There is a general cline in increasing vigour with decreasing latitude with origins from northern Oregon the most vigorous, especially on southern sites in Great Britain. Poorer growth is found in origins from the Skeena River, mainland and lower coastal British Columbia and the Puget Sound area in Washington. In contrast, seed origins from the Queen Charlotte Islands of British Columbia produce better than expected growth, although there is variation within the Queen Charlotte Islands with the low elevation seed sources from the northern and eastern parts of Graham Island having higher than average production. These origins proved to be well adapted and productive over a wide range of sites in Great Britain.

Sitka spruce timber shows a high inverse correlation between growth rate and wood density, with wood density declining with decreasing latitude. A comparison of sawlog output and quality between origins from Washington and Queen Charlotte Islands indicated that the use of Washington origins could increase plantation value through increased volume production without significant loss in the proportion of C24 grade constructional timber.

A seed origin suitability map for Great Britain has been developed to aid forest managers in selecting seed origins for particular sites, based on accumulated temperature in day degrees, a measure of continentality and latitude. This model can be modified to accommodate future changes in climate. The results of the experiments indicate the general suitability of certain Queen Charlotte Islands seed sources for use on a wide range of sites in Great Britain, with Washington and northern Oregon sources suitable for selected sites in Wales and south west England.

Resumen

Picea sitchensis (Bong.) Carr. fue introducida en Gran Bretaña por David Douglas en 1831. Desde entonces esta pícea se ha convertido en la especie forestal más importante desde el punto de vista comercial en las tierras altas de Gran Bretaña, ocupando el 36% de la superficie arbórea en el año 2004. El área de distribución natural de esta especie se sitúa a lo largo de unos 3000 km en la franja costera del Pacífico norteamericano, desde Alaska hasta California. Este amplio rango de distribución latitudinal hace que *Picea sitchensis* haya evolucionado bajo la presión selectiva de muy diferentes condiciones climáticas.

Por ello, se ha considerado fundamental determinar los orígenes de semillas más adecuados a emplear en Gran Bretaña mediante ensayos de procedencias. Bajo esta perspectiva se establecieron dos series de ensayos, el primero de ellos en 1960/61 y el segundo en 1974/75. Este último es el más completo ya que en él están representados 62 orígenes procedentes de las recolecciones de semilla efectuadas por IUFRO (International Union of Forest Research Organisations) entre 1968 y 1970. Los resultados de estos ensayos, tanto de la etapa de vivero como del comportamiento en campo, han mostrado la adaptabilidad de varios orígenes para un amplio rango de condiciones de ensayo.

La variación entre orígenes en la fecha de inicio de elongación de los brotes, es decir la susceptibilidad a daños por heladas tardías, es pequeña, por lo que este rasgo no puede ser tenido en cuenta en la selección de los orígenes más adecuados. Sin embargo, las diferencias estimadas en la fecha de finalización de la elongación, relacionada con la susceptibilidad de daños por heladas otoñales tempranas, son mucho mayores y deben tenerse en cuenta en la fase de vivero y en los primeros estadios de la plantación. Los orígenes más meridionales, que detienen el crecimiento más tardíamente, son muy susceptibles a las heladas otoñales y producen además un mayor número de brotes con crecimiento libre.

Existe una tendencia general al aumento del vigor con la disminución de la latitud del origen de las semillas, siendo los orígenes del norte de Oregón los más vigorosos, especialmente en las localidades del sur de Gran Bretaña. Los menores crecimientos corresponden a los orígenes de Skeena River, de la zona costera continental del sur de la Columbia Británica y del área de Puget Sound en Washington. Por el contrario, los orígenes de las Islas Queen Charlotte en la Columbia Británica muestran mejores crecimientos de lo esperado, aunque existen variaciones dentro de ellos, siendo los de baja altitud del norte y sur de la Isla Graham los de mayor producción promedio. Estos orígenes se han mostrado como bien adaptados y con buenas producciones en una amplia gama de sitios en Gran Bretaña.

Por otro lado, la densidad de la madera de *Picea sitchensis* muestra una correlación negativa con el crecimiento, disminuyendo la densidad al hacerlo la latitud del origen. La comparación de la producción y la calidad de la madera aserrada entre orígenes de Washington y Queen Charlotte Islands indica que el empleo de los orígenes de Washington puede incrementar el valor de las plantaciones al aumentar el volumen producido, sin pérdidas significativas en la proporción de madera estructural de la clase resistente C24.

Se ha establecido un mapa de recomendación de uso de semilla para Gran Bretaña con el objetivo de orientar a los gestores forestales sobre cuales son los orígenes más adecuados para cada sitio, basándose en la temperatura acumulada en grados día, un parámetro de continentalidad y la latitud. Este modelo puede ser modificado teniendo en cuenta cambios futuros en el clima. Los resultados de los ensayos indican la adecuación de algunos orígenes de las Islas Queen Charlotte para su uso en un amplio rango de sitios en Gran Bretaña, y la de algunos orígenes de Washington y norte de Oregón para algunas zonas específicas de Gales y el oeste de Inglaterra.

Résumé

Depuis son introduction par David Douglas en 1831, l'épicéa de Sitka (*Picea sitchensis* (Bong.) Carr.) est devenu l'espèce la plus importante pour la foresterie commerciale in Grande-Bretagne. En 2004, elle représentait 36 % du domaine forestier. L'aire de distribution naturelle de cette espèce s'étend sur 3000km le long d'une bande étroite en Amérique du Nord, le long de la cote pacifique de L'Alaska à la Californie.

Cette grande amplitude latitudinale entraîne des variations dans les conditions climatiques dans lesquelles l'épicéa de Sitka a évolué. Il est donc essentiel de déterminer à l'aide d'expérience de provenance, la meilleure origine de graines pour la Grande Bretagne. Deux séries d'expériences ont été établies en 1960/61 et 1974/75. Cette dernière expérience est la plus complète et a été réalisée sur la collection 1968/70 de l'International Union of Forest Research Organisations (IUFRO), avec 62 origines de graines représentées. Les résultats de ces expériences, en pépinière et sur le terrain ont montrée l'adaptation de plusieurs de ces origines de graines a une variété de sites.

Les différences de date de débourrement entre origines sont faibles et ne peuvent donc pas être utilisées comme facteur de sélection des sources pour éviter les dégâts liés aux gels printanniers. Par contre les variations dans la date de fin de croissance et donc la sensibilité aux dégâts liés aux gels automnaux est plus importante. Elles doivent donc être prise en compte pendant la phase de pépinière et de jeune forêt. Les origines les plus au sud pour lesquelles la fin de croissance est la plus tardive, sont très sensible aux gels automnaux et produisent le grand nombre de pousses d'été.

La vigueur augmente généralement avec les latitudes décroissantes. La provenance du nord de l'Oregon est la plus vigoureuse surtout dans les sites au sud de la Grande Bretagne. Les faibles croissances proviennent de la Skeena River, de la Colombie Britannique (intérieur des terres et côtes) et de la zone du Pudget Sound. Les graines provenant des îles Reine-Charlotte (Colombie-Britannique) produisent une meilleure croissance que prévue. Il existe une variabilité parmi cette provenance, les graines provenant de faible altitude au nord et à l'est de l'île de Graham présentant une croissance au-dessus de la moyenne. Ces provenances sont bien adaptées et productives pour un grand domaine de sites en Grande Bretagne.

Le bois d'épicéa de Sitka présente une forte corrélation entre le taux de croissance et la densité du bois, la densité du bois diminuant pour les latitudes décroissantes. Une comparaison de la production de grume et de qualité du bois entre les graines provenant de l'Etat de Washington et des îles Reine-Charlotte indique que l'utilisation de graine de l'état de Washington peut augmenter la valeur de plantation grâce à une augmentation du volume de production sans réduction significative de la proportion de bois de construction de qualité C24.

Une carte présentant les provenances adaptées à la Grande Bretagne a été développée pour aider les gestionnaire forestier à choisir les origines de graines pour un site donné. La carte est basée sur une accumulation des températures en degrés-jour, une mesure de la continentalité et de l'altitude. Le modèle peut être modifié pour prendre en compte de futur changement de climat.

Les résultats de l'expérience montrent que les graines de certaines des îles Reine-Charlotte sont bien adaptées pour un grand nombre de sites en Grande Bretagne. Les graines de l'état de Washington et du nord de l'Oregon sont elles, bien adaptées pour nombre de sites au pays de Galles et au sud-ouest de l'Angleterre.

Zusammenfassung

Seit ihrer Einführung durch David Douglas im Jahr 1831 ist die Sitkafichte (*Picea sitchensis* (Bong.) Carr.) in den britischen Hochlandwäldern zum wichtigsten Nutzholzlieferanten geworden und machte 2004 36% des gesamten Waldbestandes aus. Das natürliche Verbreitungsgebiet der Art erstreckt sich als schmaler Gürtel von etwa 3000 km entlang der nordamerikanischen Pazifikküste von Alaska bis Kalifornien.

In diesem großen Breitengradbereich hat sich die Sitkafichte unter unterschiedlichsten klimatischen Bedingungen entwickelt, und daher ist es wichtig, durch Herkunftstests die Samenherkunft zu bestimmen, die für den Gebrauch in Großbritannien am besten geeignet ist. Zwei wesentliche Versuchsreihen wurden 1960/61 und 1974/75 durchgeführt. Die letzte war die umfangreichste und basierte auf den Sammlungen der International Union of Forest Research Organisations (IUFRO, Internationaler Verband der Forstforschungsorganisationen) aus den Jahren 1968/70 mit 62 verschiedenen Samenherkünften. Die Ergebnisse dieser Studien – aus den Pflanzgarten- und Feldstadien – haben die Anpassungsfähigkeit einiger Samenherkünfte für verschiedene Standorttypen gezeigt.

Das Datum der Triebbildung variiert zwischen den verschiedenen Herkünften kaum und kann daher nicht als entscheidender Faktor für die Auswahl von Samenquellen herangezogen werden, um eventuelle Frostschäden im Frühjahr zu vermeiden. Das Datum der Wachstumseinstellung und somit der Empfindlichkeit für Schäden durch untypische Herbstfröste schwankt jedoch wesentlich stärker und muss im Pflanzgarten und in frühen Waldstadien berücksichtigt werden. Die Bäume südlicher Herkunft, die das Wachstum spät im Jahr einstellen, sind empfindlich gegenüber Herbstfrösten und produzieren außerdem die größte Anzahl an Augusttrieben.

Allgemein nimmt die Vitalität mit abnehmender geografischer Breite zu, wobei die Pflanzen aus Nordoregon besonders an südlichen Standorten in Großbritannien am kräftigsten sind. Bei Saatgut, das vom Skeena River, dem Festland und den südlichen Inseln British Columbias und dem Puget-Sound-Gebiet in Washington stammt, wird ein schlechteres Wachstum beobachtet. Auf der anderen Seite produzieren Samen, die von den Queen Charlotte Islands in British Columbia stammen, eine besseres Wachstum als erwartet; und innerhalb der Queen Charlotte Islands gibt es wiederum Unterschiede: Samen aus niedrigen Lagen der nördlichen und östlichen Teile von Graham Island führen zu einer überdurchschnittlich hohen Produktion. Es hat sich gezeigt, dass Samen aus diesen Herkunftsgebieten an zahlreiche Standorte in Großbritannien gut angepasst und dort produktiv sind.

Das Holz der Sitkafichte zeigt eine starke umgekehrte Korrelation zwischen der Wachstumsrate und der Holzdichte, wobei sich die Holzdichte mit abnehmender geografischer Breite verringert. Ein Vergleich zwischen Saatgut aus Washington und von den Queen Charlotte Islands im Hinblick auf Sägeholzertrag und Qualität hat gezeigt, dass die Verwendung von Saatgut aus Washington die Wertleistung durch eine erhöhte Volumenproduktion steigern kann, ohne dass ein signifikanter Verlust beim Anteil an Bauholz der Klasse C24 entsteht.

Es wurde eine Karte mit der Eignung der verschiedenen Samenherkünfte in Großbritannien entwickelt, die Forstverwalter bei der Auswahl von Saatherkünften für verschiedene Standorte unterstützen soll. Sie basiert auf der akkumulierten Temperatur in Taggraden, einem Maß für Kontinentalität und geografische Breite. Dieses Modell kann modifiziert werden, um zukünftige Klimaänderungen zu berücksichtigen.

Die Ergebnisse der Versuche zeigen die allgemeine Eignung von Samen aus gewissen Quellen der Queen Charlotte Islands an einer Vielzahl von Standorten in Großbritannien, und die Eignung von Quellen aus Washington und Nordoregon für Wales und Südwestengland.

Crynodeb

Ers ei chyflwyno gan David Douglas ym 1831, mae pyrwydden Sitca (*Picea sitchensis* (Bong.) Carr.) wedi datblygu'n rhywogaeth fasnachol bwysicaf coedwigaeth ucheldir ym Mhrydain ac yn 2004 roedd yn cyfrif am 36% o'r goedwig gyfan. Mae ystod naturiol y rhywogaeth yn ymestyn dros 3000 cilometr yn llain arforol gul ar hyd arfordir y Môr Tawel Gogledd America o Alasca i Galiffornia.

Mae'r ystod ledredol eang hon yn peri amrywiaeth yn yr amodau hinsoddol y mae pyrwydden Sitca wedi esblygu odanynt, ac mae felly'n hanfodol pennu drwy arbrofion tarddle beth yw'r tarddiadau hadau mwyaf addas i'w defnyddio ym Mhrydain Fawr. Sefydlwyd dwy brif gyfres o arbrofion ym 1960/61 ac ym 1974/75. Yr olaf oedd y gyfres fwyaf cynhwysfawr ar sail casgliadau 1968/70 Undeb Rhyngwladol y Sefydliadau Ymchwil Coedwigoedd (IUFRO), gyda 62 o darddiadau hadau'n cael eu cynrychioli. Mae canlyniadau'r arbrofion hyn, o'r cyfnod planhigfa a'r cyfnod maes, wedi dangos bod nifer o darddiadau hadau yn gallu ymaddasu ar gyfer ystod o fathau o safleoedd.

Mae'r amrywiaeth o ran dyddiad tyfiant rhwng tarddiadau yn fach, ac felly ni ellir ei defnyddio'n ffactor diffinio wrth ddethol ffynonellau hadau a allai osgoi niweidio gan rew yn y gwanwyn. Fodd bynnag, mae'r amrywiaeth o ran dyddiad darfod tyfu, a thueddiad felly i niwed gan rewoedd annhymhorol yn yr hydref lawer yn fwy, ac mae'n rhaid ystyried hyn yn ystod cyfnod y blanhigfa a'r cyfnod cynnar yn y goedwig. Mae'r tarddiadau deheuol, sy'n darfod tyfu yn hwyr yn y flwyddyn, yn agored iawn i rewoedd yr hydref, ac maent hefyd yn cynhyrchu'r nifer fwyaf o flagur lammas.

Mae graddfa gyffredinol mewn egni'n cynyddu wrth i ledred ostwng, a tharddiadau o ogledd Oregon yw'r mwyaf grymus, yn enwedig ar safleoedd deheuol ym Mhrydain. Ceir tyfiant salach mewn tarddiadau o Afon Skeena, tir mawr ac ardal arfordirol isaf Columbia Brydeinig, ac ardal Puget Sound yn Washington. Mewn cyferbyniad, mae tarddiadau hadau o Ynysoedd Queen Charlotte yng Ngholumbia Brydeinig yn cynhyrchu tyfiant gwell na'r disgwyl, er bod amrywiaeth o fewn Ynysoedd Queen Charlotte gyda chynhyrchiant uwch na'r cyfartaledd o'r ffynonellau hadau uchdwr isel yn rhannau gogleddol a dwyreiniol Ynys Graham. Dangosodd y tarddiadau hyn eu bod wedi ymaddasu'n dda ac yn gynhyrchiol dros amrywiaeth eang o safleoedd ym Mhrydain.

Mae pren pyrwydden Sitca yn dangos cydberthynas wrthdro uchel rhwng cyfradd dwf a dwysedd y coed, gyda dwysedd y coed yn lleihau wrth i ledred ostwng. Nododd cymhariaeth allgynnyrch ac ansawdd boncyffion wedi'u llifio rhwng tarddiadau o Washington ac Ynysoedd Queen Charlotte y gallai defnyddio tarddiadau Washington gynyddu gwerth planhigfa drwy fwy o gynhyrchiant heb golled sylweddol yng nghyfran y coed adeiladu gradd C24.

Mae map addasrwydd tarddiadau hadau ar gyfer Prydain wedi'i ddatblygu i gynorthwyo rheolwyr coedwigoedd wrth ddethol tarddiadau hadau ar gyfer safleoedd penodol, ar sail tymheredd cronedig mewn dyddraddau, mesur cyfandiroledd a lledred. Gellir addasu'r model hwn i ddarparu ar gyfer newidiadau yn yr hinsawdd yn y dyfodol.

Mae canlyniadau'r arbrofion yn dangos addasrwydd cyffredinol rhai ffynonellau hadau Ynysoedd Queen Charlotte i'w defnyddio ar amrywiaeth eang o safleoedd ym Mhrydain, ac mae ffynonellau Washington a gogledd Oregon yn addas ar gyfer safleoedd dethol yng Nghymru a de-orllewin Lloegr.

1 Introduction

History of introduction and use of Sitka spruce

In Great Britain, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) is the most widely used conifer for afforestation and replanting, accounting for 36% of the forest estate. Although the species accounted for 46% of the total area planted during 1991–1999 (61% of all conifer species), this was lower than the previous decade (1981–1990) in which it accounted for 65% of the total planted area (71% of all conifers). This change has been considerably greater within the private forestry sector (26% of all species down from 63%) than within the Forestry Commission estate (52% down from 63%). Nevertheless, since Sitka spruce continues to play the dominant role in commercial forestry in upland northern and western Britain, it is essential that seed of the most suitable origin should be used for each of the range of sites where the species is to be planted (Figure 1).

Figure 1

Wide-scale planting of Sitka spruce in Britain: a view of Kielder Forest, Northumbria showing mature, clearfelled and restocked areas.

Sitka spruce was originally discovered in 1792 by Archibald Menzies (Menzies, 1923), a Scottish naturalist, who sailed as a surgeon with Captain George Vancouver during his investigation of the coastlines of Washington and British Columbia. He did not collect seed but brought back foliage specimens which are now in the British Museum. It was introduced to Britain in 1831 by David Douglas, during his second expedition to the Pacific Northwest and was probably collected in the area of the Columbia River which is now the border between Oregon and Washington. Douglas in his Journal (1823–1827) (Douglas, 1914) gave the following description of the species (*Pinus menziesii*).

'The appearance of this species closely resembles P. Douglasii; although neither so large nor so plentiful as that species, it may nevertheless become of equal if not greater importance, as it possesses one great advantage over that one by growing to a very large size on the northern declivities of the mountains in apparently poor, thin, damp soils; and even in rocky places, where there is scarcely a sufficiency of earth to cover the horizontal wide-spreading roots, their growth is so far from being retarded that they exceed one hundred feet and eight feet in circumference. This unquestionably has great claims on our consideration as it would thrive in such places in Britain where even P. sylvestris finds no shelter.'

The species did not, however, immediately achieve the same popularity in arboreta as some of his other introductions, such as Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) or western red cedar (*Thuja plicata* D. Don), perhaps because the seed came from the more southern end of its range which has less rainfall than Britain. Subsequent collections were made in Oregon and California in the 1850s by Jeffrey and Lobb. Hunter (1883) referred to it as a Californian tree, see Figure 2. One of the first records of forest planting was in 1879 at Strathgyle, Durris (Grampian). The

Figure 2

A good quality natural stand of Sitka spruce with fine branching habit growing at Patrick's Point, Crescent City, northern California, near to the site of IUFRO collection 3020 (see Chapter 3).

plantation unfortunately blew down in the gale of January 1927 but on an exposed peat site attained 22 m at 43 years of age (Steven, 1927). A smaller plantation was established at wide spacing (20 feet) at Wooplaw (Scottish Borders) in 1866 and a few trees still remain. Other early plantations were at Corrour (Highland), Moorburnhead (Dumfries and Galloway) and Inverliever (Strathclyde). There are a few individuals emanating from Douglas' collections of 1830–32 still standing, the largest of which is at Curraghmore, Ireland. By the time the Forestry Commission was established in 1919 it was fairly well-known as a fast-growing tree, hardy in exposed conditions and capable of growing on the type of site which at that time was mainly planted with Norway spruce (*Picea abies* (L.) Karst.), see Figure 3.

Figure 3

A view within a 42 year old stand of Sitka spruce of Queen Charlotte Island origin growing at South Strome, Highland Region.

However, although Sitka spruce grew faster than Norway spruce and its timber had a high reputation in northwest America for use in aircraft construction, it was still used with caution by the Forestry Commission; until 1927 more Norway spruce was planted than Sitka spruce each year. Caution such as "Sitka spruce is not new to the country, but cannot yet be considered equally 'safe' ... it appears wise not to put too many eggs into one basket" (Robinson, 1931) was recommended. Even before this it had been noted that frost damage varied in severity on different seed origins in the nursery (Macdonald, 1927).

Most of the seed imported prior to 1922 came from the company J Rafn of Copenhagen, Denmark, who obtained the majority of their seed from Grays Harbor County, on the Pacific Coast of Washington. One of the first tasks of the Forestry Commission was to ensure reliable seed supplies of northwest American conifers and, in collaboration with the Canadian forest authorities, arrangements were made for bulk collections of Sitka spruce on the Queen Charlotte Islands (QCI), and for the building of a seed extractory to process the cones at New Westminster, near Vancouver city (Borthwick, 1924). The Queen Charlotte Islands were chosen as the preferred seed source because of their climatic and latitudinal match with Britain and the excellent growth and high quality timber of the indigenous stands (Hopkinson, 1931).

Table 1 summarises the percentages of seed imported from different regions of the Pacific Northwest and seed collected in Great Britain by decade, 1920s–1980s. The data were collated from Forestry Commission seed records which have been compiled since 1922. Until the end of the 1970s, the Forestry Commission was virtually the sole importer and supplier of seed of Sitka spruce, but during the 1980s other commercial organisations from which no data are available became involved. For the 1940s in particular, location details within British Columbia (BC) and the USA were not available but there is good evidence that those from BC continued the established pattern of collection on the Queen Charlotte Islands and that those from USA were most likely to have been of Washington origin. Table 1 shows that seed from Alaska, the mainland coast of BC, Vancouver Island and Oregon was only imported in small quantities and together they account for less than 2% of all imported seed over the full period 1922–1989.

Up to 1960, over 95% of seed used was imported and that during this period over 85% of imported seed came from the Queen Charlotte Islands (including unspecified BC lots in the 1940s). Over this same period, the main imports of Washington material (including unspecified USA lots) were

Table 1

Summary of origins of seed collections of Sitka spruce recorded by the Forestry Commission 1922–1989.

Region	Decade							Total 1922–89
	1920–29	1930–39	1940–49	1950–59	1960–69	1970–79	1980–89	
Total seed (kg)	5676	5595	13764	14232	7878	8106	9189	64440
Percentage of total seed								
Imported from North America	100.0	99.8	94.6	95.1	86.5	64.4	15.3	79.5
Home-collected in Great Britain		0.2	5.4	4.9	13.5	35.6	84.7	20.5
North American regions as % of total seed imported								
Alaska				0.4	1.4		1.6	0.3
British Columbia (mainland)		0.2			1.5			0.2
British Columbia (unspecified)			81.0	9.3			0.7	23.1
Queen Charlotte Islands	91.5	84.2		85.3	56.3	87.1	80.9	60.4
Vancouver Island				1.7	1.0	0.3		0.6
Washington		15.4	1.9	3.2	38.8	8.2	8.7	9.2
Oregon					0.9	1.3	8.1	0.8
USA (unspecified)	8.5		17.0					5.3

concentrated in the 1930s and 1940s when they contributed to an average of 17% of imports. These have resulted in many widely distributed stands of mainly Washington origin. Unfortunately, seed records of these older plantations are not always reliable, which can cause problems if seed is later collected from them (Lines *et al.*, 1971).

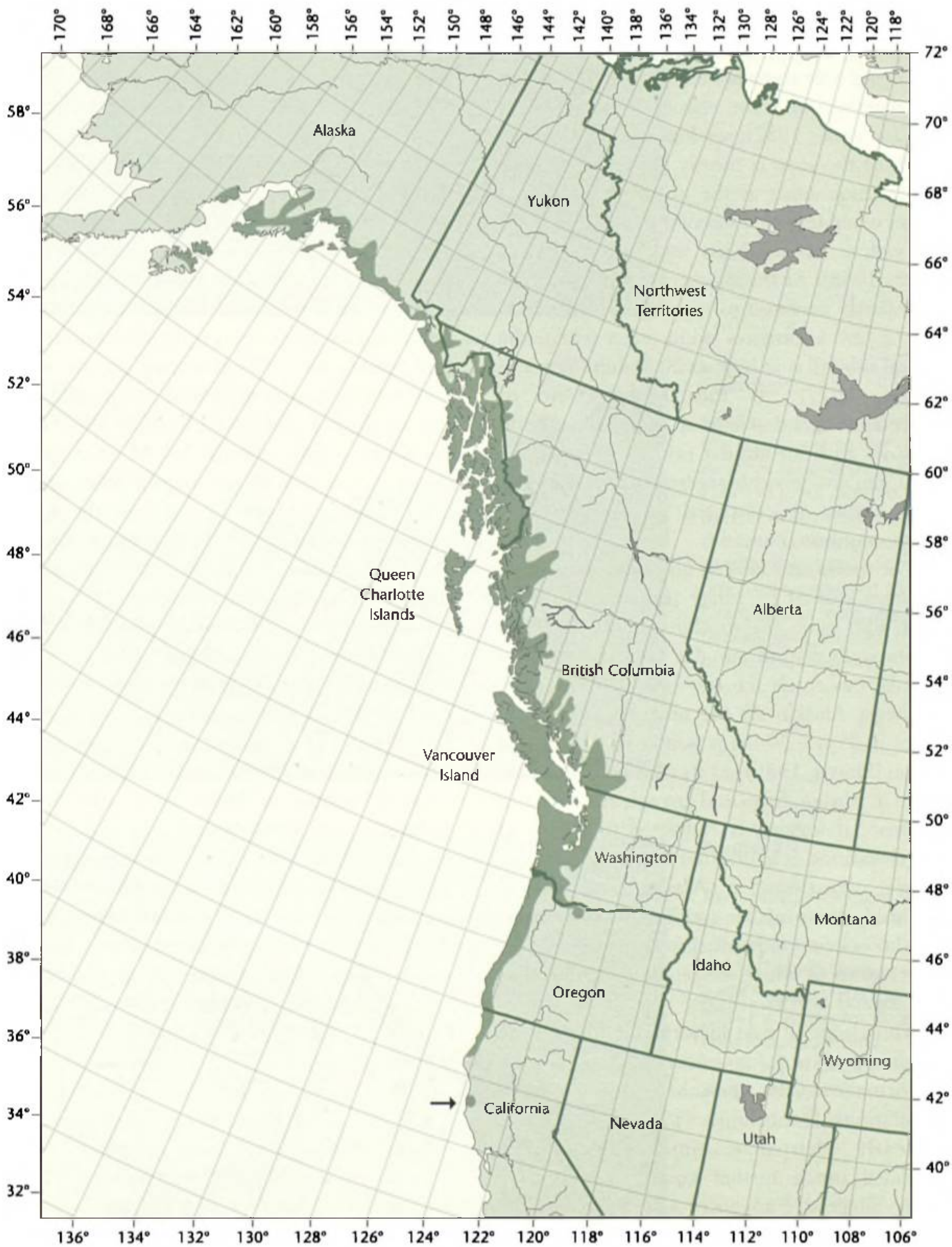
Collection of British Sitka spruce seed began as early as 1923 (from the old trees at Durris) but, because plantations of this species seldom cone abundantly until they are 30 years old (Fletcher and Faulkner, 1972), large scale collections were not possible until the 1960s. Over this and the next two decades, there was an exponential increase in the contribution to the overall supply of collections made in Great Britain. Throughout this period, opportunities were taken to collect seed following clearfelling of mature stands of superior quality during years of abundant coning. There is now potential for obtaining a large proportion of Sitka spruce requirements from British sources, although years of good seed production remain unpredictable and intermittent, due to the climatic conditions which prevail, with a frequency of abundant crops every 7–10 years. Doubts about the exact origin of candidate seed stands also remain a problem in securing seed from British plantations. Genetically improved tested material from tree breeding now makes a major contribution to the supply of planting stock. This comes from tested seed orchards and the multiplication of superior families derived from controlled pollinations by vegetative propagation using rooted cuttings.

Natural range

Sitka spruce is the largest of the world's spruces and occurs naturally throughout a narrow belt along the Pacific coast of North America extending for 3000 km from Kodiak Island, Alaska (58°N) in the northwest, through Valdez (61°N) to 41°N in California (Figure 4). There is a disjunct population at Jug Handle Creek near Casper in Mendocino County at 39°15'N. The range appears to be dependent on abundant moisture during the growing season. It is essentially a northern species, with 63% of its estimated growing stock in Alaska, 29% in British Columbia and only 8% in Washington,

Figure 4

The natural distribution of Sitka spruce (→ indicates disjunct population at Jug Handle Creek, California).



Oregon and California (Harris, 1984; Anon, 1990). Sitka spruce is unusual in having a strongly maritime distribution, growing on tidal flats in Alaska and British Columbia (an alternative common name is Tideland spruce) and being able to tolerate some salinity in the soil together with the effects of ocean spray (Krajina *et al.*, 1982), see Figures 5 and 6. The width of the strip is mostly restricted by high coastal mountains at the northern end of its range, extending to a maximum of 200 km up the valleys of the Nass and Skeena Rivers (Ruth, 1958). At the southern end of its range it is strictly confined to the 'fog belt' which is only a few kilometres wide, even where the annual rainfall is as high as 2000 mm (Farr and Harris, 1979). At the southeast tip of Vancouver Island where it grows in a 'rain shadow' with an annual rainfall of less than 1000 mm and possible severe summer drought, Sitka spruce is restricted to stream sides, beaches and tidal areas.

The species is found at low elevations at the southern end of its range (Figure 7). It may reach 880 m in the foothills of the Olympic National Park and on the Queen Charlotte Islands, but reach the tree line at 1000 m in southeast Alaska. At the northern end of its range in Prince William Sound it is found at 300 m (Harris, 1980). At its extreme altitudinal range in Alaska, form and growth are poor and commercial logging is restricted to stands at low elevations. It is unusual in that it occurs at higher elevations in Alaska and British Columbia than further south. This is contrary to other species with which it is associated, the distribution of which descends in elevation as they extend northwards.

Knowledge of past history and distribution of this species aids understanding of the performance of present day natural populations. Daubenmire (1968) showed that by early Pleistocene times Sitka spruce extended much further south than it does today. Successive advances and retreats of the ice-front severely affected or eliminated mainland and inner island populations as far south as 47°N. There is evidence for survival of spruce during the last glacial period in refugia or nunataks on the Queen Charlotte Islands (Calder and Taylor, 1968; Warner *et al*, 1982) and perhaps on some other islands. Below 47°N the genetic structure of the populations would have been affected to a lesser extent. After the glacial retreat pollen records show that spruce became established in Washington and southern British Columbia 8500 years ago, 8000 years ago in northern British Columbia and as recently as 3000 years ago on Kodiak Island (Heusser, 1960). Griggs (1934) reported that Sitka spruce, the only conifer on this island, was still advancing slowly westwards onto heathy grassland at an estimated rate of about 1 mile (1.62 km) per 100 years.

Where coastal populations of Sitka spruce come in contact with the interior white spruce (*Picea glauca* (Moench) Voss) in the Kenai Peninsula, Alaska, and in the upper Skeena River in British Columbia, natural hybridisation occurs. Roche and Fowler (1975) listed the authors who have studied both this natural cross and also artificial crosses. The interspecific hybrid has been named *Picea* x *lutzii* in Alaska (Little, 1953), where it yields fertile seed with progeny resembling the parent and looking quite uniform and similar to Alaskan origins of Sitka spruce. In British Columbia, the introgression zone (e.g. around Kitwanga on the Skeena River) contains individuals which show wide morphological differences in their cones (Daubenmire, 1968; Roche, 1968, 1969) and crown shape ranging from typical Sitka spruce to typical white spruce (Figure 8). Progeny grown in Britain from seed collected at Kitwanga show types varying in appearance from true Sitka spruce to those closely resembling white spruce (Lines, 1978). The distribution of Sitka spruce in British Columbia also overlaps with Engelmann spruce (*Picea engelmannii* (Parry) Englm.) and black spruce (*Picea mariana* (Mill.) B.S.P.).

Figure 5

Dyea, near Skagway, Alaska (IUFRO source 3022). Sitka spruce growing in a narrow band along the shoreline with lodgepole pine on the slopes behind.

Figure 6

Sitka spruce growing along the shore near to the location of seed source 70(7111)500, close to Masset in the northeast of the Queen Charlotte Islands. Large quantities of seed were imported to Great Britain from this general area through most of the 20th century.

