SECTION 5
SITKA SPRUCE (*PICEA SITCHENSIS* (BONG.) CARR.)

1. General Information

This consensus document addresses the biology of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Sitka spruce is an ecologically important species of the north temperate coastal rain forest of western North America. It is a valuable species for both pulp and lumber. Its wood offers unique qualities for manufacture of the highest quality sounding boards and tops for many musical instruments. As well, an outstanding strength-to-weight ratio made Sitka spruce strategically important during both World Wars for construction of aircraft (Brazier, 1987). While its natural range is not extensive and the species' economic importance ranks far below that of other western conifers, it is a keystone species in some of the most productive ecosystems of North America, particularly in the Queen Charlotte Islands of British Columbia (Peterson *et al*., 1997). Outside its natural range, Sitka spruce has played an important role in plantation forestry, particularly in Northern Europe (Hermann, 1987). In Great Britain, the species now accounts for almost 70% of the annual conifer planting stock (Malcolm, 1997) and plantations cover over 20% of the forest/woodland area (Cannell and Milne, 1995). Sitka spruce is also a primary plantation species in Brittany, where productivity of stands is similar to that in Britain (Vaudelet, 1982; Serrière-Chadoeuf, 1986; Guyon, 1995).

The general biology of Sitka spruce is described in the context of the species' role in natural forests and its domestication in planted stands. Taxonomic and evolutionary relationships with other *Picea* species are described. Reproductive biology is described with a focus on aspects of mating system, gene flow, seed production and natural stand establishment. The current knowledge of genetic variation within the species is reviewed, highlighting the importance of variation patterns and the potential for improvement by means of recurrent selection breeding strategies. Biological diversity and ecological interactions with higher and lower flora and fauna are discussed. Domestication and operational breeding activities are reviewed. While Sitka spruce reforestation is currently based on seed propagation, vegetative propagation of rooted cuttings is well advanced, and somatic-embryogenesis techniques are available making it a logical target for implementation of transgenic biotechnologies and the use of cloning in both breeding and deployment strategies.

This document was prepared by the lead country, Canada. It is intended for use by regulatory authorities and others who have a responsibility for conducting assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of this species.

2. Taxonomy and Natural Distribution

A. Taxonomy and nomenclature

Sitka spruce (*épinette Sitka* in French Canada, *épicéa Sitka* in France, *Sitkafichte* in Germany) is one of about 40 species of the genus *Picea* A. Dietr. (family Pinaceae) distributed throughout the cooler parts of the North Temperate Zone and higher elevations in the south. It is also one of 7 species native to North America and 5 native to Canada (Farrar, 1995). There is lack of agreement among taxonomists regarding the subdivision of the genus *Picea* (Schmidt-Vogt, 1977). Most early taxonomists suggested dividing the genus into three sections: Eupicea (or Morinda), Casicta, and Omorika. Mikkola (1969) recommended recognition of only two sections: Abies and Omorika. After extensive crossability studies, Fowler (1983, 1987) has suggested that the section Omorika be further divided into two subsections: Omorikoides and Glaucoides, with Sitka spruce assigned to the latter, together with White Spruce and Engelmann spruce.

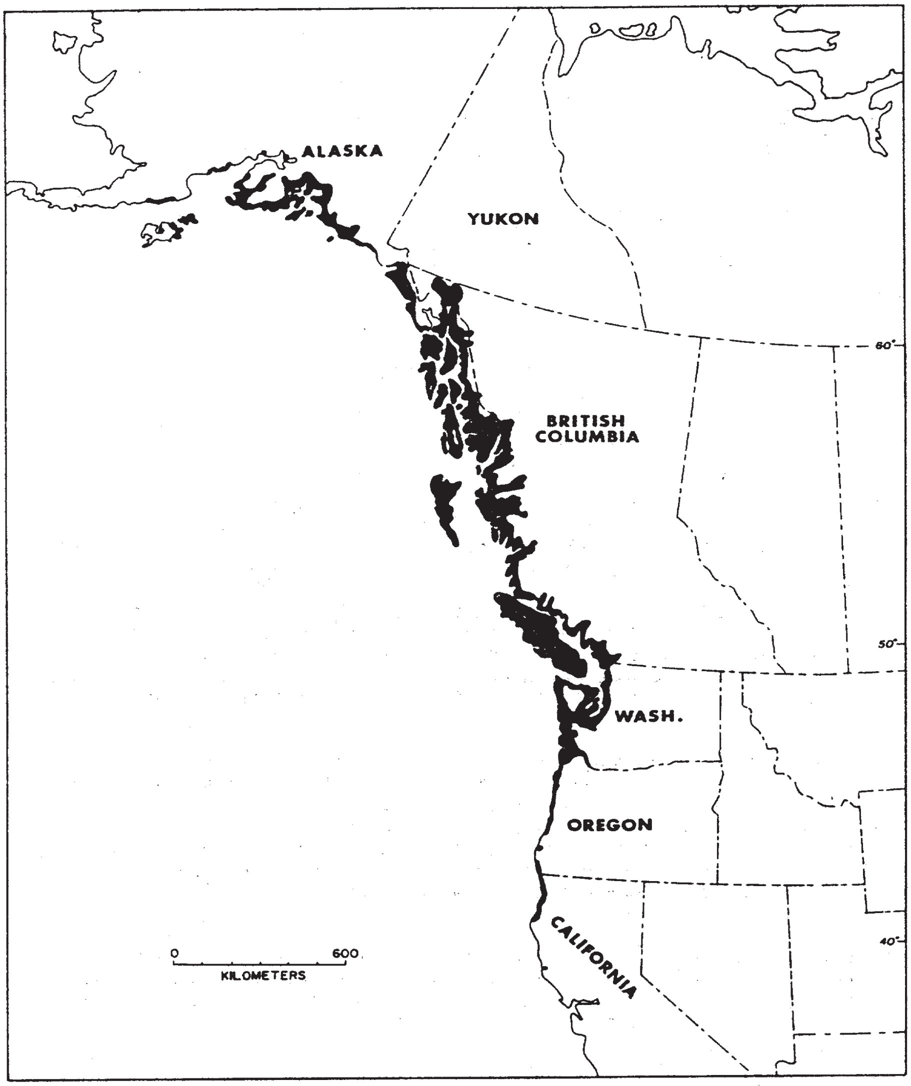
Originally introduced to Great Britain by David Douglas in the early 1800s as *Pinus menziesii*, the species was described soon after by the French botanist Bongard as *Pinus sitchensis*, referring to the origin of his specimens, Sitka Island, Alaska (now known as Baranoff Island) (Peterson *et al*., 1997). Carrière later recognised the species as a member of genus *Picea*, and the species is now well recognised as *Picea sitchensis* (Bong.) Carr. Common names are numerous, including airplane spruce, coast spruce, Menzies spruce, silver spruce, tideland spruce, western spruce, and yellow spruce. A famous rare mutant form found on the Queen Charlottes is known as golden spruce (Peterson *et al*., 1997).

