Sitka Spruce, Its Distribution and Genetic Variation

J. O'DRISCOLL[1]

Origin

THE probable origin of all conifers is reputed to be from the periphery of the north Pacific Basin. (Li, 1953). Differentiation into the various families took place during the Mesozoic Era, 225 to 75 million years ago. Eastern Asia has been suggested as the likely origin of all spruces because of the large assortment of species at present found there. In addition *P. koyamai,* a primitive spruce, is found there today (Wright, 1955). These species would have evolved toward the end of the Cretaceous Period 70 million years ago. Today approximately forty species are contained within the genus Picea. All of these are native to the cooler parts of the northern hemisphere. Their southern limit extends to the mountains of northern Mexico, southern Europe, Asia Minor, Himalayas and Taiwan (Figure 1). Over half of the species in the genus are to be found in China with only eight being native to the American continent (Wright, 1955). These include *P. mariana, P. glauca, P. engelmanii, P. rubens, P. pungens, P. sitchensis, P. breweriana* and *P. chihuahuana.* Of these eight, six have ranges in Western North America. Two of these species *P. breweriana* and *P. chihuahuana* however have little or no commercial value. The natural range of these species is mainly confined to the interior of the North American continent, the only exception being Sitka spruce whose range is entirely maritime (Figure 2). In this regard it differs entirely from all the other species in the genus.

Distribution

Paleobotanical evidence has shown that the present distribution of the species is rather similar to what it was prior to the Wisconsin glaciation which occurred during the Pleistocene period 2 million years ago. With the onset of the cold period the ice sheet spread as far south as the 48th parallel reaching a depth of 915 m. on the Queen Charlotte Islands. This effectively wiped out the northern arm of the species distribution (Daubenmire, 1968) (Fig 3). Any surviving populations north of the glacial border were probably on nunataks as has been shown by decumbent individuals of Sitka spruce found on four widely separated nunataks. (Heusser, 1952) The effect of the glaciation on the southern arm of the species distribution was to push it further south. Fossil evidence shows it

1· Research Branch, Forest and Wildlife Service, Bray, Co. Wicklow.

Figure 1
Southern limit of spruce distribution (Li, 1952).

to have occurred south of San Francisco. Remnant populations can be found today in Mendocino county of northern California which is 50 kms further south than the terminus of the present day main population. With the melting of the ice sheet simultaneously along the coast, the rapid recolonisation of former sites was made in all probability from the remnant populations surviving on the nunataks rather than from migration northwards (Daubenmire, 1968).

The present day range extends from latitude 61° in Alaska to latitude 39° in California—a distance of 1,800 miles (Figure 3). Throughout this distribution it is confined mainly to a narrow coastal belt commonly known as the fog belt. Most of the commercial stands are estimated to be within 2½ miles of the coast reaching their maximum density on the Queen Charlotte Islands. Further south this band is still narrower. Its inland penetration is usually along river basins. In this situation it has been found up to 30 miles from the sea in Oregon and Washington. Its greatest penetrations is in Alaska and British Columbia where it occurs up to 130 miles inland. At these extremes of its inland penetration it is associated with white spruce (*P. glauca*). Its elevation range is also limited throughout its distribution with the exception of Alaska where it is found up to 800 m. More usually it ranges from sea level up to 300 m. (Fowells, 1965).