Figure 7

Towards the southern end of the natural range of Sitka spruce, at Lincoln City in north Oregon (between IUFRO sources 3013 and 3014), the species, together with lodgepole pine, continues to predominate along the shoreline.

Figure 8

Spruce trees in the area north of Kitwanga, Skeena River, in the area of introgression with white and Engelmann spruces. Trees have narrow crowns and bluer foliage.

Comparison of climate in Britain and northwest America

The general climate throughout the range of the species is maritime being strongly influenced by the prevailing westerly winds from the Pacific Ocean. Rainfall is generally high, at least 1200 mm per annum. Due to the proximity to the ocean, temperature fluctuations throughout the latitudinal range are not large. The difference in average July temperature between northern California and south east Alaska is less than 5°C.

Tables of climatic data for sites within the natural range are given by Ruth (1958), O'Driscoll (1976), Farr and Harris (1979) and Schaefer (1980); this information is summarised in Table 2. Wood (1955) compared a broad range of northwest American climates with those in Britain, and by concentrating on those which most resemble Great Britain, he paid most attention to the Sitka spruce range. Day (1957) restricted his comparisons with Britain to the Queen Charlotte Islands and the Terrace area in British Columbia, about 130 km from the coast. He noted that for the British forester no perfect fit with climate is likely and '*in the search for sources of seed he will have to be content with that climate which is likely to produce the more adaptable strains for his purpose*'. Wood emphasised the overall temperature differences between the two countries, which result in a better match in Britain for places much further south in northwest America, e.g. the monthly temperatures for Ucluelet, Vancouver Island (48°55'N) are close to those for Blackpool (53°45'N), while those at Astoria, Oregon (46°12'N) are similar to Woolacombe, Devon (51°10'N). Thus the day-length will be appreciably different for places with similar temperature regimes. Day was also impressed by the complete absence of frost damage, either during spring or autumn on the Queen Charlotte Islands and by the lack of evidence for exposure to high winds even on topographically exposed sites at 1000 m.

The use of accumulated temperature (i.e. day degrees over 5°C, referred to here as AT5) offers a useful means of comparing climates. Wood showed the increase in temperature with decreasing latitude is much greater for Britain than for northwest American coastal weather stations. The main reason for these differences lies in the ocean currents. The North Atlantic Drift maintains higher temperatures in Britain just as the Japanese current brings some warmth to the Queen Charlotte Islands and southern Alaska. However, the cold Humboldt current increases the number of cloudy days and lowers the temperature in northern California and southern Oregon (Fletcher, 1976). Farr and Harris (1979) concluded that the average site index of Sitka spruce (a measure of productivity) is highly correlated

Table 2

Climatic details of Sitka spruce seed collection sites in North America and typical planting sites in Great Britain.

Region	Meteorological station	Latitude °N	Longitude °W	Altitude (m)	Mean daily temperature °C	Extreme maximum temperature °C	Extreme minimum temperature °C	ATS	Mean total precipitation (mm)	Precipitation May to August (mm)	Mean length of frost-free period (days)
Collection sites in North America											
Alaska	Ketchikan (3030)	55.21	131.39	14	7.8	30.0	-17.2	1472	3940	884	182
Queen Charlotte Islands	Masset (3048)	54.02	132.08	3	7.8	28.9	-18.9		1430	285	190
	Sandspit (3050)	53.15	131.49	7	7.8	26.7	-13.9	1455	1259	196	190
Skeena River	Prince Rupert (3044)	54.17	130.23	52	7.6	32.2	-21.1	1294	2398	505	200
Main coast BC	Ocean Falls (3054/55)	52.21	127.40	5	8.5	37.8	-18.3	1676	4490	407	190
Vancouver Island	Cape Scott (3056/57)	50.47	128.26	71	7.8	30.0	-12.7	1434	2946	364	200
	Ucluelet (68(7116)6)	48.58	125.32	5	9.4	34.4	-13.9		2890	387	195
	River Jordan (3065)	48.25	124.03	3	9.3	31.1	-15.5		1930	202	195
Washington	Bellingham (3001)	48.48	122.29	33	10.8	35.6	-17.8		911	141	165
	Clallam Bay (3002)	48.15	124.15	21	8.6	36.1	-13.9		2096	232	190
	Forks (3003)	47.57	124.22	106	9.6	38.2	-21.0	1942	2943	343	168
	Hoquiam (3008)	46.58	123.53	3	9.9	37.8	-14.5	1963	1086	178	190
	Willapa Harbour (3010)	46.41	123.47	46	10.7	39.4	15.5		2122	244	160
North Oregon	Astoria (3011)	46.11	123.50	61	10.9	38.2	-12.2	2264	2022	217	273
	Tillamook (3013)	45.28	123.51	8	10.3	38.2	-17.2	2131	2249	256	182
	Newport (3014)	44.38	124.04	41	10.7	37.8	-11.6		1541	165	248
South Oregon	Port Orford (3017)	42.44	124.30	23	11.6	35.0	-9.4	2155	1822	177	286
	Brookings (3018)	42.03	124.17	36	12.0	37.8	-8.3	2511	2054	202	269
Meteorological stations in Great Britain with examples of close experimental planting sites (see Note 4)											
N Scotland	Fort Augustus (Farigaig)	57.08	4.40	21	8.1	30.0	-14.2	1307	1096	146	216
W Scotland	Benmore (Benmore Glendaruel)	56.02	4.59	12	8.6	29.6	-13.9	1450	2206	307	230
SW Scotland	Threave (Arecleoch Glentrool)	56.56	3.57	73	8.3	29.5	-13.9	1479	1204	187	230
NE England	Redesdale (Wark)	55.15	2.16	235	6.8	28.3	-16.7	1190	1187	283	183
NW England	Newton Rigg (Thornthwaite)	54.40	2.57	171	8.1	31.1	-15.0	1345	885	150	193
North Wales	Bala (Mathrafal Clocaenog)	52.54	3.35	163	8.5	31.3	-16.5	1533	1242	179	214
South Wales	Trawscoed (Ystwyth Myherin)	52.20	3.57	63	9.3	32.5	-14.0	1778	1152	183	263
	Neath (Rhondda Rheola)	51.39	3.51	62	10.3	31.8	-9.8	1855	1267	208	283
SW England	Bastreet (Wilsey Down)	50.34	4.29	236	8.9	31.5	-11.2	1610	1662	253	200

1. British figures based on 1951–80 averages (figures at Redesdale adjusted using averages for Kielder Castle). Extreme maximum and minimum temperatures are based on 1981–90 averages where available.
2. For sites in Great Britain, the figures in the column labelled Mean length of frost free period (days) are the length of growing season (after Fairbairn, 1968).
3. AT5 – Mean number of growing degree days above 5°C per year (data for North America based on Farr and Harris, 1979).
4. Actual planting sites may contrast with meteorological stations because of local climatic variation due to altitude, rain shadows etc. Rainfall and AT5 figures may thus not be close to those given for specific experimental sites in Appendices 2 and 4.

with accumulated temperature. For sites from southern Oregon to Juneau in Alaska (58°22'N) this followed a linear relationship, but the site index fell rapidly at the northwest end of its range.

Soils and growth

In the southern part of its range Sitka spruce is found on alluvial soils, on sandy gravel of river terraces or on soils having a thick accumulation of organic material. The soils to the north of the Puget Sound in Washington which were affected by the Wisconsin glaciation are poorly developed and tend to be podsolised and acid. Day (1957) distinguished between the valley alluvia, gravels and tills on the bottomland areas, and the colluvial soils. These correspond to the two general types of Sitka spruce distinguished by Cary (1922). The first is the 'bottomland' type where the trees are characterised by large buttresses, heavy branching and short clear stems and these are normally the largest trees. The second form is the 'slope' type which are tall, without buttresses and have long lengths of stem clear of branches. The species grows best on the lower slopes of the mountains where there can be considerable rooting depth and with a relatively high nutrient status. It fails to compete with other species where there is a lack of aerated water and lower nutrient levels.

Sitka spruce occurs mainly in mixed stands with western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on well-drained soils, with western red cedar (*Thuja plicata* D. Don) on swampy and alluvial soils, and with black cottonwood *(Populus tricocarpa* Hook) and red alder (*Alnus rubra* Bong.) on alluvial floodplains. It is dominant only on the freely drained moister sites whereas on moisture- or nutrient-stressed sites it cannot compete with less exacting species such as western hemlock or western red cedar. Pure stands are found in areas strongly influenced by salt spray or in the early stages of forest succession on landslides or retreating glaciers in Alaska. Sitka spruce achieves its best growth on floodplain terraces which may occur well inland along major rivers where it can grow in open stands (Figure 9).

Sitka spruce is one of the largest trees in the Pacific Northwest and according to data assembled by Waring and Franklin (1979) it is only exceeded by western red cedar and coast redwood (*Sequoia sempervirens (*D.Don) Endl.). Typically the largest trees are 180–230 cm in diameter at breast height and 70–75 m in height and live to an age of about 500 years. The tallest tree is reputed to be the 'Carmanah Giant' in the Carmanah Valley on Vancouver Island, British Columbia, at 95 m in height with a diameter of just over 3 m.

Figure 9

Mature individuals of Sitka spruce along the banks of the Hoquiam River close to the Washington coast, near to the site of IUFRO source 3008. The trees display wide crowns and long branches, typical of older specimen trees in Great Britain.

2 Evaluating seed sources

Obtaining seedlots for testing during the early phases of seed origin research

The success of all planting programmes depends largely on the correct choice of species and seed source. The most suitable origins of seed are determined by means of provenance tests using material from throughout the natural distribution of the species. However, the early importations of Sitka spruce to Britain came from one or two restricted areas close to where seed merchants were based or where extensive fellings were taking place. In the 1950s, at the time when interest in studying intra-specific variation in northwest American species began, communication between western North America and Great Britain was limited. Seed for origin evaluation research was generally only available from seed merchants who could supply smaller quantities from major commercial collections and more detailed sampling of specific locations was more difficult to arrange. Whilst visiting research workers in the 1960s established better contacts, early evaluation experiments were often characterised by any of the following problems:

- no details of the exact location of the collection.
- no indication of the size of the population being sampled or its importance in relation to the natural distribution of the species.
- no control over the size of the sample of trees from which seed was collected.
- limited opportunities to sample the natural range systematically or in relation to its known distribution.
- limited detailed sampling of populations within a broader region.

The IUFRO seed origin collection initiative

In order to overcome these problems of a lack of source-authenticated material from a range of species, a 'Working Group on Provenance Research and Testing' was set up by the International Union of Forest Research Organisations (IUFRO) in 1962. At a meeting in France in 1965, this group drew up guidelines 'concerning the collection of seed, the design of field experiments and the evaluation of results to aid development of national and international studies of provenance' (Lines, 1967). Following this meeting, a IUFRO Working Party was established, the main aims of which were to obtain authenticated material for provenance research from a range of northwest American species. Between 1966 and 1978, seed collections were made by IUFRO teams throughout the range of five species from identified and well-documented sites which were representative of the species in that particular part of its distribution (Fletcher and Barner, 1980).

Sitka spruce was sampled during 1968–70 with collections from 84 locations within its range from Alaska southwards to California. The seed was distributed to 22 countries. These IUFRO seed collections have been the basis of many provenance experiments which have provided a better knowledge and understanding of the species.

Following a meeting in Ireland in 1972 (O'Driscoll, 1976), 13 countries agreed to establish an international provenance experiment for Sitka spruce. Due to the diverse climatic zones in which the experiment would be established, the number of common seed sources was limited to ten with each one representing a broad geographic region of the species distribution. The experiments, called the IUFRO Sitka Spruce International Ten Provenance Experiments, were designed to last for a maximum of 10 years after planting, providing data on the variation in the species during the nursery and field establishment phases (O'Driscoll, 1976). This series acted as a complement to the main IUFRO series of experiments established with a much larger but not common selection of seed sources and with larger plot sizes in order to allow growth measurement to be made to at least half rotation age.

Seed origin studies of Sitka spruce outside Great Britain

Norway

Sitka spruce has been planted in Europe for over 100 years. The earliest studies of seed origin appear to be those of Hagem (1931) in Norway who tested 49 different seedlots from Alaska, British Columbia (BC), Washington and California between 1915 and 1928 in a rather frosty nursery near Bergen. Only Alaskan origins were hardy against autumn frost. Nine field tests with the IUFRO series including between 8 and 37 seedlots from BC and Alaska were established in Norway on sites between 58°N and 62°23'N. The IUFRO International Ten Provenance experiment was planted at 60°27'N. In the nursery phase the most southern origin from Oregon was completely destroyed. All seedlots were damaged, and those from Alaska and the possible introgression area with white spruce were least affected (Magnesen, 1993). Survival was strongly positively correlated with latitude of origin.

Denmark

Opperman (1929) reported that in Denmark the best origin was from southern Alaska, while Karlberg (1961) preferred BC origins because they terminated their growth three weeks earlier than Washington seedlots and grew faster than those from Alaska. Results from experiments with up to 17 seed origins planted in 1961–65 were reported by Brandt (1970) who showed that on an exposed site, winter injury was worst on the southern seedlots, while on another less exposed site the latter were tallest. He recommended Washington sources for favourable sites. The IUFRO International Ten Provenance Experiment was planted on two sites (Madsen, 1993). On both sites at 11 years from seed the Forks, Washington, and QCI origins grew very well while the Alaskan origins had poor vigour.

Germany

Large areas of Sitka spruce have been planted in the coastal region of northern Germany and systematic research began in 1880. However, problems from climatic stress, insects and fungi have caused a reduction in its use during the last 40 years (Kleinschmit, 1980). Two unreplicated trials were planted in 1930–33 at Gahrenberg near Hann Munden with eight seed origins at one site and seven origins at another (Schober, 1962). They are of particular interest because some of the same origins were planted in Great Britain, three at Radnor Forest in 1929 and two at Kilmun Arboretum in 1930. For volume production, the four Washington origins were best, followed by Queen Charlotte Islands and then Oregon. 25% of the Oregon trees and 50% of those from California did not survive a severe winter frost in 1939–40. Differences in flushing time between origins were much less than between individuals within a seedlot. The most recent tests based on the IUFRO collections were planted on four sites in north Germany. 43 seed origins were sown in the nursery and they showed the usual increase in height growth for decrease in latitude, although the most southerly origins were severely frosted (Kleinschmit and Sauer, 1976). The heavy losses in the nursery among southern origins, meant that only 39 seed origins were planted out. Survival continued to be a problem in the field for Oregon and California origins; even northern Oregon origins had accumulated losses of over 50%. The data for budset, length of growing season and height growth demonstrated a strictly clinal pattern with up to 80% of the variation being explained by the three geographical variables, latitude, longitude and elevation (Kleinschmit and Svolba, 1993). At eight years from seed the fastest growing provenances were from Washington except at the higher elevation sites (440 m) when some of the provenances from BC were at least as good.

Belgium

In Belgium, 19 of the IUFRO seedlots were sown in two replicated nursery experiments (Nanson, 1976). Flushing, bud set, needle colouration and height growth were studied in the nursery. Bud set was under moderate genetic control and followed a latitudinal cline. Needle colour changed from light green in southern Oregon to blue in north BC and Alaskan provenances. The provenances were planted out on a rather frosty site and the two origins from mid and south Oregon suffered badly. Results at 12 years from seed showed that, for a combination of good height growth and reasonable frost tolerance, Washington Coast origins appear most suitable for Belgium. In these tests the percentage of lammas shoots, early frost damage and forking decreased significantly with increasing latitude (Nanson, 1993).

The Netherlands

In the Netherlands, Sitka spruce is of some importance and 48 origins from the IUFRO collection were selected to cover the range from northern BC to southern Oregon (Kranenborg and Kriek, 1980). The provenances were planted on two sites. At 10 years from seed, survival of the provenances from BC, Washington and northern Oregon was very good but for those from mid to south Oregon it was poor. Survival of the Oregon provenances decreased from north to south. As regards height growth the best performing provenances were from northern Oregon followed by Washington coastal areas. Provenances from Vancouver Island were superior to those from QCI and provenances from the latter area exhibited a large degree of variation.

France

In France there are now 50 000 ha of Sitka spruce mainly at lower elevations in Brittany (Deleporte, 1984a). Seed origin comparison began in 1967 with three experiments containing 16 provenances in Brittany. At seven years of age the provenance from southern Oregon was the tallest (5.4 m) while the one from the Queen Charlotte Islands (3.6 m) was the smallest. There was a clear latitudinal cline for growth vigour at all three sites.

France participated both in the main IUFRO provenance experiment as well as the International Ten Provenance Experiment. 73 of the IUFRO seedlots together with 36 commercial seedlots were planted on three sites, in Brittany, southwest France and the Massif Central. At 11 years from seed on all three sites, the southern Oregon provenances were superior, closely followed by northern Californian and northern Oregon and then Washington coastal sources which always out-performed those from the Puget Sound. However, the southern provenances, although vigorous, showed a high degree of lammas growth, which may lead to occasional autumn frost damage and defective branching (Roman-Amat, 1993a). The International Ten Provenance Experiment was planted at the Massif Central site following a four year nursery phase. Results from the nursery showed that for budset, length of growing period and frequency of secondary growth or lammas shoots there was a strong clinal pattern of variation with latitude of origin. As regards flushing there was no pattern since there were only five days between the earliest and latest compared to five weeks for budset (Birot and Le Couvier, 1980). At 11 years from seed the mean provenance heights were strongly related with their latitude of origin. The only exception was the provenance from Queen Charlotte Islands which has the growth rate expected of an origin from further south. The ranking of the provenances for height was constant from 4–11 years of age. The fast rate of growth appeared to be strongly and positively correlated with the production of numerous lateral branches and the capacity to produce lammas shoots (Roman-Amat, 1993b).

Northern Ireland

In Northern Ireland, Sitka spruce is a most important species which has accounted for about 85% of the forest land planted since 1945. There are 26 experiments in two main series, the first planted in 1967 with nine origins, but as the range of origins is narrow and plants of different age were used, the results are difficult to interpret (Savill and Milner, 1980). The second series covered 17 of the IUFRO seedlots planted on 14 sites including the International Ten Provenance Experiment. Results two years after planting indicated that early and late frosts both in the nursery and the field rendered the use of provenances from much further south than 50°N too risky. However height growth indicated the superiority of more southern provenances.

Ireland

Sitka spruce is also an important species in the Republic of Ireland (O'Driscoll, 1976). Because plantations of the commonly used Queen Charlotte Islands origins grew well, investigation of more southerly origins did not start until 1960, when 10 origins (the same as in the British 1960/61 series) were planted at Killarney, which has an unusually mild climate. Results showed the clear superiority of the Washington provenances (Pfeifer, 1993). The International Ten Provenance Experiment was described by O'Driscoll (1976) at the nursery stage and its results after three years in the forest at three sites by O'Driscoll (1980). The pattern of height growth was similar at all sites with the tallest seedlot from Necanicum, Oregon. There were also significant differences in flushing, growth cessation and frost damage. The overall pattern of flushing on all the field sites was similar to that in the nursery with the southern provenances first to flush but with only a maximum of seven days between the provenances. The pattern for growth cessation was also similar to that in the nursery but was greatly increased with a maximum of 64 days between sources at the Kenmore site. There was a strong clinal pattern for growth cessation with the most southerly provenances the last to cease.

In addition to these experiments, the main IUFRO collection of 67 provenances was planted on nine sites covering a wide range of conditions. As with the International Ten Provenance Experiments, these also showed that the pattern for height growth after nine years was very similar to that at the end of the nursery stage. Height at both ages was closely correlated with latitude of seed origin. The southern Oregon and northern Californian provenances were the fastest growing decreasing progressively to Alaska except for the Nass and Skeena Rivers (BC) provenances whose height was lower than expected for that latitude. The provenances from mid Oregon southwards all had autumn frost damage in the nursery but all the provenances were hardy in the field once past the tender seedling stage. Damage due to late spring frost was experienced at one field site but there were no differences in its effect on the different provenances due to the small range among them in flushing date (Pfeifer, 1993).

Wood density and branching characteristics were measured on six selected provenances at four of the most contrasting sites, when the material was 12 years old (Murphy and Pfeifer, 1990). The results showed that wood density is negatively correlated with growth rate but positively correlated with latitude of seed origin. However, site type has a greater influence on wood density than seed origin, but seed origin has a greater influence on branch size and number than site type, with the slow growing origins from Alaska and BC having larger sized branches in relation to stem diameter than those from Washington and Oregon. Large increases in growth do not necessarily result in decrease in wood density of a corresponding magnitude. There was an increase of 50% in diameter from north to south but the decrease in wood density was only 10%. This work is described in greater detail in Chapter 5.

Six of the sites were re-measured after 19 growing seasons for top height (Thompson and Pfeifer, 1995). The results continued to show that height growth increased from north (QCI) to south (Washington and Oregon) until it began to decrease in Northern California. An increase of two or three yield classes could be achieved by planting southern Washington (YC 24) and Oregon (YC 26) provenances rather than QCI (YC 18). The earlier growth studies demonstrated that the southern provenances produced fewer and smaller branches, thus adding to the advantages these provenances have, especially on mild coastal sites. On colder, more exposed sites the northerly provenances of QCI and Vancouver Island performed better.

Canada – British Columbia

In British Columbia, Illingworth (1976) noted that 4 million Sitka spruce plants are needed for reforestation annually, despite the ease with which Sitka spruce regenerates naturally. The International Ten Provenance Experiment showed that at the end of the second year in the nursery, height was correlated with latitude, linearly for the Alaskan and British Columbian seedlots, but formed a discontinuity with those from Washington and Oregon. The Big Qualicum River source from Vancouver Island was taller than the Washington and Oregon lots. The forest stage of this experiment was planted on four sites, two on Queen Charlotte Islands, one on Vancouver Island and one on the northern mainland in the Kitimat Valley, (Illingworth, 1980). Growth after three years was poorest on this mainland site and best at the southern site on Vancouver Island. Some cold injury was recorded on the most southerly origins during the first two winters after planting at the Kitimat site. These had by now overtaken the Big Qualicum River origin at all four sites. The percentage of plants with lammas growth was assessed three years after planting and there was a linear increase with decrease in latitude except for the material from Hoquiam. A second series with similar provenances to those in the International Ten Provenance Experiments was established on a further four sites covering the outer coast, inner coast and higher elevation sites. In this series material from Brookings in southern Oregon was included and this was very heavily affected by cold injury at the three northern sites.

The two series of experiments were measured for height at 3, 6, 10, 15 and 20 years of age. Three of the sites were heavily attacked by the weevil *Pissodes strobi* Peck. (Ying, 1991) which can have a severe effect on site productivity and could have potentially caused a reduction in growth of 3 m at age 20 (Alfaro, 1989). The latitudinal trend for height was strong at early ages at all sites and this trend was maintained to 20 years on the mild sites with strong maritime influence. At inland sites or sites with heavy weevil attack the geographic pattern of provenance performance changed from a linear north-south latitudinal one to a more west-east longitudinal one. In addition the superiority of the fastest growing provenances declined as age increased and the performance of the provenance climatically closest to the experiment site was converging with the best by age 20 (Ying, 1995).

In BC, the main series of 38 IUFRO seedlots concentrated on seed origins from BC and Alaska. Falkenhagen (1977) measured the seed origins during their nursery phase for flushing, budset and height and at the end of the second year showed a clinal relationship with latitude, while there was a decrease in height with distance from the coast for seed sources sampled from the course of the Skeena River. Pollard *et al.* (1976) used controlled environment chambers to study the International Ten Provenance Experiment origins at Petawawa, Ontario. Their findings showed that growth rate was rather uniform, being only slightly faster among northern provenances but growth duration was strongly controlled by photoperiod and hence latitude. The critical photoperiods for sustained growth were up to four hours shorter for southern origins than for northern ones. In their studies of the morphogenesis of the terminal bud following cessation of extension growth, at first, northern seedlots had more primordia than southern ones, but later in the season this reversed. The protracted period of development of primordia shoots in overwintering buds gives southern origins an advantage when grown on southern sites.

Experiments have also been established in Newfoundland (Khalil, 1977, 1980, 1993 and Hall, 1990) and Ontario (Ying and Morgenstern, 1982),

Other countries

Other countries or states which have tested different seed origins of Sitka spruce include Iceland (Benedikz, 1976), Latvia (Pirags, 1976, 1993), Yugoslavia (Dokus and Gracan, 1980) and Australia (Pederick, 1980, 1993) but in these countries conditions are so different from those in Britain that little further need be said. In New Zealand, where conditions in the South Island are somewhat closer to those in Britain, Sitka spruce has been used to a limited extent. Eleven of the IUFRO seedlots from Washington to California were planted on nine sites. After 12 years there was a strong inverse relationship between tree height and diameter and latitude of origin, but attacks by aphids were severe and this species is not considered to be suitable for wide-scale planting in New Zealand (Miller and Shelbourne, 1993).

The International Ten Provenance Experiments

This was designed to allow comparisons of the same set of origins over a very wide range of site types. Samuel (1993) analysed height growth 7–11 years after planting at 19 sites ranging from Norway to Yugoslavia in Europe and including the Canadian experiments. In most experiments, at least average performance could be expected from Queen Charlotte Islands or lower Skeena River origins, whilst for all areas except Scandinavia and the Baltic States, origins from Washington could give better growth on sites in which survival would not be jeopardised by extreme climatic conditions.

Summary of seed origin studies outside Great Britain

The results of seed origin comparison in a number of western European countries indicate that:

- On milder sites, seed sources from Washington and northern Oregon give the fastest rates of growth.
- Origin choice must be tempered by the effects of frost, especially in the nursery and early field stages.
- Survival of origins from southern Oregon and northern California was generally found to be poor in comparison with more northerly sources.

3 British seed origin experiments – introduction, phenology and morphology

Introduction

Appendix 1 lists all the seed origin experiments of Sitka spruce which have been planted in Britain, together with their geographic coordinates and a summary of the seed sources they contain[1].

As there was general satisfaction with the main seed source (the Queen Charlotte Islands), the Forestry Commission (FC) paid less attention to seed origin variation in Sitka spruce compared with other species during the first 30 years from its foundation in 1921. This is evident from the details of the experiments planted up to 1950. These had a number of defects, such as the use of plants of different age and type, plants raised in different nurseries, vague descriptions of origin and poor experimental design (Lines, 1964). Results were thus sometimes conflicting and difficult to interpret. The experiments planted between 1950 and 1959 tested only part of the range. In this period, broad-scale comparisons were made by Forestry Commission management staff, using 100 pairs of plots throughout Britain to compare the performance of Alaskan with standard Queen Charlotte Island origins. Research staff monitored a sample of these (Lines and Mitchell, 1965; 1968). A similar survey was carried out in stands resulting mainly from Washington seed sources imported in 1962–66 when there was difficulty in obtaining sufficient seed from the Queen Charlotte Islands. There had been serious frost damage in the nursery with these seedlots, and it was considered necessary to follow up the performance of the surviving plants in the 80 forests where they had been planted. A sample of one third

[1]Although forest experiments in Great Britain have been uniquely identified by the name of the local forest unit and a serial number (both given in Appendix 1), they are referred to in this text by their forest name only. A small number of names are common to two series of experiments but no confusion should arise from this. The convention of referring to the year of planting as the P year (P74 = planted in 1974) is also used.

of these forests showed that survival and later growth were almost always satisfactory (Lines *et al.*, 1971).

The first comprehensive range-wide collection was sown at three nurseries in 1958 with 12 commercial seedlots from North America and a Danish provenance believed to be of Washington origin (Aldhous, 1962). Fourteen forest experiments were subsequently planted in 1960/61 and four sets of demonstration plots established in 1959 close to research nurseries to enable phenological observations and detailed growth measurements to be made (Lines and Mitchell, 1966b). Appendix 2 gives details of the planting sites together with a summary of the experimental designs and plot sizes used; the distribution of the nursery and forest planting sites is shown in Figure 10. All available details of the seed origins used in the experiments are given in Appendix 3 together with letter codes by which their locations in northwest America may be identified on the maps in Figures 11a and 11b. The Alaskan source, Lawing, appears at only one site and the British collections from Devon and Cardiganshire at one and two sites respectively.

In Appendix 3 the origins are grouped into broad regions. This structure is used, particularly in studying growth characteristics, to establish trends in performance on a wider geographical and ecological scale. This collection has the disadvantage that each major region is represented by only one or two origins. This was not thought to be a problem with the Queen Charlotte Islands region (QCI), since little variation between origins on these islands was expected. Indications that this was not true, however, came first from a later experiment planted at Glendaruel in Argyll in 1968, which contains 37 of the seed origins studied by Burley (1966a). This experiment has given useful information but as the plots are small, only short term data were provided and some of the material is represented only at this single site. Details of this experiment are included in Appendix 1.

A small experiment at Shin (P72), with seed origins from the most westerly part of its range in the Cook Inlet and Kodiak Island area of Alaska extends the range of the IUFRO collection and this experiment has provided useful information on precocious flowering (Lines, 1978).

In view of the importance of Sitka spruce in Britain, the opportunity was taken to participate in evaluating the comprehensive IUFRO 1968–1970 collection (Fletcher, 1976). The 62 seedlots selected for use in Britain provide an excellent cover of the main part of the distribution. They also give a good indication of the amount of variation between sources within each broader seed region. The main IUFRO collection was sown at three nurseries in 1973 (Lines *et al*, 1973) and was planted at 18 sites covering the full range of latitude in mainland Britain from Caithness to Cornwall in 1974/75 (Lines, 1976). Appendix 4 gives details of the planting sites together with the experiment designs used. These included small plot sizes for short to medium term evaluation with larger long-term plots at some sites. These are referred to as 'intensive' and 'extensive' sections in other parts of this text. The distribution of the nursery and field planting sites used for this series is also shown in Figure 10. Details of the origins used in the IUFRO series are presented in Appendix 5 which includes a number reference through which their locations within northwest America can be found on the maps presented as Figures 11a and 11b. For such a large sample of the natural range, two levels of grouping of the origins are considered, one (8 groups) on a broad basis similar to that used in the P60/61 series and a more detailed one (16 groups) in which further more local sub-division is considered. Descriptions of the 16 groups are given in Appendix 5 and Figure 11b outlines the boundaries of both these levels of grouping (the map omits a number of origins in northern Alaska which are shown in Figure 11a).

Figure 10

Distribution of the nursery and forest planting sites used in the P60/61 and the IUFRO series in Great Britain.

Figure 11a

Locations of seed sources evaluated in the P60/61 and IUFRO experiments.