Introgressive hybridisation between Sitka and White Spruce (*Picea glauca* (Moench) Voss) occurs in sympatric areas in north-western British Columbia and Alaska, with the hybrid known as *Picea* × *lutzii* Little (Little, 1953; Daubenmire, 1968; Roche, 1969; Hanover and Wilkinson, 1970; Copes and Beckwith, 1977; Yeh and Arnott, 1986; Woods, 1988). Introgressive hybridisation between white and Englemann spruce (*Picea englemannii* Parry ex Engelm.) is common where the two are sympatric in western Canada, Montana and Wyoming, and the hybrids have given rise to the variety *Picea glauca* var. *albertiana* (S. Brown) Sarg., commonly known as "interior spruce" (Roche, 1969; Roche *et al*., 1969; Daubenmire, 1974). Sitka spruce hybridises with Englemann spruce through controlled crosses (Johnson, 1939; Roche, 1969; Jeffers, 1971; Fowler and Roche, 1977; Kiss, 1989), and there is evidence suggesting that hybrids among Sitka, white and interior spruce also occur naturally (Woods, 1988; Sutton *et al*., 1991a, b, 1994; Coates *et al*., 1994; Grossnickle *et al*., 1996a, b). Several horticultural varieties, most of them dwarf phenotypes, have been recognised (Krüssmann, 1985; Griffiths, 1994).

B Natural distribution

The natural range of Sitka spruce spans a narrow strip on the north Pacific coast of North America, extending for 2 900 km from 61°N latitude in south-central Alaska to 39°N in northern California. Throughout this tremendous north-south range, Sitka spruce is a coastal species, occupying islands of the Alexander Archipelago in Alaska and the Queen Charlotte Islands in British Columbia, and, with the exception of river valleys, they rarely reach more than a few kilometers from the coast along a narrow mainland strip. The southern limit of the species is an isolated population in Mendocino County, California (Harris, 1978). The natural range of Sitka spruce is illustrated in the map given in Figure 3.5.

Figure 3.5 The natural range of Sitka spruce



Source : Harris, 1978

C. Evolution and migrational history

Conifers probably originated around the periphery of the north Pacific basin (Li, 1953). Fossil records indicate that divergence of modern genera in Pinaceae occurred some 135 million years ago during the late Jurassic or early Cretaceous period (Florin, 1963). Based on comparative immunological studies, Prager *et al.* (1976) have suggested that *Picea* was among the first genera to emerge. Although not supported by fossil evidence, Wright (1955) suggested eastern Asia as the likely origin of *Picea*, based on the abundance of species and particularly the presence of *Picea koyamai* Shirasawa, which he felt was a primitive species. *Picea* is then thought to have migrated to North American in one or more waves of migration via a land bridge between Siberia and Alaska (Wright, 1955).

Phylogenetic relationships within coniferous genera are commonly interpreted from species crossability studies, where it is assumed that the more related are two species, the more easily they can be crossed (Wright, 1955; Critchfield, 1975). The close phylogenetic relationship between the north-western American “white” spruces (Sitka, white, and Engelmann spruce) and the eastern Asiatic *Picea jezoensis* (Sieb et Zucc.) Carr. (Wright, 1955; Roche and Fowler, 1975) supports this theory, at least for the members of the subsection Glaucoides in section Omorika, and suggests that speciation occurred after their arrival in North America.

The fossil record of *Picea* during the Pleistocene era in North America is incomplete, but it is believed that many conifer populations were fragmented and isolated in various refugia during the glacial period (Critchfield, 1984). Sitka spruce probably occupied roughly its present-day range before glaciation, surviving at higher elevations on hills and mountains, and reoccupying lower areas of the long coastal strip in British Columbia and Alaska soon after (Daubenmire, 1968; Page and Hollands, 1987).

3. Reproductive Biology

A. Reproductive development

Sitka spruce is monoecious. Development of the reproductive structures follows a 2-year cycle typical of most conifers in the northern hemisphere, other than *Pinus* species and members of the Cupressaceae family (Owens and Blake, 1985). Bud scales are initiated at the terminal apex and at newly initiated axillary apices within the enlarging vegetative buds, from about mid-April (Owens and Molder, 1976a; Cannell and Bowler, 1978). Apices differentiate as vegetative, pollen cone, or seed cone buds around mid-July, at the cessation of shoot elongation. Pollen cones typically develop from small axillary apices on vigorous distal shoots or terminal apices on less vigorous, proximal shoots. Seed cones usually develop on distal axillary positions on vigorous shoots or from smaller terminal apices on less vigorous shoots (Moir and Fox, 1975a; Owens and Molder, 1976b).

Pollen cone bud development is complete, although meiosis has not occurred before they become dormant at the end of October. Seed cones also do not undergo meiosis prior to becoming dormant in late November (Owens and Molder, 1976b). By the time buds become dormant, all microsporophylls, microsporangia, bracts and functional ovuliferous scales, and leaves have been initiated. The overwintering seed cone, pollen cone, and vegetative buds are small and similar in shape: broadly conical, greenish-brown and covered in a bloom of light grey resin (Moir and Fox, 1975a; Eis and Craigdallie, 1981).

Reproductive and vegetative buds break dormancy at about the same time, in response to photoperiod, while subsequent development is regulated by temperature. Meiosis and subsequent development of pollen occur immediately, followed by maturation of the megagametophyte (Moir and Fox, 1975b; Owens and Molder, 1980). Flushing of reproductive buds precedes that of vegetative buds, and pollen is released over a one-week period, in late-April on Vancouver Island (Owens and Molder, 1980) and by mid-May in Scotland (Moir and Fox, 1975a). The pollen enters receptive seed cones and adheres to the sticky micropylar arms. A week later, a "pollination drop" draws the pollen into the micropyle (Owens and Blake, 1984). Fertilisation occurs 4 to 5 weeks later, and embryo development is completed in mid-August. Without fertilisation, no embryo is formed and the megagametophyte tissue degenerates, leaving a normal-sized, but empty seed (Owens and Molder, 1980).