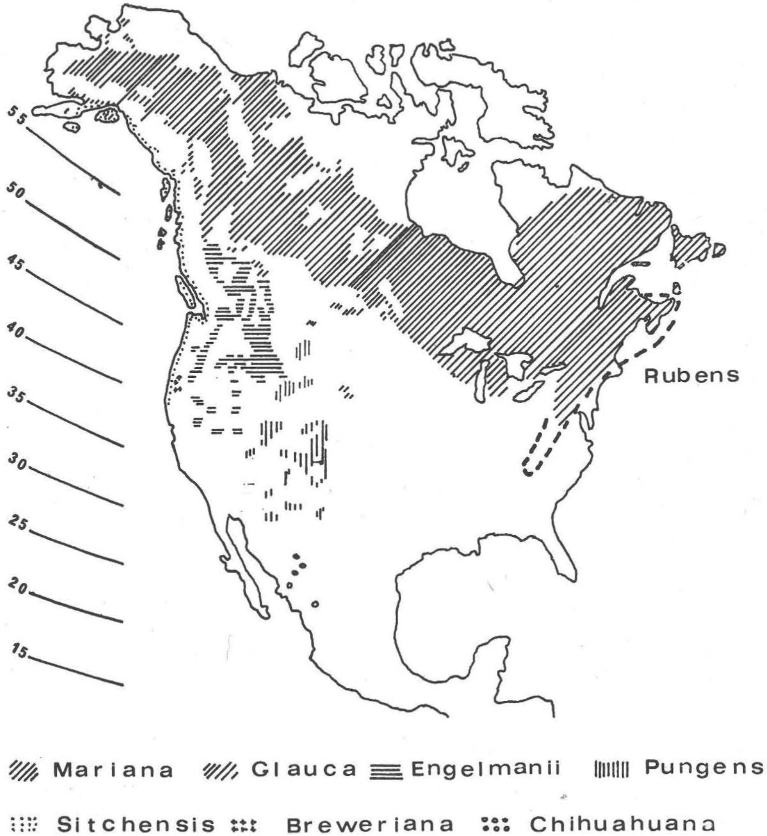

Figure 2
Distribution of North American Spruces (Wright, 1955).

Climate

The general climate throughout the range is a maritime one dominated by westerly winds from the Pacific Ocean and is characterised by equable temperatures, long frost free periods, high precipitation, cloudiness and absence of extreme cold. Precipitation is usually in the region of 1250 mm per annum occurring mainly in the period September to April. It can however reach 2000-3,000 mm in the wetter areas of the Olympic Peninsula. Throughout the summer, rainfall is negligable. Frequent fog and low clouds help to make up any deficit during this period (Franklin, 1973). The length of the growing season ranges from 300 days in southern Oregon to 140 days in Alaska (Fletcher, 1976).

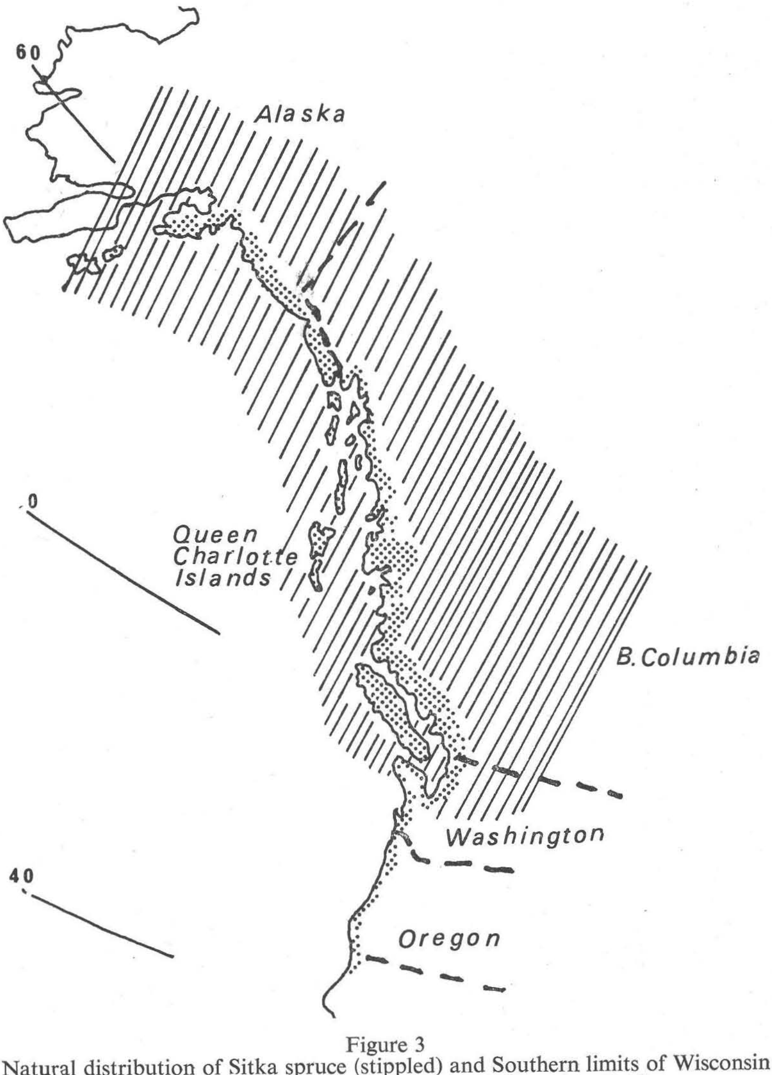

Figure 3
Natural distribution of Sitka spruce (stippled) and Southern limits of Wisconsin Glaciation (hatched). (Fowells, 1965; Daubenmire, 1968).