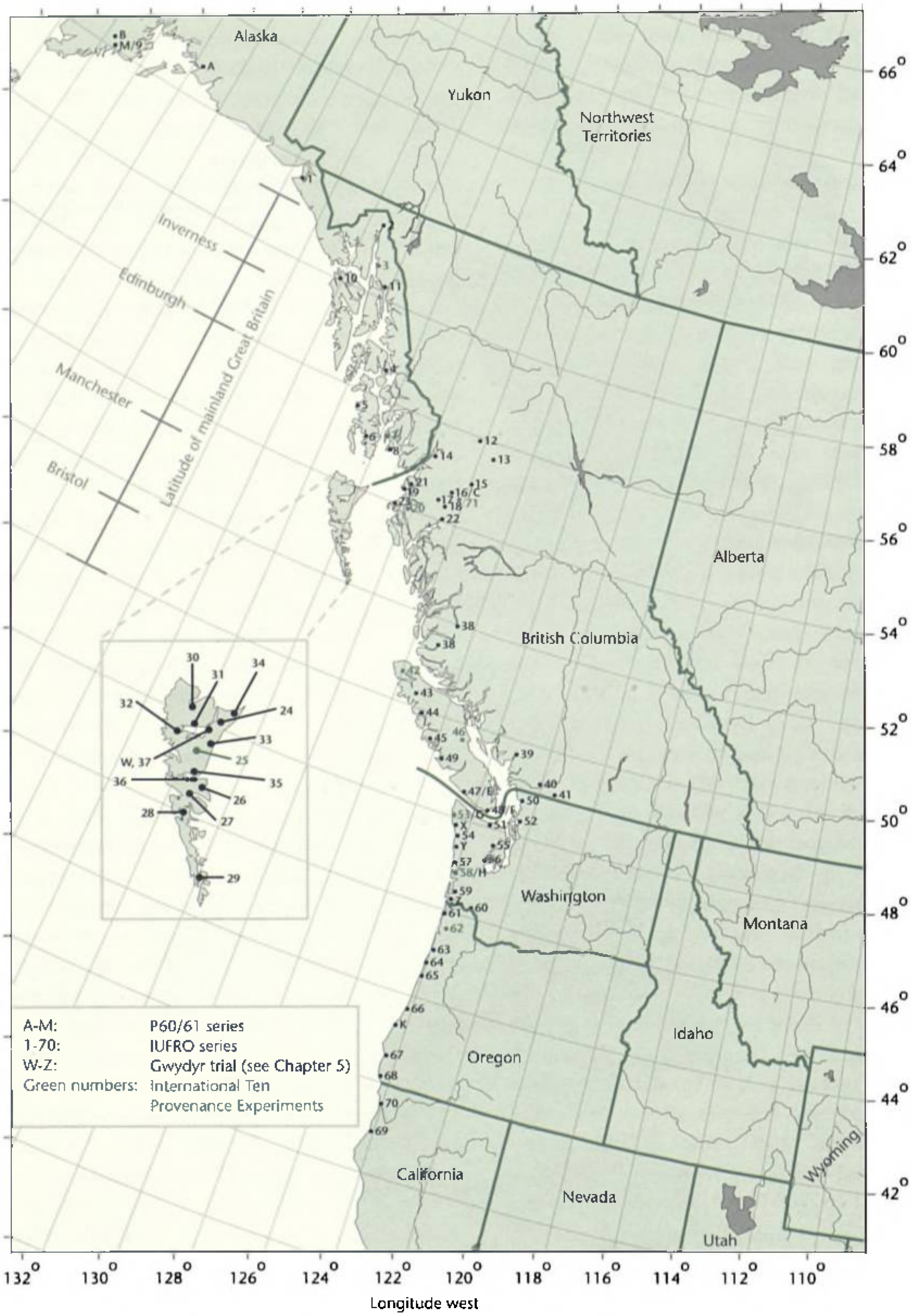
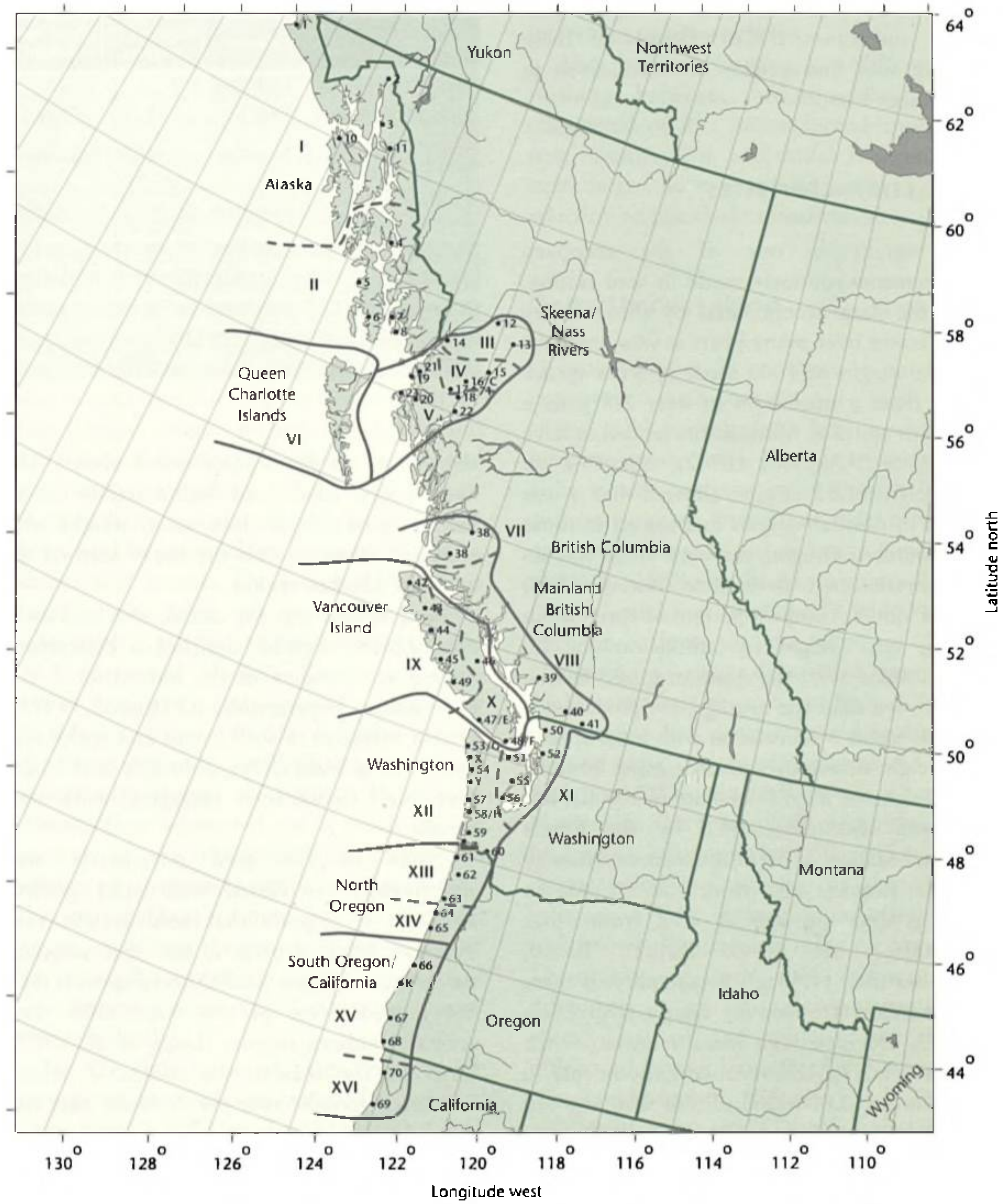


Figure 11b

Regional and sub-divisional groupings (I-XVI) of sources in the P60/61 and IUFRO experiments.



Two small experiments were established in south Scotland and in Wales as part of the International Ten Provenance Experiments (Lewis and Lines, 1976). Details of these planting sites and origins are also given in Appendices 4 and 5.

Seed characteristics

Seed weight is one of the standard measurements routinely made in seed testing. From the data accumulated by the Forestry Commission over many years it was apparent that the weight of 1000 seeds of Sitka spruce varied from a maximum of over 2.8 g to a minimum of 1.5 g. Alaskan lots tended to have heavier seed. Aldhous (1962), reporting on seed weight of 12 origins, showed that it was highest in Alaskan origins and lowest in those from southern Oregon, although there was no clear correlation with latitude. Burley (1965) found a similar complex pattern of variation in relating seed weight to latitude among 30 origins, again with the Alaskan group having heavier seed than the average. He pointed out that this trend is unusual as with most species seed weight decreases with increasing latitude. Seed weight of the 71 seedlots in the IUFRO collection was determined by the Forest Research Station at Stend in western Norway with the heaviest seed from Yakutat, Alaska (2.96 g) and the lightest seed from Hays Mountain, near Prince Rupert, British Columbia (BC) (1.44 g). A summary of these measurements grouped by region is given in Table 3. Detailed seed measurements of the International Ten Provenance Experiments in 11 countries (O'Driscoll, 1976) also showed the Alaskan seedlot from Duck Creek, Juneau, Alaska, to be significantly heavier than the mean, while the lightest seed was from Holberg at the northern end of Vancouver Island.

While it is evident that there is no clinal relationship between seed weight and latitude, there is a suggestion of a regional pattern in the data from all the studies noted above. The Skeena/Nass River seed region stands out as having particularly low seed weight and contrasts strongly with the heavy seed of the adjacent Alaskan region.

Table 3

Weight of 1000 seeds (g) of 71 IUFRO seed origins averaged over region. (Tested in Stend, Norway).

Region	Range	Number of origins	Mean seed weight
Alaska	1.99–2.96	9	2.55
Skeena/Nass River	1.44–2.55	18	2.08
Queen Charlotte Islands	2.15–2.84	10	2.41
Mainland coast of BC	2.06–2.65	5	2.30
Vancouver Island	2.03–2.39	8	2.22
Washington	2.16–2.44	11	2.33
North Oregon	2.09–2.64	5	2.30
South Oregon and California	2.30–2.62	5	2.51

Seed weight was the character which most consistently showed significant differences among seed origins in the International Ten Provenance Experiments (O'Driscoll, 1978). Origin variation in seed length and width was usually of a lesser order, although seed length was often significantly correlated with seed weight.

None of the seed parameters was significantly correlated with later growth although it appears that seed weight may influence height growth of one year seedlings up to August, since Alaskan origins with their heavy seeds were at this stage taller than several southern origins (Lines *et al*, 1973). Later in the season, the southerly origins continued growth after the Alaskan ones had set buds.

Flushing

Flushing or bud-burst in Sitka spruce has been shown to be dependent on the number of day degrees >5°C after 1 February and the amount of winter chilling (Cannell and Smith, 1983). Flushing has been assessed in British seed origin experiments with Sitka spruce on many occasions since 1954 (Lines, 1964). Fairly intensive assessments were made in 1960 and 1961 in plots specially laid out to study phenology and growth rate during the growing season at three sites (Lines and Mitchell, 1966a). Lateral buds flushed about one week before terminal buds. There was much greater variation in flushing date between individual trees within a seed origin than between the mean values of different origins. The northern origins tended to take longer than southern ones to pass from the bud swelling stage to the fully-flushed stage. Burley (1966a) found differences of 10 days between the earliest and latest dates of flushing for 47 seed origins. There was no correlation with latitude, but they could be grouped into regions related to climate and source. The group with earliest flushing was from the Skeena/Nass River valleys, while the last to flush were from the coast of central Oregon. Kraus and Lines (1976) showed only small differences (significant at p <0.05) between seven latitudinal groups in the IUFRO series. When 64 seed origins were divided into 15 regional groups, these accounted for a much greater amount of the variation and differences between groups became significant at p < 0.001. The two earliest-flushing of the regional groups were from the area near the mouth of the Fraser River, and the upper Skeena and Nass Rivers. Oregon and Californian groups were late flushing.

In the International Ten Provenance Experiment, flushing was recorded at ten sites across Europe and Canada (O'Driscoll, 1976) and there was a broad consistency in results. Big Qualicum River, Vancouver Island, BC, was the earliest to flush (except in Canada and Norway) while the two Alaskan and the Hoquiam, Washington origins tended to be late flushing. Kleinschmit (1980) showed a difference of only 11 days between earliest and latest of 43 seed origins tested in Germany, while in France Deleporte (1984a) put this interval at only seven days.

For practical forestry, the differences in flushing between seed origins must be considered of low importance. However, for tree improvement, individual differences are quite large and it would be useful to confine selection to late flushing individuals.

Growth cessation

Growth cessation in autumn is a much more important characteristic of seed origin variation, as it affects both frost hardiness and inherent productivity. First year seedlings of Sitka spruce continue active growth into the autumn for much longer than older transplants or mature trees. In the series of experiments sown in 1958 at three nurseries, Aldhous (1962) noted that there was a wide variation between origins in the time of budset, amounting to more than three months. All Alaskan seedlots began to set buds in July and their growth had virtually ceased by the end of August while Oregon seed origins did not set buds on 50% of the seedlings until late November. The controlling mechanism is day length or photoperiod. Vaartaja (1959) demonstrated the existence of photoperiodic ecotypes in Sitka spruce and the effect is now well known. Experiments using the same set of 12 origins at four sites, showed large differences in growth cessation at two and three years of age, which were strongly influenced by the latitude of the seed origins (Lines and Mitchell, 1966b).

Pollard *et al.* (1976) studied the effect of photoperiod on origins from the International Ten Provenance Experiments using growth chambers. Their results demonstrated the critical effect of photoperiod on growth cessation, e.g. at 11 hours day-length there was no detectable shoot growth on any of the seedlings in the most northerly origin (Juneau, Alaska), while all of the 16 seedlings of the most southerly origin (Necanicum, Oregon) were in active growth. The full IUFRO collection provided an excellent opportunity to study growth cessation of large numbers of seed origins from the greater part of the natural range. Many authors (Kraus and Lines, 1976; Kleinschmit and Sauer, 1976; Falkenhagen, 1977; Kranenborg and Kriek, 1980) showed essentially the same relationship between length of growing season or progress of bud-setting, which was correlated linearly or curvilinearly with latitude (and hence photoperiod). Nanson (1976) found a correlation of 0.81 (significant at $p < 0.001$) between budset and latitude, while Kraus and Lines (1976) obtained a correlation of 0.91.

The length of the growing season is less easy to assess in the forest stage because of the difficulty of making frequent observations at distant sites. However it was assessed in the two International Ten Provenance Experiments in Britain. At Tywi, the growing season in 1977 (third since planting) varied between 65 and 135 days for the Juneau, Alaska, and Forks, Washington, origins respectively. There was the usual latitudinal cline for increasing growth period with decreasing latitude. Total height increment during the second and third growing seasons was highly correlated with growing season length ($r = 0.814$, significant at $p < 0.01$). In the Glentress experiment this was assessed two years later (fifth since planting). The date when 80% of the final shoot length had been attained gave the best discrimination between origins (differences significant at $p < 0.001$). This occurred at 74 days after the commencement of flushing for the most southerly origin (Necanicum, Oregon) compared with 42 days for the Juneau origin. The differences were well correlated with total height increment between the third and sixth growing seasons.

Lammas growth

'Lammas' or 'free' growth is the elongation of stem units formed a few months beforehand, in contrast to the spring flush of 'predetermined' growth, which is the elongation of stem units in the overwintering bud (Cannell *et al.*, 1976; Jablanczy, 1971). Pollard and Logan (1976) investigated the significance of lammas growth in its contribution to total shoot growth in ten seed origins of four year old black spruce (*Picea mariana* (Mill.) BSP). They found a greater amount of free growth on southern origins than on northern ones, although northern origins could be stimulated into free growth by extending the photoperiod artificially. The study by Pollard *et al.* (1976) with Sitka spruce seedlings clearly showed they had free growth in their first year. However, the potential for free growth diminishes between five and ten years and the potential of the primordial shoot in the overwintering bud therefore assumes increasing importance as a determinant of shoot growth. Nevertheless, in some origins of Sitka spruce obvious lammas shoots are produced, even when they are 10 or 12 years old, while others produce very few or none. The production of lammas shoots is not solely governed by the inherent potential of a particular seed origin to produce them, as it also depends on the site conditions and any previous injurious influence such as frost damage.

Lammas shoots are easily recognisable in the forest, and assessments of their frequency have been made in 19 British experiments, commencing in 1956 (Wood and Lines, 1959). This study showed that six Washington origins had 4–10 times as many lammas shoots as a QCI origin. One of the distinguishing features of the wide-scale comparison plots of Alaskan and QCI origins, established in the 1950s, was the virtual absence of lammas shoots on the Alaskan seed lots, while there were sometimes many on those from the QCI (Lines and Mitchell, 1968). However, in an experiment on an exposed hill-top at 457 m elevation in southwest Scotland (Watermeetings P59), even trees of presumed Washington origin had virtually no lammas shoots, while trees of the same origin on a favourable site in Wester Ross (Ratagan, P59), produced lammas growth.

Seven of the 1960 series of experiments were assessed for incidence of lammas shoots, which varied from 0% (Seward, Alaska) to 25% (Jutland, Denmark of Washington origin). There was a broad correlation with latitude, although a fast-growing origin from Sooke, Vancouver Island had more trees with lammas growth than the most southerly seedlot from North Bend, Oregon on six of the seven sites. However, at Glendaruel (P68) the incidence of lammas shoots was correlated more closely with latitude than with tree height at six years (Lines, 1975).

In the IUFRO series of experiments, eight were assessed for incidence of lammas growth three years after planting (Table 4). Seed origin differences were very highly significant at each site and the same general pattern of increase in percentage of lammas shoots with decreasing latitude was found. There were anomalous results at Benmore and Blairadam, both sites where the most southerly origins suffered severe early frost damage and as a result lammas shoot production may have been inhibited. At Benmore, an assessment of lammas growth in the tenth year (see right hand column, Table 4) showed a complete reversal, with the southern Oregon/California group now having the most lammas development, whereas at three years it had even less lammas growth than the Alaskan group. For Wilsey Down, the general pattern noted above was examined to see whether there was any further relationship between tree height and lammas growth or whether the apparent correlation was simply due to both being correlated with latitude. To remove the effect of latitude from both data sets, linear regressions were calculated separately for each. Even after adjusting for the effect of latitude, there was a clear correlation between the score for lammas growth and tree height.

Table 4

IUFRO series: incidence of lammas shoots at eight planting sites three years after planting. Ranked 1–8 (most–least growth). Further data for lammas growth 10 years after planting at Benmore appear in the right hand column.

Region	Craigellachie	Ratagan	Farigaig	Achaglachgach	Blairadam	Benmore	Wark	Wilsey Down	Benmore 10 years
Alaska	8	8	8	8	7	7	8	7	7
Skeena/Nass River	7	7	6	7	6	6	7	6	8
Queen Charlotte Islands	6	6	7	5	2	3	2	5	5
Mainland Coast of BC	3	5	3	6	5	5	3	..	6
Vancouver Island	5	4	4	3	1	2	3	4	4
Washington	4	3	5	4	3	1	5	3	3
North Oregon	2	2	2	2	4	4	1	2	2
South Oregon and California	1	1	1	1	8*	8*	6	1	1

*Considerable frost damage affected lammas shoot production

General summary of flushing, growth cessation and lammas growth

- Flushing or bud burst showed differences between seed origins which were statistically significant and clearly genetically controlled.
- Flushing was not correlated with latitude and because of the relatively short period between the earliest and latest origin to flush, it is not a characteristic to be evaluated in selecting a seed source.
- Growth cessation or bud set is a far more important characteristic with differences between origins of up to two months or more. It is highly correlated with latitude, southern sources which continue growth over a longer period being susceptible to autumn frosts.
- Lammas (secondary or free growth) is under strong genetic control and is highly correlated with latitude, increasing with decreasing latitude, although especially site conditions and elevation can influence production.
- Lammas growth in early years contributes significantly to tree height and can be susceptible to early autumn frosts.

Frost susceptibility

Sitka spruce may be damaged by spring, autumn or winter frosts. Much of the winter damage is not due to frost itself but to excessive water loss when the roots are not able to take up sufficient water from the cold or frozen soil (Peace, 1962). Peace stated that '*autumn frost is much less important than spring frost*', *noting that Sitka spruce 'can be damaged in the nursery, though not in the forest*'. There is no doubt that this statement is still true today for Queen Charlotte Islands origins of Sitka spruce, although certainly not for the most southerly origins. Because of the small differences in flushing time between seed origins, the forest manager can have little influence on the risk of spring frost, apart from changing from Sitka spruce to late flushing origins of Norway spruce for use in frost hollows (Lines, 1973). The opportunity to reduce autumn frost damage by selecting origins which are best adapted to early growth cessation and autumn hardening is much greater.

Most of the pioneer work in Britain on frost damage to forest trees was carried out by Day and Peace (1934 and 1946). Recent frost damage studies by Redfern and Low (1972) and Redfern and Cannell (1982) have drawn attention to autumn frost damage on Sitka spruce in the nursery and on young trees in the forest. They showed that needle browning damage was associated with grass minimum temperatures of -5° to -8° C, particularly when frosts followed a warm spell in September. Southern origins were more severely damaged than those from the Queen Charlotte Islands and Alaska. Damage symptoms could be reproduced in a freezing chamber. These studies were continued by Cannell (1984 and 1985); Cannell and Sheppard (1982); Cannell and Smith (1983, 1984 and 1986); Cannell *et al.* (1985); and Sheppard and Cannell (1985). This area of research has concentrated on the physiological status of Sitka spruce of different seed origins and their reaction to freezing in growth cabinets, while at the same time attempting to correlate and forecast the probability of frost injury from a study of meteorological records. It covers both spring and autumn frost damage and is based on:

- knowledge of the tissue temperatures which kill buds and shoots at different times of the year.
- an estimate of the screen air temperatures associated with lethal tissue temperatures.
- information on dates of budburst and shoot hardening, based on empirical models of thermal time and chill days for budburst and on minimum temperature

and daylength for shoot hardening (different origins showing very different responses to changes in daylength).
- knowledge of the probabilities of frost occurrence in spring and autumn.

Comparison is also made with conditions in northwest America and Cannell (1984) noted that Scottish upland sites (e.g. Eskdalemuir at 242 m altitude) experience air frosts of -2.5° C about four weeks later in the spring than Masset on the coast of the Queen Charlotte Islands. Illingworth (1980) noted that cold injury to Sitka spruce was not recorded at any of the sites of his seed origin experiments on the Queen Charlotte Islands or Vancouver Island, even though these included the Oregon seedlot from Necanicum.

Frost damage in earlier British experiments

Frost damage in British seed origin experiments has been recorded over a period of nearly 60 years, beginning with Steven's (1928) observation that 'in the autumns of 1926 and 1927, seedlings raised from Siskiyou, California and Siuslaw, Oregon were damaged, the terminal buds being frosted before they had ripened. In neighbouring plots, seedlings raised from seed from Queen Charlotte Islands, BC were not injured'. Frost injury to other pre-1939 Sitka spruce seed origin experiments was described by Lines (1964) and included both spring and autumn frost damage.

In post-1945 experiments the first record of frost damage was on a frosty site at Kielder (P50) (Wood and Lines, 1959); there were very highly significant differences in autumn frost damage, assessed as the percentage of trees with dead leaders, between a QCI origin with 7–10% dead leaders and six Washington seed sources with from 55–67% with dead leaders.

Frost damage at another site in Kielder (P54) in spring 1958, which resulted in death of the leading buds, caused stem-forking the following year. Assessments showed 48% of an Alaskan origin with forking, while the Queen Charlotte Island and an Argyll provenance (originally from Washington) had 56% and 35% respectively (Lines and Aldhous, 1961).

Frost damage in the P60/61 experiments

Little frost damage occurred in the mild autumns of 1958, 1959 and 1960 when the 11 seed origins were at risk in three nurseries (Aldhous, 1962). Only the most southerly origin from North Bend, Oregon (latitude 43°N) had losses of 10–25%. There was no spring frost damage in the nursery.

This collection was planted on 14 sites, of which two (Glentrool and Wark) frost hollows were chosen to give a severe test of frost resistance in subsections of the main experiment. These sections are distinguished (suffix B) from the main experimental areas (suffix A) in Table 5 in which frost damage in this series is given. A similar experiment was planted in a frost hollow at Bannau. To reduce site variation to a minimum at this site, a design using single tree plots with 12 replicates was used.

At Glentrool in the frost hollow section, autumn frosts in 1960 did no damage to northern origins, while those from Washington and Oregon suffered damage; the difference was statistically highly significant, although the degree of injury was slight (see Table 5, column 6). Frosts in the last week of May 1962 also caused more widespread damage as the plants had flushed, but again it was fairly light (Table 5, column 1). Seed origin differences were significant at $p < 0.001$, although there was no relationship with either tree height or latitude. Hoquiam, Washington and Skidegate, Queen Charlotte Islands, origins were worst affected, but the most southerly origin (North Bend, Oregon) had similar damage to that from

Table 5
P60/61 series: summary of frost damage at five planting sites.

	Site												
	Glen-trool 18B	Wark 2B	Bannau 1	Deer 3	Wark 2A	Glen-trool 18B	Wark 2B	Glen-trool 18A	Wark 2A	Wark 2A	Glen-trool 18B	Shin 1	Deer 3
	Spring frost years					Autumn frost years		Winter frost years					
	1962	1967	1961	1965	1965	1960	1964	1962/63	1962/63	1962/63	1962/63	1962/63	1962/63
Cordova	1.4	0.35	3.54	-	3.17	0.00	2.70	-	18.3	85.3	80	2	(0.50)
Lawing	1.8	0.37	2.84	1.07	3.60	0.07	2.40	77.6	24.0	84.6	88.2	1	0.65
Juneau	2.3	0.53	-	1.93	3.47	0.07	3.27	62.5	11.0	90.0	84.6	18	0.98
Sitka	2.1	0.69	3.96	-	3.33	0.00	3.07	-	16.0	77.0	79.7	5	(0.89)
Terrace	2.7	0.85	3.96	1.97	3.60	0.59	3.57	59.1	17.7	88.0	63.5	18	0.92
Skidegate	3.1	0.46	3.88	1.73	3.60	0.31	3.23	39.0	16.7	89.0	54.3	34	1.30
San Juan R.	2.7	0.64	4.00	2.23	3.63	1.10	3.60	37.7	30.0	92.0	55.4	52	1.41
Sooke	2.8	0.67	3.83	2.97	3.63	0.70	3.87	39.3	37.3	85.3	46.3	64	1.87
Forks	2.8	0.65	3.92	2.47	3.53	2.31	3.83	-	44.7	85.7	42.5	50	1.71
Hoquiam	3.0	0.73	3.83	-	3.37	1.93	3.87	21.3	32.3	81.3	49.6	69	(1.42)
Jutland ex Washington	2.4	0.76	4.00	2.57	-	1.87	3.70	-	-	-	38.0	-	1.78
Jewell	2.6	0.76	3.91	2.43	3.33	1.87	3.93	46.2	26.7	80.3	47.4	34	1.40
North Bend	2.4	0.65	3.75	2.60	3.23	1.80	3.33	28.6	30.3	83.7	49.9	55	1.50
Differences significant at:	***	***	**	NS	***	***	***	***	NS	not analysed	***	***	***
Notes	Score 1–5	Score 1–5 Trans-formed by ridits	Score 1–5	Score 1–5	Score 1–5	Score 1–5	Score 1–5	Survival % in July 1963	% trees with dead leading bud in June 1963	% trees with winter blast damage	Height in June 1963 as a % of height in Nov. 1962	% leaders with dieback	Score 0–4
Column number (see text)	1	2	3	4	5	6	7	8	9	10	11	12	13

Figures in parenthesis are from unreplicated plots

Where a scoring system is used, a lower number implies a smaller effect of frost.

A and B suffixes to experiment names: A = main site area, B = frost hollow.

Significance tests: ** significant at 1% probability level, *** significant at 0.1% probability level, NS not significant.

Juneau, Alaska. The winter of 1962/63 was outstanding for the long, exceptionally cold spell, which lasted from Christmas 1962 until early March 1963 (Wood, 1964). At Glentrool snowfall during this period was slight, so that the peat became frozen to such a depth that moisture uptake by the roots could not replace water loss caused by desiccating winds in late February when the daily maximum temperature was usually above 0°C. This resulted in considerable dieback and even death of well-established three year old trees. Dieback varied from 12% for Lawing, Alaska to 62% for Jutland (Washington origin) (Table 5, column 11). Differences were very highly significant and correlated with latitude.

In the parallel experiment at Wark, there was a severe frost on 1 June 1962, but no differences in damage among seed origins, presumably because they were all well-flushed by this date. In autumn 1964, frosts caused significantly greater damage at this site in the seed origins from Vancouver Island southwards than in those from north of this latitude, although within the southern group there was no relationship with latitude (Table 5, column 7). The two origins worst affected were Sooke, Vancouver Island and Jewell, Oregon, while the most southerly origin from North Bend, Oregon was affected to the same degree as the one from Terrace, BC. In 1967, spring frost caused serious damage to the seed origins (Table 4, column 2). When damage was assessed on 2 June 1967 there were highly significant differences, the worst affected being Terrace, closely followed by the Washington and Oregon seed sources. Alaskan origins were much less affected.

At Bannau, a severe frost at the end of May 1961 caused serious damage, with only the Lawing origin being significantly less affected (Table 5, column 3). Lawing was again the least damaged origin in May 1964 when Skidegate had the most damage. An assessment at 10 years of age showed that as a result of frosting, 55% of the trees from Sooke, Vancouver Island and Jewell, Oregon had multiple leaders, while Terrace and North Bend had 18% and 11% respectively. There was no latitudinal pattern.

In the remainder of the 1960/61 series of experiments none escaped frost injury completely, although at Wilsey Down in Cornwall, frost damage was never serious enough to have much effect on growth. This contrasts strongly with the most northerly experiment at Shin in Sutherland, where growth of all seed origins was checked by repeated frosting. All seed origins were severely damaged by a late May frost in 1961, then they had shoot dieback during the severe 1962/63 winter. The four Alaskan lots had between 1% and 18% of their leaders frosted back, while the more southerly origins from Vancouver Island, Washington and Oregon had 34–69% dieback (Table 5, column 12). The experiment at Forest of Deer, Grampian escaped the May 1961 frost, but had shoot dieback during the 1962/63 winter with a similar pattern of damage to that at Shin (Table 5, column 13). In both experiments the Sooke, Vancouver Island origin was more severely damaged than most of the Washington and Oregon sources. At this site, a late spring frost in May 1965 damaged all seed origins with less damage on the northern and more on the southern seed lots (Table 5, column 4).

In the main experiment at Wark there was widespread needle-browning on 80–90% of the trees in most seed origins following the severe winter of 1962/63 (Table 5, column 10). This damage was probably due to the period of low humidity at the end of February, when wind speeds of 15 knots were recorded and the soil temperature at 30 cm depth was below –2°C for a whole week. The percentage of trees with dead leading buds the following June varied from 11–45%, corresponding inversely with latitude, but seed origin differences were non-significant (Table 5, column 9). A spring frost on 19 May 1965 at Wark damaged all seed origins quite badly (Table 5, column 5).

Greatest damage occurred on those from the middle latitudes 54°–48°N with least damage on Cordova, Alaska and North Bend, Oregon.

In the main experiment at Glentrool the severe winter of 1962/63 had a devastating effect, causing the death of over 50% of all trees. Survival ranged from 77% for Lawing, Alaska to 21% for Hoquiam, Washington, when assessed the following July (Table 5, column 8).

Frost damage in the IUFRO experiments

Damage at the nursery stage

Autumn frost damage to seedlings at the nursery stage of the IUFRO collection was restricted to the six most southerly origins, i.e. from Florence 44°07'N southwards. Slight frosts in September 1972 did not damage any origin, but a severe frost on 21 October injured the southern seedlings which had not yet hardened (Lines *et al.*, 1973). The experiments at Bush and Fleet nurseries were both damaged in spring 1973 after the plants were lined out. Temperatures of -9°C were recorded at the end of April and, as the trees had flushed, damage occurred in all seed origins at Fleet. At Bush, where flushing was later than at Fleet, the damage was less universal and an assessment on 8 May 1973 showed very highly significant differences, most of which could be accounted for by the differences between regional groups rather than among individual origins within groups. There was a highly significant inverse correlation between this damage and latitude except for the most southerly group, which had been so badly damaged by autumn frosts that flushing had been delayed.

The transplants at Fleet made a steady recovery from frosting throughout the 1973 growing season with the Alaskan origins appearing to have had little damage. By early October, all seed origins from above 49°N had set bud. Frosts in October and November (-11°C) damaged the un-hardened shoots of the southern origins, see Figure 12. Frosting is expressed as a score on a scale of 0 (no damage) to 4 (all plants with severe damage to leader and side shoots). Transplants at Wareham were not damaged by frost in either spring or autumn 1973.

Autumn frost damage in the forest experiments

Table 6 shows the distribution of damage to the eight main regional groups of seed origins. The analyses were made on individual values before grouping and in most cases refer to trees showing any kind of autumn frost damage, although at Benmore the assessment in 1980 was limited to trees showing dieback of the 1980 leading shoot. There was a very clear exponential increase in damage in the more southerly groups. For example, at Arecleoch a curvilinear regression of frost damage on latitude explained 88% of the variation. In several experiments omitted from the table, damage was not assessed, as it was confined only to the south Oregon and California group. However, it is also evident that on the most testing sites, e.g. Rumster, significant autumn frost damage can occur on origins as far north as the Queen Charlotte Islands.

Spring frost damage in the forest experiments

The pattern of spring frost damage is very different (Table 7), being poorly correlated with latitude of seed origin, although the Alaskan group were usually below the mean, while the south Oregon and Californian group were above the mean. Many assessments refer to the spring of 1975 when damage was widespread. Trees in those experiments which had been badly damaged by autumn frost in 1974 were either delayed in flushing or had no live buds able to flush. This probably accounts

Figure 12

IUFRO series: the effect of autumn frost at the nursery stage, scores from 0–4 (no to severe damage).

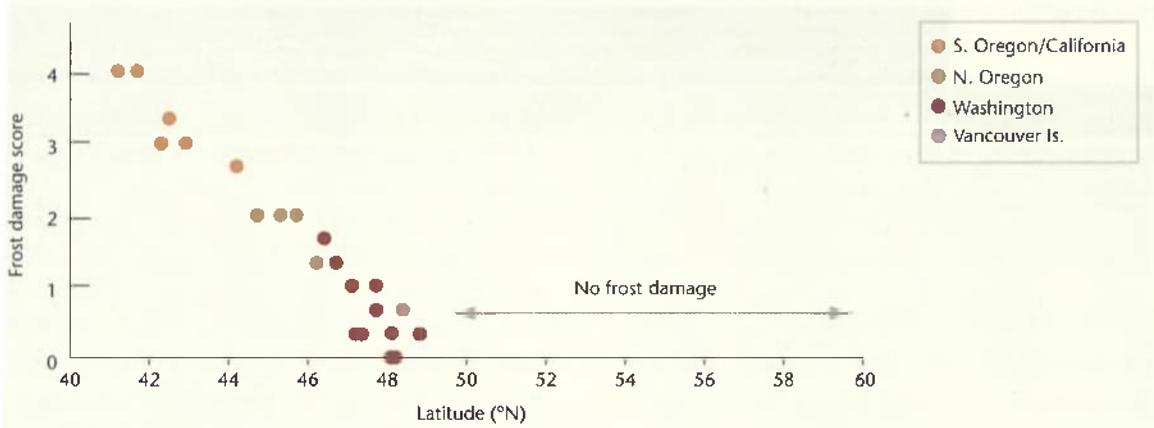


Table 6

IUFRO series plus Glendaruel (P68) experiment: autumn and winter frost, percentage of trees damaged.