B. Mating system and gene flow

Sitka spruce is a wind-pollinated, monoecious species, and outcrossing is by far the most prevalent mating system (Cottrell and White, 1995). Self pollination occurs to some degree, as the period of pollen release and female receptivity coincide for an individual tree (Owens and Molder, 1980; El-Kassaby and

Reynolds 1990). Female strobili are usually found at the ends of primary branches in the mid- to upper-crown, while males are more prevalent at the ends of secondary branches lower in the crown (Tompsett, 1978; Philipson, 1997), although the effectiveness of this zonation against selfing is questionable (Nienstaedt and Teich, 1972). In the open-grown conditions in a seed orchard, the outcrossing rate was greatly reduced for seeds produced in the lower crown (Chaisurisri *et al.*, 1994). The two-step pollination mechanism, whereby pollen is collected in the sticky micropyllar arms over the receptive period, and only then drawn *en masse* by the pollination drop, ensures that pollen from many sources has a chance to fertilise any given ovule (Owens and Blake, 1984; Runions *et al.*, 1995).

Gene flow in *Picea* is mediated by small pollen grains, 70-85 µm at their widest point (Eisenhut, 1961), whose bladdery wings make them well-adapted for aerial transport (Di-Giovanni and Kevan, 1991). Various studies of pollen dispersal in conifers indicate that over 90% of the pollen comes to rest less than 100 m from the source (Wright, 1976). Nevertheless, conifer pollen may remain viable for several days and a substantial quantity may travel great distances (Lindgren *et al.*, 1995; Lindgren and Lindgren, 1996). Gregory (1973) cites reports that pollen of *Pinus* and *Picea* may travel as far as 600 to 1 000 km, and several authors have concluded that isolation distances of less than 1 km often have little impact on contamination rates in conifer seed orchards (see review by Di-Giovanni and Kevan, 1991). While pollen dynamics are not well known in Sitka spruce, a recent study of pollen dispersal dynamics in a black spruce seed orchard indicated that "large amounts" of pollen rose to a height of 300 m above ground level (Di-Giovanni *et al.* 1996). At a steady wind speed of 5 $m \cdot s^{-1}$, the authors calculated that spruce pollen reaching this altitude would drift about 47 km.

C. Seed production

Sitka spruce begins to produce seed at 20 to 25 years of age, with heavy crops occurring at intervals of 3 to 5 years (Malcolm, 1987; Philipson, 1987b). Crop intervals are somewhat longer, 5 to 8 years, in the northern part of the range (Harris, 1969). It is a prolific seed producer and, in a good seed year, an old-growth stand may produce as much as 14.5 kg of seed per hectare (Peterson *et al.*, 1997). The seeds themselves are small, and average cleaned seed weight is about 2.2 g/1000 seeds (Safford, 1974).

Initiation and duration of seed dispersal are weather and site dependent. The mature cones open as they lose moisture and the scales flex in dry weather, re-closing during wet periods. Seed dispersal begins in the fall, with over 70% of the seeds dispersed within the first 6 weeks, 90% by February, and the remainder released over the next growing season (Ruth, 1958; Harris, 1969). The seeds are winged and wind-dispersed. The actual distance reached from the source depends on several factors, including height and position of the seed source, local topography and wind conditions (Harris, 1967, 1978). While 80% of the seed usually falls within 30 metres the parent tree, some may travel up to several hundred metres (Mair, 1973).

D. Natural regeneration

Sitka spruce seeds exhibit weak dormancy, and both the rate and total amount of germination can be increased by exposure to low temperatures under moist conditions, *i.e.*, cold stratification (Pintaric, 1972; Gordon *et al.*, 1976; Gosling, 1988; Chaisurisri *et al.*, 1992; Jinks and Jones, 1996). While not always employed in nursery practice, moist-chilling of Sitka spruce seed is often beneficial, particularly when moisture content and temperature are carefully controlled (Gosling and Rigg, 1990; Jones *et al.*, 1993; Jones and Gosling, 1994), and stratified seed will tolerate redrying (Jones and Gosling, 1990; Jinks and Jones, 1996; Poulsen, 1996). In the wild, Sitka spruce seeds normally germinate the following spring, as soon as soil surface temperatures are warm enough and provided there is adequate moisture.

Unlike its highly shade tolerant associates western hemlock and western red cedar that can germinate and survive on organic seedbeds, Sitka spruce is more restricted in its seedbed and light requirements and tends to be more disturbance dependent (Taylor, A.H., 1990; Peterson *et al*., 1997). Sitka spruce regenerates naturally on landslides, newly exposed alluvial sites, and openings created by windthrow. Regeneration cutting systems in Sitka spruce must generate sufficient ground exposure and disturbance, by clear cutting, shelterwood or seed-tree methods (Harris and Johnson, 1983; Weetman and Vyse, 1990). Regarding thinning operations in mixed western hemlock, Sitka spruce stands will normally favour regeneration of the hemlock over the spruce, particularly in older stands where thinning intensity is light (Deal and Farr, 1994). Dense natural regeneration has been more commonly observed after harvesting of first-generation planted stands in Britain, with up to several hundreds of thousands per hectare and requiring spacing (Nelson, 1991; Adam and Berg, 1996).

E. Vegetative reproduction in nature

Vegetative reproduction of Sitka spruce is rare under natural conditions or in plantations, although layering can occur on moist sites (Cooper, 1931; Roche and Fowler, 1975). Rooting is most likely to occur when lower branches of open-grown trees come in contact with the ground and become covered by soil or organic materials on the edges of bogs or near the timber line (Harris, 1978).

4. Crosses

Potential crosses with Sitka spruce are summarised in Table 3.7. Natural hybrids between Sitka and White Spruce were first collected in North America by H.J. Lutz on the Kenai Peninsula, Alaska, and given the name *Picea* × *lutzii* by E.L. Little (1953). Before this, white-Sitka spruce hybrids had been observed in Denmark as a result of natural crossing between adjacent plantations (Thaarup, 1945; Bornebusch, 1946). Populations resulting from introgressive hybridisation have since been documented in the Skeena, Nass, and Bulkley river valleys in British Columbia where the two species are sympatric (Daubenmire, 1968; Roche, 1969). The hybrid has frequently been made artificially with parents from outside the sympatric area (Fowler, 1987), often in the hope of imparting the resistance of White Spruce to the white pine weevil. The degree of cold hardiness of the hybrid is related to the proportion of White Spruce germplasm (Ying and Morgenstern, 1982), and growth performance of the hybrid depends greatly on the origin of the parents (Sheppard and Cannell, 1985). Though *Picea breweriana* and *Picea sitchensis* can cross successfully, *P. breweriana* has a very small range that is rarely, if ever, sympatric with *P. sitchensis* given that the populations are separated by elevation. The category of "easily crossed, probably occurring naturally" indicates species that readily cross with *P. sitchensis* if grown together in artificial plantations, but are not naturally sympatric.