Soils

On account of its narrow distribution, the soils on which Sitka spruce is found are rather similar in development. These soils usually have a high organic matter content reaching 20% in the upper horizons.

Best growth is to be found on alluvial soils with a relatively high nutrient status. Where drainage is impeded growth is restricted. Day (1957) found on Queen Charlotte Islands that the best growth was on well drained soils allowing maximum root development. Competing species were suppressed on these site types. On less fertile sites the opposite was the case. In the northern part of its distribution the species is found on coarse textured thin soils while to the south it is restricted to alluvial soils or sandy bottoms along streams (Fowells, 1965).

Associated Species

Pure stands of Sitka spruce are found only where disturbance has taken place. Under more stable conditions it is commonly associated with western hemlock (*Tsuga heterophylla*). The proportion of each species varies according to the region. In Alaska, Sitka spruce represents 20% of the spruce-hemlock forest, while in Oregon it represents up to 80%. It is also found in association with western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), red alder (*Alnus rubra*), redwood (*Sequoiadendron sempervirens*) and Lodgepole pine (*Pinus contorta*). The only spruce with which it is associated is white spruce (*P. glauca*) with which it is known to hybridise along the Skeena river valley, British Columbia and in Alaska (Fowells, 1965; Roche, 1969).

Growth

In its native habitat Sitka spruce is a vigorous fast growing tree which reaches its maximum development on the west side of the Olympic peninsula, Washington and north Oregon coast. In this region maximum volume production is found in stands of mixed spruce hemlock with a mean annual increment of 11.9m^3 per hectare at 80 years. The tallest tree, located in Washington, when measured was 5 m. in diameter and 87 m. in height. In Alaska, the largest old growth tree measured was 2.4 m. in diameter. Growth in younger stands is in the region of 24 m. in height and 24 cm. in diameter (Fowells, 1965; Ruth, 1964).

Discovery

Discovery of the species is accredited to the Scottish naturalist Archibald Menzies who sailed as surgeon on the Discovery captained by George Vancouver. It was during the voyage of 1792 that he first identified the species in Admirality Inlet on Puget Sound, Washington (Fletcher, 1976). The first introduction to these islands was in 1831 by David Douglas who named it *Abies menziesii* in 1833 in honour of the discoverer (Veitch, 1881). It, however, had also been discovered by Mertens on Sitka island now Baranof Island Alaska, and described by Bongard as *Pinus sitchensis* in 1832. Following reclassification of the genus to Picea by Carriere in 1855 this has become the accepted name of the species. (Burley, 1965) Some of the plants raised from the David Douglas collection were reputed to have been sent to Curraghmore estate, Co. Waterford (Mitchell, 1972).

Since its first introduction to Europe, Sitka spruce has been planted extensively outside its natural range. A high percentage of

