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CONSENSUS DOCUMENT ON THE BIOLOGY OF PICEA GLAUCA (MOENCH)  
VOSS (WHITE SPRUCE)

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OECD Environmental Health and Safety Publications

Series on Harmonization of Regulatory Oversight in Biotechnology

**No. 13**

**Consensus Document on the Biology of  
*Picea glauca* (Moench) Voss (White Spruce)**

**Environment Directorate**

**Organisation for Economic Co-operation and Development**

**Paris 1999**

## **About the OECD**

The Organisation for Economic Co-operation and Development (OECD) is an intergovernmental organisation in which representatives of 29 industrialised countries in North America, Europe and the Pacific, as well as the European Commission, meet to co-ordinate and harmonize policies, discuss issues of mutual concern, and work together to respond to international problems. Most of the OECD's work is carried out by more than 200 specialized Committees and subsidiary groups composed of Member country delegates. Observers from several countries with special status at the OECD, and from interested international organisations, attend many of the OECD's Workshops and other meetings. Committees and subsidiary groups are served by the OECD Secretariat, located in Paris, France, which is organised into Directorates and Divisions.

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**or contact:**

**OECD Environment Directorate,  
Environmental Health and Safety Division**

**2 rue André-Pascal  
75775 Paris Cedex 16  
France**

**Fax: (33) 01 45 24 16 75**

**E-mail: [ehscont@oecd.org](mailto:ehscont@oecd.org)**

## FOREWORD

The OECD's Working<sup>1</sup> Group on Harmonization of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of **Consensus Documents** that are mutually recognised among Member countries. These Consensus Documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, Consensus Documents are being developed on the biology of certain plant species, on specific genes and resulting proteins that, when introduced into a plant, result in the expression of specific traits; and on biosafety issues arising from certain general trait modifications made to plants.

This Consensus Document addresses the biology of white spruce (*Picea glauca* (Moench) Voss). White spruce is one of the most economically important tree species in North America, where it is used primarily for wood pulp and general-purpose lumber. It is found in all forested regions of Canada except on the Pacific coast. White spruce is a dominant species in reforestation programmes in every Canadian province and throughout the north-central and northeastern United States.

The general biology of white 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 also described. Reproductive biology is discussed 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 clinal and edaphic variation patterns and the potential for improvement by means of recurrent selection breeding strategies. The species' biological diversity and the complexity of ecological interactions with higher and lower flora and fauna are addressed. White spruce has been the most commonly planted forest tree species across its natural range. Domestication and operational breeding activities are examined. While white spruce reforestation is currently based on seed propagation, vegetative propagation techniques for cuttings and regeneration of somatic embryos are well-advanced, making this species a logical target for implementation of transgenic biotechnologies and the use of cloning in both breeding and deployment strategies.

The document was prepared by a lead country, Canada. It has been revised based on comments received from other OECD Member countries. It is intended for use by regulatory authorities and others who have responsibility for assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of this species.

The Joint Meeting of the Chemicals Committee and Working Party on Chemicals has recommended that this document be made available to the public. It is published on the authority of the Secretary-General of the OECD.

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1. In August 1998, following a decision by the OECD Council to rationalise the names of Committees and Working Groups across the OECD, the "Expert Group on Harmonization of Regulatory Oversight in Biotechnology" became the "Working Group".



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## Preamble

OECD Member countries are now commercialising and marketing agricultural and industrial products of modern biotechnology. They have identified the need for harmonization of regulatory approaches for the assessment of these products, in order to avoid unnecessary trade barriers.

In 1993, **Commercialisation of Agricultural Products Derived through Modern Biotechnology** was instituted as a joint project of the OECD's Environment Policy Committee and its Committee on Agriculture. The objective of this project is to assist countries in their regulatory oversight of agricultural products derived through modern biotechnology – specifically in their efforts to ensure safety, to make oversight policies more transparent and efficient, and to facilitate trade. The project is focused on the review of national policies, with respect to regulatory oversight, that will affect the movement of these products into the marketplace.

The first step of this project was to carry out a survey concentrating on national policies in regard to regulatory oversight of these products. Data requirements for products produced through modern biotechnology, and mechanisms for data assessment, were also surveyed. The results were published in *Commercialisation of Agricultural Products Derived through Modern Biotechnology: Survey Results* (OECD, 1995).