Table 3.7 Species cross compatibility with Sitka spruce

Species	Origin	References
Commonly occurring in sympatric range		
P. glauca (Moench) Voss.= *Picea* × *lutzii* Little	Canada, Northeast USA	Daubenmire, 1968; Roche, 1969; Fowler,1987; Woods, 1988
Easily crossed, probably occurring naturally		
P. englemannii Parry ex Engelm.	Canada, Western USA	Johnson, L.P.V. 1939; Roche, 1969; Jeffers, 1971; Fowler and Roche, 1977; Kiss, 1989
P. breweriana Wats.	Northwest USA	Langner 1952
P. mariana (Mill.) B.S.P.	Canada, Northern USA	Fowler, 1983
Successful crosses		
P. jezoensis (Sieb. & Zucc.) Carr.	Japan	Wright, 1955; Roulund, 1969
P. omorika (Pancic) Purkyne	Western Serbia, Eastern Bosnia	Johnson, 1939; Langner, 1959; Roulund, 1971; Geburek and Krusche, 1985
Possible crossability		
P. abies (L.) Karst (=*P. excelsa* (Lam.) Link)	Northern, Central, Eastern Europe	Langner, 1952
P. likiangensis (Franch.) Pritz.	China	Roche and Fowler, 1975
P. pungens Engelm.	Western USA	Roche and Fowler, 1975
P. wilsonii Mast.	China	Roulund, 1969

5. Genetics

A. Cytology

Sitka spruce vegetative cells normally have $2n = 24$ chromosomes (Burley, 1965b; Fox, 1987), although some trees exhibit a small 13th pair (Moir and Fox, 1972; Kean *et al*., 1982). These supernumerary or B-chromosomes seem to be restricted to provenances in the southern half of the species range (Moir and Fox, 1977), but have not been associated with any detectable effect on growth (Moir and Fox, 1976).

B. Genetic variation

Population-level variability

Before 1970, information on population variation of Sitka spruce was only available from small studies with limited sampling. Even in these first limited trials, there was strong evidence of clinal variation for many traits, associated with latitude, elevation, and distance from the coast (Burley, 1965a; Roche and Fowler, 1975). In 1969/70, an extensive sampling of seed sources from across the entire range was organised by the International Union of Forest Research Organizations (IUFRO). Ten of these sources were widely planted in field tests in North America and many European countries (O'Driscoll, 1978).

Clinal variation patterns are expressed for phenological traits such as cessation of growth (Lines and Mitchell, 1966; Pollard *et al*., 1975; Kraus and Lines, 1976), and is greater among provenances than within

(Falkenhagen, 1977; Deleporte, 1984). Southern coastal provenances produce up to 100% more height growth than northern inland sources (Cannell, 1974; Cannell and Willett, 1975; Cannell and Willet, 1976). While southern sources grow faster, they are more susceptible to frost damage, particularly in the nursery (Magnesen, 1986; Lines, 1987b; McKay, 1994). Provenance trials in the former Federal Republic of Germany showed a north-south trend in growth, with latitude accounting for over 80% of the among-provenance variation (Kleinschmit, 1984). Results of a 19 year provenance trial in Ireland demonstrated that the most productive provenances of Sitka Spruce for the mild, coastal conditions in Ireland originated from southern Washington and northern Oregon (Thompson and Pfeifer, 1995).

Ecotypic variation related to bioclimatic and physiographic factors has been demonstrated among provenances for seed and cone traits (Falkenhagen, 1978; Falkenhagen and Nash, 1978). Even for growth traits that normally exhibit clinal variation patterns, substantial variation may be present at the microgeographic level, attributable to such local site factors as slope and aspect (Campbell *et al*., 1989). Variation in biochemical composition appears to be clinal for sources from Alaska to north Washington, while more southerly sources show no geographic trends, perhaps reflecting the post-glacial recolonisation of northern parts of the range (Forrest, 1975b, 1980; Wellendorf and Kaufmann, 1977).

Population differences have also been demonstrated for susceptibility to insect attack. Provenances from Kitwamga (inland Skeena River) and Big Qualicum (SE Vancouver Island) suffer less damage from the white pine weevil (Alfaro and Ying, 1990; Tomlin and Borden, 1994; Ying and Ebata, 1994). Density of green spruce aphids attacking a provenance test in northern Ireland was related to latitude of seed origin, with southern provenances especially susceptible (Day, 1984). Lignified stone cell masses in spruce bark are considered an important physical defence against insects and fungi, and there is a clinal increase in bark lignin with increasing latitude of provenance origin (Wainhouse and Ashburner, 1996).

In contrast to many other characters, geographic variation at polymorphic allozyme loci appears to be weak. In a study of the 10 IUFRO provenances, only 8% of the diversity at polymorphic loci was due to differences among populations, whereas 92% resided within populations (Yeh and El-Kassaby, 1980).

Individual-level variability

While variation among provenances is important in determining the risks and benefits of transferring seed sources, genetic improvement from mass selection relies primarily on variation within-populations as the source of genetic gains. For productivity traits, on average, 40% of the genetic variation for Sitka spruce is at the provenance level, while 60% is within provenance (Fletcher, 1992).

Estimates of narrow-sense heritabilities for height growth during the first six years was around 25% for open-pollinated progeny of randomly selected trees in a single population (Samuel and Johnstone, 1979), while another study estimated heritability at over 40% for height after eight years (Birot and Christophe, 1983). Other quantitative estimates of additive genetic variation in growth traits have also varied widely (Falkenhagen, 1977; Yeh and Rasmussen, 1985; Samuel, 1991), but narrow-sense heritability is normally more than sufficient for individual tree selection and breeding to be effective, particularly when provenance and family performance are combined in a multiple-trait selection index (Christophe and Birot, 1983). Height superiority of individual trees is not necessarily associated with production of "free growth", although progeny of plus-trees have been noted to improve their height rankings over the first six years on better sites by production of free growth (Cannell and Johnstone, 1978).

Perhaps the most precise estimates of genetic variance for Sitka spruce have been reported for a 7-tree diallel cross, planted at two test sites in Scotland and Wales (Samuel *et al*., 1972; Samuel, 1991). In this experiment, genetic variation for height growth, although under some additive genetic control, was predominantly controlled by non-additive effects, whereas diameter was only controlled by additive effects. Practically all the variation in monoterpene composition for these crosses was attributable to additive genetic effects, and reflected the differences in parental means in additive combination with little significant deviation due to specific combining ability or reciprocal effects (Forrest and Samuel, 1988).

The ease of vegetative propagation of Sitka spruce offers opportunities to capture additional gains earlier in the breeding cycle. Clonal selection has been demonstrated to be highly effective in Sitka spruce, for characters such as planting stock phenology, frost resistance (Nielsen and Roulund, 1996), root-growth potential (Deans *et al*., 1992), early height and diameter growth, and branching habit (Cahalan, 1981) . Clonal testing has also demonstrated that it is possible to select clones that combine good growth with high wood density (Costa e Silva *et al*., 1994).