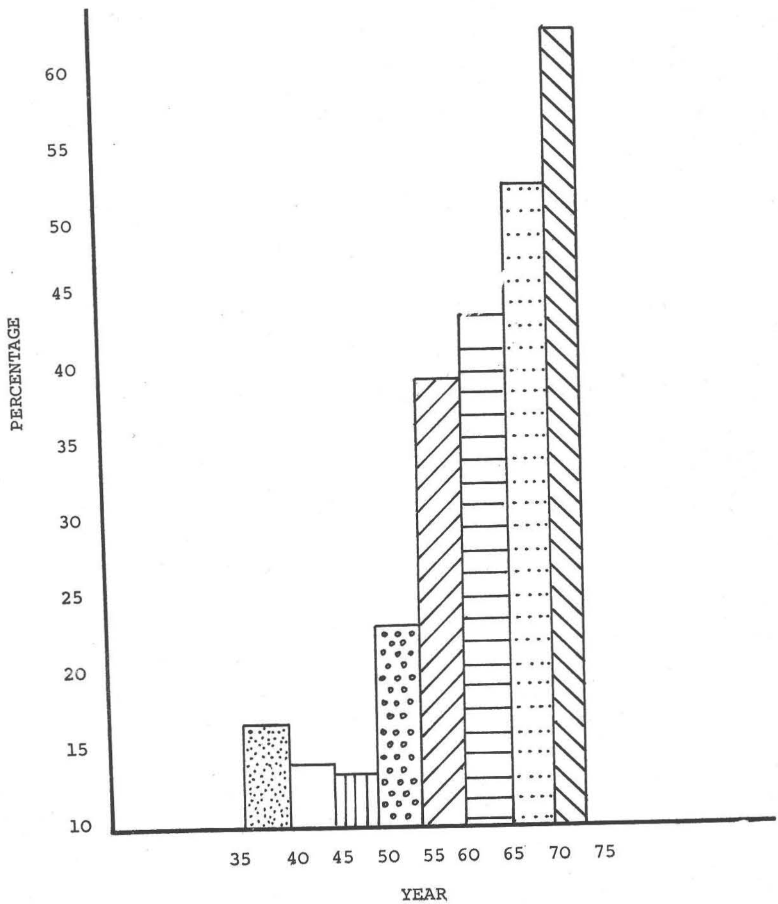

Figure 4

Percentage land area planted with Sitka spruce.

the annual planting programme in Ireland and Britain is composed of Sitka spruce (Figure 4). In continental Europe, Sitka spruce is a species of moderate importance in Denmark, Norway, Germany, Netherlands, Belgium and France. In the southern hemisphere, it is only of minor importance, in New Zealand and Australia.

Genetic Variation

During the glacial period the northern arm of the species distribution would have been subject to severe selection pressure which would have favoured biotypes tolerant to low temperatures. The effect of this would have been to greatly deplete the gene pool. The southern arm of the species distribution would not have been subjected to similar selection pressures and would have evolved under quite different ecological conditions.

Though the species has a considerable natural distribution, study of the species s variation has been carried on outside its natural range—mainly in Europe.

Seed Characteristics

Differences in seed weight have been recorded between provenances with those from Alaska being the heaviest. These differences do not confer any enhanced vigour to the developing seedling nor are they in any way correlated with latitude. Differences in seed length, but not seed width, also occur between provenances but these do not follow any set pattern (Aldhous, 1962; Burley, 1966; O'Driscoll, 1976a).

Variation within seed parameters is greatest among the Washington, Oregon and Lower Skeena Valley provenances (Illingworth, 1976). The former is probably due to the inherent genetic variability undisturbed since earliest times and the latter due to introgression with white spruce (*P. glauca*).

Patterns of variation in germination rate do exist between provenances but these differences are not correlated with any of the seed parameters or latitude. Germination capacity also varies between provenances, those from northern and outer coast provenances being poorest. This characteristic, allied with slow germination rate, could be used as a measure of fitness, as those with poor germination rate and capacity would not be likely to colonise a new site. Cotyledon number has been found to vary from 3 to 8 with a general mean of 5. Within provenance, the number can vary over entire range. This characteristic is therefore of little value in the identification of different provenances (O'Driscoll, 1976a).

Growth

Experiments have shown that the pattern of variation in height growth follows a geographic gradient, though evidence of some ecotypic variation has been found in provenances from Alaska (Burley, 1966). Generally, the pattern of growth in Ireland is such that with decreasing latitude there is an increase in height growth. (O'Driscoll, 1972, 1976a). An apparent break in this clinal pattern occurs at the Straits of Juan de Fuca separating Vancouver Island and Washington. South of these Straits the clinal pattern is reinstated. Two possible explanations can be given for this break. The Straits form a barrier to effective gene flow between adjacent subpopulations thus giving rise to differentiation at this point (Koski, 1970). The Straits also represent the southern limit of the spread of the Wisconsin ice sheet. Populations to the south have had many more generations in which to evolve and adapt to their environments than have populations to the north. Though variation does occur between provenances in root collar diameter growth at the nursery stage, it does not follow a geographic gradient. Evidence would suggest that it is more under the influence of the environment than under genetic control (O'Driscoll, 1976a).

Morphological Variation

Growing Points: At first sight Sitka spruce do not appear to have the same degree of variation in branch numbers as do pines. Studies within and between provenances are limited. The 1972 IUFRO provenance experiment indicated that the number of growing points was strongly correlated with height growth (O'Driscoll, 1976a). This would seem to imply that the more southerly provenances had more branches. However, these branches would be spread over a greater surface area and branching would in fact appear less dense than their more northerly relatives.