Subsequently, an OECD Workshop was held in June 1994 in Washington, D.C. with the aim of improving awareness and understanding of the various systems of regulatory oversight developed for agricultural products of biotechnology; identifying similarities and differences in various approaches; and identifying the most appropriate role for the OECD in further work towards harmonization of these approaches. Approximately 80 experts in the areas of environmental biosafety, novel food safety and varietal seed certification, representing 16 OECD countries, eight non-member countries, the European Commission and several international organisations, participated in the Workshop. *Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* was also published by the OECD in 1995.

As a next step towards harmonization, the Working Group on Harmonization of Regulatory Oversight in Biotechnology instituted the development of **Consensus Documents** that are **mutually recognised** among Member countries. The purpose of these documents is to describe common elements in the safety assessment of a new plant variety developed through modern biotechnology, to encourage information sharing and to prevent duplication of effort among countries. These common elements fall into three general categories: the biology of the host plant species, or crop; the introduced genes and gene products conferring the novel trait; and biosafety issues arising from the introduction of certain general trait types into plants.

This Consensus Document is a “snapshot” of current information that may be relevant in a regulatory risk assessment. It is meant to be useful not only to regulatory officials, as a general guide and reference source, but also to industry and others carrying out research and product development.

It is anticipated that the Consensus Documents related to genes and products that confer novel traits, together with the relevant Consensus Documents on plant species biology and those providing information on biosafety issues arising from the use of general trait types in plants, will be of use in the biosafety assessment of genetically modified plants.

Reference to two other OECD publications that have appeared in recent years will also prove useful. *Traditional Crop Breeding Practices: An Historical Review to Serve as a Baseline for Assessing the Role of Modern Biotechnology* presents information concerning 17 different crop plants. It includes sections on phytosanitary considerations in the movement of germplasm and on current end uses of the crop plants. There is also a detailed section on current breeding practices. *Safety Considerations for Biotechnology: Scale-Up of Crop Plants* provides a background on plant breeding, discusses scale dependency effects, and identifies various safety issues related to the release of plants with “novel traits”.<sup>1</sup>

To ensure that scientific and technical developments are taken into account, OECD countries have agreed that Consensus Documents will be updated regularly. Additional areas relevant to the subject of each Consensus Document will be considered at the time of updating.

Users are therefore invited to provide relevant new scientific and technical information, and to make proposals concerning additional areas that might be considered in the future. ***A short, pre-addressed questionnaire is included at the end of this document. The information requested should be sent to the OECD at one of the addresses shown.***

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1. For more information on these and other OECD publications, contact the OECD Publications Service, 2 rue André-Pascal, 75775 Paris Cedex 16, France. Fax: (33) 01.49.10.42.76; E-mail: PUBSINQ@oecd.org; or consult <http://www.oecd.org>

Also see the BioTrack Online web page at <http://www.oecd.org/ehs/service.htm>

## Section I - Forestry Practices

White spruce is the most commonly planted tree species in Canada, accounting for more than one-third of all reforestation throughout the (Kuhnke 1989). Active tree breeding and orchard programmes exist in every Canadian province, a distinction not shared by any other species (Fowler and Morgenstern 1990; Lavereau 1995). Breeding programmes in the United States are active, with productive white spruce seed orchards in New England, New York and the Lake States (Carter and Simpson 1985; Carter 1988; Stine *et al.* 1995). ). White spruce is the dominant reforestation species in the upper Lake States (Rauscher 1987). In Germany, *Picea glauca* has had limited use as a species with potential for reclaiming badly polluted industrial areas (Weiss 1986). Elsewhere in the world, white spruce is of much less importance. With the exception of limited ornamental use, it is not generally planted outside its North American range.

### A. Deployment of reforestation materials

White spruce has a long history as a preferred species for reforestation across its range. In the early years, most planting stock were produced as seedlings or transplants in bareroot nurseries (Stiell 1976). Following developments in nursery technology, most planting stock for white spruce are now produced from seed in containerised systems, in soil-less growing media. 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 (Landis *et al.* 1989, 1990a, b, 1992, 1995).

White spruce planting stock can also be produced by means of vegetative propagation. The simplest approach is to bulk-up (vegetatively multiply) tested crosses between selected individuals. White spruce cuttings taken from the seedlings can then be rooted to produce stecklings for deployment (Russell and Ferguson 1990).