A provenance test in British Columbia demonstrated significant difference in susceptibility to white pine weevil, both among provenances and among families within provenances (Alfaro and Ying, 1990; Ying, 1991). Unfortunately, a study of variation within a resistant provenance found that taller families were more likely to be attacked (Alfaro *et al*., 1993).

Variation in biochemical composition for trees within provenances is high (Forrest, 1975a, b; Wellendorf and Kaufmann, 1977), a trend that is also found for variation at polymorphic enzyme loci (Yeh and El-Kassaby, 1980). While southern provenances are generally less resistant to frost, there is sufficient variation within populations to select frost resistant, fast-growing individuals (Nicoll *et al*,. 1996).

Genotype-environment interactions are of concern to tree breeders who generally seek broad adaptability within bred material. A seedling test of provenances grown under controlled environments found that provenances near the centre of the range were more broadly adapted (Mergen *et al*., 1974). A test of families originating from the latitudinal range of Sitka spruce and planted at eight locations in Britain found highly significant family-site interaction for six-year height, but found that above-average families could be selected that were broadly adapted (Johnstone and Samuel, 1978). A progeny test established at 3 locations in Denmark demonstrated genetic control of growth, stem form, wood density (pilodyn penetration), frost resistance and resistance to aphids, in addition to substantial genotype–environment interaction for growth characters (Jensen *et al*., 1996). Another clonal test in Denmark found that 15% of the clones contributed over 50% of the GE interaction variance (Nielsen and Roulund, 1996).

C. Inbreeding depression and genetic load

Self pollination in Sitka spruce has severe effects on seed set, early growth, and survival (Samuel *et al*., 1972). Among those that survive, strong inbreeding depression continues with selfed individuals only 68% as tall as outcrossed trees at 15 years of age (Samuel, 1991). Inbreeding depression is also exhibited by progeny originating from seed collections in small stands (Phillips, 1984).

D. Breeding programs

Breeding strategies for Sitka spruce generally utilise a system of progeny testing and recurrent selection for generation advancement, combined with clonal seed orchards for production of improved seed. Flowering of Sitka spruce grafts can be stimulated by means of various cultural treatments, particularly those involving gibberellin $A_{4/7}$, and this has facilitated the turnover of breeding cycles (Philipson, 1985a, b, 1987a, 1992; Philipson *et al*., 1990; Ross, 1991; Owens *et al*., 1992). While most seed orchards currently in production were established by grafting cuttings from plus-trees, and their placement in cultivated field environments, some programs have also experimented with the management of containerised Sitka spruce orchards, with the possibility of vegetative multiplication of small quantities of seed by rooted cuttings (John and Mason, 1987; Philipson and Fletcher, 1990).

Breeding programs have been established in all the areas where Sitka spruce is an important plantation species. In British Columbia, where planting of Sitka spruce is severely limited due to risk of damage by the white pine weevil, the breeding plan emphasises weevil resistance. Currently, more than 250 open-pollinated families and 300 clones are included in weevil-resistance screening trials (King, 1994; King *et al*,. 1998). The intensive breeding program in Britain began in the early 70's (Fletcher and Faulkner, 1972), and is by far the most ambitious. From an initial 2 800 plus-tree selections, the breeding population now consists of 200 tested parents, subdivided into sub-populations targeted for different geographic areas (Faulkner, 1987; Fletcher, 1992; Malcolm, 1997). Breeding programs are also carried out in Denmark (Roulund, 1990) and in northern France (Deleporte and Roman-Amat, 1986), where Sitka spruce is an important component of plantation forestry operations.

E. Conservation of genetic resources

Domestication of a key species such as Sitka spruce can influence diversity of genetic resources: (1) indirectly, by the method of seed collection, extraction, and storage, and by nursery and plantation culture; and (2) directly, by intentional selection to increase the frequency of genes for desirable traits (Chaisurisri and El-Kassaby, 1994; Morgenstern, 1996). The inadvertent loss of genes by natural processes and human activity can have negative consequences on the adaptability of populations and the potential for future gains from breeding. The need for gene conservation for a species can be assessed by evaluating (1) its current status of protection, (2) its frequency of occurrence, (3) the extent of its botanical range, (4) ease of natural regeneration, and (5) its representation in genetic testing and breeding programs (Lester, 1996). Using this approach, Yanchuk and Lester (1996) ranked the need of Sitka spruce for gene conservation as higher than some of its associates (Douglas-fir, western red cedar and western hemlock), but lower than others (mountain hemlock, amabilis fir, yellow-cedar and western white pine).

In the case of Sitka spruce, *in situ* conservation of genetic resources is practised by protection of ecological reserves, special areas, and parks (Pollard, 1995), and integrated with domestication activities that control the movement of seed, active management of existing stands to maintain biological diversity, and protection of isolated, small populations (Yanchuk, 1995). *Ex situ* conservation, by cryopreservation of germplasm, by off-site maintenance of populations in arboreta and clone banks, and by multi-population breeding strategies (Eriksson *et al*., 1993; Namkoong, 1995), has been practised to a much lesser extent, although many provenances and families are now represented in field tests and seed bank collections (Edwards and El-Kassaby, 1993). Such "active" forms of gene management must be accelerated in preparation for response to rapid environmental and climate changes (Ledig and Kitzmiller, 1992; Yanchuk and Lester, 1996).

6. Ecology and associated species

A. Habitat

In its natural range, Sitka spruce is primarily a coastal species, but may extend well inland where optimum environmental conditions occur (Harris, 1990). It is primarily a low elevation species and is uncommon at elevations above 500 m. It is, however, much less restricted by edaphic factors than by climate and physiography (Roche and Haddock, 1987).

Climate

The natural range of Sitka spruce is restricted to an area of maritime climate with abundant moisture throughout the year, relatively mild winters and cool summers. Annual precipitation is high throughout the range, but somewhat greater in the north where summer precipitation as light drizzle and fog are frequent. Summer temperatures in these coastal habitats lack the extremes of more continental areas and, while moderated by the ocean current of the north Pacific, decrease northward. Although winters are mild, accumulated heat input varies with latitude and probably accounts for much of the variation in productivity, soil development, and associated species (Harris, 1978).

Soils and site type

While Sitka spruce grows on soil derived from a variety of parent materials, their best development is on deep, moist, well-aerated soils. Growth is poor on swampy sites. Sitka spruce commonly occupies alluvial soils along streams, coarse-textured soils, or soils with a thick accumulation of organic matter. In Alaska, it is a pioneering species on immature soils exposed by glacial retreat or uplift from the sea. Soils in the natural range are acidic, with pH values varying from 4.0 to 5.7 (Harris, 1978).