	Site										
	Rumster	Craigellachie	Farigaig		Blairadam	Benmore		Castle O'er	Arecleoch	Glendaruel	Ystwyth
Region	Autumn 1974	Autumn 1974	Autumn 1974	Autumn 1975	Autumn 1974	Autumn 1974	Autumn 1980	Autumn 1975	Autumn 1974	Autumn 1973	Winter 1981/82
Alaska	2	0	18	1	0	6	16	0	5	1	0.17
Skeena/Nass Rivers	14	0	21	0	0	5	16	0	8	2	0.73
Queen Charlotte Islands	37	0	26	2	0	8	13	1	15	0	0.70
Mainland coast of BC	64	3	46	4	0	24	19	11	30	0	-
Vancouver Island	65	0	33	17	0	13	18	6	39	4	1.00
Washington	84	1	37	31	1	18	12	8	37	3	0.85
North Oregon	89	7	38	50	10	25	21	14	53	15	1.12
South Oregon and California	99	20	35	80	44	40	56	43	98	16	3.04
Differences between regions significant at:	*	NA	***	***	NA	***	***	NA	***	NA	***
Notes			Intensive plots only	Extensive plots only			% trees with dieback on 1980 leader		Both sections of experiment damaged to same degree		Score 0–4 (no–severe damage)

Significance tests: * significant at 5% probability level, *** significant at 0.1% probability level, NA not analysed.

Table 7
IUFRO series: summary of spring frost damage.

	Site								
	Rumster	Craigellachie	Blairadam	Benmore	Glentress	Mathrafal	Ystwyth	Ratagan	Farigaig
Region	1975	1975	1975	1975	1975	1975	1975	1981	1981
Alaska	2.37	1.01	0.97	67	2	76	1.42	2.34	2.39
Skeena/Nass River	2.57	1.02	0.91	77	4	77	1.66	2.60	2.64
Queen Charlotte Islands	2.50	1.02	0.99	72	10	70	1.46	2.64	3.23
Mainland coast of BC	2.60	1.02	1.09	62	27	-	-	3.24	3.10
Vancouver Island	2.57	1.04	0.98	70	36	77	1.70	3.11	3.46
Washington	2.61	1.12	1.12	69	56	77	1.12	3.07	2.96
North Oregon	2.14[1]	1.72	1.39	54	80	85	0.97	3.18	3.57
South Oregon and California	1.58[1]	3.55	3.08	4[1]	97	89	0.76	3.66	3.38
Differences between regions significant at:	NA	NA	**	**	NA	NA	***	***	***
Notes	Score 1–5	Score 1–5	Score 1–4	% of trees damaged	% of trees damaged	% of trees damaged	Score 0–3	Score 1–5	Score 1–5

NA = Not analysed.
[1]Trees affected by serious dieback in autumn 1974.
Scoring system: lowest number = least affected except at Ystwyth where highest number = least affected.
Significance tests: ** significant at 1% probability level, *** significant at 0.1% probability level.

for the low values recorded for the Oregon groups at Rumster, Benmore and Ystwyth. At Ystwyth, which is a high elevation site (510 m), it was observed that the northern origins were flushing at the end of April 1975, while buds on the southern origins had only reached the stage when they were beginning to swell. On this particular site these phenological differences may account for some of the variation in damage. Note that the scoring system used at Ystwyth was 0–3 (instead of 1–5) so that the worst group, Vancouver Island at 1.70 is approximately equivalent to 2.61 for the Washington group at Rumster. Results suggested that it was not possible to select seed origins which can resist late spring frosts and there were no examples of individual seed origins within a group showing consistently higher resistance on a range of sites.

The damage in 1981 at Ratagan and Farigaig was of a very unusual kind, caused by exceptionally warm weather at the end of March and the beginning of April when daily maxima of 17–20°C were recorded (Redfern, 1982). A severe frost occurred on the night of 22/23 April over the north west Highlands, with screen minima down to -10°C. Although the trees had not flushed, the stem and branch cambium had been activated on some trees by the earlier warm spell. Death of this cambium girdled the trees, causing the crowns to die back to about 1–2 m above the ground on trees up to 3 m tall (see Figure 13). Very few trees were completely killed and over the next few years a good recovery was made. The Alaskan group was least damaged (Table 7) which suggests that these northern origins may either require a higher accumulated temperature to activate the stem cambium, or that in some way they are inherently more resistant to freezing temperatures in the spring.

A combined analysis of the 39 seed origins which are common to both sites showed no significant difference between sites in severity of damage while the interaction of seed origin with site was significant at the 5% level of probability. By far the largest amount of variation was due to that between the geographical groups. The correlation of 0.745 between the mean score for damage at both sites and latitude of each seed origin was found to be highly significant when tested by Spearman's Rank Correlation Coefficient.

Winter frost damage in the forest experiments

During the years before mutual shelter began to develop, there were no winters as testing as 1962/63. Sporadic observations of damage after the winter of 1981/82 were made in this series, although frost injury was mainly confined to one or two seed origins in the south Oregon/ California group. However, at Ystwyth more widespread damage occurred in this winter, when the mean height was less than 2 m (i.e. before canopy closure). The pattern of damage shown in Table 6 was similar to that for autumn frost damage and confirms the very hardy nature of the Alaskan origins and the greater susceptibility of the south Oregon and California group to winter blast.

Frosting during the autumn–winter period of 1976/77 was assessed at Farigaig on 2 May 1977 (before flushing). Incidence of lammas shoots had been recorded on 23 November 1976 and individual trees were noted as having either light green or dark green lammas shoots, perhaps indicating an increased level of growth cessation (dark green). Overall, 40% of the trees had no lammas growth, 40% had dark green and 20% light green shoots. Of those with dark green or none, only 1% of the trees were frosted, but one-third of all those with light green shoots were frosted, i.e. frosting was almost entirely associated with trees having light green lammas shoots. The winter of 1976/77 at Farigaig was unusually severe and a comparison of frost damage recorded in November with frost damage assessed the following May shows a considerable increase for the Oregon and Californian seed origins, e.g. Newport, Oregon increased from nil to 17%, while the most southerly origin, Big Lagoon, California increased from 28% to 80% and Brookings, Oregon which had only 4% damaged trees in November increased to 79% by May.

Figure 13

Damage following low temperature in late April in the IUFRO origin 3012, Necanicum, Oregon, at Farigaig (Highland Region), seven seasons after planting.

General conclusions from the analysis of frost damage data

- In the nursery, seedlings and transplants can be damaged by both late spring or early autumn frosts. Early frosts cause more damage to southern origins. Frost damage at the nursery stage can be minimised by means of cultural techniques such as the use of netting covers over beds.
- In the forest, prevention of frost damage is not an option. Due to the small differences between flushing times between origins, all origins will be more or less equally affected by a late spring frost.
- Origins with late bud set or high incidence of lammas growth are more susceptible to early autumn frosts. Southern origins, especially those from Oregon and California and even from Washington should not be planted on sites where early autumn frosts are likely.

Infestation by green spruce aphid

Attack by the Green spruce aphid (*Elatobium abietinum* Walker) has a powerful influence on growth of Sitka spruce in the early stages (Carter, 1977). In trees felled in natural stands in the Queen Charlotte Islands, BC, seed collectors have noted a pattern in ring widths associated with a 10 year cycle of *E. abietinum* outbreaks. In Britain, Carter (1977) emphasised how the average frequency of outbreaks varied with winter severity from three years in southern England to six years in other parts of Britain with a reduction in leader growth in young trees of up to 61%. However, on average, reduction in height increment is in the region of 10–30% (Straw *et al.*, 1998). Very few of the 47 seed origin experiments in Britain have escaped an attack completely, although some showed severe defoliation, e.g. Wark and Rheola (P60/61) and Rhondda (IUFRO), while others may have been infested by *E. abietinum* without showing extensive defoliation.

Infestation reaches a peak at the end of May or the beginning of June but, apart from needle discolouration, the severity of attack only becomes fully apparent following needle fall, which may remove nearly all older needles, leaving the tree in early summer with only the newly flushed needles. For this reason, assessments of *E. abietinum* were made on the percentage of trees in each class of defoliation from 1 = undamaged to 4 = severe damage and 5 = dead.

The first major assessment was made in an experiment at Kielder nine years after planting in 1950 (Aldhous, 1961). This experiment contains six Washington origins and one from the Queen Charlotte Islands. In general the Washington origins were both taller and worse infested than the QCI origin, although with only a few replicates, the differences were not statistically significant. In the 1960 series of experiments, Rheola was severely defoliated by *E. abietinum* in 1976 followed by another severe infestation in 1977. These attacks were so severe that they overrode any seed origin differences. At Loch Goil, all seed origins proved equally susceptible in 1967, including the Alaskan lots, which were only two-thirds the mean height of the experiment. At Glentrool, there were no apparent differences among origins in defoliation in either 1967 or 1972. At the Forest of Deer, a relatively light defoliation in 1966 showed a very high correlation with tree height, but after removing the effect of height by covariance, the remaining seed origin differences in defoliation were not significant. Only at Wark were there highly significant differences in defoliation among seed origins. Because it was such a severe attack the comparison was made between the percentage of trees which were completely defoliated rather than using an average score. No geographical pattern emerged, since both the worst (Juneau with 57%) and the least defoliated (Lawing with

10%) were from the Alaskan group. Skidegate had 50% totally defoliated, while the Oregon seedlots Jewell and North Bend had 45% and 15% defoliated respectively. Covariance to remove the effect of height also reduced the significance of the difference among seed origins.

Four of the IUFRO experiments were assessed for defoliation: Benmore in 1979 and 1981 and Mathrafal, Rhondda and Achnaglachgach in 1981. There were significant differences between regional groups in each experiment, generally at the level $p < 0.001$ (Table 8).

At the Rhondda experiment, defoliation was not assessed on individual trees, but a general score was given to each plot on the basis of 1 = least to 3 = most defoliation. Thus the score of 2.62 for the South Oregon and Californian region represents severe defoliation. It was not possible to use the Rhondda data in an analysis across sites. However, data from the other three sites were combined for the joint analysis of the 1981 assessments. They showed significant overall differences between origins and between sites, although in no case were there significant differences within a seed region, while the site x origin interaction was only barely significant. By far the largest part of the variation was that between the regional groups, which were significant at $p < 0.001$. However, as seen from the overall defoliation percentage given in Table 8, the differences between the main regional groups of seed origins which are widely used (i.e. Queen Charlotte Islands to North Oregon) was small and may not be of practical significance.

When the data for defoliation were compared with tree height at six years, a high correlation was found at each of the four sites. When the overall mean height of the 26 origins at Achnaglachgach, Benmore and Mathrafal sites was compared with their overall defoliation by *E. abietinum* a correlation of $r = 0.767$, significant at $p < 0.001$ was found.

Day (1993) studied aphid intensity on a range of six provenances in a IUFRO experiment in Northern Ireland at eight years of age. Significant differences were found between provenances with aphid intensity apparently inversely related to latitudinal

Table 8

IUFRO series: defoliation by *Elatobium abietinum* (%) in 4 experiments.

Region	Benmore	Achaglachgach	Benmore	Mathrafal	Combined analysis over three sites[1]	Overall mean height at 10 years at three sites (m)	Rhondda
	July 1979	May 1981	June 1981	June 1981			May 1971 (defoliation score)
Alaska	14.99	3.59	32.30	14.42	13.87	3.14	1.95
Skeena River	18.19	3.36	50.42	14.51	17.44	3.19	1.89
Queen Charlotte Is.	33.50	10.88	56.21	43.83	38.14	3.93	2.50
Vancouver Island	30.13	8.31	58.07	39.00	35.79	4.00	2.50
Washington	24.48	6.14	52.18	44.54	34.47	4.06	2.42
North Oregon	16.10	16.10	41.10	46.13	33.38	4.28	2.00
South Oregon and California	7.77	12.81	46.30	52.29	35.91	3.77	2.62
Significance of difference between regions	***	**	***	***	***		*

[1]These data refer to the assessments of May/June 1981 at Benmore, Achaglachgach and Mathrafal. For the two northern sites they are regional means based on 59 origins common to both sites. In the combined analysis only 26 origins are included.

Significance tests (based on angular transformation of data): * significant at 5% probability level, ** significant at 1% probability level, *** significant at 0.1% probability level.

origin of the seed, i.e. the more southerly provenances were more susceptible. A later assessment was made on a greater range of provenances at the same site when the trees were 19 years old and had closed canopy (Harding *et al.*, 1998). Again there were marked differences between provenances but now there was a direct relationship between population density and latitudinal origin of the seed source, with the northern provenances most heavily infested.

In an experiment in Denmark based on 61 of the IUFRO origins, using percentage needle loss of the previous year's foliage as an index of resistance, there was no correlation between susceptibility and latitude of seed origin (Harding *et al.*, 1998). However, the assessment did indicate that there was large variation in susceptibility to defoliation between individuals within an origin. The study also demonstrated that the degree of damage was related to tree height.

It is not enough to consider only the relationship between seed origin variation and defoliation, as there are very likely differential responses in recovery following a serious attack. A preliminary study in the Rhondda experiment by Carter and Nichols (1993) following severe infestation in 1980, showed that while leader growth dropped dramatically in 1980 in each of five seed origins throughout the latitudinal range, the recovery of shoot growth in 1981 differed greatly, with Crescent City, California having much less loss in leader growth, compared to 1979, than Necanicum, Oregon, Masset, QCI and Duck Creek, Alaska. These authors have also drawn attention to the relationship between amino-acid content of the needles and dormancy. They suggest that origins with a long dormant period (i.e. northern origins) would be at a greater risk from the more damaging early winter attack and that they may have the tendency to carry greater over-wintering populations, since feeding and proliferation takes place during the dormant period of the host tree.

Leader breakage

Leader breakage occurs more often in Sitka spruce than in any other common conifer grown in Britain. Although it may occur at any time, it is most common following strong winds in summer or early autumn, before the woody tissues have become fully lignified. There is some evidence that trees on which the leader has lost turgor in a dry period, while the shoot is rapidly extending, suffer from a whiplash effect. The incidence of leader breakage is usually higher on more exposed, fertile sites than on sheltered, less fertile ones (Baldwin, 1993). On those in extremely exposed conditions repeated leader breakage will have a cumulative effect on height growth and thus make yield class prediction uncertain. This is probably less important than the effect on timber properties. A new leader forms below the point of breakage, thus producing more grain distortion than is found at a normal node (Aldhous, 1985; Brazier[2], personal communication, 1986). This 'swirl' in the grain pattern forms a point of weakness which is revealed during structural stress grading.

Leader breakage was assessed in five of the 1960 series of experiments and in the IUFRO series it was recorded in five experiments at six years and in two experiments at 10 years (Tables 9 and 10). The trees were between 1.5 m and 3.5 m tall at the time of these assessments, so that the point of leader breakage would affect timber quality within the lowest, most valuable sawlog. Leader breakage in the upper pulpwood section of a log is of little importance.

Tables 9 and 10 show that leader breakage is usually associated with growth vigour. At the three Welsh sites planted in 1960 (Table 9), Sooke, Vancouver Island had less leader breakage at six years than would be expected

[2] J D Brazier, Head of Wood Structure (retired), Forest Products Laboratory, Princes Risborough, UK.

Table 9 P60/61 series: leader breakage (%).

Origin	Deer	Wark		Tarenig	Myherin		Taliesin	
	10 years	6 years		5 years	6 years	10 years	5 years	10 years
	%	%	Adjusted for height (transformed)	%	%	%	%	%
Cordova	(0)	45.2	46.1	0	20.0	3.2	0	5
Lawing	12	15.4	29.1	0	17.0	4.2	0	0
Juneau	14	49.3	45.8	-	-	-	-	-
Sitka	(3)	42.0	43.2	0.8	23.8	5.2	5	5
Terrace	16	28.9	35.9	1.1	25.2	10.2	5	5
Skidegate	30	48.5	42.1	7.8	40.5	18.5	25	15
San Juan River	19	37.1	35.3	6.1	29.5	13.5	25	20
Sooke	26	44.3	41.2	5.7	24.8	13.0	5	15
Forks	34	23.3	27.8	11.3	27.8	22.0	30	20
Hoquiam	(17)	33.1	30.6	9.9	23.5	12.5	20	20
Jewell	27	45.3	38.0	7.9	29.2	12.5	15	30
North Bend	25	39.5	35.3	8.8	29.5	16.0	20	35
Differences significant at:	NS	*	*	***	**	**	NA	NA

NA = Not analysed.

Figures in parenthesis at Deer are from unreplicated plots.

Significance tests (based on angular transformation of data): * significant at 5% probability level, ** significant at 1% probability level, *** significant at 0.1% probability level, NS not significant.

Table 10 IUFRO series plus Glendaruel (P68) experiment: leader breakage (%).

Region	Achag-lachgach	Blairadam	Benmore	Glentress	Mathrafal	Castle O'er	Wark	Glendaruel
	6 years	6 years	6 years	6 years	6 years	10 years	10 years	6 years
Alaska	7.4	9.0	7.7	28.2	4.8	29.4	11.7	1.0
Skeena/Nass	11.0	5.9	8.8	17.6	1.5	29.2	15.7	2.3
Queen Charlotte Islands	7.8	15.3	26.4	29.9	2.1	32.7	19.0	2.0
Mainland Coast BC	11.2	4.2	19.8	14.2	-	46.0	15.7	3.0
Vancouver Island	7.9	15.2	28.1	18.4	4.0	40.8	12.0	3.8
Washington	7.3	9.4	22.7	16.9	10.3	30.7	21.6	5.3
North Oregon	11.1	10.8	21.8	17.8	17.5	51.4	26.0	4.0
South Oregon/California	6.2	3.5	2.3	3.0	33.5	(87.0)	61.6	5.0
Differences between regional means significant at	NS	NA	***	**	***	***	***	NA

NA = Not Analysed.

Significance tests (based on angular transformation of data): ** significant at 1% probability level, *** significant at 0.1% probability level, NS not significant.

on the basis of its tree height and it was suggested (Lines and Mitchell, 1966b) that this apparently greater resistance to shoot breakage might be partly responsible for its good height growth at six years. Sooke proved less resistant to shoot breakage in the Wark and Forest of Deer experiments, while the mean value for the Vancouver Island seedlots in the IUFRO series was close to the overall average for shoot breakage. In general, the Alaskan and Skeena River seed origins had the least number of broken leaders (except at Wark and Glentress) while the QCI seedlots were just as badly damaged as those from most southerly origins. This topic requires further investigation especially in respect to its effect on timber strength properties.

Stem and crown form

Within its native range, Sitka spruce develops pronounced buttress roots and basal swelling. This is more often found on trees which have germinated high up on old rotting stumps or fallen trunks and is of common occurrence in mature forests in British Columbia and Washington. It is too early to say whether seed origin differences will occur in basal swelling under British conditions; the oldest isolated Sitka spruce in Britain and Ireland already have very impressive buttress roots (see Figure 36 in Karlberg (1961) for typical buttress roots in European stands). However, it is unlikely that serious reduction in utilisable timber will result from buttressing under normal lengths of rotation in Britain. Also within its native range, there are striking differences in crown shape and branching pattern between individuals in the introgression zone with white spruce in the upper Skeena River valley.

Foliage colour

In trees from the Skeena River and in most Alaskan populations, the foliage colour of young trees is much lighter blue – green than in populations from below 54°N. The colour difference appears to be due to a much thicker waxy coating on the upper surface of the needles. The differences were highly significant in a nursery experiment at Benmore at the transplant stage of the P60/61 series and in the IUFRO series at Bush at the seedling stage. Burley (1966b) and Falkenhagen (1977) found a similar result.

Crown characteristics

Crown form varies both within and between origins. Detailed analysis of branching patterns have been made by Cannell (1974) on small samples from five seed origins growing at Glendaruel, and Cahalan (1981) used four clones from each of five seed origins taken from the P60/61 experiment at Wark to study their height growth and branch characteristics at two contrasting sites. Cannell showed a three-fold difference in total length of needle-bearing shoot per tree among seed origins. This was controlled by the amount of leader extension per year and the number of lateral branches produced. Cannell constructed a model predicting the branch formation of a particular seed origin, given that its height growth was known on that site. Cahalan showed that while there were significant differences between origins in branch number and angle, with southerly ones generally producing more branches than northerly ones, there were also significant differences between individual clones with some of those from the Queen Charlotte Islands having many more branches than those from North Bend, Oregon.

Delaporte (1984b) assessed various aspects of stem and branch form at seven years on eight origins which could be accurately placed within the natural range of Sitka spruce from Yakutat at 59°30'N to Curry County, Oregon, at 42°N. Branch angle varied by less that 8°, ranging from 55°24'N to 63°N and was independent of both vigour and latitude of origin. Most other characters, or the relationships between them, were influenced by vigour or latitude, e.g. the ratio of tree height to breast height diameter varied between 102.7 for Yakutat and 65.3 for Curry County. Differences in forking were not significant, and stem straightness was negatively correlated with vigour.

Apart from the detailed studies reported by Cannell (1974) and Cahalan (1981), there have been few studies of form in British seed origin experiments. This aspect has been investigated to some degree in numerous British progeny tests, mainly by scoring assessments. As these experiments commonly include three standard origins from Alaska, the Queen Charlotte Islands and Washington as well as the test families, some information can be gained from these, although the results are not appropriate for tests of significance. In general, they show small differences in branch angle. Relative crown width was greatest on Alaskan and least on Washington origins, with those from the Queen Charlotte Islands intermediate (Lee, 1988).

The experiment at Glendaruel was assessed at six years for branch angle using a scoring system with the percentage of each of three classes (horizontal, upswept, acutely upswept) recorded. The best discriminator between regional groups was the combined classification of upswept with acutely upswept and the results are summarised in Table 11. Differences between regional groups were significant (p >0.001), although there was no latitudinal trend. Relative crown width was assessed in four classes which reflected the ratio of crown width to total tree height. The best discriminator was the percentage of trees with crowns less than one quarter of total tree height, also given in Table 11, and differences between regions were again significant (p >0.001). There was a marked decrease in relative crown width with decreasing latitude. It should be noted that within the Vancouver Island region there were marked differences, with narrower crowns on the northern seedlots. An assessment of the ratio of crown width to height was also carried out at the same age. The results, also given in Table 11, showed highly significant differences between origins, and a fairly good correlation between these and relative crown width assessed by the same method. In both, therefore, the narrowest crowns were found in the two most southerly regional groups, while Alaskan seed origins had the broadest crowns.

General conclusions on infestation by green spruce aphid, leader breakage and stem and crown form

- Green spruce aphid can cause reductions in height growth of between 10% and 20% and the experiments indicated that the more southerly origins were more severely defoliated. The pattern however is not clear and the rate of recovery by seed origins following defoliation may be more important. The degree of damage is related to tree height.
- Leader breakage most commonly occurs following strong winds in late July and early August prior to the shoots becoming fully lignified. The incidence is higher on exposed and fertile sites and is associated with growth vigour.
- Variation in branch angle was small and there was no latitudinal trend. There was a marked decrease in relative crown width with decreasing latitude.

Table 11 Glendaruel (P68) experiment: branch and crown characteristics, six years after planting.

		Branch angle		Relative crown width			
		Trees with horizontal and slightly upswept branches		Trees with crowns less than one quarter height		Ratio of crown width to height	Region mean
Burley's No[1]	Seed origin	%	Region mean	%	Region mean		
	Alaska						
31	Chugach	85	71.4	3.3	3.24	93.8	95.8
48	Kodiak Is	68		0.0		103.5	
33	Duck Creek	99		1.8		90.0	
	Skeena/Nass						
19	Nass River	95	82.6	4.8	10.14	95.0	90.3
18	Kalum Valley	97		5.0		85.8	
3	Terrace	97		3.5		90.3	
	Mainland BC coast						
5	Bella Coola	94	80.1	6.0	9.92	82.5	82.5
	Queen Charlotte Islands						
4	Masset	84	75.3	6.0	9.85	78.5	85.7
16	Juskatla	95		4.0		89.3	
40	Moresby Island	93		4.0		89.3	
	Vancouver Island						
41	Quatsino	99	82.6	1.0	11.63	94.0	87.8
17	Green Central Lake	96		2.3		86.3	
36	Port Alberni	97		12.0		81.5	
7	Port Renfrew	96		8.5		89.5	
	Washington						
8	Hoko	95	83.6	21.5	20.57	78.5	81.6
9	Forks	95		15.5		80.8	
13	Wiskah	99		10.3		82.0	
11	Hoquiam	99		12.5		78.0	
45	Cedarville	95		10.8		87.5	
44	Cranberry Bogs	98		11.3		81.8	
12	Long Beach	99		19.5		83.0	
	North Oregon						
14	Jewel	92	76.7	13.5	23.34	86.3	78.6
26	Siuslaw Nat Forest	93		19.8		71.0	
	South Oregon and California						
15	North Bend	96	74.5	20.8	27.04	79.3	80.4
37	Crescent City	87		22.5		81.5	
	Differences significant at:	***		***		**	

Significance tests (based on angular transformation of data): ** significant at 1% probability level, *** significant at 0.1% probability level.
[1]Burley's number: see Burley, 1966a.

4 British seed origin experiments – growth studies and production

Introduction

Seed origin testing for Sitka spruce in Britain can be considered in three main experimental phases: early experiments planted before 1960; the series planted in 1960/61; and the IUFRO series planted in 1974/75 (see Appendix 1).

There was no clear pattern in the rate of growth of different seed origins in the experiments planted up to 1960 due to poor experimental design and losses from frost and fire (Lines, 1964). The results indicated faster growth of Washington seed origins than of the standard Queen Charlotte Island sources, but most of the experiments had been established on less demanding sites, somewhat unrepresentative of the wide range of site types on which Sitka spruce would be planted as the predominant commercial conifer from the 1960s onwards. They did suggest, however, that there might be good reasons for using Washington origins in milder areas, especially in southern Britain. No further detailed consideration is given to these experiments here.

The P60/61 series and the IUFRO series included range-wide collections established over a set of contrasting site types and as such lend themselves to more detailed consideration. Routine assessments of height (HT) were made at 1, 3, 6 and 10 years after planting. The first of these may still reflect nursery differences but it is used to compare initial survival of sources. Changes in ranking of entries has been found in provenances (Kleinschmit, 1993; Kleinschmit and Svolba, 1993) and in breeding material in Sitka spruce up to six years after planting (Samuel and Johnstone, 1979), but closer correspondence between six and ten years in the experiments reported here indicated that more predictable differences are likely to be encountered after the sixth year. In both these series of experiments, therefore, height at 10 years will be considered as the definitive indication of comparative early vigour up to around the time of canopy closure. After 10 years, for practical reasons, diameter measurements at breast height (DBH) were substituted for height and carried out at intervals. These enabled the calculation of basal area per hectare (BA) in those experiments based on plot sizes of 100 trees or more. During this later phase of evaluation, measurement was constrained by resources and the ages at which assessments were carried out were not consistent within a series of experiments. In the IUFRO experiments, DBH assessments were confined to the extensive sections of experiments which had been established with large plot sizes.

Presentation of data

A standard format for summarised growth data (HT and BA) is adopted throughout. Origin means are presented as a percentage of the mean for a chosen standard QCI origin. This provides a consistent and easier way of comparing the performance of different origins at a range of sites in tabulated data. QCI was selected as the standard since seed from either Graham Island or Moresby Island has been used almost exclusively in Britain in commercial forestry over the last 50 years. Within both series of experiments, origins have also been assembled into the regional groupings discussed in Chapter 3 so that comparisons of group means and origins within groups can be made. Details of the basis upon which origins have been grouped are given in Appendices 3 and 5. For the P60/61 series, tables summarising performance include both individual origin and group means. Within the IUFRO series, however, where up to 69 origins are included in experiments, full tables detailing the performance of each origin at each site are restricted to Appendices 6 and 7; any tables included in the text will only present data at the regional grouping level.

Statistical methods used in the analysis of growth data

The field experiments reported here are typical of those in which adaptive genetic variation among a range of sources is evaluated across contrasting sites. When data from all sites are combined, analysis of variance can be used to examine the significance of differences between sites and between origins across all sites. Due to the wide range of site types deliberately chosen in the evaluation of Sitka spruce origins, highly significant differences between site means were always found and, because the species has such a range of latitudinal distribution, significant differences between origins were always present. However, when data summarising origin performance at a range of sites are examined (see, for example, Appendix 6), changes of rank among origins between different sites are common. This is detected in analysis of variance as a significant origin x site interaction. It may occasionally be so prominent as to obscure the interpretation of overall origin performance. The regression analysis proposed by Finlay and Wilkinson (1963) and extended by Perkins and Jinks (1968) has been used to examine growth performance data combined across sites wherever possible.

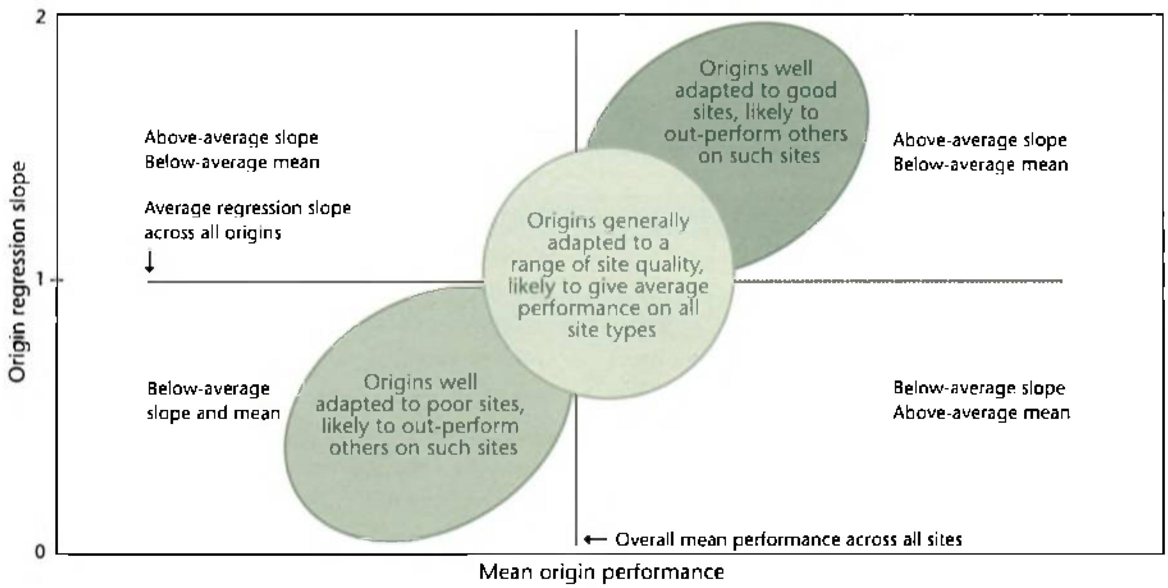
The methods use the mean height of all seed origins at a site (the site mean) as an index of the total environmental potential of that site, reflecting climatic, topographic and edaphic conditions. Linear regressions can then be derived for individual origin performance on this site index across all sites. The size of the regression coefficient (the regression slope) indicates the way an origin responds to better or poorer site conditions which may be referred to as its adaptability. The coefficients may be greater or less than the expected mean of 1.0. Thus an origin with the ability to respond to very favourable conditions will have a coefficient well above 1.0, while for those which fail to respond in growth on a good site the coefficient will be below 1.0. The significance of the deviations from the fitted regression line needs to be examined for each origin since their significance would reduce the confidence with which the regression slope could be used to predict likely origin performance on particular sites. As well as applying these techniques at the origin level, regressions may be fitted at the group mean level and the significance of deviations of individual origins from these groupings may be further examined.

One of the most easily interpreted presentations of the results of this approach is a scatter diagram relating origin mean to origin regression slope. A generalised representation is given in Figure 14. The scatter can be considered within four sectors defined by the intersection of two lines denoting the overall mean performance across all origins and sites and the expected average regression slope of 1.0. Origins with high mean and slope will only perform well on the most beneficial sites and will appear in the upper right sector whilst in contrast, those with low mean and slope will outperform others only on the poorest sites and will appear in the lower left sector. Occurrence in the other two sectors will be less common but many origins showing general adaptation to a range of site types will fall around the central intersection. When examining seed origin variation in most species, a positive linear relationship between mean and slope will be evident. It should be noted that overall origin means used in such scatter diagrams are calculated on the basis of raw site means weighted by the number of blocks at each site.

Regression analysis will be less reliable when the number of sites is small but it has been used as an adjunct to analysis of variance across sites for all assessments of vigour to be presented. Scatter diagrams will be used as the main basis for detailing the results of regression analysis. Analysis of variance tables will not be given but detailed aspects of appropriate analyses and significance tests will be referred to in the text where necessary.

Figure 14

Scatter diagram relating regression slope and mean performance of origins analysed across a range of experimental sites.