Techniques for the initiation and regeneration of somatic embryos have been available for white spruce for about 10 years (e.g., Hakman and Fowke 1987; Lu and Thorpe 1987; Hakman and von Arnold 1988). In fact, work on *Picea glauca* has been responsible for many *in vitro* technologies now used with coniferous plants. Since then, technical progress has been rapid, and the production of white spruce planting stock is also now possible by means of somatic embryogenesis. In addition to *P. glauca* somatic embryogenesis has also been achieved in *P. engelmannii* and in *P. glauca engelmannii* complex (Wilson and Thorpe, 1995). Work by Lulsdorf *et al.* (1993) also describes the development of encapsulation of somatic embryos. While embling production systems have not yet achieved operational status in white spruce, nursery and field testing has demonstrated that performance of emblings is comparable to that of seedling stock (Grossnickle and Major 1994a, b; Grossnickle *et al.* 1994). Embryogenic lines can be successfully regenerated after cryostorage (Cyr *et al.* 1994; Park *et al.* 1994), making it possible to maintain genotypes in a completely juvenile condition during clonal testing. White spruce embling propagation systems are also being automated further through the application of bioreactor technology to produce "synthetic" seeds (Attree *et al.* 1994).

The advancement of *in vitro* propagation of *P. glauca* has played an important role in the more recent success in genetic transformation of the species. *P. glauca* was the second coniferous species to be stably transformed (Ellis *et al.* 1993). The number of stably transformed coniferous species remains rather low (five to ten species).

The use of direct seeding as a regeneration technique for white spruce has fluctuated, and results have been erratic (Waldron 1974; Stiell 1976). Its operational use has been largely restricted to Alberta, where direct seeding of white spruce is often performed as a species mixture with *Pinus contorta* (Kuhnke 1989).

### **B. Provenance transfer**

A long history of provenance tests has demonstrated the general wisdom of using local white spruce seed sources in the absence of tested alternatives. While some movement of genetic material from point of collection to site of establishment is inevitable, these transfers are normally controlled either a set of transfer rules, regulating distance of movement, or seed zones, where it is assumed that adaptation of populations has been shaped by climate and other ecological factors (Morgenstern 1996). Both are appropriate for a species like white spruce, where genetic variation is predominantly clinal. Seed zones have been most commonly used throughout the range of white spruce, where they are normally based on ecological classification schemes (e.g., Fowler and MacGillivray 1967; Konishi 1979). With provenance test data in hand, white spruce seed zones may be revised to recognise the amplitude of genetic variation and stability over regions (Govindaraju 1990).

While local seed sources are generally recommended for white spruce, some provenance transfers have been demonstrated to be particularly promising. Provenances from the Ottawa Valley region have continued to perform better than local sources in several field experiments, to the point that breeding programmes based on this material have been recommended in the Lake States (Nienstaedt and Kang 1983), New Brunswick (Fowler 1986) and Quebec (Beaulieu 1996).

### **C. Breeding programmes**

With experimental evidence that substantial genetic variation was to be found within populations, selection of plus-trees has been a common starting point for most improvement programmes. The actual improvement realised through plus-tree selection systems may vary considerably, depending on the techniques used and the stand situations, all of which affect selection intensity, genetic variance and heritability for traits of interest (Morgenstern and Mullin 1988; Cornelius 1994). In white spruce it is particularly important that sampling of the founder population by selection be balanced, and that breeding strategies maintain this balance to avoid rapid loss of genetic diversity in the breeding population (Nienstaedt and Kang 1987).

Breeding programmes are now well established throughout the range where white spruce is planted. Regional breeding strategies have been prepared which generally utilise a system of progeny testing and recurrent selection for generation advancement, combined with clonal seed orchards for production of improved seed and usually involving multi-agency co-operation (e.g., Carter and Simpson 1985; Fowler 1986; Dojack 1991; Lamontagne 1992; Stine *et al.* 1995). Flowering of young white spruce grafts can be stimulated by means of various cultural treatments, particularly those involving gibberellin A<sub>4/7</sub>, and this has facilitated the turnover of breeding cycles (Greenwood *et al.* 1991; Daoust *et al.* 1995).

Most seed orchards currently in production were established by grafting cuttings from plus-trees, and establishment in cultivated field environments. Early data indicated that such orchards would average over 1 million viable seeds per hectare by the time they entered their productive period (Nienstaedt and Jeffers 1970; McPherson *et al.* 1982). Many of these first-generation orchards are now in production, and some regional nursery requirements are now met completely by orchard seed. Some programmes have also experimented with the management of containerised white spruce orchards. While container orchards can be conveniently managed to maximise genetic value and to promote flower production, the yield has seldom been more than 10-15 filled seed per cone and requires further development of cultural protocols (Webber and Stoehr 1995).