Sitka spruce is relatively nutrient demanding, particularly at young ages prior to crown closure (Miller and Miller, 1987). It is most productive on nitrogen rich soils, but also requires relatively large amounts of calcium, magnesium and phosphorus (Krajina, 1969). Nitrogen and phosphorus have been found to be limiting on sites in both British Columbia and Britain, and applications of fertilisers may be necessary for successful plantation establishment (McIntosh, 1981, 1983; Miller and Miller, 1987; Taylor, C.M.A., 1990; Taylor and Tabbush, 1990; Prescott and Weetman, 1994).

B. Synecology and associated species

Sitka spruce occurs most commonly in mixed stands, usually associated with western hemlock (*Tsuga heterophylla*) (Harris and Johnson, 1983). Red alder (*Alnus rubra*) and black cottonwood (*Populus trichocarpa*) are associated throughout the range. Other associates vary with latitude: Douglas-fir (*Pseudotsuga menziesii*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), western white pine (*Pinus monticola*), redwood (*Sequoia sempervirens*), and bigleaf maple (*Acer macrophyllum*) are limited to the south; shore pine (*Pinus contorta* var. *contorta*) and western red cedar (*Thjua plicata*) extend into south-east Alaska; while yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and Sitka alder (*Alnus sinuata*) are limited to northern sites and higher elevations in the south (Harris, 1978). In Alaska and the Skeena, Nass, and Bulkley river valleys of British Columbia, Sitka spruce is associated with White Spruce (*Picea glauca*), and hybrid populations are found (Daubenmire, 1968; Roche, 1969). Pure stands of Sitka spruce are common on tidewater areas that receive quantities of salt spray, and in early succession situations following disturbance. Sitka spruce is an aggressive pioneer and, by itself or together with intolerant associates such as alder or cottonwood, will invade landslides, dunes, uplifted beaches and glaciated terrain.

Due to the latitudinal spread of the Sitka spruce range and the variation in precipitation and exposure, the species is a component of several ecological associations, characterised by available moisture and nutrient regimes. On the mid- to upper-slopes of the Queen Charlotte Islands, the western hemlock – Sitka spruce forest is typically associated with Alaska blueberry (*Vaccinium alaskaense*), red huckleberry (*V. parifolium*), ovalleaf huckleberry (*V. ovalifolium*), and several mosses (*Rhytidiadelphus loreus*, *Hylocomium splendens*, and *Mnium glabrescens*). On exposed coastal locations, pure stands of salt-tolerant Sitka spruce are associated with reed grass (*Calamagrostis nutkaensis*), salal (*Gaultheria shallon*) and finger moss (*Stokesiella oregana*). Sheltered alluvial sites find Sitka spruce and its associates western hemlock and red alder on grass meadows with *Trisetum cernum*, *Gymnocarpium dryopteris*, *Hylocomium splendens* and *Leucolepis menziesii* (Roche and Haddock, 1987; Hanley and Hoel, 1996; Hanley and Brady, 1997).

Inland valleys and eastern slopes of coastal mountains tend to be drier. It is on these areas that Sitka spruce is most likely to be sympatric with White Spruce and hybridisation can occur. Within this drier zone, valley bottoms and mountain slopes typically support mixed conifer forests with ground vegetation dominated by Alaska blueberry, ovalleaf huckleberry, red huckleberry, and rustyleaf menziesii (*Menziesia ferruginea*). Devil's club (*Oplopanax horridus*) appears within this zone on fluvial sites of the Skeena and Nass Rivers, and skunk cabbage (*Lysichiton americanum*) and salmonberry (*Rubus spectabilis*) are found on the driest sites in flat areas (Roche and Haddock, 1987; Harris, 1990).

C. Competition and stand structure

While Sitka spruce is rated as tolerant to shade, it is less tolerant than its usual associate, western hemlock (Daniel *et al*., 1979; Minore, 1979; Kobe and Coates, 1997), so that the general successional tendency is toward a western hemlock climax type, although few climax stands proceed to pure hemlock. As Sitka spruce is physically large, long-lived, and able to invade small openings resulting from windthrow, it is commonly maintained as a stand component, even under climax conditions. In south-east Alaska, mixed stands of hemlock and spruce are regarded as the climax stand type, with Sitka spruce regenerating on mineral soil mixtures exposed by windthrow and other disturbance, and hemlock seeding in on organic substrates (Harris, 1990; Deal *et al*., 1991; Peterson *et al*., 1997).

Sitka spruce is one of few conifer species that produce epicormic shoots along the stem. These shoots may originate from either dormant or adventitious buds (Stone and Stone, 1943) in response to light intensity (Isaac, 1940; Herman, 1964). Increasing exposure of stems to sunlight by thinning of stands will stimulate epicormic branching and affect the future quality of the trees (Farr and Harris, 1971).

D. Ecosystem dynamics

Many abiotic factors interact with Sitka spruce in natural and planted forests, and some may cause significant damage. Windthrow is probably the most serious damaging agent, particularly in plantations of Sitka spruce that are established in Great Britain where shallow rooting on unfavourable soils and exposure to strong winds results is risk of instability (Miller, 1986; Coutts and Philipson, 1987; Mason and Quine, 1995; Malcolm, 1997). Elsewhere in Europe, planted Sitka spruce has suffered significant wind damage, but has proven more wind-firm than other conifers such as *Picea abies*, *Abies* spp. and *Pinus sylvestris* in France (de Champs *et al*,. 1983; Touzet, 1983), Denmark (Neckelmann, 1981) and Norway (Lohmander and Helles, 1987). In North America, Sitka spruce is considered less wind-resistant than *Pseudotsuga menziesii* and *Thuja plicata*, but more-so than *Tsuga heterophylla* and *Abies amabilis* (Minore, 1979).

While Sitka spruce is among the least fire-resistant species in coastal forests, wild fires are not a major cause of damage within the native range (Minore, 1979; Agee, 1990). On the other hand, Sitka spruce regeneration benefits rather more from slash burning than several of its conifer associates (Hawkes *et al*., 1990; Otchere-Boateng and Herring, 1990). Frost heaving can cause severe damage, particularly to container seedlings planted on finer-textured soils (Shaw *et al*,. 1987; Goulet, 1995). Autumn frost is a particular problem in Great Britain, where faster-growing southern provenances are particularly susceptible (Redfern and Cannell, 1982; Lines 1987b; Nicoll *et al*,. 1996).

In the following table, other species interactions with Sitka Spruce are shown.