Comparison of 6 and 10-year height in the P60/61 series

Results after six years for the series of 14 experiments planted in 1960/61 were presented by Lines and Mitchell (1968) and after 10 years by Lines *et al.* (1971). A general summary of the performance and trends observed through the early assessments illustrates some of the ranking changes which become less noticeable by around the tenth year after planting. Seed origins from the four most northerly sources were consistently slower growing than those from Skidegate, QCI, and further south. The origins from Lawing and Cordova, Alaska were the slowest growing, while those from Terrace, BC maintained an intermediate position between the Alaskan and more southerly sources. Among the southern group, that from Sooke, Vancouver Island was tallest at both six and ten years. The origins from Jewell, Oregon and Hoquiam, Washington grew poorly at first, partly associated with winter dieback in 1962/63 (Lines and Mitchell, 1966b), but by the 10th year they ranked second and third respectively. Skidegate, QCI and North Bend, Oregon, which were second and third tallest one year after planting, fell in rank to sixth and fifth place respectively by the tenth year. The Forks, Washington origin maintained an average position among the southern sources, while that from San Juan, Vancouver Island was consistently the poorest of the southern group.

Height at 10 years in the P60/61 series

Mean height at 10 years for each origin at each site is summarised in Table 12. The table includes data from the site at Killarney in the Republic of Ireland, which have been analysed with those from the British sites. Performance has been expressed as a percentage of the single QCI lot from Skidegate. Mean height (m) for each site is given at the bottom of the table and overall origin mean in the right-hand column. In Britain, site means range from 0.87 m at the severe site at Mynydd Du to 3.21 m at the relatively sheltered west coast site at Loch Goil (see Appendix 2 for site details). Growth at the Killarney site (3.91 m) exceeds this considerably.

Examination of the overall origin means in this table shows a clear inverse latitudinal cline in height growth with slow growth being found among Alaskan sources and faster growth among those from Washington and Oregon. However, averaged across all sites, the growth of Skidegate, QCI is comparable to that of more southerly origins, and the fastest growing source overall is Sooke from Vancouver Island.

When the data presented in the main body of Table 12 are considered (growth expressed as a percentage of Skidegate, QCI), it can be seen that the tallest origins at the most northern (and frosty) site at Shin and at the high elevation exposed site at Mynydd Du were both from the Alaskan group. In contrast, origins from Washington and Oregon had below-average growth at these sites. Among the Scottish sites, this trend tends to persist at the less optimal sites of Deer and Glentrool, whilst in the milder western site of Ratagan, Washington and Oregon origins generally had the fastest growth rates. This effect was well-established throughout the English and Welsh sites with the fastest growth among origins from Vancouver Island southwards, and in the more favourable sites, with the growth of Oregon sources exceeding that of those from Washington. In the lower part of Table 12 summaries by regional grouping are presented in which the same data are displayed (see also an equivalent bar chart in Figure 15). However, some of the clear variation previously observed between individual origins within regional groups is no longer evident here. At Shin and Mynydd Du, for example, the QCI origin is now the fastest growing overall. Figure 15 shows of the general superiority of the QCI source over many others at a wide range of sites.

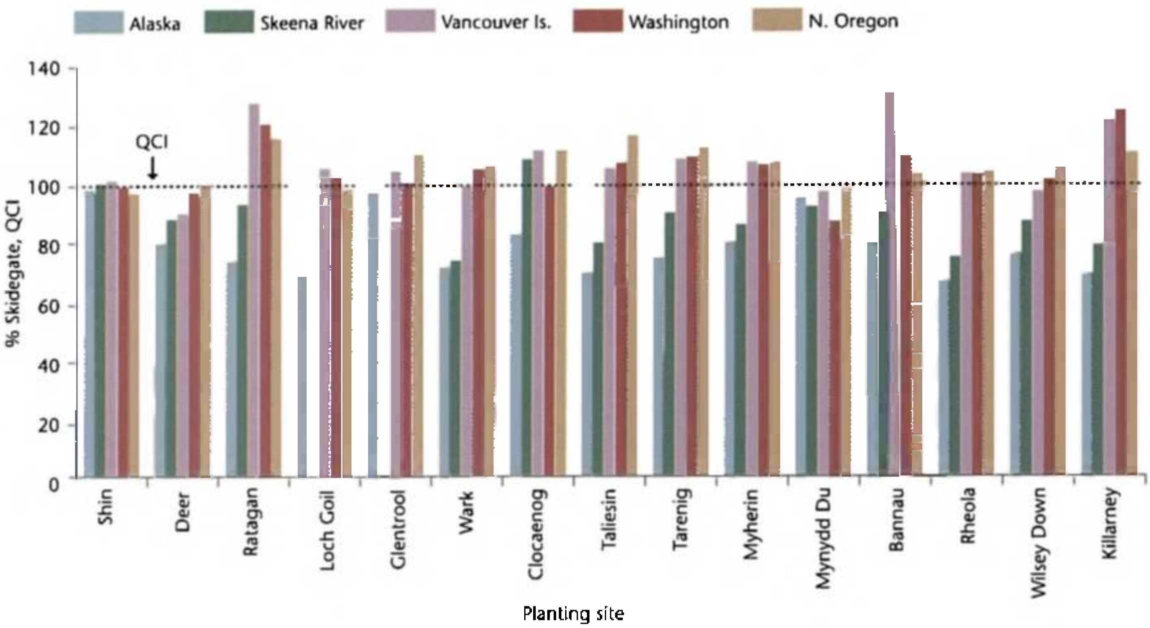
Table 12 P60/61 series: height at 10 years after planting at 15 sites expressed as % Skidegate, QCI.

Origin	Region	Latitude of origin	Shin	Deer	Ratagan	Loch Goil	Glentrool	Wark	Clocaenog	Taliesin	Tarenig	Myherin	Mynydd Du	Bannau	Rheola	Wilsey Down	Killarney	Overall origin mean (m)
UK latitude			58.00	57.50	57.25	56.00	55.00	55.00	53.00	52.50	52.25	57.50	52.00	51.75	51.50	50.50	52.00	
Cordova	Alaska	60.50	103	62	46	56	100	71	81	61	78	78	102	86	65	76	66	1.79
Lawing	Alaska	60.00	104	83	79	71	90	63		74	64	80	89	72	60			1.79
Seward	Alaska	60.00	95	84	83		98						76			65		1.94
Juneau	Alaska	58.25	93	89	71		90	78					90			70		1.95
Sitka	Alaska	57.00	85	72	83	76		67		68	78	76	109	76	70	85	68	1.92
Skidegate	QCI	53.00	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2.50
Terrace	Skeena River	54.50	98	86	91		89	72	106	78	88	84	90	88	73	85	77	2.06
Sooke	Vancouver Island	48.25	96	89	132	109	118	95	119	108	116	114	100	139	107	98	130	2.79
San Juan River	Vancouver Island	48.50	102	86	118	98	86	100	99	99	95	96	89	118	95	93	108	2.48
Forks	Washington	48.00	97	105	109	100		97	97	105	102	112	85	106	104	100	125	2.65
Hoquiam	Washington	47.00	97	85	126		98	109	97	106	111	95	85	108	98	98	119	2.52
Jewell	Oregon	46.00	92	104	113	101	119	105	113	114	105	111	102	100	105	108	114	2.69
North Bend	Oregon	43.00	99	92	112	91	98	102	105	114	115	99	90	103	99	99	103	2.53
Jutland	Denmark		81	103		122			128	107	123	120	91	89	122	116		2.61
Site mean height (m)			1.68	2.67	3.16	3.21	2.10	2.42	2.46	1.97	1.97	2.32	0.87	1.46	2.74	2.74	3.91	

	Region	Shin	Deer	Ratagan	Loch Goil	Glentrool	Wark	Clocaenog	Taliesin	Tarenig	Myherin	Mynydd Du	Bannau	Rheola	Wilsey Down	Killarney
By region	Alaska	96	78	72	67	95	70	81	68	73	78	93	78	65	74	67
	QCI	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	Skeena River	98	86	91			72	106	78	88	84	90	88	73	85	77
	Vancouver Is.	99	88	125	103	102	97	109	103	106	105	95	128	101	95	119
	Washington	97	95	118	100	98	103	97	105	107	104	85	107	101	99	122
	Oregon	95	98	113	96	108	104	109	114	110	105	96	101	102	103	108
	Denmark	81	103		122			128	107	123	120	91	89	122	116	

Figure 15

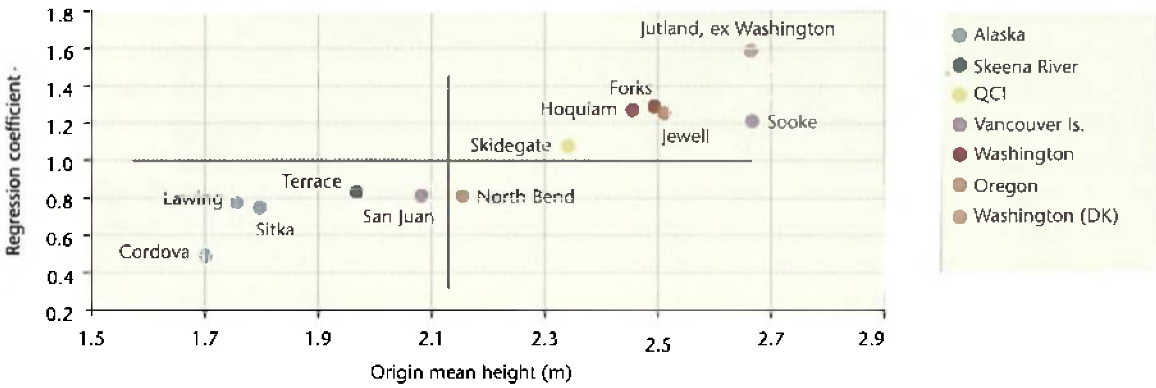
P60/61 series: regional mean height at 10 years after planting expressed as % of Skidegate, QCI.



Despite the shortcomings already referred to of low within-region representation in this series of tests, rank change between origins across sites are very clear. The results of considering this indication of origin x site interaction through regression analysis appear in a scatter diagram relating overall mean and regression slope for each origin in Figure 16, where each regional grouping from Table 12 is plotted using a different colour, and the material of Washington origin from Denmark has been separated from the other two Washington sources. The two Alaskan sources, Seward and Juneau, which are poorly represented across all sites, were omitted from any statistical analysis. Because of the incomplete distribution of origins to sites, there were no data for a further 15 cells. The statistical (Genstat, 2005) routines used in this and later analyses estimate missing values for such cells. The diagram provides a clear summary of those trends already noted in the data in Table 12. Alaskan origins, which have low means and regression slopes, are likely to be poor performers on all but the most demanding sites, whilst in contrast, Washington origins have above average growth and high regression slopes and will be likely to show particular growth advantages on better quality sites. The single QCI source used in this series of experiments has above average growth but has a regression slope close to 1.0, indicating that it is likely to perform well across a range of sites. However, there is a contrast between the two origins from Vancouver Island. Although occurring in relatively close proximity at the south of the Island, the Sooke material showed above-average growth, performing as if it were a coastal Washington source at almost all sites. Likewise there is a similar contrast between the Oregon sources. Here there is a difference of 3° in latitude of origin with the northern Jewell source showing growth and adaptation similar to the Washington origins whilst the southern source from North Bend is likely to be adapted to sites and climate types which lie outside the British range.

Figure 16

P60/61 series: scatter diagram relating regression slope and origin mean for height at 10 years after planting.



These more detailed observations from the scatter diagram were supported by significance tests within the analysis of variance applied to the data. Tests for mean height showed that differences between regional group means were significant. However, although tests between origins within groups were non-significant for the Alaskan and Washington regions, there were significant differences between origins within the Vancouver Island and Oregon regions. Similar tests applied to regression slopes found significant differences between slopes at the regional group level but only within the Oregon region was the difference between individual origin slopes significant. Individual regression slopes were all significant fits but there were higher standard errors for San Juan River and North Bend.

This detailed examination of the P60/61 data confirms that the regional grouping of these origins is sound but that there would be considerable benefit in wider sampling of populations within regions. There is some suggestion that variation within regions can be high and the IUFRO series based on up to 70 origins offers the opportunity to investigate this further.

Height at 10 years in the IUFRO series

A total of 70 seedlots was raised in nurseries for the 18 forest stage experiments established in 1974 and 1975. In the listing and description of these given in Appendix 5, the 62 origins forming part of the IUFRO collection are identified in the 3000 number series. The further eight origins were raised from commercial seedlots for comparison purposes and are identified by the seed identity numbers for such material used in Britain at that time. Three of these are from Alaska, four from QCI and one from Vancouver Island. The individual experiments covering Scotland and northern England each included between 63 and 70 origins. However, in the sites distributed through Wales and southwest England, the decision was made, based on the early results of the P60/61 series, to concentrate on the more southerly sources from Washington, Oregon and California and a common set of 27 origins was used.

At all the northern planting sites, an experimental design of 4 replicates of 9 (3 x 3) plant plots was used. At three of the sites (Farigaig, Arecleoch and Wark), the number of origins present in this intensive section was reduced, those removed being established in a further extensive section based on three replicates of larger plots of 225–255 plants. At the southern sites, where only 27 origins were present, all experiments except Mynydd Du had intensive (three replicates of 25 plant plots) and extensive (two replicates of 196 plant plots) sections containing all origins. These details are summarised in Appendix 4. Early height measurements were made at 1, 3 and 6 years after planting; those made at three years were summarised by Lines (1980).

Two of the experiments, Farigaig and Ratagan, were damaged by an unusual frost in April 1981. Recovery from this was so poor at Farigaig that no measurement of height was made at 10 years, but the experiment had recovered sufficiently for DBH to be measured later. At Ratagan, recovery was better and an assessment at 10 years was carried out. As indicated in Chapter 3, the intensive sections were intended to provide growth data up to the point of canopy closure after which inter-plot competition could be influential. The 10 year height assessment was therefore the last to be made in the intensive sections of each site. The extensive sections present at three of the northern sites were also measured to provide data on all origins, the origin means from the extensive section being weighted by the block effects calculated for the intensive section and included with other intensive data for analysis. The complete dataset summarising 10 year height for all origins at all sites is given in Appendix 6 where individual origin height has been expressed as a percentage of the commercial QCI seedlot, SS70(7111)Lot2. From this it is clear that some origins remain unrepresented at some sites. Because of poor survival and growth at Mynydd Du, no height data were collected after six years. Lines and Samuel (1993) presented an early summary of the data for height at 10 years after planting.

The considerable detail in this appendix is summarised in Table 13 where the origins have been grouped by regions, as in the P60/61 series. The regional grouping, because of wider sampling of the natural range now includes a combined grouping from the Skeena and Nass Rivers and a small set of origins from the mainland coast of British Columbia (BC). Sources from south of Washington have been split into two regional groups. It is clear that no set of origins has a mean height which exceeds the commercial QCI lot in growth on the more northerly of the Scottish sites except at Ratagan in the milder northwest of Scotland where material from as far south as Oregon has grown equally well. At test sites at lower latitudes from southern Scotland southwards through Wales and southwest England, the superiority of QCI origins is less evident and the increased performance of all regional groupings from Vancouver Island southwards becomes increasingly clear. However, the sources from the mid-mainland coast of BC grow slowly at all sites (see Figure 17).

A more detailed grouping of origins made possible by the large number of sources in test is given in Table 14. Among the five Alaskan and Skeena River groups, those from the upper Skeena River area (iii) perform poorly in comparison with other sources, particularly on more southerly sites. These origins were sampled at the extreme edge of the distribution of Sitka spruce in a zone in which its introgression with white spruce (*Picea glauca*) and Engelmann spruce (*Picea engelmannii*) is recognised. The mainland coast of BC groupings (vii and viii) also grow slowly as do origins from within the Puget Sound (xi). When the Puget Sound material is separated from the remaining coastal Washington sources (xii), a general improvement in performance of the latter is clear across all but one site. This superiority of coastal Washington origins on all sites from southern Scotland southwards is only exceeded by those from Oregon on the fastest growing sites where the northern and central Oregon groups (xiii and xiv) are often superior. Any superiority of sources from

Table 13

IUFRO series: summary of height at 10 years after planting, at the regional grouping level expressed as % 70(7111)Lot2, QCI.

		North Scotland			Central and southern Scotland						Northern England			Wales and SW England			
By Region	Origins	Rumster	Craigellachie	Ratagan	Blairadam	Benmore	Achaglach-gach	Glentress	Castle O'er	Arecleoch	Wark	Thorn-thwaite	Dalby	Mathrafal	Ystwyth	Rhondda	Wilsey Down
Alaska	12	88	82	77	80	87	79	93	87	84	79	77	81	75	85	71	79
Skeena/ Nass Rivers	12	81	85	76	81	84	80	91	88	77	78	73	84	82	88	72	78
Queen Charlotte Is.	14	98	93	91	97	103	102	101	104	94	96	94	100	101	102	98	102
Mainland B.C.	4	79	81	75	86	88	89	92	86	82	85	84	83				
Vancouver Island	8	93	95	86	97	101	105	101	101	94	96	97	101	100	102	129	106
Washington	11	89	93	92	97	104	106	99	103	99	94	90	101	109	100	95	97
North Oregon	5	95	94	100	93	104	119	101	91	98	88	101	109	110	106	98	112
S.Oregon/ California	5	83	88	101	64	80	122	78	48	76	61	84	99	100	91	95	114
Site mean height in m		2.97	2.43	3.62	3.50	3.71	4.03	2.17	2.32	3.11	2.45	3.64	3.34	3.40	2.75	3.01	4.64

southern Oregon and California is restricted to the very fast-growing soft sites (those with longer growing seasons and frost-free periods) of Achaglachgach and Wilsey Down.

In Figure 18, the overall mean height of each origin across all sites has been plotted against the latitude of its source. A different colour is used to represent each of the eight regions identified in Table 13 with changes of colour used to separate the more detailed grouping within each region used in Table 14. The overall trends already noted from Tables 12–14 are quite clear in this figure, particularly the clinal variation with latitude, and the superior performance of QCI origins compared with Skeena River and main coast BC origins from similar latitudes. The unsuitability of southern Oregon and Californian sources together with those from mainland BC is also evident. There is great variability across the narrow latitudinal range of the Skeena/Nass Rivers material, none of which matches the performance of QCI sources. Within the Skeena River area, a trend in diminishing growth rate from west to east, as noted by Ying (1995), can be seen. A very distinct separation of Washington origins collected within the Puget Sound from those from the Pacific coast of the Olympic Peninsula also emerges. Sources from east and west Vancouver Island do not separate so clearly, but the single origin from Muir Creek, near Sooke, appears to perform in a similar way to the coastal Washington origins. This mirrors the performance of material from this area in the P60/61 series and suggests that Sitka spruce from the extreme south of Vancouver Island can be considered to have the potential of material from the Olympic coast (both areas are combined in the data presented in Figure 19).

Several authors have demonstrated that there is a clinal pattern of variation in growth and phenological characters in Sitka spruce (Kleinschmit and Svolba, 1993; Pfeiffer, 1993;

Table 14

IUFRO series: summary of height at 10 years after planting, at the detailed grouping level expressed as % 70(7111)Lot2, QCI.

By detailed grouping		Origins	North Scotland			Central and southern Scotland						Northern England			Wales and southwest England			
			Rumster	Craigellachie	Ratagan	Blairadam	Benmore	Achaglachgach	Glentress	Castle O'er	Arecleoch	Wark	Thornthwaite	Dalby	Mathrafal	Ystwyth	Rhondda	Wilsey Down
i	North Alaska	6	84	83	77	74	80	77	90	86	76	76	75	75	72	82	64	76
ii	South Alaska	6	93	82	78	87	95	82	94	91	93	81	79	84	81	89	77	82
iii	Upper Skeena/Nass Rivers	3	82	85	75	81	83	68	85	84	62	77	67	76	61	70	65	52
iv	Middle Skeena/Nass Rivers	3	80	86	74	81	81	79	90	83	80	77	77	83				
v	Lower Skeena/Nass Rivers	6	81	84	77	81	86	86	95	93	85	80	75	89	92	97	76	91
vi	Queen Charlotte Islands	14	98	93	91	97	103	102	101	104	94	96	94	100	101	102	98	102
vii	Mainland coast BC	1	98	93	68	89	95	87	93	92	78	97	76	78				
viii	Vancouver/lower Fraser River	3	73	77	78	85	85	90	92	83	83	81	87	84				
ix	North/west Vancouver Island	5	96	91	82	98	101	104	102	106	99	95	94	98				
x	South/east Vancouver Island	3	84	104	92	94	102	108	98	94			102	107	100	102	129	106
xi	Straits and Puget Sound	5	87	90	87	94	96	101	97	98	94	88	87	91	99	87	93	98
xii	Olympics and Pacific coast	6	92	96	96	100	111	111	101	107	103	100	93	109	112	104	96	96
xiii	North Oregon	3	89	95	94	97	106	115	101	95	102	88	98	110	109	103	99	107
xiv	Central Oregon	2	105	93	108	87	102	125	99	85	91	88	105	107	111	109	98	120
xv	South Oregon	3	87	96	104	71	76	121	84	48	80	67	80	105	101	97	100	118
xvi	California	2	76	76	94	52	86	127	61		70	53	96	90	100	81	87	108

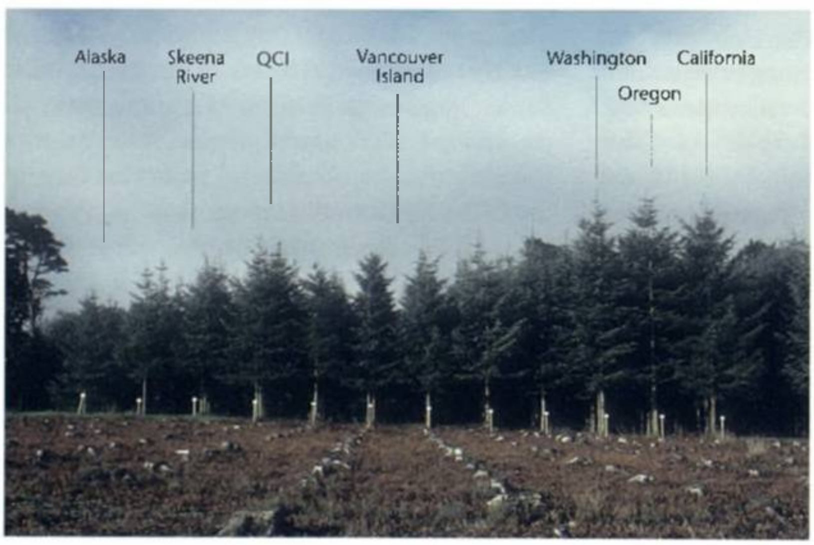


Figure 17

A demonstration of a range of origins of Sitka spruce growing in Britain at the Forestry Commission research station near Edinburgh, Scotland.

Figure 18

IUFRO series: relationship between height at 10 years and latitude of origin, based on detailed regional grouping (see Table 14).

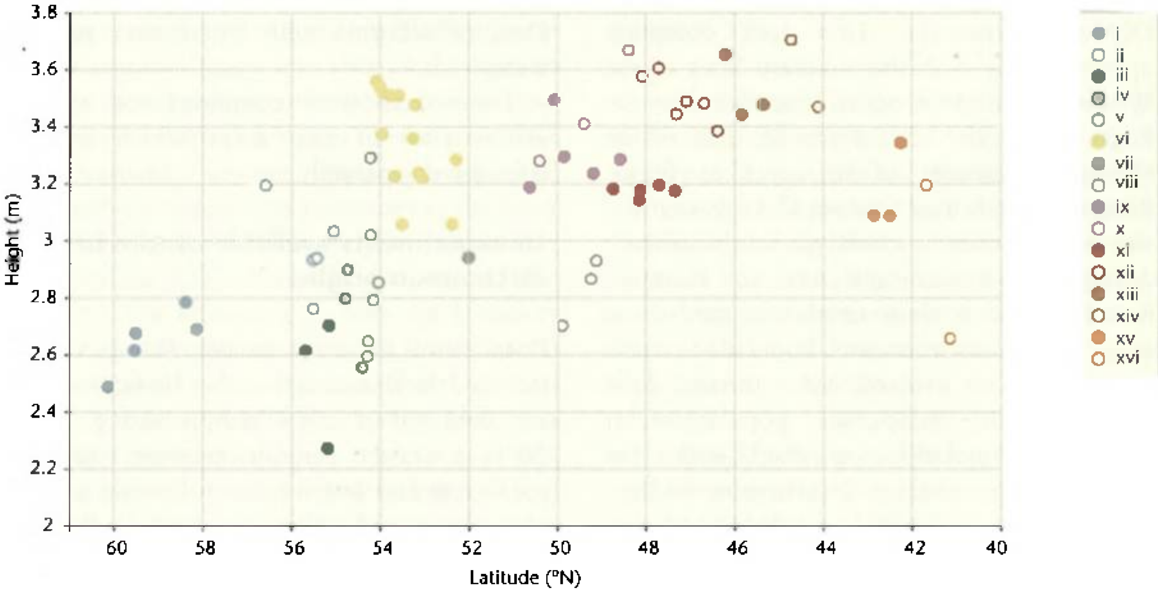
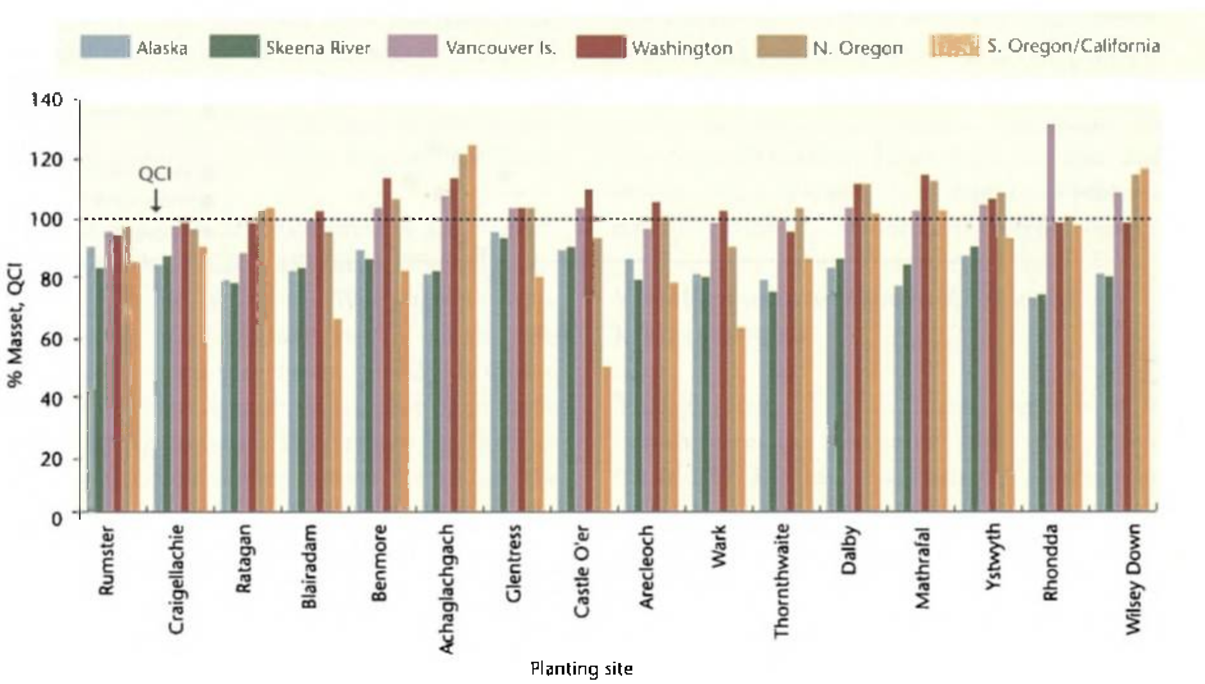


Figure 19

IUFRO series: height at 10 years after planting as % of 70(7111)Lot2, Masset, QCI.



Kranenborg, 1993; Illingworth, 1976, 1980). Their data also indicate that there is possibly a discontinuity in the clinal pattern in the region of the south of Vancouver Island and the Olympic Peninsula. This area coincides approximately with the southern limit of the Wisconsin ice sheet which extended into the Puget Sound and on the western side of the Olympic Peninsula as far south as Forks. Illingworth indicated that populations south of the ice sheet were free from glacial disturbance during the last major glaciation and therefore have had many more generations to evolve and adapt to their environments. Populations to the north may have evolved, either through gene migration from the southern populations, or from relict populations on refugia within the glaciated area (nuntaks) (Daubenmire, 1968).

The data presented in Table 14 are produced as a bar chart in Figure 19 which concentrates on those groupings which are of the greatest interest as potential sources of seed in Britain (QCI, Vancouver Island, coastal Washington with Muir Creek and northern Oregon) together with more extreme sources from Alaska, Skeena/Nass Rivers and southern Oregon/California with which they may be compared.

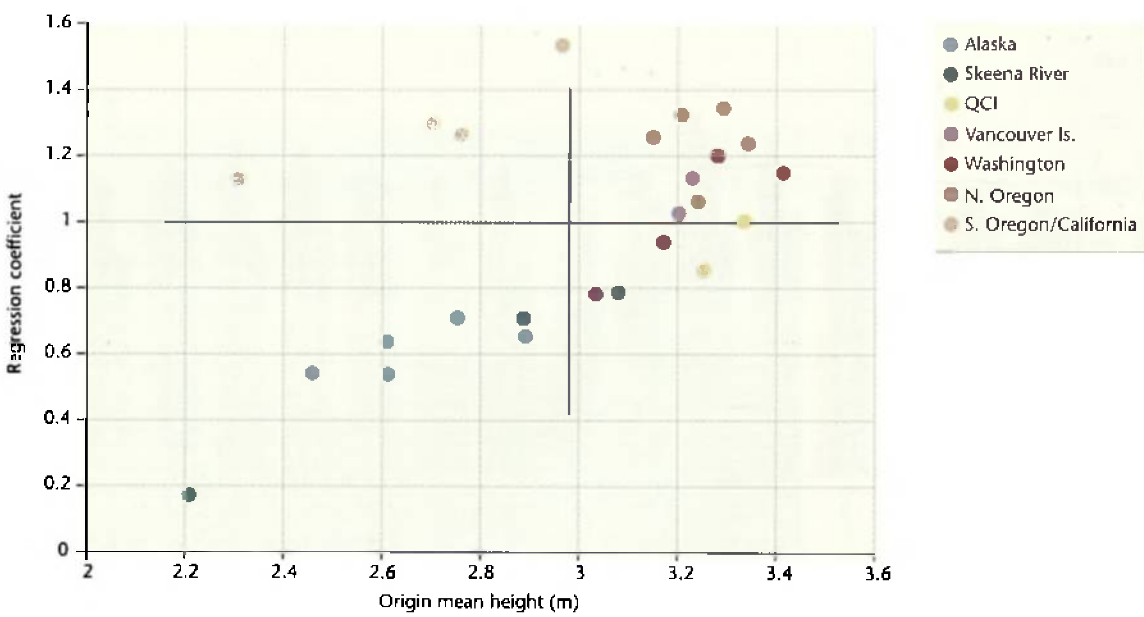
These data were combined for analysis across sites in two ways which will be considered separately.

16 experiments available on the basis of 26 common origins

Data from all sites except Ratagan were included in this analysis; the 26 origins used are identified in italics in Appendix 6. Figure 20 is a scatter diagram relating regression coefficient and origin mean following analysis of variance with joint regression analysis for this combination of origins and sites. Seven of the eight major groupings used in Table 13 are represented among the 26 origins present and

Figure 20

IUFRO series: scatter diagram relating regression slope and origin mean for height at 10 years, northern and southern sites combined.



are identified by the use of different colours. The trends already observed in Figure 16 (P60/61 series) are substantiated here but the benefits of greater representation of origins and an extension of sampling to further south in the natural range are also clear. Alaskan origins have consistently poor means and regression slopes whereas there is some improvement among those from the Skeena/Nass Rivers. The exception to the latter is the single point in the lower left of the scatter representing 3032, Kitwanga, a source from well into the introgression area. QCI sources show above average mean with a slope close to 1.0 continuing to confirm their general adaptation to a wide range of sites. There is a general improvement in regression slope among Vancouver Island origins but a fall in those from Washington. The five sources from northern Oregon have high slopes combined with high means, indicating their advantageous adaptation to sites of high growth potential. The southern Oregon and Californian sources, however, appear in marked contrast with high regression slopes but below average means. This indicates that they retain the potential to respond to fast growing sites but that their growth remains variable, resulting in the lower mean height. This is a clear indication that such origins are likely to have unpredictable survival and high variability in growth in Great Britain.

Within groups other differences are evident. The position of 3032 (Kitwanga) has already been noted but within the Washington group, the single point with lower mean and regression slope represents 3005, Brinnon, from the Puget Sound area rather than from the Washington coast. This reflects a difference that was noted among means based on the detailed grouping in Table 14. Within the south Oregon/California group, those origins which are most displaced from the central intersection are the two from California (3019, Big Lagoon, and 3020, Crescent City). All regression slopes are significant fits at the 5% significance level; 3032, Kitwanga, only marginally exceeds this.