Cone variation

Variation in cone size and length/width ratio of cone scale has been found to be clinal, increasing from north to south (Daubenmire, 1968). A different pattern of variation occurs in the Skeena Valley which suggests that the population here is a hybrid one with white spruce (Roche, 1969).

Phenological Variation

Flushing: Significant differences in time of flushing have been recorded between provenances. The pattern of variation is correlated with latitude of origin but does not follow a geographic gradient. There is some disagreement between the two studies carried out as to which end of the range flushes first. Aldhous (1962) found that Alaskan provenances were the first to flush while the 1972 IUFRO experiment found that the more southern provenances were first (O'Driscoll, 1976b). Generally speaking there is considerable within provenance variation. Northern provenances are also found to flush over a longer period of time. Flushing in Sitka spruce is considered to be predominantly a temperature response (Lines and Mitchell, 1966; O'Driscoll, 1976a).

Cessation of growth: The pattern of variation of cessation of growth is very strongly clinal and this characteristic is very obviously under the control of length of photoperiod. The northern provenances are the first to enter domancy with the more southerly ones the last. This has the effect of making southerly provenances more prone to early Autumn frosts when they are moved to northern climes (Magnesen, 1976). This was very obvious in the IUFRO SS experiment, when all the Oregon provenances suffered frost damage in November 1974. Length of growing season is positively correlated with height, growth, the longer the growing season the better the growth (Kraus and Lines, 1976; O'Driscoll, 1976a).

Wood Characteristics: Considerable differences have been recorded within provenances in wood density, tracheid length, spiral grain and seasoning properties. Jeffers (1959) recorded significant differences in density between four provenances. Few studies, as yet, have been carried out on the between tree within provenance variation. Environmental effects represented 33% of the variation in density in trees from 20 stands in Alaska (Farr, 1972). Site quality differences have been shown to effect density. Sunley (1961) reported that Quality Class 3 stands had a higher density than either Q.C. 1 of Q.C. 2 stands. Incidence of spiral grain was also found to be higher in faster grown trees (Brazier, 1967).

Hybridisation: At only two locations throughout its natural range does Sitka spruce grow in close proximity with another spruce, white spruce (*P. glauca*). In the Skeena river valley it forms a natural hybrid with white spruce. The entire valley is a zone of introgression between the two species (Daubenmire, 1968; Roche, 1969). A hybrid swarm is also considered to exist on the Kenai Peninsula, Alaska where the hybrid *Picea x Lutzii* was first recognized (Little, 1953). Through its ability to hybridise naturally with white spruce, its possible evolutionary path can be traced via the *P. jezoensis* × *P. glauca* cross to China which is considered to be the cradle of all spruces. Successful man-made crosses have been made between Sitka spruce and Norway spruce, Serbian spruce (*P. omorika*), Yeddo spruce (*P. jezoensis*) and Engelman spruce (*P. engelmanii*) (Roche and Fowler, 1975). It can be stated that generally genetic variation in Sitka spruce is of a clinal type though further ecotypic variants to that referred to by Burley (1966) may yet be found.

Practical Implications of Sitka spruce variability

Studies to date in Ireland have shown that none of the metrical parameters of Sitka spruce seed have any worthwhile practical implication. This is in contrast to such species as Douglas fir and Lodgepole pine where large seed size of inland provenances can give an initial boost to seedling growth in the first years. Variability of cotyledon number is not sufficiently definite for specific provenance identification.

When the growth parameters are considered, exploitation of the variability in height growth between provenances offers the most positive response. The recently completed nursery stage of the IUFRO experiment has shown that the further south the seed is collected from within the species distribution the better is the growth. The pattern of variation follows very closely that of an earlier experiment at Killarney, planted in 1960 (Figure 5). Both experiments indicate that the most productive provenances for Irish conditions are from the south Vancouver Island–North Washington region. Traditionally we have imported our Sitka spruce seed from the Queen Charlotte Islands. Experimental evidence shows that