Table 3.8 Species Interactions with Sitka Spruce

Insects	
Common name	**Agent**
White pine weevil [Johnson, 1965; McMullen, 1976; Alfaro, 1982; Martineau, 1984; de Groot, 1985; Wallace and Sullivan, 1985; Hulme, 1986, 1987; McMullen *et al*,. 1987; Alfaro, 1989a,b; Hulme and Harris, 1989; McLean, 1989; Alfaro and Omule, 1990; Alfaro and Ying, 1990; Warkentin *et al*., 1992; Fraser and Heppner, 1993; Alfaro, 1994; Fraser and Szeto, 1994; Hulme, 1994; Sahota *et al*., 1994; Spittlehouse *et al*., 1994; Tomlin and Borden, 1994; Alfaro *et al*., 1995; Hulme, 1995; Alfaro, 1996a,b; de Groot and Zylstra, 1996; Tomlin *et al*., 1996; and, Tomlin and Borden, 1997a,b:]	*Pissodes strobi;* The most serious economic insect pest of Sitka spruce in North America. Larvae tunnel down the inner bark of the shoot, killing the leaders. Not yet a pest where Sitka spruce is planted in Europe.
Green spruce aphid [Powell and Parry, 1976; Carter, 1977; Dixon, 1977; Koot, 1983; Evans, 1987; Nichols, 1987; Carter, 1989; Sutherland *et al*., 1989; Finck *et al*., 1990; Seaby and Mowat, 1993; Straw, 1995; Schwenke, 1972]	*Elatobium abietinum;* a sap sucking insect, can result in mortality at high infestations levels
Bark beetles (Scolytidae) Spruce beetle Great spruce bark beetle [Bejer-Petersen, 1976; Lemperiere and Bailley, 1986; Fielding *et al*., 1991; Kirkeby-Thomsen, 1992; Rose *et al*,. 1994, and Reynolds and Holsten, 1996]	*Dendroctonus rufipennis;* feeds and breeds in galleries between bark and wood. *D. micans* (ditto)
Fungi	
Disease	**Agent**
Annosus root rot [Pratt, 1979a, b; and Morrison *et al*., 1986]	*Heterobasidoion annosum;* causes butt-rot and can lower yield and quality
Armillaria root rot [Boullard and Gaudray, 1975; Redfern, 1978; and Morrison, 1981]	*Armillaria mellea* complex; may kill younger trees
Laminated root rot [Nelson and Sturrock, 1993; and Thies and Sturrock, 1995]	*Phellinus weirii;* butt decay that may kill younger trees
Rhizinia root rot [Phillips and Young, 1976; Gregory and Redfern, 1987; and Callan, 1993]	*Rhizinia undulata;* can affect young seedlings and pole sized trees

For other rust fungi, stem decay, nursery moulds and diseases of seed and cones see: [Gregory and Redfern, 1987; Sutherland *et al*., 1987, 1989 and Sutherland and Hunt, 1990]	
Animals	
Common name	**Species name**
Sitka spruce stands provide cover for many species of fish (salmon and trout species), mammals and birds [Hartman and Brown, 1988; and Staines *et al*., 1987]	
Black-tailed deer [Sullivan *et al*,. 1990] Red deer Sika deer Roe deer Fallow deer [Welch *et al*., 1987, 1991, 1992; Hannan and Whelan, 1989 and de Jong *et al*., 1995]	*Odocoileus hemionus columbianus;* heavy numbers may cause browsing damage *Cervus elaphus* *C. nippon* *Capreolus caprelous* *Dama dama* All may cause damage by bark stripping and browsing
Porcupine [Sullivan *et al*., 1986]	*Erethizon dorsatum;* may feed cause slight damage
Red squirrel [Syme, 1985]	*Tamiasciurus hudsonicus;* damages shoots in removing cones
Seed-eating birds	Many bird species commonly eat quantities of seed, as well as insects associated with Sitka spruce.

E. Symbiotic Relationships - Mycorrhizae

Relatively little research has been done on mycorrhizas of Sitka spruce, although results from forest trials show that inoculation with selected mycorrhizal fungi can give significant early growth effects (Walker, 1987). For example, seedlings inoculated with E-strain fungi, the dominant mycorrhizal fungi of nurseries, were smaller than those inoculated with either *Thelephora terrestris* or *Laccaria laccata* (Thomas and Jackson, 1983). The dominant mycorrhizal fungus in the nursery, the 'E-strain', decreases in frequency with age after planting out. Some mycorrhizal types are found at all forest sites in Britain: of these types, *Thelephora terrestris* has been found on all age classes of Sitka spruce. Other mycorrhizal species recorded on Sitka spruce include *Amanita rubescens, Laccaria amethystea, Lactarius hepaticus, L. tabidus, L. turpis* and *Russula ochroleuca* (Thomas *et al*., 1983). The successions of fruit bodies of mycorrhizal fungi under differently aged British plantations of Sitka spruce were determined to be *Laccaria/Paxillus-Inocybe-Cortinarius-Lactarius* (Dighton *et al*., 1986).

Eighty-four potentially mycorrhizal macrofungi have been recorded with Sitka spruce in Scotland. They derive primarily from the native flora of birch and pine and many are fungi with a wide host range. Specific mycorrhizal associates do not occur. The saprotrophic macrofungi are species that are common in a range of vegetation types (Alexander and Watling, 1987). In nurseries in the Irish Republic, *Piceirhiza horti-inflata* was the most frequent mycorrhizal association during the first year of growth but appeared to be replaced by *Hebeloma* sp. and *Amphinema byssoides* in 2-year-old seedlings. There was a greater diversity of mycorrhizas on container-grown seedlings, which included *Thelephora terrestris*, *Hebeloma* sp. and *Piceirhiza guttata* (Grogan *et al*., 1994). Sitka spruce trees in a plantation established in Normandy in 1956 were affected by *Armillaria mellea* root rot and it is suggested that the formation of mycorrhizae on *P. sitchensis* in France (where the tree is an exotic) is in some way incomplete and affords inadequate protection against *A. mellea* (Gaudray, 1973).

The ability of six ectomycorrhizal fungi (*Thelephora terrestris, Hebeloma crustuliniforme* strains Siv and 81a, *Paxillus involutus, Laccaria laccata* and *Lactarius rufus*) to form mycorrhizas on plantlets of Sitka spruce derived from somatic embryos was investigated by Sasa and Krogstrup (1991). Mycorrhizal synthesis was achieved only on the oldest plantlets during the third week after inoculation. The rate and development of mycorrhizal formation varied according to the fungal species, with infection by *T. terrestris* the highest (92% of the total number of root tips), and *Lactarius rufus* failing to form any mycorrhizas.