12 northern experiments with up to 69 origins

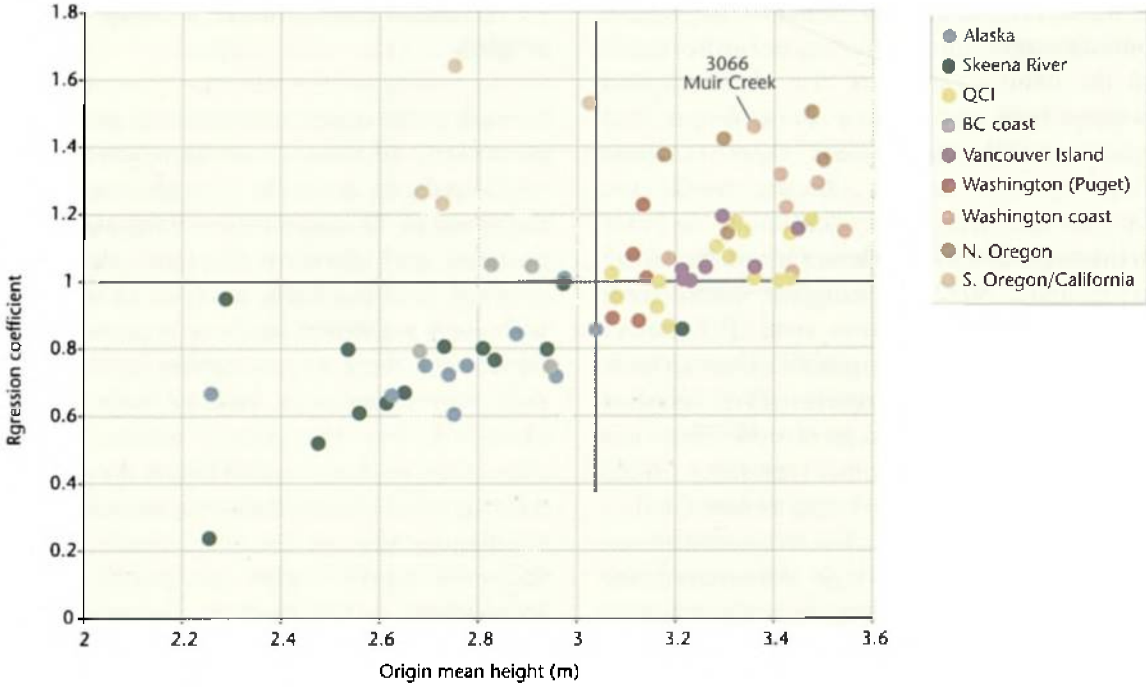
A much wider sampling of regional groupings, particularly of those from Vancouver Island northwards, is available through considering the group of 12 larger experiments planted in Scotland and northern England. A scatter diagram resulting from analysis of variance with joint regression analysis is presented in Figure 21 where origins within each of the eight major groupings used in Table 13 are identified by the same colour. These correspond to those used in Figure 20 with the addition of a new grouping for origins from the mainland coast of British Columbia. This enhanced representation of specific groups consolidates earlier findings. Below average height growth and slope is virtually confined to sources from Alaska, Skeena/Nass Rivers and the BC coast whilst the remaining origins with below-average height are from southern Oregon/California. There are now 10 sources from Washington, those from the Puget Sound area having lower means and regression slopes similar to sources from Vancouver Island. The remainder from the Pacific coast of the Olympic Peninsula have high means and slopes, their means, but not their slopes, equalling those of the northern Oregon sources.

Variation among Queen Charlotte Islands origins

The majority of Sitka spruce seed used in British forestry has come from the Queen Charlotte Islands. Nowadays, commercial collections of seed are taken from cone caches made by squirrels but before 1950, most seed was collected from areas of active logging on Moresby Island or Graham Island, due to the absence of squirrels on this island grouping at that time. In the 1940s and 1950s, collections

Figure 21

IUFRO series: scatter diagram relating regression slope and origin mean for height at 10 years, northern sites only.



were made by native communities on the eastern side of the islands and a commercial seed extraction plant was located at Masset. QCI material has always performed well throughout Britain and the IUFRO collections were the first opportunity to test a wide range of sources from this specific area. Fourteen origins were planted on the 12 northern sites in the intensive sections of the experiments.

In British Columbia, Sitka spruce forms a major component of the Coastal Western Hemlock Zone (Krajina, 1973, 1980; Banner *et al.*, 1983). This zone can be further subdivided into a number of sub-zones, one of which is QCI. At this level several ecosystem associations are recognised which are sufficiently different to conclude that the Sitka spruce populations they contain may be genetically distinct (Roche and Haddock, 1987). The effect of the Queen Charlotte Mountains is to produce a clear contrast in precipitation between the west and the east coast of the islands. The sub-montane part of the sub-zone, which extends up to approximately 350 m in altitude, includes most of the eastern part of Graham Island and northeastern Moresby Island. Sitka spruce, western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) are the major species here. Although Sitka spruce was restricted to the areas south of the Puget Sound and the Olympic Peninsula during the last glaciation, it is believed that it may have existed in refugia or nunataks on the Queen Charlotte Islands (Calder and Taylor, 1968).

In Figure 21 it is clear that QCI sources are distributed in a positive linear pattern performing better than the overall mean and those with higher means having regression slopes greater than 1. It is therefore relevant to consider whether this trend is related to the limited records of variation made at each collection site. The correlations of mean height and regression slope with latitude, longitude and altitude of the collection sites (see Appendix 5) were considered. There was little variation in altitude data, all collections being made below 100 m with many in low ranges from which the mid-point was used. There were only two relatively strong correlations reaching significance, between height and altitude (-0.564, $p < 0.05$) and height and latitude (0.532, $p = 0.05$). Whilst the former is to be expected, the latter contradicts clinal variation with latitude observed on a wider scale across the species' range. Figure 22 shows the details of this correlation, each point being identified by the origin number and a map reference number through which its collection location can be identified in the detailed map of QCI in Figure 11a. The lower rainfall of the eastern side of the islands compared with the western and southern parts is closer to that found in areas of Great Britain to which the species is adapted best. This may explain the apparently contradictory relationship between growth rate and latitude. The fastest-growing sources all come from low elevation sites in the northern and eastern parts of Graham Island, indicating that material from this area of the Queen Charlotte Islands is likely to be most superior in growth under British conditions.

General conclusions from the analysis of 10th year height data

- Throughout the natural range of Sitka spruce, there is strong clinal variation in growth rate associated with latitude.
- Northerly origins (Alaska) grow slowly on all but the most demanding sites; their use in Britain would thus be limited to exposed sites in the north of Britain.
- Origins from the traditional collecting areas in the Queen Charlotte Islands (northern and eastern parts of Graham Island) have higher than average performance across a wider range of sites than other origins.
- Material from the Skeena River area grows relatively slowly compared to QCI material, together with origins from the mainland BC coast which have no growth advantages and are not recommended for use in Britain.
- Southern origins from the extreme south of Vancouver Island, coastal Washington and northern Oregon show considerable height growth advantages on faster-growing sites, but origins from other parts of Washington around the Puget Sound perform poorly.
- Origins from southern Oregon and

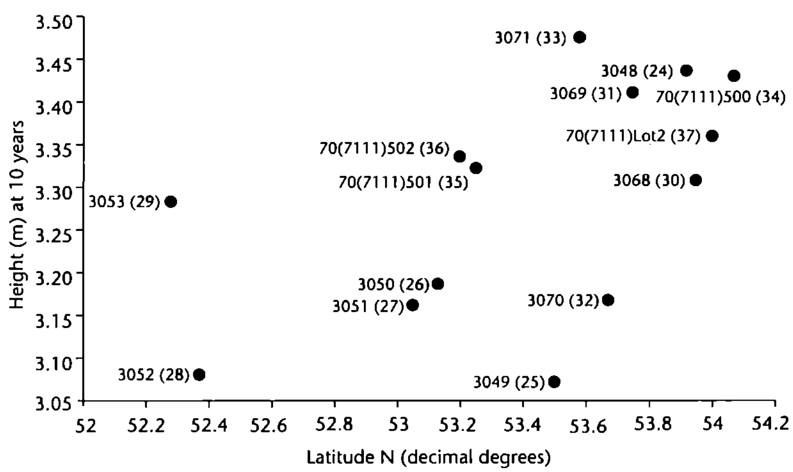


Figure 22

IUFRO series: correlation between height at 10 years and latitude among the 14 QCI sources.

California are likely to be variable in growth rate and survival and are not suitable for use in Britain.

Basal area assessments

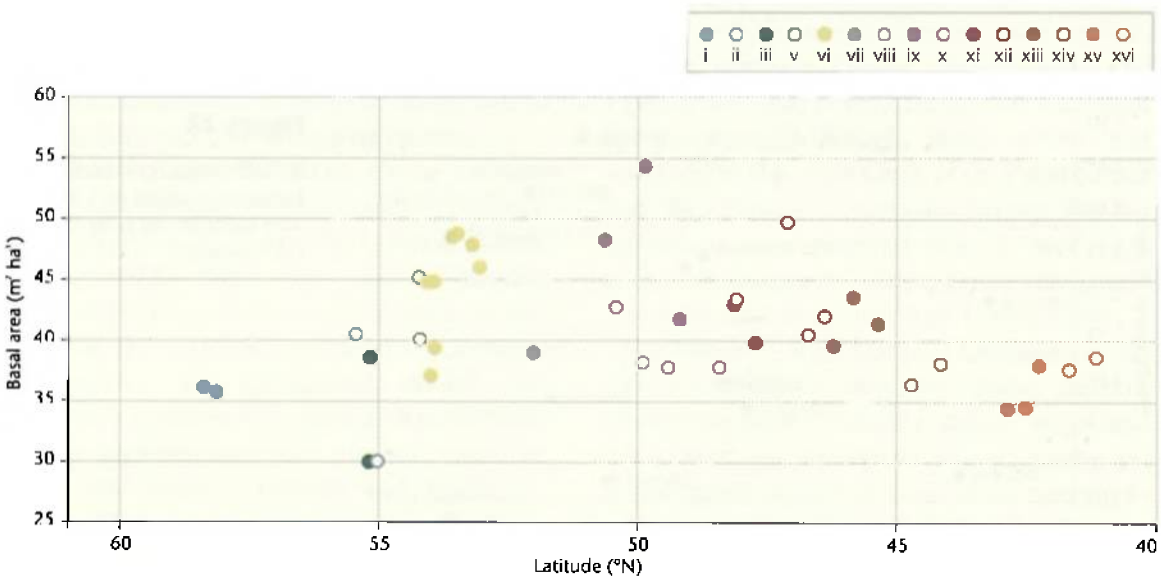
In the IUFRO series, diameter at breast height (DBH) was measured at 20–22 years after planting. DBH had also been measured at the same age at five sites in the P60/61 series but, since a wider range of sources and sites was available in the IUFRO experiments, data from these will mainly be considered. Nine sites in the P60/61 series were assessed during the period of 26–37 years after planting and these data will also be presented because they provide information on volume production at a later age.

Basal area, 20–22 years after planting in the IUFRO series

In the IUFRO series, diameter at breast height was measured at 20 years after planting in the extensive sections (196 tree plots) of all the southern experiments. However, in the northern experiments this was restricted to the three sites (Farigaig, Arecleoch and Wark) in which extensive sections had been established (238, 255 and 225 tree plots respectively) and took place at 20–22 years after planting. Also in these experiments, measurements were restricted to a smaller number of origins (25) in the extensive plots, and on some sites a number of origins from the extremes of the distribution range in which growth and survival had been poor were not measured. This has resulted in smaller sets of data representing regional group means than those used in the 10 year height data previously presented and, at some sites, the absence of data from the Alaskan and south Oregon/California groupings. In Figure 23 overall mean basal area across all sites has been plotted against latitude of origin for each source represented using different colours for each region and colour shades to separate groups within regions. The trends observed in Figure 18 (for height at 10 years) are less clear, particularly because there was a wider spread

Figure 23

IUFRO series: relationship between mean basal area per hectare at 20–22 years and latitude of origin across seven sites.



of performance within each grouping. Also, the Washington coast, north and central Oregon sources, which had the greatest height growth relative to QCI, showed a decline in basal area production. Within Vancouver Island, the western grouping of origins clearly out-perform the eastern grouping and there was no indication that 3066 (Muir Creek, Sooke) performed in a similar way to coastal Washington sources. In contrast to the data for height, therefore, this origin has been included among the Vancouver Island sources in basal area data and analysis.

A summary of all basal area measurements is given in Appendix 7 where each is expressed as a percentage of 3048, Masset Sound, QCI, the only QCI source common to all sites. It should be noted in Appendix 7 that regional and detailed groupings of origins are represented by different sources at each site. In particular, data from Oregon and Californian sources from the three northern sites are very limited; therefore those for south Oregon/California were omitted from further summaries and analysis. Table 15 summarises basal area at the regional level only with sources from the Puget Sound separated from those from the Olympic coast of Washington; Figure 24 gives a bar chart from which mainland BC origins have been omitted. The poorer performance of Alaskan, Skeena River and mainland BC origins is clear, and those from Puget Sound, whilst always lower than those from coastal Washington, have above-average performance on faster-growing sites.

Farigaig was the most northerly site measured and both the table and the figure show that the performance of the common QCI origin (3048) is only slightly exceeded by those from coastal Washington and, as might be expected, Alaskan material has responded well to the more demanding site conditions. At Arecleoch, Skeena River material performs almost as well as QCI but this can be traced to the single origin representing the group at this site which is the origin that is nearest to the coast. Washington origins are superior to QCI at all sites but at the most southern ones, their performance is matched or exceeded by those from northern Oregon. This is markedly so at Ystwyth, an exposed site in west Wales in which growth has been slow overall. At Wilsey Down, southern Oregon/California origins have produced the greatest basal area.

Figures 19 and 24 compare the rankings of regional group means at each site for basal

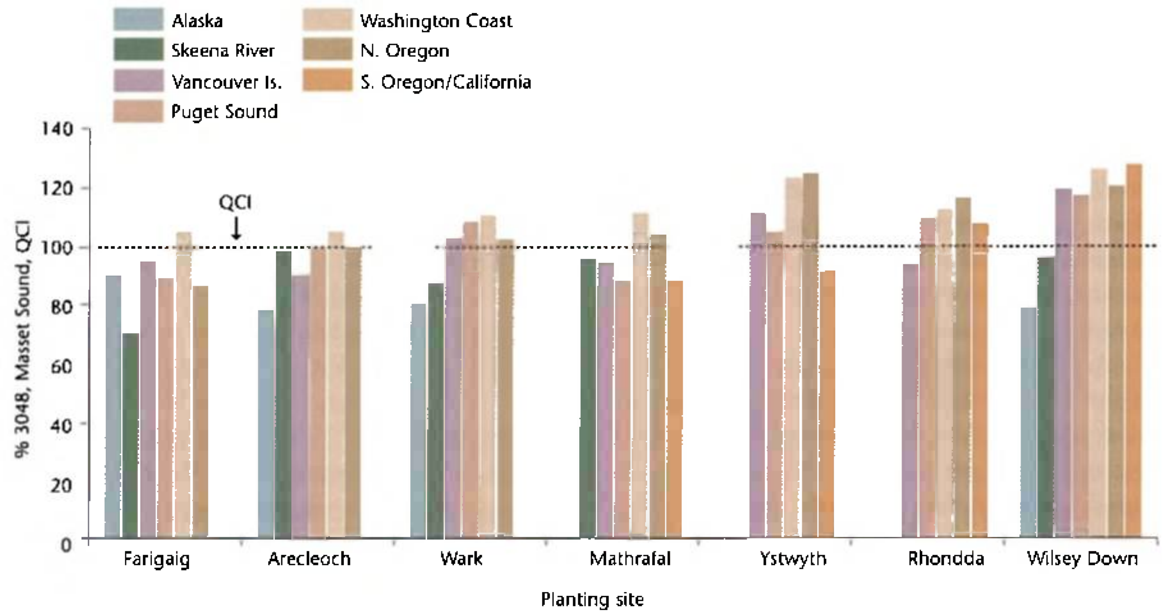
Table 15

IUFRO series: summary by region of basal area, 20–22 years after planting expressed as % QCI, 3048, Masset Sound.

	Farigaig	Arecleoch	Wark	Mathrafal	Ystwyth	Rhondda	Wilsey Down
Region	Age 21	Age 22	Age 20	Age 20	Age 20	Age 20	Age 20
Alaska	88	76	79				77
Skeena/Nass Rivers	68	96	85	94			94
Queen Charlotte Is.	107	96	103	98	113	103	103
Mainland BC	76	84	92				
Vancouver Island	93	88	100	92	109	91	117
Puget Sound	87	97	106	86	102	107	114
Washington	103	103	108	109	120	110	123
North Oregon	85	97	100	102	122	114	118
S. Oregon/California				86	89	105	125
Site mean basal area ($m^2 ha^{-1}$)	41.06	41.52	46.51	36.12	30.58	31.34	47.88

Figure 24

IUFRO series: basal area per hectare 20–22 years after planting as % of 3048, Masset Sound, QCI, on seven sites.



area production with those for 10 year height growth. No height data were available at Farigaig at this age but the variation among regional group means for six year height was similar to that for basal area at this site. Compared with QCI, most groups show a greater degree of superiority in basal area than for height at Wark whilst this situation is reversed at Mathrafal. At Ystwyth and Rhondda, basal areas are greater than for height growth for the more southerly groupings and, at Wilsey Down, there is a marked improvement in the production of basal area of Washington origins.

Appendix 7 shows that representation of origins across sites presents major problems in assembling a sufficient dataset for analysis of basal area data either across a wide enough range of site types or incorporating sufficient origins; indeed, only eight are common to all sites. Further statistical analysis of the basal area data has therefore not been carried out.

Basal area, 26–37 years after planting in the P60/61 series

The basal area measurements made in the IUFRO series at around 20 years after planting represented plots which had passed canopy closure but in which no thinning had been carried out or, if so, it had been so recent as to have little effect on basal area production. The P60/61 series offer the opportunity to study basal area measured at a later stage ranging between 26 and 37 years after planting at nine sites, during which period silvicultural thinning to optimise volume production would have been undertaken. These data are summarised for each origin as percentages of the mean of the QCI source at each site in Table 16, together with a further summary based on regional grouping of origins. Where possible, these figures are for the main crop plus any thinnings removed, representing, therefore, total basal area production to date. Also the data are compared in Figure 25.

Table 16

P60/61 series: most recent basal area assessments, 26–37 years after planting expressed as % 57(7111)2, Skidegate.

Location	Region	Shin	Deer	Ratagan	Glentrool	Wark	Clocaenog	Tarenig	Myherin	Wilsey Down
		Age 26	Age 27	Age 32	Age 32	Age 29	Age 29	Age 30	Age 30	Age 37
Cordova	Alaska	108		87		76	102	61	84	75
Lawing		96	81	71	66	74		48	70	
Seward										69
Juneau		95	91	67	76	81				76
Sitka		87		82		79		76	79	74
Skidegate	QCI	100	100	100	100	100	100	100	100	100
Terrace	Skeena River	97	98	88	90	90	105	91	88	87
Sooke	Vancouver Is.	92	95	105	83	91	85	100	90	89
San Juan River		106	103	98	85	103	103	110	94	107
Forks	Washington	96	97	78		95	99	104	107	107
Hoquiam		95		100	79	98	117	108	94	106
Jewell	Oregon	95	97	98	63	99	125	107	96	100
North Bend		95	97	82	79	97	95	107	100	96
Jutland	Denmark						117	113	100	96
Devon	Great Britain						98			
Cardigan							99			93
Site mean basal area (m^2ha^{-1})		40.37	46.02	53.55	44.40	54.57	55.72	25.04	30.92	45.75
By region	Alaska	97	86	77	71	77	102	62	78	74
	QCI	100	100	100	100	100	100	100	100	100
	Skeena River	97	98	88	90	90	105	91	88	87
	Vancouver Is.	99	99	102	84	97	94	105	92	98
	Washington	95	97	89	79	96	108	106	100	106
	Oregon	95	97	90	71	98	110	107	98	98
	Denmark						117	113	100	96
	Great Britain						98			93

At northern sites as far southwards as Wark, basal area production for almost all groups is lower than that of QCI. This effect is less pronounced in the remaining southern sites where origins from the south approach or exceed QCI more consistently. The information in Figure 25 can again be compared for relevant sites with the same information for 10 year height given in Figure 15. Overall for basal area, the production from QCI was more rarely exceeded by other origins than was the case for height. However, despite this, similar distribution patterns for the regional groupings are evident at most sites, although clearer changes of ranking between the two assessments are to be seen at Glentrool, Clocaenog and Wilsey Down. Of these, the most notable difference is at Glentrool where basal area for all regions is well below the QCI level and there is an increasing fall in basal area in origins from Vancouver Island southwards. Whilst height growth is assessed on a per tree basis, basal area, calculated on an area basis, will be reduced by lower survival. The data in Table 17 summarise survival for these three sites at the same regional grouping level and indicate that at Glentrool, percentage survival is lower in most origins from Vancouver Island

Figure 25

P60/61 series: basal area per hectare 26–37 years after planting as percentage of Skidegate, QCI source on nine sites.

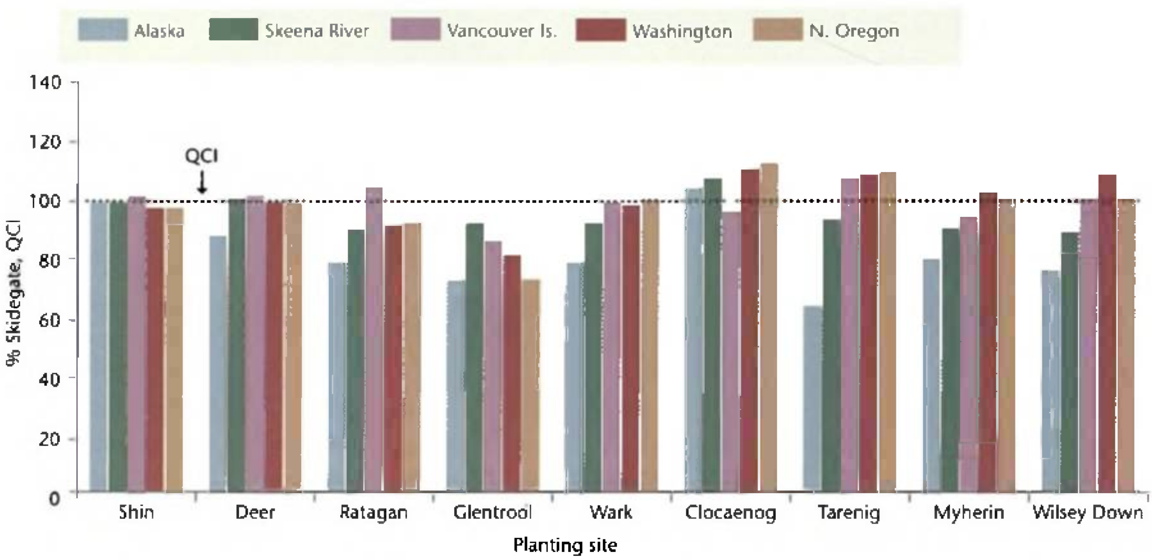


Table 17

P60/61 series. Percentage survival at final basal area assessment on three sites.

Region	Location	Glentrool	Clocaenog	Wilsey Down
Alaska	Lawing	95		
	Cordova		78	56
	Seward			54
	Juneau	78		45
	Sitka			55
Skeena River	Terrace	86	74	59
Q.C.I.	Skidegate	91	85	62
Vancouver Island	San Juan R.	70	82	72
	Sooke	73	71	62
Washington	Forks		83	68
	Hoquiam	59	82	67
Oregon	Jewell	45	85	66
	North Bend	64	80	58

southwards leading to the decrease in basal area already observed. At Clocaenog, the most interesting comparison is the basal area of the single Alaskan source from Cordova, the most northerly point sampled in this series, which is slightly higher than that of QCI, although proportionally much lower for height at 10 years. At this site survival of all origins is similar, thus the superiority of this source remains unclear. At the most southerly site, Wilsey Down, the low basal areas among the Alaskan and Skeena River origins, reflecting a trend already established for 10 year height. Survival in origins from these two regions is also lower. However, the Oregon origins are not as productive as might be expected at such a mild and fast-growing site, although survival is comparable to that of origins from other regions. This suggests that early, fast height growth in sources from the most southerly part of the range in suitable sites may not be reflected in later volume production and that the form or taper of the trees may be different, although this has not been specifically measured.

General conclusions from the analysis of basal area data

- The results presented must be interpreted with caution because representation of origin groupings varies between sites.
- Measurements made before half-rotation age (i.e. 20–22 years as in the IUFRO series) indicate similar variation among regional groupings to that observed for height at 10 years, although there is variation between sites.
- At this age, Washington origins are more closely comparable to the more productive Oregon origins at fast-growing sites.
- By half-rotation age and later (i.e. 26–37 years as in the P60/61 series), basal area production for most other regional groups on sites in northern Britain do not exceed that of QCI.
- At half rotation age and later, Washington origins are the most consistently productive on southern sites, with the earlier superiority of Oregon sources appearing to decrease.

5

Studies on timber quality in Sitka spruce

Many studies have shown considerable variation in wood properties among individual trees and between sites in Britain, e.g. Bryan and Pearson (1955), Sunley and Lavers (1961), Brazier (1967). In North America, the best virgin stands of Sitka spruce on the Queen Charlotte Islands were an important source of high quality 'aircraft spruce' for constructing wooden aircraft during World War I and again for Mosquito aircraft in World War II (Brazier, 1987). Dinwoodie (1962) illustrated timber core samples from seven North American sites, all except one from virgin stands. They show a much narrower ring pattern than most British timber samples, with a more pronounced differentiation of early and late wood. However, these samples are not necessarily typical of the majority of Sitka spruce timber now available from North America.

Wood density

In 2005, over 80% of wood products used in the United Kingdom are imported, and of sawnwood, approximately 75% is imported (Forestry Commission, 2005). Although Sitka spruce accounts for a high proportion of British sawnwood production its contribution to more profitable construction end uses is around 10% (Gillam[3], personal communication). To provide the greatest contribution to this sector, it is essential that Sitka spruce should produce as much high-strength timber as possible. Wood density is a good indication of the overall timber strength and in Sitka spruce it is found to be on average 340 kg m^{-3}, which is low compared with other conifers grown in the UK such as Scots pine (420 kg m^{-3}), Douglas fir (410 kg m^{-3}) and European larch

[3]Simon Gillam, Head of Economics and Statistics, Forestry Commission, Edinburgh, UK.

(450 kg m^{-3}) (data presented by Lavers, 1983). Brazier (1987) stated that the average wood density of Sitka spruce grown in North America is higher (340–390 kg m^{-3}) than that for the species grown in the UK, due to its slower growth rate. In Sitka spruce the inverse correlation between growth rate and wood density is high and it is therefore important that any increases in growth rate through seed origin choice are not associated with reductions in timber strength. The correlation first came to attention when wood density was found to be highest in the QCI origin and lowest in the Oregon origin in the experiment planted at Radnor in 1929 (see Appendix 1) when it was sampled 30 years after planting (DSIR, 1958; Broughton, 1962). Only five thinned stems were taken from each plot in this unreplicated trial located on a fairly steep slope with considerable differences in early stocking (from 662 trees per hectare in the Oregon plot to 2004 trees per hectares in the QCI plot). Samples covered the range of sizes in each plot; thus the mean of the samples from the QCI plot had a diameter of 15.4 cm, while the Oregon samples had a mean diameter of 20.4 cm. Origin differences were found in wood density and the percentage of summerwood. This was complicated because the Oregon trees had grown very fast at first and had then slowed down over the last 10 years, whereas this trend was less apparent in the QCI and Washington trees. Brazier (1970) summarised the main effects of vigorous growth as causing a reduction in overall wood density, with a lower minimum earlywood density. Brazier[4] (personal communication) has also pointed out that, because the sample of trees in Radnor varied so widely in volume (0.068 m^3 to 0.31 m^3), by plotting tree volume of all samples against the average specific gravity of the two lowest discs taken, a curvilinear relationship is found. This indicates that what appears to be seed origin differences may be merely an effect of tree vigour. This is similar to the findings of Cannell *et al.* (1983) on much younger clonal material of different provenances.

A preliminary study of 12 seed origins in the P60/61 series was made by Brazier (1972) on trees which had been established as unreplicated demonstration plots (six tree lines) at two nurseries eight years after planting (nine years from seed). For each tree, discs were taken at the mid-point of each internodal section for which average volume and weight were measured and average wood density calculated. The results are given in Table 18. Among the origins at Bush nursery, there were unexplained faster growth rates in Lawing and Juneau than would be expected from others in the Alaskan region. In general, an increase in volume and weight of wood was associated with decreasing latitude, with wood density increasing with increasing latitude. The figures given for wood density in Table 18 are higher than those previously referred to. This is because the study sampled material from the juvenile core of the tree where density values are higher (Bryan and Pearson (1955), Brazier (1967), Wood (1986).

Detailed studies of ring structure and wood density were made on the same material using a 10 micron section of wood from a fixed position in each tree (1966 ring at the second internode from ground level) using a C14 labelling method. This seventh ring from the pith still lay within the juvenile core. The relationships between ring width and wood density, ring width and the percentage of latewood, and wood density and the percentage of latewood were examined. Northern origins tended to have higher wood density for their ring width whereas those from Washington and Oregon together with San Juan River (Vancouver Island) tended to be lighter in weight in comparison to their rate of growth. The pattern of variation in the percentage of latewood appeared to have little association with seed origin.

[4] J D Brazier, Formerly Head, Wood Structure, Forest Products Laboratory, Princes Risborough, UK.

Table 18

P60/61 series: average volume, weight and wood density of 12 seed origins.

Seed Origin	Site							
	Bush				Wykeham			
	No of trees	Average volume cm^3	Average weight g	Density g cm^{-3}	No of trees	Average volume cm^3	Average weight g	Density g cm^{-3}
Alaska								
Cordova	5	740	342	0.460	6	223	112	0.500
Lawing	4	3398	1345	0.398	4	120	60	0.500
Juneau	5	3459	1248	0.361	5	1337	636	0.475
Sitka	4	1457	668	0.458	5	657	331	0.503
British Columbia								
Terrace Skeena River	6	2143	990	0.463	3	779	350	0.450
Skidegate QCI	6	3048	1173	0.385	6	1783	771	0.433
San Juan River Vancouver Island	5	1856	750	0.405	5	1800	701	0.390
Sooke Vancouver Island	6	3770	1551	0.410	6	1671	739	0.441
Washington								
Forks	6	3475	1293	0.371	6	1829	784	0.428
Hoquiam	6	3342	1250	0.375	5	3088	1209	0.391
Oregon								
Jewell	6	2786	1070	0.385	6	2245	915	0.409
North Bend	6	4661	1823	0.390	5	4386	1676	0.381

Other than the work reported above which was based on small sample sizes, there have been no direct measurements of wood density in comprehensive seed origin experiments of Sitka spruce in Britain. However, a study was made in Ireland on six origins at four sites forming part of the International Ten Provenance Experiments (Murphy and Pfeifer, 1990). These were:

- 3024 Duck Creek, Alaska
- 3040 Usk Ferry, Skeena River (not in main UK series)
- 3049 Link Road, Juskatla, QCI
- 3062 Big Qualicum River, Vancouver Island
- 3003 Forks, Olympic coast, Washington
- 3012 Necanicum, North Oregon

Appendix 5 and Figure 11a give more details.

Cores were extracted from the sixth internode from the top of the trees at 12 years after planting, and wood density was assessed on the cores using the water displacement method (Olesen, 1971). There were highly significant differences between sites and between origins, all generally reflecting a clear trend of low wood density associated with faster growth. The range of wood density encountered across sites was 0.4490–0.3586 gm cm^{-3} and among origins was 0.4246–0.3824 gm cm^{-3}. There were significant relationships overall between wood density and DBH (negative) and between wood density and latitude of origin (positive). However, the north Oregon source (3012) had a consistently higher wood density than the Washington source (3003) at all sites and exceeded both the Vancouver Island (3062) and QCI (3048) sources at the two fastest growing sites. These data suggest that, although overall regional trends exist, there may be consistent variation within these. Wood densities of the southern origins were up to 5% lower than that of QCI material.

Delaport (1984b) assessed the density of cores taken from 12 of the IUFRO seed origins grown at Arne, in Brittany, France and at the JF Kennedy Park in Ireland. There was a strong inverse correlation of wood density with growth vigour at both sites. Delaport suggested that it is possible to select or eliminate trees in the juvenile phase of growth, simply by measuring the torsional moment of the largest trees.

Measuring wood density using core extraction and gravimetric methods or X-ray densitometry require considerable resources. However, use of the Pilodyn® provides a non-destructive method of screening individual trees for wood density. This device, developed for timber rot detection, fires a captive 2.5 mm diameter bolt into the stem of the tree at a pressure of 6 joules, giving a reading of the distance penetrated by the bolt which is inversely correlated to wood density (see Figure 26). Assessments using this method are carried out at breast height with an area of bark removed. Because of the initial assumption of the need to avoid juvenile core wood, measurements are made at 15 years from planting. Studies by Wood (1986) have shown that the Pilodyn® provides a measurement which is well correlated to whole tree wood density.