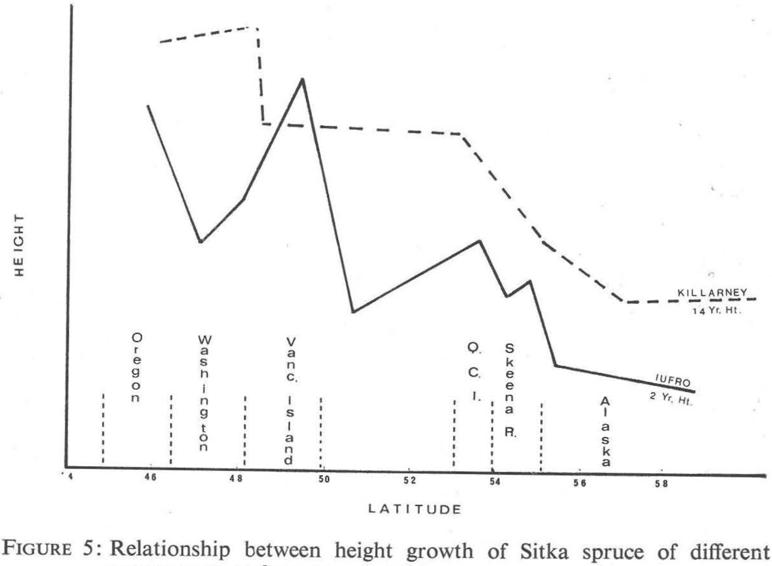

FIGURE 5: Relationship between height growth of Sitka spruce of different provenances at 2 years and at 14 years.

there is a difference of two yield classes between these two regions, 20 for the Queen Charlotte Islands region and 24 for the south Vancouver Island–North Washington region. Over the rotation of the stand this would mean a difference in yield of 198 m^3 which is equivalent to an estimated £1,980. Of the 97,000 hectares planted up to 1972 with Sitka spruce approximately 30% have been planted with seed from *known* Vancouver Island–North Washington provenances. This implies that the production in the remaining 64,000 hectares is below the optimum level and that it could have been increased appreciably by choice of correct provenance or by use of home collected lots from stands of proven quality. Home collected lots were however not available in any quanity up to 1972.

Further increase in growth could be achieved by using still more southerly provenances. These provenances however have the major drawback in that they are more susceptible to early autumn frost. Provenances which do not cease growth by mid September are particularly prone to such damage. Experimental evidence has shown that provenances from South Washington and further south are more liable to early frost damage because of their extended growing season. Optimum length of growing season would appear to occur in these provenances from Vancouver Island–North Washington region.

Sitka spruce is also susceptible to late Spring frost. Here provenance choice offers few options. It has been found that most provenances flush in or about the same time. Though northern provenances flush slightly later the difference is so insignificant to be not worth pursuing. Any improvement in this characteristic would be gained by exploiting between tree within provenance differences where these are proven to be worthwhile.

Branching habit in Sitka spruce follows no distinct pattern by provenance as is found with Lodgepole pine. In fact all provenances appear to exhibit the complete range of branching types. If improvement is to be gained in this characteristic it will be best achieved by the selection of individual trees with definite whorls within the chosen provenances. These can then be placed in a seed orchard to produce progeny with the desirable branch format.

Though the main objective in the exploitation of the genetic variability of Sitka spruce would appear to be that of increased growth, the end product must not be forgotten. There is a danger of a reduction in density with increased vigour. This would have an adverse affect on the strength properties, pulp yields and pulp and paper qualities of the end product (Harris, 1970). Further study may reveal considerable variation in density between trees in fast growing provenances. This will allow the selection of these higher density trees for further propagation and the establishment of a specific orchard for the production of high density reproductive material.

Tracheid length on the other hand was not influenced by vigour and so would not be affective by choice of vigorously growing provenances. Improvement would be best achieved by exploiting between tree within provenance variation. It is therefore, very important at all times to consider the end product when planning to exploit the genetic variability of Sitka spruce.

References

Brazier, J. D. 1967. Timber improvement, I. A. study of the variation in wood characteristics in young Sitka spruce. Forestry **40,** 117-128.

Burley, J. 1965. Genetic variation in *Picea sitchensis* (Bong.) Carr. A literature review. Comm. Forestry Rev. **44,** 47-58.

Burley, J. 1966. Genetic variation in seedling development of Sitka spruce *P. sitchensis* (Bong.) Carr. Forestry **39,** 68.94.

Daubenmire, R. 1968. Some geographic variations in *Picea sitchensis* and their ecological interpretation. Canad. J. of Bot. **46,** 787-797.