7. Domestication

In 1930, Sitka spruce seedlings were among those planted in British Columbia's first reforestation project in the Fraser River Valley, near Vancouver (Young, 1989). While previously planted at a level of about 10 million seedlings per year in British Columbia, Sitka spruce has been all but eliminated from reforestation programs in North America, due to damage from the white pine weevil (King *et al*., 1998). Today, less than 2 million seedlings are planted each year, primarily on cool, coastal areas of the Queen Charlotte Islands. Meanwhile, Sitka spruce is the backbone of plantation forestry in Great Britain, accounting for about 70% of the seedlings planted (Malcolm, 1997), and is a commonly planted species in other European countries such as France and Denmark (Hermann, 1987). In spite of the good growth potential of Sitka spruce in the former Federal Republic of Germany, planting has been drastically reduced due to frost damage, drought and storm damage, and foraging by deer (Kleinschmit, 1978).

A. Deployment of reforestation materials

While Sitka spruce planting stock has traditionally been produced in bare root nurseries as 2+0 seedlings or 1+1 transplants, an increasing proportion is now produced in containerised growing systems, particularly in North America (Daniels and Simpson, 1990; Van Eerden and Gates, 1990; Aldhous and Mason, 1994). A variety of containers are used and stock is raised in both heated and unheated greenhouse structures. Cultural techniques have become highly sophisticated, ensuring that high-quality planting stock can be produced reliably and efficiently.

Sitka spruce planting stock can also be produced by means of vegetative propagation. Practical propagation systems have been developed (Kleinschmidt, 1992). Juvenile cuttings are easily rooted to produce planting stock as "stecklings" (Mason, 1984, 1992; John and Mason, 1987; Mason and Keenleyside, 1987) whose performance after planting is comparable to that of conventional transplant stock (Roulund, 1978; Roulund and Bergstedt, 1982; Baldwin and Mason, 1986; Mason *et al*., 1989). While steckling planting stock has been actively promoted in Great Britain, higher nursery production costs have kept annual production to a few million (Mason, 1991, 1992; Mason and Sharpe, 1992). Despite the higher production costs for steckling stock, the ability to bulk-up (vegetatively multiply) scarce seed sources and tested crosses between selected individuals is expected to more than compensate by realising potential genetic gains earlier (Gill, 1983; Mason and Gill, 1986; Mason and Harper, 1987; Lee, 1992).

Techniques for the initiation and regeneration of somatic embryos are available (Krogstrup *et al*., 1988), and embryogenic lines can be successfully regenerated after cryostorage (Find *et al*., 1993; Kristensen *et al*., 1994), making it possible to maintain genotypes in a completely juvenile condition during clonal testing. Sitka spruce plantlets derived from tissue culture propagation systems are also being automated further through the application of bioreactor technology (Moorhouse *et al*., 1996).

Sitka spruce has been established by direct seeding on an experimental basis, where it has been shown that the seedlings produce a much smaller amount of adventitious roots, compared with bare root transplants (Coutts *et al*., 1990). However, direct seeding has not been used operationally as a regeneration technique for Sitka spruce. Its use in British Columbia is considered a poor option, due to the very slow growth of germinants, which predisposes them to drought and competition (Mitchell *et al,*. 1990).

B. Provenance transfer

Within the native range, plantations established on sites with a strong maritime climate will be faster growing if seeds are transferred from more southerly latitudes. Conversely, transfers of seed from coastal origins to planting sites further inland involve higher risk (Lester *et al*., 1990; Ying, 1990).

Sitka spruce seedlots from British Columbia have also been certified under the OECD scheme for sale in Europe (Pollard and Portlock, 1990; Portlock, 1996). In Britain, southern provenances (below 47°N latitude) grow fastest, but are susceptible to spring and autumn frosts (Lines, 1987a, b), although clonal testing has demonstrated substantial variation in frost hardiness within provenances and potential for selecting southern genotypes with low risk of frost damage (Nicoll *et al*., 1996). Material from the Queen Charlotte Islands is generally recommended over much of Britain, although origins further south in Washington are better for south-west England, Wales, and parts of west Scotland (Fletcher, 1992). In the north of Germany, provenances from Washington are recommended, while fast-growing sources from Oregon are deemed to be too susceptible to frost damage (Stratmann and Tegeler, 1987). Provenances have been recommended for use in France, where plots have been established at four locations to demonstrate seed source differences (Bastien and Lemoine, 1986; François, 1986; Steinmetz, 1986). In Denmark, naturalised seed sources of the second and subsequent generations have grown faster and shown better adaptation than trees from seed imported directly from North America (Nielsen, 1994). In Germany, provenances from British Columbia (Canada) are also recommended.

8. Summary

Sitka spruce is an economically important species of the north temperate coastal rain forest of western North America. While not as commercially important as other conifers within its native range, it is a keystone species in some of the most productive ecosystems in North America. Sitka spruce is now widely planted in North Europe, where it forms the backbone of plantation forestry and is of enormous economic value in some regions. It is closely related to the other North American "white" spruces, *Picea glauca* and *P. englemannii*. As an outcrossing, wind-pollinated species and prolific seed producer, it can transfer its genes rapidly to neighbouring populations and to other related spruces.

Sitka spruce exhibits clinal variation for many growth traits, associated with latitude, elevation, and distance from the coast. Population differences are also demonstrated for resistance to insect attack. While there is great variation among populations, more than half of the genetic variation in many growth traits is found among individuals within populations. Heritabilities for growth and quality traits are sufficiently high to expect substantial genetic gain from conventional recurrent-selection breeding programs. The species is readily propagated by rooted cuttings, offering potential to capture non-additive genetic variance and to accelerate the pace of genetic improvement. Statistically significant genotype-environment interactions have been observed, but broadly adapted individuals are rather common.

The distribution of Sitka spruce is limited to an area of maritime climate with abundant moisture. It may occur as pure stands, particularly on exposed coastal sites, but more commonly occurs in mixtures with western hemlock. While Sitka spruce is tolerant to shade and may occur in climax forest types, it is dependent on disturbance for regeneration and can be an aggressive pioneer in earlier stages of succession. The white pine weevil is by far the most serious threat to stands in North America, killing the leader and seriously affecting growth and merchantability. While the weevil does not affect planted stands in Europe, the green spruce aphid, various species of deer, and windthrow can cause significant damage.

Sitka spruce is well suited to artificial regeneration. While constituting a minor component of the reforestation effort within its native range, Sitka spruce plantation programs are well developed in some parts of Europe. Genetically improved materials from local seed orchards now constitute a significant portion of deployed planting stock. While most Sitka spruce reforestation is currently based on seed propagation, vegetative propagation techniques for cuttings and regeneration of somatic embryos are well advanced, making it a logical target for implementation of transgenic biotechnologies and the use of cloning in both breeding and deployment strategies.

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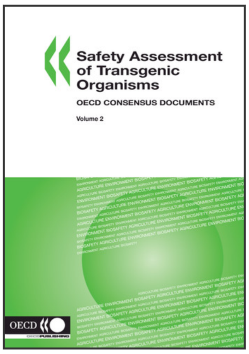

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