Figure 26

Using the Pilodyn® in which a pin is fired at the tree with a fixed force. The length of pin-penetration gives a relaible correlation with whole tree density.

Wood density was measured in this way in two of the IUFRO experiments in Wales, Mathrafal and Rhondda at 16 and 20 years after planting, in an attempt to see if greater use of southern origins in Wales would cause penalties in lower wood quality. Although assessed at different ages, penetration data should be reasonably comparable across sites and the site mean values (Table 19) show a lower wood density at Mathrafal than at Rhondda. For comparison, site means for height at 10 years and basal area at 20 years are also given in the table. These confirm that Mathrafal is the faster growing site; the relationship between wood density and growth rate at these sites is therefore similar to that found across the range of Irish sites studied by Murphy and Pfeifer (1990). Not all origins in these experiments were assessed, concentrating on a sample of those from regions in which potential growth rate advantages had already been established. In Table 19, penetration is given as an inverse percentage of that for the standard QCI commercial source 70(7111)Lot2, since greater penetration implies lower wood density. It can be seen that at both sites the majority of origins from Washington (including 3066, Muir Creek, Vancouver Island) and Oregon have lower wood density values than the QCI source. There are some exceptions to this but the average fall in wood density in both the Washington and north Oregon groupings does not exceed 8%. In the single origin from southern Oregon, Brookings, noted for its fast growth rate at a number of sites, wood density decreases by 9–12% below that of QCI. As previously noted in the Irish study, some southern origins have higher wood density values than QCI, but there is less consistency in these results and 3012, Necanicum, has generally lower rather than higher values.

Table 19

IUFRO series: wood density (mm Pilodyn® penetration) 16–20 years after planting expressed as % 70(7111)Lot2, QCI.

IUFRO number	Location	Region	Group	Mathrafal Age 20	Rhondda Age 16
70(7111)Lot 2	Massett (Commercial lot)	QCI	vi	100	100
3066	Muir Creek (Sooke)	Vancouver Island	x	103	97
3003	Forks	Washington	xii	92	103
3009	Raymond		xii	82	90
3010	Naselle		xii	93	104
Mean of Washington coastal sources				92	99
3011	Astoria	North Oregon	xiii	87	97
3012	Necanicum		xiii	91	89
3013	Tillamook		xiii	92	97
3014	Newport	North Oregon	xiv	96	108
3015	Florence		xiv	105	98
Mean of northern Oregon sources				94	98
3018	Brookings	South Oregon	xv	88	91
	Site mean (Pilodyn® penetration, mm)			19.30	13.46
	Site mean, basal area at 20 years ($m^2 ha^{-1}$)			36.12	31.35
	Site mean, height at 10 years (m)			3.40	3.10

Note: Values indicating Pilodyn® penetration indicate higher wood density.

Sawlog output and quality

These fairly limited studies of wood density, using direct and indirect methods of measurement, highlight the possibility of a loss in timber strength resulting from the use of faster growing more southerly sources on appropriate sites, as noted by Fletcher (1992).

Lee *et al.* (1999) examined the out-turn of sawlogs from the experiment planted at Gwydyr in 1950 (see Appendix 1) at the end of its rotation (44 years), see Figure 27. At this site, four origins were considered, one from QCI and three from coastal Washington. Details of these origins are given in Table 20.

Table 20

Origins used in the Gwydyr sawlog out-turn study.

Region	Location	Nearest IUFRO origin	Figure 11a symbol
QCI	Not specific	70(7111)Lot2	W
Washington	Hoh River	Forks (3003) Kalaloch (3004)	X
Washington	Copalis River	Humptulips (3007) Hoquiam (3008)	Y
Washington	Columbia River	Naselle (3010) Astoria (3011)	Z

Figure 27

Alan Fletcher standing in a plot of Washington origin in the early seed origin test at Gwydyr, North Wales used for timber quality testing, 42 years after planting.

Table 21 summarises cumulative basal area, felled volume at the end of rotation, the distribution of products into large sawlogs/small sawlogs/pulpwood and the distribution of the large sawlogs into strength classes. Basal area and volume data are expressed as percentages of the values for QCI material and it shows that, although Washington origins were more productive than QCI, the Copalis River origin performed less well than the other two Washington origins.

The three Washington origins produced greater numbers of large logs than QCI, similar numbers of small logs and less pulpwood material. Thus the use of these faster-growing sources should increase the production of greater quantities of logs which meet larger constructional specifications for size. However, this would be of less value if such production were at the expense of meeting strength specifications.

In the Gwydyr study, the large logs were converted into standard battens for strength testing as determined by using calibrated Machine Stress Graders (BS4978:1988). In Table 21 the higher outturn of battens in the Washington sources reflects the increased number of large logs produced. Poor performance of material from the Copalis River source continues to be evident. The percentage of battens which were graded at SC4 (now classified as C24 (BS4978:1996)) in the Hoh River and Columbia River origins was less than that for QCI, but there was a considerable increase in the percentage of SC3 battens (now classified as C16). However, when the numbers of battens graded at SC4 are considered (given in parentheses), the figures for SC4 are comparable to those obtained from QCI. Therefore it is suggested that using either of the two faster-growing Washington origins would increase the value of future timber crop plantations without any loss of out-turn of high strength constructional timber.

Branching characteristics

Wood density is not the sole influence on the quality and strength of timber. Apart from anatomical characteristics such as tracheid length (the principal water conducting cells comprising 90% of the volume of softwoods are long and narrow), a major effect of strength properties is the number, size and distribution of knots. These can be studied in the forest through the assessment of branching traits and data are available from the International Ten Provenance series in Ireland (Murphy and Pfeifer, 1990). The ratio of

Table 21

Product and outturn data for four origins from a trial planted at Gwydyr in 1950 (after Lee *et al.* 1999).

Region	Cumulative basal area %QCI	Felled volume %QCI	Produce %			Out-turn of large logs			
			Large logs	Small logs	Pulp	Battens	% SC4 (No)	% SC3 (No)	% Reject (No)
QCI	100	100	38	32	30	121	31 (38)	52 (63)	17 (20)
Hoh River	121	115	46	30	24	165	22 (37)	64 (105)	14 (23)
Copalis River	110	84	44	36	21	133	17 (23)	60 (79)	23 (31)
Columbia River	123	110	47	33	20	175	23 (41)	57 (100)	20 (34)

Cumulative basal area includes an estimate of that removed in earlier thinnings.
Large logs meet the specification of 5 m length with minimum 18 cm top diameter under bark.
Small logs meet lesser sawlog specifications, 3.75–2.1 m with 14–18 cm top diameter under bark.
Pulpwood meets the specification of 2.3 m length with 7–14 cm top diameter under bark.
SC4 and SC3 are equivalent to the current European Standard for constructional timber of C24 and C16 respectively.

branch diameter to adjacent mid-internode diameter (branch:diameter ratio) was calculated, together with the ratio of the number of branches at a whorl to its adjacent internode length (branch number:internode length ratio). Measurements were made on the same six origins as those used in the wood density study above.

For branch:diameter ratio, there was a strong, positive relationship with latitude. The slower growing origins from Alaska and Skeena River had larger branches relative to stem size than those from further south, among which (including QCI) there were no significant differences. The Washington and Oregon sources had smaller ratios than those from QCI and Vancouver Island which suggests that the use of faster growing sources will not jeopardise timber strength through the development of differentially larger knots. The results for branch number:internode length ratio were similar, again indicating that there would be no increase in branch number per whorl resulting from the use of faster growing sources. This work is encouraging, but a fuller understanding would need to take into account the distribution of branches within whorls and the frequency and density of internodal branching.

These findings generally accord with those of Maun (1992) who examined Sitka spruce battens under stress grading and predicted that a decrease in knot surface area of 10% combined with an increase of 10% in the spacing between adjacent knots on battens would increase outturn of SC4 (C24) battens by 8%. If a decrease in wood density of 10% was included, the increase in out-turn of SC4 battens was reduced to 1%. This work also suggests that the use of faster growing material such as more southerly origins, from which similar changes to these are likely, should not have an adverse effect on the structural quality of timber produced.

General summary of work on timber quality

- There is a strong negative correlation between wood density and growth rate in Sitka spruce.
- Through the natural range of the species, wood density declines with decreasing latitude.
- In faster growing southern origins within the Washington coast/north Oregon origins, wood density may be lower than QCI by up to 8%.
- The increased volume produced by southern origins results in the production of more timber which meets the C16 strength class without a decrease in the amount reaching the higher C24 grade.
- Limited study of branching characters suggests no increase in either branch number or branch size:diameter ratio in faster growing sources, indicating that increased knot-related problems in the timber of these sources should not adversely affect the out-turn of structural grade timber.

6 Seed origin suitability for use in Great Britain

Grouping of origins within the natural range of Sitka spruce

In the early experiments and the P60/61 series, sampling of origins was on a broad scale and most major geographical areas were represented by only one or two sources. However, in the IUFRO collection, and, to a lesser extent the collection planted at Glendaruel, sampling of many sources within each region was carried out. In routine analysis of variance for height and other characteristics, either at single sites or across all sites in a series, tests of significance both between regional groupings of origins and between individual origins within each group were routinely carried out. Non-significance at the latter level commonly indicated that the origins selected were representative of that region. Less commonly, significance at this level suggested that further details such as altitudinal differences or introgression need to be taken into consideration. Those origins which are consistently poorer than the regional mean on many sites should be considered as unrepresentative and recommendations should indicate that they should be avoided. Link Road, Juskatla, (3049) is such an example (see Appendix 6 and Figure 22) and indicates the danger of using this single origin to represent a whole region in the International Ten Provenance Experiments.

This raises a further question of how regional boundaries are positioned. For example, in some studies on Sitka spruce, arbitrary groupings based on latitude have been used (e.g. Kraus and Lines, 1976). These tend to obscure any variation associated with distance from the coast. For northern British Columbia and Washington in particular, differences in several characteristics appear to be equally strongly related to this as to latitudinal changes. The groupings used in the analysis of ten-year height in the IUFRO series (eight regions or 16 more refined sub-regions) were based on knowledge of the species in its native range gained when the seed collections were made. The fact that in statistical analysis, the variation between these groups accounts for a high percentage of the total variation, gives clear reassurance that the groupings accord with the inherent pattern of variation present.

Prediction of future growth from early measurements

Seed characteristics were poorly correlated with later growth. First year seedling height in the nursery for the IUFRO series would have given a grossly inflated prediction of later growth of the most southerly group on most sites, although it indicated accurately the poor later growth of Alaskan and Skeena/Nass River origins. The inherently long autumn growth of the southern origins was evident from the glasshouse study under controlled conditions of Pollard *et al.* (1976) and from the nursery experiment of Kraus and Lines (1976). From these studies, the susceptibility to autumn frost of the most southerly origins was also predictable. Routine height measurements during early years in forest stage tests have indicated that reliable prediction of later growth can be obtained from 6–10 year height. Studies of juvenile:mature and age:age correlations indicate that height at about ten years after planting is a good indicator of diameter at mid–late rotation age (Lambeth, 1980; Gill, 1987; Lee, 1992, 1997).

Development of a suitability map

As an aid to the forest manager in choosing the most appropriate seed origin for any particular planting site, an origin suitability map has been developed for Great Britain. The most comprehensive set of data across the widest range of sites is available for height at 10 years in the IUFRO series and this has been used, together with the known variation in a range of environmental variables at each site, to provide generalised guidance on provenance choice.

Ten-year height data were available from 16 of the 17 planting sites in the IUFRO series (see Figure 10). Three of these, (Blairadam, Craigellachie and Dalby) were considered to represent sites at which Sitka spruce would not be a primary species choice and data from these sites were omitted from further analysis. Initial relationships between growth rate and site factors at the remaining 13 sites were explored for each of the four regional groupings of interest:

- Alaska (AL).
- Queen Charlotte Islands (QCI).
- Olympic coast of Washington, including 3066, Sooke, Vancouver Island (see Chapter 4) (WA).
- North Oregon Coast (southwards to and including 3015, Florence) (OR).

For each of these groups, the means of all origins at each planting site were used as dependent variables in multiple regressions using site variables available from geographic information system (GIS) data as independent variables. Following an examination of correlations among the range of factors available, the following three independent variables were selected as the most important.

- National Grid northings (reflecting latitude).
- Accumulated temperature in day degrees above 5°C (AT5).
- Distance from sea.

Stepwise multiple regression routines were used to investigate the predictive quality of each of these variables and their combinations. They were found to be sufficiently independent in effect for regression equations based on all three variables to have the best explanation of the variation present. Four predictive equations were therefore developed, one for each regional grouping. The details of these are given in Appendix 8.

Using these equations, 10-year heights were predicted for each of the four regional groups using a grid of 250 metre squares across the whole of Great Britain, the minimum level at which data were available from GIS for each of the variables. At each point on this grid, the predicted performances of the other three regional groupings (AL, WA and OR) were calculated and compared with that of QCI and for each region, a series of maps was developed based on percentage thresholds by which the growth of the regional group exceeded that of QCI. Where the group concerned exceeded the threshold, a different plotting colour was used.

A set of maps for Washington sources based on threshold percentages of 5, 6 and 7 is presented in Figure 28. Those areas on the map which are coloured black are recognised as generally unsuitable for planting Sitka spruce using the criteria available from the Ecological Site Classification system (ESC) (Pyatt *et al.*, 2001; Ray, 2001). The area in which Washington sources would be expected to grow 5% faster than QCI material extends throughout southwest England, most of Wales, the coastal land of the Lake District and the coast of southwest Scotland. If a 6% threshold is considered, this area is now confined to south and west Wales and southwest England and if this is raised to 7%, only the southern fringe of the south Wales coast and a reduced part of southwest England is indicated. Experience of past planting practice, establishment success and subsequent growth rates suggests that the map based on a 5% threshold would provide an appropriate framework upon which to base the use of Washington origins.

In considering origins from north Oregon, their increased susceptibility to frosting must be taken into account. Because of this risk, recommendations to use such sources are only justifiable if growth potential thresholds well above those of Washington origins were considered. Maps for north Oregon origins, based on higher threshold percentages of 10, 11 and 12, are presented in Figure 29. Predictions of suitable areas for this grouping are confined to a coastal band which widens in the south of Great Britain. Increasing the threshold to higher percentage levels has the effect of progressively narrowing this band leading to its elimination in northern parts of the range. The map based on a 10% threshold provides a suitable framework for considering the use of north Oregon sources.

The same techniques were applied using the predictive equation for Alaskan sources but no points emerged at which predicted growth exceeded that of QCI material.

Choosing a seed origin using the suitability map

For reference purposes, an origin suitability map in which areas for both Washington (5% above QCI) and Oregon (10% above QCI) are superimposed is presented on a larger scale in Figure 30.

This map has been developed using predictive models which, whilst based on significant linear relationships between growth rate and site variables, do not explain all the variation in growth to be observed (see Appendix 8). Although it provides clear guidance on origin choice, it is important to emphasise that its use should be taken as a starting point in the refinement of a final decision. Further consideration must be given to two alternatives in making a decision for any individual planting site:

- on any part of the map in which an alternative to QCI is indicated, specific site conditions (such as frosting and leader breakage) might adversely affect growth and survival. In these circumstances, in a part of the map in which Washington is indicated, it might

Figure 28

Maps showing 5%, 6% and 7% increase over QCI in predicted height at 10 years for the coastal Washington origins.

Figure 29

Maps showing 10%, 11% and 12% increase over QCI in predicted height at 10 years for the northern Oregon origins.

Figure 30

Areas in Great Britain in which Washington and Oregon origins of Sitka spruce can be expected to show increased height at 10 years over Queen Charlotte Islands origins of 5% and 10% respectively.

be better to use QCI, or in a part in which Oregon is indicated, it might be better to use Washington.

- conversely, on any part of the map in which QCI or Washington are indicated, specific site conditions may be so favourable as to allow Washington or Oregon to be considered respectively. This is particularly so on the west coast of Scotland, together with the Inner Herbrides where forest managers should be encouraged to consider routinely the potential of specific sites for the use of Washington sources.

At the nursery stage, frosting can be a factor both in spring and in the autumn. However, it is possible to give protection to seedlings and transplants in the nursery whereas this is not possible after planting out on forest sites. All the experiments which have measured flushing, both in Britain and in Ireland and western Europe, found that there was limited variation in flushing time between origins with a maximum range of three weeks. Therefore, origins cannot be differentiated with respect to their susceptibility to spring frosts. However, there is a clear clinal relationship between growth cessation and latitude and thus susceptibility to autumn frosts. Origins from southern latitudes cease growth up to three months later than northern ones. The primary environmental factor to be considered, therefore, will be the potential for damaging frost.

Survival in the IUFRO experiments in Great Britain was on average above 90%, but the far southern origins from south Oregon and California had poor survival of 40–60% (Lines, 1980). A similar picture was found in Northern Ireland (Savill and Milner, 1980). In the main IUFRO experiments in Belgium, which had a restricted number of origins, survival of Oregon material from Brookings and Necanicum was less than 65%. In the Netherlands, at age 10 years on two sites with

48 origins, survival of those from QCI, Vancouver Island, mainland BC and Washington averaged over 85% but it decreased from north to south in Oregon with Brookings and Gold Beach at under 40% (Kranenborg, 1993). Data from three sites in northern Germany containing 43 origins indicated a similar picture. Accumulated losses in the nursery and field up to age 8 years for origins from southern Oregon and northern California exceeded 90%, with origins from north and mid Oregon at 50% or more. Losses in more northern origins from BC and Washington were normally less than 35% (Kleinschmit and Svolba, 1993).

The use of more southerly origins must therefore be chosen with reference to the likely effect of unseasonal frosts at the planting site. Aspect and slope will play an important role in avoiding deleterious frosts. Sites which do not include valley bottoms but incorporate generally warmer south-facing slopes can be considered for more southerly origins than those which do not combine these advantages.

Exposure must also be considered in selecting a suitable Sitka spruce seed origin for a site. The more rapid growth rate of more southerly seed origins will inevitably produce longer leading shoots which are more vulnerable to wind damage on an exposed site. Susceptibility to prevalence of winds between mid July and early August may be important since leader breakage normally occurs during the period before full lignification of the leader has taken place.

Sitka spruce has a poor ability to restore apical dominance following repeated leader damage, and this can result in multiple leaders and a significant loss of growth (Perks *et al.*, 2005). Hale *et al.* (1998) suggested that a threshold DAMS (Detailed Aspect Method of Scoring wind; see Quine and White, 1993) score of 20.5 represents the exposure growth limit for QCI, growing at yield class 10. This score would need to be reduced for any situations in which a faster level of growth was anticipated, either because of site quality or because of the growth potential of more southerly origins. For Washington and Oregon sources, DAMS thresholds of 17 or below might need to be considered. This would help to avoid losing the growth advantage of Washington and Oregon sources on exposed sites.

Whilst the suitability recommendations suggested by the map in Figure 30 are based on comparatively low increases in height at 10 years (5% for Washington, 10% for Oregon), it is likely that these will represent more substantial volume gains. In a detailed study of 11 families of Sitka spruce, Lee and Matthews (2004) compared 10-year height with felled volume yields 38 years after planting, comparing each with QCI material. Only one family produced less volume increase than height increase, the remainder producing between one and four-fold increases in volume compared to height.

7 Conclusions and recommendations

General trends

Sitka spruce became the dominant plantation species in Britain in the 1950s and continues to retain this position in areas where production of timber and pulpwood are considered as the primary forestry objectives. The species has more than twice the natural latitudinal range occupied by mainland Britain, extending almost 10 degrees further south. The variation present can therefore not only be used to choose the best sources of seed based on climatic matching, but also to seek greater growth potential from origins outside the more limited British latitude range. Both of these approaches have been used in the analysis of field experiment data.

Few planting sites in Britain compare with the very specific site conditions in which Sitka spruce is found naturally, but the species has been grown with considerable success across a wide range of sites in Britain through which the main limitation has been found to be climatic conditions which are too dry or altitudes where exposure and cold are extreme.

It is very fortunate that at the start of the afforestation programme of the 20th century, firstly that Sitka spruce was selected as one of the main species to be used (Robinson, 1931); secondly that the Queen Charlotte Islands were the preferred seed source due to climate and latitudinal matching; and thirdly that adequate supplies of seed were available due to an agreement with the Canadian government (Borthwick, 1924). All later investigations into this seed source have indicated its general superiority across a wide range of non-limiting sites. Only very occasionally at extreme northern sites where low temperatures may have limiting or damaging effects, have Alaskan origins been found to outperform QCI material but this has not been sufficiently consistent for any recommendation to use Alaskan sources to be made.

Sources of seed from latitudes to the south of those of Britain have been shown to have the potential for faster growth than QCI material on sites characterised by a milder, wetter climate and a longer growing season. The potential of Washington origins in these conditions is clear but, on the mildest sites, origins from Oregon may be considered. However, as will be indicated below, close attention must be paid to the potential for damage from frost during the first few years after establishment.

In addition to these major trends, the experiments have also identified other areas of the natural range of Sitka spruce from which poorly performing sources have been found. Those from coastal areas of British Columbia (BC) around the Skeena River (v) do not compare with material from QCI (at a similar latitude) and the more inland of these, where introgression with interior spruce species is likely, are notably poor (iii and iv). Other populations on the mainland coast of BC (vii), as well as those from the Fraser River area (viii) and the Puget Sound, Washington (xi), contrast with material from the west coast of Vancouver Island (ix) and the west coast of the Olympic peninsula (xii). In the extreme south of the range, sources from southern Oregon (xv) and California (xvi) have grown slowly with poorer survival. Therefore none of these groupings should be considered for use in Britain.

The conclusions which have been drawn from these experiments are based on results obtained under current climatic conditions. However, it is now widely accepted that over the next century atmospheric carbon dioxide, and consequently temperatures, are set to rise above their current levels (Hulme, 2002). This will lead to forest growth rates increasing except in areas where there is an increase in moisture deficit. Ray *et al.* (2002) using the Ecological Site Classification (ESC) model (Pyatt *et al.*, 2002) which is based on accumulated temperature (AT), moisture deficit (MD), wind exposure (DAMS) and continentality have produced climate suitability maps for Sitka spruce over the next century. These show that in southwest and mid England, due to the development of a warm, dry climate in a westerly direction, the area where Sitka spruce can be considered as a suitable or very suitable species will decrease. However, in Scotland and northern England, due to the predicted increase in AT, the area which can be considered very suitable will increase considerably. The increases in temperature will cause spring flushing to be advanced, but the risk of spring frost is unlikely to change (Redfern and Hendry, 2002). The results of the current studies have shown that the differences in flushing time between seed origins are very small, and origin choice would therefore not be affected. On the other hand, autumn frosts may become more important, especially in England, and this could influence the choice of origin. The increased temperatures would indicate in certain areas that Oregon origins could displace others from Washington, but this should be avoided because the risk of unseasonal frost damage will remain. The latitudinal clinal variation in growth and morphology which has been noted in this species should provide sufficient variation and adaptability to accommodate changes in origin recommendations in Great Britain which are likely to involve increases in the area in which more southerly sources can be used.

Conclusions

In summary, the experiments have shown that:

- Seed origins of Sitka spruce are rather uniform in morphology and, apart from the generally more blue-green foliage of Alaska origins, cannot be distinguished easily on appearance alone.
- By contrast, origins show very wide differences in their phenology,

particularly in the time at which they cease growth and set buds in autumn.

- Flushing differences are greater between individuals within a seed origin than between the mean values for different origins.
- Lammas shoot production often differs significantly between origins, although it is also greatly influenced by growing conditions.
- These phenological differences have a direct influence of susceptibility to frost, with late-maturing southerly origins being frequently damaged by early autumn frosts on some sites. The danger from frost is greatest in the nursery stage. Late spring frosts can damage all seed origins, although there is some evidence for greater hardiness of Alaskan sources.
- There appears to be a pattern of increasing defoliation by *Elatobium abietinum* as tree vigour increases, hence southerly origins are more heavily infested than northerly ones. However, the pattern is not particularly clear and apparent seed origin differences in recovery following defoliation may be of greater importance than differences in initial susceptibility.
- Leader breakage is a frequent phenomenon in stands of Sitka spruce, and at some sites it was highly significantly correlated with tree height. It could have an important negative influence on timber strength by causing a sharp change in grain angle.
- In a limited study, differences in crown form (as measured by crown width:tree height ratio) were highly significant with the broadest crown in Alaskan origins and the narrowest in southern ones.
- After about 6–10 years in the forest, the pattern of growth becomes less variable and later rank changes among origins are mainly associated with recovery of certain origins from early frost damage. Basal area production generally follows similar patterns to early height growth.
- There are several exceptions superimposed on the general cline of increasing vigour with decreasing latitude are several exceptions. Poorer growth in relation to latitude is found in the far northeast of the species range in the upper Skeena River valley, the mainland coast of British Columbia, the lower Fraser River basin, the Puget Sound, the most southerly parts of Oregon and northern California. In contrast, better growth than expected can be found in Queen Charlotte Islands and some Vancouver Island origins. In general, those from coastal Washington and northern Oregon are the most vigorous.
- There is variation within the Queen Charlotte Islands with low elevation sources from the northern and eastern half of Graham Island having higher than average production.
- Wood density varies significantly with seed origin, but is influenced by vigour so the importance of origin alone is not clear. Origins from the Washington coast and north Oregon groupings have a wood density which may be lower than that for QCI by up to 8%.
- A major study of Washington and QCI sources showed that the Washington origins produced a greater quantity of sawlogs which met constructional specifications for size and an increase in battens falling into the SC3 (C16) strength category. However, the number of battens meeting the SC4 (C24) specification did not decrease compared to QCI.

The choice of seed origin in Sitka spruce in Great Britain based on growth must be based on an overall recommendation of using QCI sources with more specific guidance on sites where Washington or Oregon sources could be considered.

Reconciling the use of British and imported seed

As a general principle, using seed from local populations is advantageous, even of introduced species. However, while they may appear satisfactory, they may be growing significantly more slowly than the rate which could be achieved by a superior seed origin. In 2005, the weighted general yield class (GYC) for Forestry Commission Sitka spruce woodlands in Britain approaches 14 (Halsall[5], personal communication). At several sites, the GYC has been estimated within the range 18–22+ for the fastest growing origins. Despite the fact that the national average will be depressed by those stands which had experienced sub-optimal silvicultural treatment or were planted on difficult sites, there appears to be scope for increasing GYC by choosing optimal seed origins.

Variation among origins from QCI was also noted. This suggests that some of the commercial imports of large quantities of seed from this region in the past could have led to potential seed sources in Britain with slower growth rates. Likewise, ill-defined origins of older imports (e.g. 'USA' or 'Washington') could also leave doubts about the suitability of other potential stands for British seed collection. However, the possibility of beneficial adaptation in first generation British material must not be disregarded. This has been clearly shown in *Abies grandis* Lindl. (Samuel, 1996) where material collected from a first generation British stand grew faster than native material re-collected from the original parental source.

Gains of 5–10% in growth rate appear possible from the results of seed origin experiments. Even allowing for possible higher nursery production costs (due to losses from frost or the need to protect stock), Corcoran (1985) estimated net discounted revenue gains of £200–300 per hectare, simply by changing from QCI to Oregon seed origins in some areas of Wales. For northern England and Scotland, the scope for increasing revenue could be similar on the better sites (e.g. Achaglachgach, Ratagan and Benmore), although on poorer sites with more testing climatic conditions, it would be safer to concentrate on specific vigorous seed origins from more northerly sources, specifically QCI.

Reconciling seed origin choice with the use of improved Sitka spruce from the British breeding programme

In parallel with the investigations on provenance reported in this publication, a tree breeding programme in Sitka spruce has been carried out in Britain. This work has been based on conventional plus-tree selection with comprehensive progeny testing of all candidates. (Fletcher and Faulkner, 1972: Lee, 2001). Proven high quality parents have then been re-selected to form the components of tested seed orchards or family mixtures for vegetative propagation using cuttings (Mason and Gill, 1986), see Figures 31 and 32. Parents have deliberately been selected because their progeny have performed well across a range of sites where tests have been conducted, retaining thereby, the adaptive characteristics of QCI material. From all improved material currently available, average predicted increases in growth rate across a range of site types are of the order of 15–20% higher than unimproved QCI. These clearly exceed the levels of gain upon which the suitability maps were constructed and many of the gains observed among faster-growing origins in the experiments reported here. Furthermore, parents in the breeding programme have also been selected for an increase in stem quality (straightness and branching habit). This means

[5] Lesley Halsall, Systems and Data Manager, Operational Support Unit, Forestry Commission, Edinburgh, UK.

Figure 31

Increasing amounts of improved seed of Sitka spruce now come from tested seed orchards resulting from tree breeding work. Gains in vigour and tree form, without loss of timber density, can be expected.

Figure 32

Mass vegetative propagation of cuttings from small quantities of improved seed make a major contribution to bringing the latest products of Sitka spruce tree breeding into commercial use.

that plantations based on improved material are likely to produce a higher out-turn of sawlogs of acceptable quality than those based on provenance choice alone. In Sitka spruce, because of the strong negative correlation between growth rate and wood density, parents are also selected to prevent any overall decrease in wood density occurring due to the increased vigour of improved material (Lee, 2001).

Improved Sitka spruce is therefore likely to out-yield all unimproved origins across most site types in Britain. Thus today, the first choice of planting stock of Sitka spruce for timber production should be improved material, and choice of unimproved seed origins will arise only in the following circumstances:

- **Supply:** because of the oceanic climate in Britain, flowering of Sitka spruce is unpredictable and erratic, resulting in abundant seed production only every 5–10 years. There is therefore insufficient continuity of supply of seed from orchards to meet annual demands on a regular basis. Choice of the most productive unimproved seed origin will be necessary in years when the supply of improved planting stock is inadequate.
- **Direct seeding:** this places heavy demands on seed supply which are unlikely to be met from seed orchards. Origin choice will be important where this is practiced but particularly close attention to potential frosting will be necessary.
- **Cost:** plants and cuttings of improved material may be at least twice as expensive as unimproved stock, although vigorous growth has been shown to reduce overall establishment costs through a lower need for herbicides. Where there are constraints on the cost of planting stock, particularly if the planting site is within the Washington or Oregon suitability zones, choice of unimproved material of the appropriate origin may be necessary, provided the loss in total production is acceptable.

The long-term aim will be full provision of improved planting stock from the tree breeding programme, either as seed from tested clonal seed orchards or as vegetatively propagated planting stock from tested family mixtures, but, if there is insufficient planting stock from these sources, then the correct choice of seed origin will continue to be of great importance.

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Appendix 1

List of all seed origin experiments of Sitka spruce planted in Great Britain between 1929 and 1975.