#### **D. Conservation of genetic resources**

Domestication of a key species such as white spruce can influence diversity of genetic resources (1) indirectly, through the method of seed collection, extraction and storage, and through nursery and plantation culture; and (2) directly, through intentional selection to increase the frequency of genes for desirable traits (Morgenstern 1996). The inadvertent loss of genes through natural processes and human activity can have negative consequences for the adaptability of populations and the potential for future gains from breeding.

Throughout most of the range of white spruce, *in situ* conservation of genetic resources is practised by protecting of ecological reserves, special areas and parks (Pollard 1995), and is integrated with domestication activities that control the movement of seed, active management of existing stands to maintain biological diversity, and protection of small isolated populations (VanBorrendam 1984; Dhir and Barnhardt 1995; Villeneuve 1995; Yanchuk 1995). As outcrossing rates in white spruce stands can be lower than those of other conifers, inbreeding depression related to population size is a concern for *in situ* conservation efforts. Studies have been initiated to develop guidelines on minimum viable population size (Mosseler *et al.* 1995).

*Ex situ* conservation, through cryopreservation of germplasm, off-site maintenance of populations in arboreta and clone banks, and multi-population breeding strategies (Eriksson *et al.* 1993; Namkoong 1995), has been practised to a much lesser extent, although many white spruce provenances and families are now represented in field tests and seed bank collections (Plourde *et al.* 1995). Such "active" forms of gene management must be accelerated in preparation for response to rapid environmental and climate changes (Ledig and Kitzmiller 1992).

## Section II - Taxonomy

White spruce (*épinette blanche* in French Canada) 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, and one of seven species native to North America and five native to Canada (Farrar 1995). Its scientific name is now well recognised as *Picea glauca* (Moench) Voss, although it has also been referred to in the literature under an array of botanical synonyms including *Picea canadensis* B.S.P. and *Picea alba* Link. (Sutton 1970; Krüssmann 1985). Its colloquial synonyms are even more numerous. They include cat spruce, skunk spruce and Canadian spruce in English, and *épinette à bière*, *épinette des champs* and *sapinette blanche* in French (Sutton 1970).

A variety is generally recognised as Porsild spruce (*Picea glauca* var. *porsildii* Raup) in northern Alberta, the Yukon and Alaska (Farrar 1995). Introgressive hybridisation between white and Englemann spruce (*Picea engelmannii* Parry ex Engelm.) is common where the two are sympatric in western Canada, Montana and Wyoming, and the hybrids have given rise to a variety known as *Picea glauca* var. *albertiana* (S. Brown) Sarg. (Roche 1969; Roche *et al.* 1969; Daubenmire 1974). Introgressive hybridisation between white and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) also occurs in sympatric areas in northwestern British Columbia and Alaska, with the hybrid known as *Picea* × *lutzii* Little (Roche 1969; Copes and Beckwith 1977; Yeh and Arnott 1986). A rare natural hybrid between white and black spruce (*Picea mariana* (Mill.) B.S.P.), known as “Rosendahl” spruce, has been recognised in the southern part of the range (Little and Pauley 1958; Riemenschneider and Mohn 1975) and has been reported as occurring commonly in northwestern Canada (Larsen 1965; Roche 1969), but its F1 hybrid status has been questioned (Parker and McLachlan 1978). Many named horticultural varieties are recognised (Krüssmann 1985; Griffiths 1994).

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, 1987a) has suggested that the section Omorika be further divided into two subsections, Omorikoides and Glaucoides, with white spruce assigned to the latter together with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Englemann spruce (*Picea engelmannii* Parry).

### Section III - Centres of Origin/Diversity

#### A. Natural distribution

The natural range of white spruce extends from the Atlantic to within 100 km of the Pacific Ocean, and from the northern tree limit across North America south into northern New England, New York and the Lake States (Sutton 1970). Over this tremendous range it is found at elevations ranging from sea level to 1 520 m (Nienstaedt and Zasada 1990). Alone or with black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch), white spruce forms the northern limit of tree-form growth. Outlier populations have been reported as far south as the Black Hills in Wyoming and South Dakota (Sutton 1970).

Several range maps have been prepared for white spruce, but that drawn by E.L. Little, Jr. and presented in Fowells (1965) has formed the basis for maps found in current reference publications (Nienstaedt and Zasada 1990; Farrar 1995). Little's map is shown in Figure 1.

#### B. Evolution and migrational history

Fossil records indicate that divergence of 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.