Day, W. R. 1957. Sitka spruce in British Columbia, Bulletin, 28, For. Comm., Lond.

Farr, Wilbur, A. 1972. Specific gravity of Western Hemlock and Sitka spruce in South East Alaska, Wood Sci. **6,** 9-13.

Fletcher, R. 1976. Seed collection in north-west America with particular reference to a Sitka spruce seed collected for provenance research. IUFRO Sitka spruce International Ten Provenance Experiment—Nursery Stage Results, pp. 4-20. Forest and Wildlife Service, Dublin, Ireland.

Fowells, H. A. 1965. Silvics of Forest Trees of the United States U.S.D.A. Forest Service Agriculture Handbook 271.

Franklin, J. and Dryness, C. T. 1973. Natural Vegetation of Oregon and Washington. U.S. Forest Service General Technical Report PNW8.

Harrish, A. S. and Ruth, Robert, H. 1970. Sitka spruce a bibliography with abstracts. U.S.D.A. Forest Service Research Paper PNW 105.

Harris, J. Madden 1970. Breeding to improve wood quality. Unasylva **24,** 32-36.

Heusser, Calvin J. 1952. Nunatak flora of the Juneau Ice Field, Alaska. Torrey Bot. Club. Bull. **81** (3).

Illingworth, K. 1976. Sitka spruce International Ten Provenance Experiment in British Columbia. Phase I and II (nursery) results. IUFRO Sitka spruce International Ten Provenance Experiment—Nursery Stage Results, pp. 280-289. Forest and Wildlife Service, Dublin, Ireland.

Jeffers, J. N. R. 1959. Regression models of variation in specific gravity in four provenances of Sitka spruce. Journal Instit. Wood Sci. **4,** 44-59.

Koski, V. 1970. Study of pollen dispersal as a mechanism of gene flow in conifers. Communicationes Institute Forestalis Fennica.

Kraus, J. and Lines, R. 1976. Patterns of shoot growth, growth cessation and bud set in a nursery test of Sitka spruce provenances. Scot. For. **30,** 16-24.

Li Hui-Lin 1952. Present distribution and habitats of conifers and taxada. Evolution. **7,** 245-261.

Lines, R. and Mitchell, A. F. 1966. Differences in Phenology of Sitka spruce provenances. Report on Forest Research for year ended March 1965, Forestry Commission, London, pp. 173-184.

Little, E. L. Jr 1953. A natural hybrid in Alaska. J. For. **51,** 745-747.

Magnesen, S. 1976. The International Sitka spruce ten provenance experiment in West Norway—nursery results. IUFRO Sitka spruce International Ten Provenance Experiment—Nursery Stage Results Report, pp. 218-236, Forest and Wildlife Service, Dublin, Ireland.

Mitchell, A. F. 1972. Conifers in the British Isles. Booklet 33. For. Comm., Lond.

O'Driscoll, J. 1972. Sitka spruce provenances. Forest Research Review, Forest and Wildlife Service, Dublin, Ireland, pp. 12-20.

O'Driscoll, J. 1976a. Sitka spruce International Ten Provenances Experiment Nursery Stage Results in Ireland. IUFRO Sitka spruce International Ten Provenance Experiment—Nursery Stage Results Report, pp. 142-163. Forest and Wildlife Service, Dublin, Ireland.

O'Driscoll, J. 1976b. IUFRO Sitka spruce International Ten Provenancc Experiment—Nursery Stage Results Report. Forest and Wildlife Service, Dublin, Ireland.

Roche, L. 1969. A genecological study of the genus Picea in British Columbia. New Phytol. **68**, 504-554.

Roche, L. and Fowler, D. P. 1975. Genetics of Sitka spruce. USDA Forest Service Research Paper WO 26.

Ruth, Robert H. 1964. Silviculture of the coastal Sitka spruce/Western hemlock type. Proceedings of the Society of American Forestels, Denver, Colorado, pp. 32-36.

Sunley, J. P. and Lavers, G. M. 1961. Variation in the strength and specific gravity)of Sitka spruce grown in Great Britain. J. Inst. Wood Sc. London **7**, 15-27.

Veitch, J. 1881. A Manual of the Coniferae.

Wright, J. 1955. Species crossability in spruce in relation to distribution and taxonomy. For. Sci. **1**, 319-349.

Wright, J. 1976. Introduction to Forest Genetics.