Planting year	Forest and experiment number	Latitude °N	Longitude °W	Number of origins	
1929	Radnor 20	52.29	3.19	4	
1933–39	Leanachan 1	56.85	5.02	16	
1936–38	Kielder 29	55.19	2.53	11	
1938–40	Newcastleton 5	55.17	2.77	11	
1950	Kielder 53	55.21	2.37	8	
1950	Glendaruel 1	56.06	5.16	9	
1950	Gwydyr 1	53.05	3.82	6	
1954	Strathy 4	58.48	4.01	3	
1954	Kielder 72	55.21	2.38	3	
1959	Watermeetings 1	55.36	3.63	5	
1959	Naver 4	58.34	4.26	5	
1959	Ratagan 1	57.24	5.50	5	
1960	Ratagan 2	57.24	5.50	13	
1960	Glentrool 18	55.12	4.62	11	
1960	Wark 2	55.05	2.44	12	
1960	Loch Goil 2	56.19	4.93	10	
1960	Bannau 1	51.77	3.46	12	
1960	Myherin 3	52.39	3.78	12	
1960	Rheola 8	51.67	3.68	12	
1960	Taliesin 16	52.50	3.86	12	
1960	Tarenig 5	52.38	3.73	12	
1961	Forest of Deer 3	57.57	2.18	14	
1961	Shin 1	58.08	4.39	14	
1961	Clocaenog 44	53.10	3.55	10	
1961	Mynydd Du 3	51.95	3.12	14	
1961	Wilsey Down 19	50.60	4.61	13	
1968	Glendaruel 5	56.06	5.13	25	
1972	Shin 39	58.14	4.46	11	
1974	Rumster 11	58.53	3.25	64	
1974	Craigellachie 2	57.48	3.09	64	
1974	Farigaig 32	57.24	4.46	69	
1974	Blairadam 6	56.24	3.54	62	
1974	Benmore 16	56.06	4.91	64	
1974	Arecleoch 6	55.07	4.75	69	
1974	Wark 19	55.10	2.32	69	
1974	Dalby 128	54.25	0.65	63	
1974	Mathrafal 5	52.63	3.47	27	
1974	Mynydd Du 7	51.95	3.11	27	
1974	Rhondda 3	51.71	3.53	27	
1974	Wilsey Down 21	50.55	4.53	27	
1974	Ystwyth 8	52.40	3.74	27	
1975	Ratagan 4	57.23	5.47	64	
1975	Glentress 26	55.72	3.26	64	
1975	Achaglachgach 2	55.80	5.35	62	
1975	Castle O'er 11	55.26	3.14	63	
1975	Thornthwaite 7	54.61	3.23	64	
1975	Glentress 31	55.67	3.16	10	
1975	Tywi 49	52.19	3.78	10	

	Range covered	Notes
	QCI; Washington; Oregon; California	Unreplicated large plots
	Kitimat BC; QCI; Vancouver Is; N Washington	Replicated; frost, fire and pollution affected results
	QCI; Vancouver Island; N Washington	Replicated; frost and fire affected results
	Kitimat BC; QCI; Vancouver Island; N Washington	Replicated; plant age varied, severe frost
	QCI; Washington (6 origins)	Replicated; frosty site
	QCI; BC; Washington (6); USA	Replicated; little frost
	QCI; BC; Washington (5)	Replicated; little frost
	Alaska; QCI; Scotland (Washington)	Replicated
		Replicated
	Alaska; QCI; Scotland (Washington)	Replicated
		Unreplicated
		Unreplicated
	Alaska; Skeena River; QCI; Vancouver Island; Washington; Oregon	This series includes some seedlots which are not replicated on all sites. The sites cover a wide range of climatic and soil factors. Mainly 3 replications per site. Plot size varies from 60 to 361 plants except for Bannau and Taliesin which have 12 and 25 replications of single tree plots respectively.
	Alaska; Skeena R.; Vancouver Is.; Washington; Oregon; California	Includes 12 additional origins in unreplicated plots
	Alaska (10); QCI	Plants from Icelandic Forest Service
	Alaska; Skeena River; QCI; Coast BC; Vancouver Island; Washington; Oregon; California	The main IUFRO series. *Intensive* sections: mainly 4 replicates of 9 plants plots (25 plant plots at Welsh sites and Wilsey Down) *Extensive* sections: large plots (225–255 plants) with 3 replicates at Farigaig, Arecleoch and Wark. 2 replicates of 196 plant plots at Welsh sites and Wilsey Down.
	Alaska; Skeena River; QCI; Vancouver Island; Washington; Oregon	IUFRO International Ten Provenance Experiments

Appendix 2

Description of planting sites used in the P60/61 series of experiments.

Forest and Experiment number	Planting year	Latitude °N[1]	Longitude °W[1]	Altitude (m)	Rainfall (mm)	
Shin 1	1961	58.08	4.39	152	1020	
Deer 3	1961	57.57	2.18	140	850	
Ratagan 2	1960	57.24	5.50	122	1778	
Loch Goil 2	1960	56.19	4.93	145	2160	
Glentrool 18	1960	55.12	4.62	213	1524	
Wark 2	1960	55.05	2.44	251	1066	
Clocaenog 44	1961	53.10	3.55	402	1270	
Taliesin 16	1960	52.50	3.86	450	1270	
Myherin 3	1960	52.39	3.78	472	1800	
Tarenig 5	1960	52.38	3.73	412	2000	
Mynydd Du 3	1961	51.95	3.12	732	1780	
Bannau 1	1960	51.77	3.46	335	2000	
Rheola 8	1960	51.67	3.68	335	2000	
Wilsey Down 19	1961	50.60	4.61	310	1270	

[1]Latitude and longitude are expressed in decimal degrees.
[2]Accumulated temperature (day-degrees) above 5°C.
[3]DAMS = Detailed Aspect Method of Scoring.
[4]Plots are normally square in shape (361, 196, 100, 64) or rectangular (210, 60).
[5]At Shin 1, 5 plot sizes were used: 140, 160, 168, 180 and 224.
[6]At Ratagan 2, 3 plot sizes were used: 196 (rep 1), 192 (rep 2), 198 (rep 3).

	ATS[2]	Wind (DAMS)[3]	Soil type	Previous land use	Number of origins	Number of trees per plot[4]	Replicates
	1045	16	Deep peat (*Molinia* spp., *Juncus* spp.)	Poor hill grazing	12	140–224[5]	3
	1115	15	Peaty gley, deep peat (*Calluna* spp.)	Pasture	10	196	3
	1178	12	Flushed peaty gley	Moorland	12	192–198[6]	3
	1273	11	Peaty gley	Moorland	6	210	3
	1223	17	Peaty gley	Pasture	9	196	3
	1177	16	Peaty gley	Poor pasture	12	361	3
	1099	18	Peaty gley	Hill grazing	12	196	2
	1062	17	Peaty gley, brown earth/intergrade	Hill grazing	12	1	25
	1053	17	Upland brown earth	Hill grazing	12	100	4
	1047	17	Raised bog	Hill grazing	12	196	4
	609	20	Peaty gley	Poor hill grazing	16	100	4
	1505	15	Raised bog	Moorland	12	1	12
	1295	16	Peaty gley, deep peat	Moorland	12	196	4
	1505	20	Shallow peat over granite	Pasture	14	64	4

Appendix 3

Details of seed origins used in the P60/61 series of experiments (ND = no data supplied).

Identity number	Origin	Region	Latitude °N	Longitude °W	Altitude (m)	Map[1]
57(7985)1	Cordova	Alaska	60.50	ND	ND	A
56(798)500	Lawing	Alaska	60.00	149.20	ND	B
58(7985)3	Seward	Alaska	60.10	149.40	<100	M
56(7987)1	Juneau	Alaska	58.25	134.40	ND	N
57(7986)1	Sitka	Alaska	57.00	ND	ND	O
57(7114)1	Terrace	Skeena River	54.50	ND	ND	C
57(7111)2	Skidegate	Queen Charlotte Islands	53.00	ND	ND	D
57(7116)500	San Juan	Vancouver Island	48.50	ND	ND	E
57(7116)3	Sooke	Vancouver Island	48.25	ND	ND	F
57(7971)1	Forks	Washington	48.00	ND	ND	G
57(7972)2	Hoquiam	Washington	47.00	123.90	0–500	H
57(7951)4	Jewell	Oregon	45.80	123.40	700	J
57(7952)1	North Bend	Oregon	43.00	ND	ND	K
55/121	Jutland	Denmark ex. Washington	56.00	ND	ND	L
58(4225)	Devon	Great Britain	50.50	ND	ND	P
58(4291)	Cardigan	Great Britain	51.25	ND	ND	Q

[1]Code letter used to identify location on map in Figure 11a.

Appendix 4

Description of planting sites used in the IUFRO series of experiments.

Forest and Experiment no.	Planting year	Latitude °N[1]	Longitude °W[1]	Altitude (m)	Rainfall (mm)	ATS[2]	
Main IUFRO series							
Rumster 11	1974	58.53	3.25	30	825	1130	
Craigellachie 2	1974	57.48	3.09	290	950	940	
Ratagan 4	1975	57.23	5.47	76	1780	1234	
Farigaig 32	1974	57.24	4.46	230	1000	1040	
Achaglachgach 2	1975	55.80	5.35	152	1524	1281	
Blairadam 6	1974	56.24	3.54	290	1270	1041	
Benmore 16	1974	56.06	4.91	20	2286	1435	
Glentress 26	1975	55.72	3.26	440	1020	866	
Castle O'er 11	1975	55.26	3.14	280	1524	1127	
Arecleoch 6	1974	55.07	4.75	140	1270	1365	
Wark 19	1974	55.10	2.32	190	1016	1266	
Thornthwaite 7	1975	54.61	3.23	487	1530	857	
Dalby 128	1974	54.25	0.65	183	836	1346	
Mathrafal 5	1974	52.63	3.47	358	1400	1199	
Ystwyth 8	1974	52.40	3.74	510	1600	933	
Rhondda 3	1974	51.71	3.53	440	2400	1084	
Mynydd Du 7	1974	51.95	3.11	735	1400	516	
Wilsey Down 21	1974	50.55	4.53	285	1778	1436	
International Ten Provenance Experiments							
Glentress 31	1975	55.67	3.17	304	1016	1062	
Tywi 49	1975	52.18	3.77	425	2000	1105	

[1]Latitude and longitude are expressed in decimal degrees.
[2]Accumulated temperature (day-degrees) above 5°C.
[3]DAMS = Detailed Aspect Method of Scoring.
[4]Figures in parentheses for origins, plot size and reps relate to the extensive sections (long term); those without parentheses to the intensive sections (short term).

Wind (DAMS)[3]	Soil type	Previous land use	Number of origins[4]	Number of trees per plot[4]	Replicates[4]
16	Brown earth	Pasture	64	9	4
15	Humus iron podzol	Moorland	64	9	4
13	Brown earth	European larch YC10	64	9	4
15	Imperfectly drained ironpan	Mixed conifers YC12	42 (25)	9 (238)	4 (3)
15	Deep peat	Poor hill grazing	64	9	4
14	Surface water gley	Hill grazing	64	9	4
9	Alluvial	Forest nursery	64	9	4
20	Ironpan	Poor hill grazing	64	9	4
16	Peaty gley	Hill grazing	64	9	4
16	Peaty gley over induration	Poor pasture	42 (25)	9 (255)	4 (3)
14	Peaty gley	Poor pasture	42 (25)	9 (225)	4 (3)
14	Upland brown earth	Norway spruce	64	9	4
13	Ironpan	Japanese larch	64	9	4
18	Peaty gley to peat	Hill grazing	27 (27)	25 (196)	3 (2)
18	Deep peat	Poor hill grazing	27 (27)	25 (196)	3 (2)
17	Flushed Blanket bog	Hill grazing	27 (27)	25 (196)	3 (2)
25	Peaty gley	Poor hill grazing	27	25	3
18	Peaty gleyed podzol	Hill grazing	27 (27)	25 (196)	3 (2)
12	Brown earth	European larch	10	9	9
17	Deep peat	Hill grazing	10	9	9

Appendix 5

Details of seed origins used in the IUFRO series of experiments.

IUFRO/identity number	Origin	Region	Group[1]	Latitude °N	Longitude °W	Altitude (m)	Map[2]
3021	Yakutat	Alaska	i	59 .52	139 .70	12	1
3022	Dyea, Skagway area		i	59 .50	135 .35	0	2
3024[3]	Duck Creek, Juneau area		i	58 .37	134 .58	30	3
66(7985)3	Seward Kenai, Peninsula		i	60 .12	149 .62	0–15	9
69(7986)3	Hoonah, Chicagof Island		i	58 .13	135 .50	0–15	10
3025	Ohmer Creek, Mitkof Island	Alaska	ii	56 .58	132 .73	0–15	4
3027	Craig, Prince of Wales Island		ii	55 .50	133 .13	0	5
3028	Old Hollis, Prince of Wales Island		ii	55 .47	132 .67	0	6
3030[3]	Ward Lake, Ketchikan		ii	55 .42	131 .70	15	7
3035	Moss Point, Annette Island		ii	55 .03	131 .58	0	8
69(7986)	Craig, Prince of Wales Island		ii	55 .50	133 .13	–	5
3026	Derrick Lake, Nass River	Skeena/ Nass Rivers	iii	55 .68	128 .68	245	12
3032	Kitwanga, Hazelton area		iii	55 .17	127 .87	670	13
3033	Zolap Creek, Nass River		iii	55 .15	129 .22	15	14
3038	Pacific, Skeena River	Skeena/ Nass Rivers	iv	54 .77	128 .25	110	15
3039	Kitsumkalum Lake, Terrace		iv	54 .72	128 .77	140	16
3040[3]	Usk Ferry, Skeena River		iv	54 .64	128 .42	160	71
3041	Shames, Skeena River		iv	54 .40	128 .95	30	17
3042	Kasiks River, Skeena River	Skeena/ Nass Rivers	v	54 .28	129 .42	30	18
3043	Hays Mountain, Prince Rupert		v	54 .27	130 .32	670	19
3044[3]	Inverness, Prince Rupert		v	54 .20	130 .25	0–30	20
3045	Aberdeen Creek, Skeena River		v	54 .20	129 .92	0	21
3046	Wedene River, Kitimat		v	54 .13	128 .62	170	22
3047	Humpback Creek, Porcher Island		v	54 .03	130 .37	300	23
3048	Masset Sound, Graham Island	Queen Charlotte Islands	vi	53 .92	132 .08	0	24
3049[3]	Link Road, Juskatla, Graham Island		vi	53 .50	132 .17	90	25
3050	Copper Creek, Sandspit, Moresby Island		vi	53 .13	131 .80	80	26
3051	Moresby Camp, Moresby Island		vi	53 .05	132 .07	60	27
3052	Tasu Creek, Moresby Island		vi	52 .37	132 .08	15	28
3053	Jedway, Moresby Island		vi	52 .28	131 .22	15	29
3068	Naden Harbour, Graham Island		vi	53 .95	132 .60	0–30	30
3069	Ain River, Masset, Graham Island		vi	53 .75	132 .42	0–30	31
3070	Dinan Bay, Masset, Graham Island		vi	53 .67	132 .67	0–30	32
3071	Tlell, Graham Island		vi	53 .58	131 .93	0–60	33
70(7111)500	Tow Hill, Masset, Graham Island		vi	54 .07	131 .77	0–30	34
70(7111)501	Queen Charlotte City, Graham Island		vi	53 .25	132 .08	0–60	35
70(7111)502	Skidegate, Maud Island		vi	53 .20	132 .08	0–60	36
70(7111)Lot2	Masset (Commercial Seed Lot)		vi	54 .00	132 .00	0–15	37
3054	Noeick River, Bella Coola area	Mainland BC	vii	52 .10	126 .55	260	38
3055	Cuckwalla River Rivers Inlet		vii	51 .77	127 .12	140	38
3060	Squamish River, north of Vancouver	Mainland BC	viii	49 .88	123 .25	30	39
3063	Haney, east of Vancouver		viii	49 .23	122 .60	90–300	40
3064	Vedder, Chilliwack		viii	49 .12	121 .93	30	41

Details of seed origins used in the IUFRO series of experiments (continued).

IUFRO/identity number	Origin	Region	Group[1]	Latitude °N	Longitude °W	Altitude (m)	Map[2]
3056[3]	Holberg	Vancouver Island	ix	50 .62	128 .12	30	42
3057	Holberg		ix	50 .58	128 .07	210	42
3059	Fair Harbour		ix	50 .05	127 .03	30	44
3061	Tahsis Inlet, Nootka Island		ix	49 .83	126 .67	0	45
3065	Port Renfrew		ix	48 .58	124 .40	0–15	47
68(7116)6	Tofino		ix	49 .17	125 .83	0–15	49
3058	Salmon Bay	Vancouver Island	x	50.38	125.95	0	43
3062[3]	Big Qualicum River		x	49.38	124.62	0	46
3066	Muir Creek, near Sooke		x	48.38	123.87	0	48
3001	Bellingham	Washington	xi	48.75	122.63	15–30	50
3002	Port Angeles		xi	48.15	123.73	110	51
3067	Stillaguamish River		xi	48.12	121.75	300–370	52
3005	Brinnon		xi	47.70	122.88	0–3	55
3006	Shelton		xi	47.35	123.15	0–6	56
3003[3]	Forks	Washington	xii	48.07	124.30	120–140	53
3004	Kalaloch		xii	47.70	124.42	0–30	54
3007	Humptulips		xii	47.13	123.95	60	57
3008	Hoquiam		xii	47.08	124.05	6	58
3009[3]	Raymond		xii	46.68	123.87	15–30	59
3010	Naselle		xii	46.37	123.78	0–15	60
3011	Astoria	North Oregon	xiii	46.20	123.97	0–15	61
3012[3]	Necanicum		xiii	45.82	123.77	45	62
3013	Tillamook		xiii	45.33	123.88	90–100	63
3014	Newport	North Oregon	xiv	44.70	124.07	15–30	64
3015	Florence		xiv	44.12	124.12	150	65
3016	Denmark	South Oregon/ California	xv	42.85	124.45	150	66
3017	Gold Beach		xv	42.50	124.42	30	67
3018	Brookings		xv	42.25	124.38	90	68
3019	Big Lagoon	South Oregon/ California	xvi	41.13	124.15	10–15	69
3020	Crescent City		xvi	41.67	124.18	10–15	70

[1]See detailed descriptions in Table 14.
[2]Code number used to identify location on map in Figure 11a.
[3]Origin used in the International Ten Provenance Experiments.

Appendix 6

IUFRO series: height at ten years after planting expressed as % QCI, 70(7111)Lot(2).

Region	Group	IUFRO Number[1]	Location	
Alaska	i	*3021*	Yakutat	
	i	3022	Dyea, Skagway area	
	i	*3024*	Duck Creek, Juneau area	
	i	*66(7985)3*	Seward Kenai, Peninsula	
	i	*69(7986)3*	Hoonah, Chicagof Island	
Alaska	ii	3025	Ohmer Creek, Mitkof Island	
	ii	3027	Craig, Prince of Wales Island	
	ii	69(7986)	Craig, Prince of Wales Island	
	ii	3028	Old Hollis, Prince of Wales Island	
	ii	*3030*	Ward Lake, Ketchikan	
	ii	*3035*	Moss Point, Annette Island	
Skeena/Nass River	iii	3026	Derrick Lake, Nass River	
	iii	*3032*	Kitwanga, Hazelton area	
	iii	3033	Zolap Creek, Nass River	
Skeena/Nass River	iv	3038	Pacific, Skeena River	
	iv	3039	Kitsumkalum Lake, Terrace	
	iv	3041	Shames, Skeena River	
Shames, Skeena River	v	3042	Kasiks River, Skeena River	
	v	3043	Hays Mountain, Prince Rupert	
	v	*3044*	Inverness, Prince Rupert	
	v	*3045*	Aberdeen Creek, Skeena River	
	v	3046	Wedene River, Kitimat	
	v	3047	Humpback Creek, Porcher Island	
Queen Charlotte Islands	vi	*3048*	Masset Sound, Graham Island	
	vi	3049	Link Road, Juskatla, Graham Island	
	vi	3050	Copper Creek, Sandspit, Moresby Island	
	vi	3051	Moresby Camp, Moresby Island	
	vi	3052	Tasu Creek, Moresby Island	
	vi	3053	Jedway, Moresby Island	
	vi	3068	Naden Harbour, Graham Island	
	vi	3069	Ain River, Masset, Graham Island	
	vi	3070	Dinan Bay, Masset, Graham Island	
	vi	3071	Tlell, Graham Island	
	vi	70(7111)500	Tow Hill, Masset, Graham Island	
	vi	70(7111)501	Queen Charlotte City, Graham Island	
	vi	70(7111)502	Skidegate, Maud Island	
	vi	*70(7111)Lot(2)*	Masset (Commercial Seed Lot)	

[1]Origin identities appearing in italics are those used in the combined analysis of data from all sites except Ratagan

	Rumster	Craigellachie	Ratagan	Blairadam	Benmore	Achaglachgach	Glentress	Castle O'er	Arecleoch	Wark	Thornthwaite	Dalby	Mathrafal	Ystwyth	Rhondda	Wilsey Down	Origin mean (m)
	94	79	69	72	80	74	87	83	77	71	72	81	53	76	61	81	2.61
	82	83	82	75	83		89	85	75	80	74						2.67
	91	89	81	80	86	78	94	84	70	75	78	83	79	87	65	73	2.78
	77	74	75	64	67	73		65				62					2.45
	75	90		76	84			99	82	76			79	83	65	73	2.69
	101		81	90	96	87	92		97	81	85	84					3.19
	88	72	73	84	92	75	96	93	85	75		80					2.76
													78	82	69	78	2.78
	93	83	78		98		86		90	86	76	91					2.93
	97	77	81	85	92	83	90	92		83	81	84	79	89	77	82	2.94
	87	95	77	90	97	83	107	88	99	81	75	80	83	97	86	87	3.03
	81	88		83	83	72	76	92	75	75	68	74					2.62
	80	78	71			56	85	81	49	77	59	72	61	70	65	52	2.27
	85	88	78	80	82	75	93	79	63	77	75	80					2.70
	72	90	84	89	89	81	92	74	85	79	74	76					2.80
	84			83			96	89			90	90					2.90
	84	81	64	71	73	78	83	86	74	74	68						2.56
	76	73	78	77	77	81	86	74	75	70	70	76					2.60
	73		70	68		71		83			67	77					2.65
	90	90	99	96	98	93	96	121	100	89	83	106	95	97	77	94	3.29
	84	88	79	90	90	87	91	92	80	98	76	97	89	97	75	89	3.02
	81	89	62	88	76	90	97	88	78	75	75	92					2.79
	81	79	74	70	89	93	106	100	93	69	76	86					2.85
	109	97	89	102	112	101	98	100	97	102	96	112	101	103	97	104	3.52
	100	79	69	97	102	91	97	90	83	93	86	91					3.06
	94	92	90	87	99	99	107	113	98	85	86	98					3.24
	101	90	92	100	99	92	100	102	86	93	91	88					3.22
	82	80	67	90	95	96	99	102	99	89	83	100					3.06
	101	92	79	99	101	103	97	102	95	93	97	98					3.28
	99	99	97	94	106	108	104	103	86	97	93	100					3.37
	106	101	110	98	103	107	102	113	99	99	91	105					3.51
	81	94	92	98	97	103	103	107	92	86	89	95					3.23
	98	92		100	110				103	112		106					3.51
	103		101	98	104	110	106	108	95	110	98	96					3.56
	100	95	101		104	103	92	101	103	88	97	107					3.36
	104	95	96	95	113	111	104	102	86	96	111	103					3.48
	100	100	100	100	100	100	100		100	100	100	100	100	100	100	100	3.54

IUFRO series: height at ten years after planting expressed as % QCI, 70(7111)Lot(2) (continued).

Region	Group	IUFRO Number[1]	Location	
Coastal British Columbia	vii	3054/55	Noeick River, Bella Coola area	
Coastal British Columbia	viii	3060	Squamish River, north of Vancouver	
	viii	3063	Haney, east of Vancouver	
	viii	3064	Vedder, Chilliwack	
Vancouver Island	ix	3056/57	Holberg	
	ix	3059	Fair Harbour	
	ix	3061	Tahsis Inlet, Nootka Island	
	ix	3065	Port Renfrew	
	ix	68(7116)6	Tofino	
Vancouver Island	x	3058	Salmon Bay	
	x	*3062*	Big Qualicum River	
	x	*3066*	Muir Creek, near Sooke	
Washington	xi	3001	Bellingham	
	xi	3002	Port Angeles	
	xi	3067	Stillaguamish River	
	xi	*3005*	Brinnon	
	xi	3006	Shelton	
Washington	xii	*3003*	Forks	
	xii	3004	Kalaloch	
	xii	3007	Humptulips	
	xii	3008	Hoquiam	
	xii	*3009*	Raymond	
	xii	*3010*	Naselle	
North Oregon	xiii	*3011*	Astoria	
	xiii	*3012*	Necanicum	
	xiii	*3013*	Tillamook	
North Oregon	xiv	*3014*	Newport	
	xiv	*3015*	Florence	
South Oregon/California	xv	*3016*	Denmark	
	xv	*3017*	Gold Beach	
	xv	*3018*	Brookings	
South Oregon/California	xvi	*3019*	Big Lagoon	
	xvi	*3020*	Crescent City	
			Site mean (m)	

[1]Origin identities appearing in italics are those used in the combined analysis of data from all sites except Ratagan

	Rumster	Craigellachie	Ratagan	Blairadam	Benmore	Achaglachgach	Glentress	Castle O'er	Arecleoch	Wark	Thornthwaite	Dalby	Mathrafal	Ystwyth	Rhondda	Wilsey Down	Origin mean (m)
	98	93	68	89	95	87	93	92	78	97	76	78					2.94
	70	72	81	79		82	91	88	75	89	91	64					2.70
	69	71	78	88	88	92	95	82	88	77	82	94					2.86
	80	88	75	86	82	98	89	80	87	78	88	95					2.93
	91	97	80		98	100	103	90	99	94	90	103					3.19
	111	93	89	103	103	110	104	108	106	103	101	98					3.49
	90	89	71	107	103	100	104	111	103	97	95						3.29
	102	84	89	91	99	106	99	104	98	93	97	91					3.28
	89	92	80	92	104	104	102	113	91	87	88	102					3.23
	92	94	90	91	99	102	98	110	90	93	93	103					3.28
	76	114	86	96	104	106	101	83	84	99	103	111	100	100	102	102	3.41
			100			114	95	87	79	99	109		100	103	156	110	3.67
	85	76	90	99	102	106	96	94	103	81	82	100					3.19
	86	103	88	93	92	108	103	98	95	81	82	82					3.14
	86	99	82	96	93	94	96	97	88	98	94	98					3.18
	92	84	84	89	91	96	97	94	92	101	86	91	99	87	93	98	3.20
	86	87	91	93	104	102	96	109	94	78	93	82					3.17
	95	91	96	103	110	114	102	100	102	109	100	115	115	102	99	94	3.58
	97	101	103	102	118	116	104	125	112	94	90	108					3.61
	90	91	84	97	110	106	101	124	106	104	88	116					3.44
	102	103	100	92	118	111	101	89	103	101	91	111					3.49
	84	98	86	112	100	117	105	96	110	88	100	105	113	104	91	95	3.48
	82	91	104	94	107	101	92	105	83	102	89	101	107	104	98	99	3.39
	87	101	108	96	107	117	100	104	112	87	107	125	109	103	101	109	3.65
	92	92	88	101	100	110	104	96	91	99	89	111	107	102	93	108	3.44
		93	87	95	111	119	101	85	103	78	97	95	112	104	102	105	3.47
	105	97	122	95	109	122	103	89	101	83	112	113	111	109	93	119	3.70
		89	94	80	95	127	96	81	82	92	98	100	111	108	103	121	3.47
	87	92	98	70	72	116	90	44	77	66	79	93	106	94	105	113	3.09
		98	108	60	71	124	79	54	73	63	76	98	92	99	100	114	3.09
	86	97	106	85	85	122	82	47	91	72	85	123	104	99	95	128	3.34
	76	69		52	83				72	48		75	93	71	87	101	2.66
		83	94	52	89	127	61		67	58	96	106	106	90	86	114	3.19
	2.97	2.43	3.62	3.50	3.71	4.03	2.17	2.32	3.11	2.45	3.64	3.34	3.40	2.75	3.01	4.64	3.20

Appendix 7

IUFRO series: basal area at 20–22 years after planting expressed as % QCI, 3048, Masset Sound.

Region	Group	IUFRO number	Location	Farigaig (age 21)	Arecleoch[1] (age 22)	Wark (age 20)	Mathrafal (age 20)	Ystwyth (age 20)	Rhondda (age 20)	Wilkey Down (age 20)	Mean m^2 ha^{-1}
Alaska	i	3024	Duck Creek, Juneau	83	76	77					36.1
	i	69(7986)3	Hoonah, Chicagof Island							83	35.7
	i	66(7987)500	Juneau	95		72					38.5
Alaska	ii	3030	Ward Lake, Ketchikan	87		87					40.4
	ii	3035	Moss Point, Annette Island							70	30.1
Skeena/ Nass Rivers	iii	3032	Kitwanga, Hazelton	60		70				69	30.0
	iii	3033	Zolap Creek, Nass River	80		86					38.6
Skeena/ Nass Rivers	v	3044	Inverness, Prince Rupert							105	45.2
	v	3045	Aberdeen Creek, Skeena River	65	96	100	94			107	40.2
Queen Charlotte Islands	vi	3048	Masset Sound, Graham Island	100	100	100	100	100	100	100	39.3
	vi	3049	Link Road, Juskatla, Graham Is.	111	99	109					48.7
	vi	3051	Moresby Camp, Moresby Island	108	97						46.0
	vi	3068	Naden Harbour, Graham Island	98	95	100					44.7
	vi	3071	Tlell, Graham Island			101					48.5
	vi	70(7111)500	Tow Hill, Masset, Graham Island		89	104					44.7
	vi	70(7111)502	Skidegate, Maud Island	119	94						47.8
	vi	70(7111)Lot2	Masset (Commercial Seed Lot)				97	126	106	106	37.0
Coastal BC	vii	3054/5	Noeick River, Bella Coola area	84	81	90					39.0
Coastal BC	viii	3060	Squamish River, N. of Vancouver	69	86	94					38.2
Vancouver Island	ix	3056/7	Holberg	108		99					48.1
	ix	3061	Tahsis Inlet, Nootka Island			113					54.2
	ix	68(7116)6	Tofino		93						41.7
Vancouver Island	x	3058	Salmon Bay	95	87	96					42.6
	x	3062	Big Qualicum River	79	91	96	101	116	81	113	37.8
	x	3066	Muir Creek, near Sooke	88	82	96	84	102	102	121	37.7
Washington	xi	3067	Stillaguamish River	82	99	101					43.1
	xi	3005	Brinnon	92	95	112	86	102	107	114	39.8
Washington	xii	3003	Forks	91	105	118	104	126	117	120	43.5
	xii	3008	Hoquiam	113	109	103					49.7
	xii	3009	Raymond				111	114	116	128	40.6
	xii	3010	Naselle	104	93	104	112	121	96	122	42.0
North Oregon	xiii	3011	Astoria				100	142	98	122	39.5
	xiii	3012	Necanicum	98	109	105	106	110	126	125	43.5
	xiii	3013	Tillamook				99	131	123	129	41.3
North Oregon	xiv	3014	Newport				103	122	104	99	36.3
	xiv	3015	Florence	72	86	95	100	104	119	113	38.0
South Oregon/ California	xv	3016	Denmark				82	85	109	118	34.3
	xv	3017	Gold Beach	102			77	76	100	110	34.5
	xv	3018	Brookings		83		84	108	118	132	37.9
South Oregon/ California	xvi	3019	Big Lagoon				101		79	127	38.6
	xvi	3020	Crescent City				87	86	119	137	37.6
			Site mean (m^2 ha^{-1})	41.06	41.52	46.51	36.12	30.58	31.34	47.88	

[1]Arecleoch was thinned in 1994 but no records of the volume removed are available.

Appendix 8
Predictive equations used in the development of origin suitability maps.

Dependant variable

Height at 10 years (m) in the IUFRO series (HT).

Independant variables

1. Accumulated temperature in day-degrees above 5°C (AT5).
2. National grid northings (NO).
3. Distance from sea (km) (DS).

Sites

Rumster, Ratagan, Benmore, Achaglachgach, Glentress, Castle O'er, Arecleoch, Wark, Thornthwaite, Mathrafal, Ystwyth, Rhondda, Wilsey Down.

Predictive equations

Alaska

HT = 2.31 + 0.00108(AT5) – 0.000043(NO) – 0.0231(DS)
Percent variation accounted for: 48.45
Significance: $p = 0.0297$

Queen Charlotte Islands

HT = 2.94 + 0.00155(AT5) – 0.000127(NO) – 0.0289(DS)
Percent variation accounted for: 48.35
Significance: $p = 0.0299$

Washington

HT = 3.06 + 0.00172(AT5) – 0.000151(NO) – 0.0314(DS)
Percent variation accounted for: 52.95
Significance: $p = 0.0201$

Oregon

HT = 3.49 + 0.00169(AT5) – 0.000181(NO) – 0.0413(DS)
Percent variation accounted for: 44.27
Significance: $p = 0.0414$

Sam Samuel has worked in Forest Research since 1970 at both the Alice Holt and Northern research stations, providing support in the analysis and interpretation of data from the seed origin evaluation and tree breeding programmes. He was head of Tree Improvement Branch from 1996 to 2004.

Alan Fletcher worked in Forest Research from 1963 to 1997, leading the breeding programme for Sitka spruce. During the 1970s and 1980s he made frequent visits to the Pacific Northwest to organise surveys and seed collections of important conifer species, building up an unrivalled local knowledge of the region. He led the team which collected Sitka spruce seed in Alaska and British Columbia for the International Union of Forest Research Organisations. He was head of Tree Improvement Branch from 1992 to 1996.

Roger Lines joined the Silviculture (North) Branch of Forest Research in 1952 and among his responsibilities was research in seed origin evaluation, concentrating particularly on the important conifers species native to North America, until he retired in 1986. He was influential in devising the guidelines for provenance seed collection of behalf of the International Union of Forest Research Organisations.

Forest Research

Forest Research is an Agency of the Forestry Commission and is the leading UK organisation engaged in forestry and tree related research. The Agency aims to support and enhance forestry and its role in sustainable development by providing innovative, high-quality scientific research, technical support and consultancy services.

Sitka spruce is one of the most important and widely planted conifer species in Great Britain today. It plays a key role in the production of timber and is also important for other multipurpose forestry uses. Due to the extensive latitudinal distribution of its natural range along the Pacific Northwest coastline, it was necessary to establish seed origin studies to identify the most well-adapted sources for planting in Great Britain.

This Bulletin summarises the results emanating from over 70 years of research. The growth and production data have been used to produce a series of suitability maps which can assist forest managers in their decisions on the choice of seed origins for planting. The Bulletin is recommended reading for forest managers, advisors and researchers alike – as well readers interested in the development and use of species from the Pacific Northwest in British forestry.

Forestry Commission

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