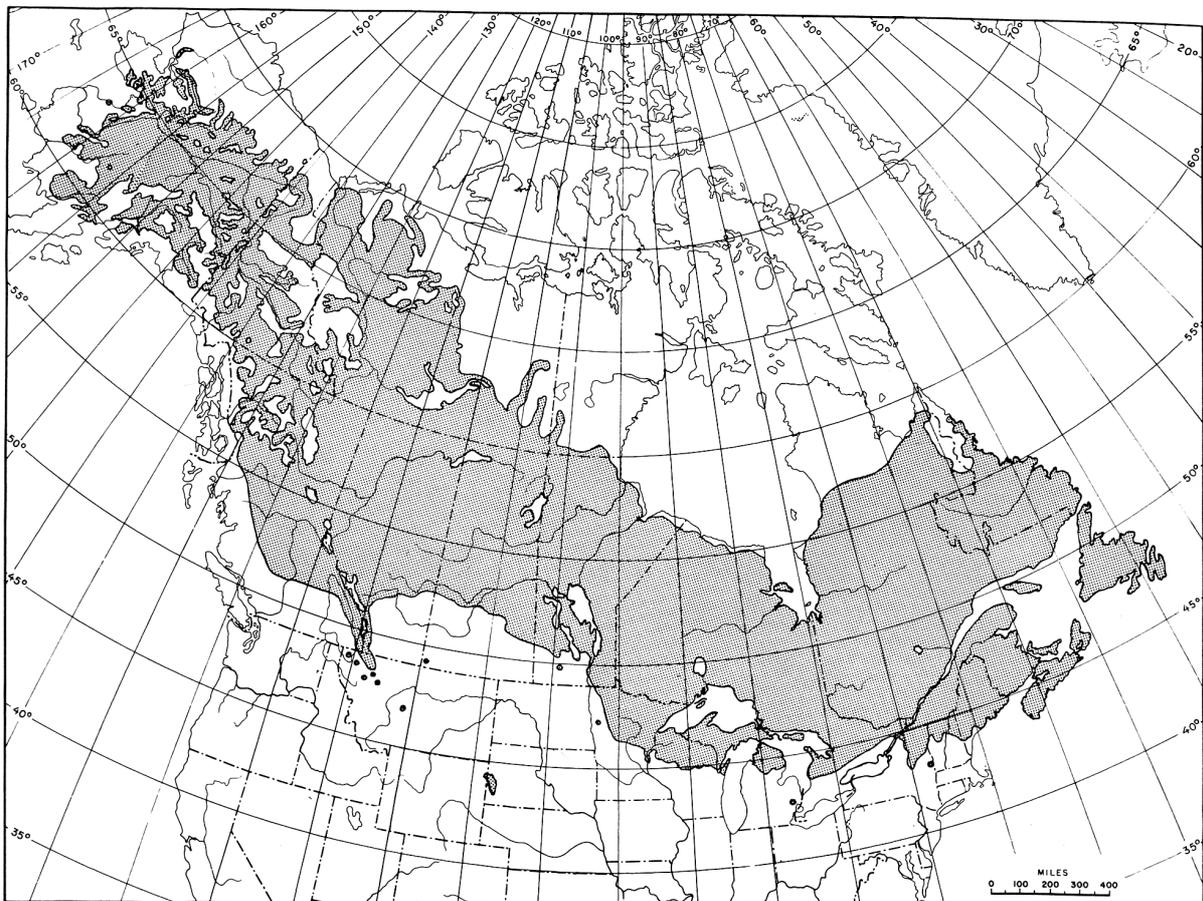
Although not supported by fossil evidence, Wright (1955) suggested eastern Asia as the likely origin of *Picea*, based on the abundance of species and particularly the presence of *Picea koyamai* Shirasawa, which he felt is a primitive species. *Picea* is then thought to have migrated to North America in one or more waves via a land bridge between Siberia and Alaska (Wright 1955). Critchfield (1984) cites fossil evidence that the white spruce extended in a broad, shifting pattern across much of North America by the Late Pleistocene.

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 1973). The close phylogenetic relationship between the northwestern American "white" spruces (white, Sitka and Engelmann spruce) and the eastern Asiatic *P. jezoensis* (Sieb et Zucc.) Carr. (Wright 1955; Roche and Fowler 1975) supports this theory, at least for the members of subsection *Glaucooides* in section *Omorika*.

Fossilised cones of an extinct species, *Picea banksii*, found on Banks Island in Arctic Canada can only be distinguished from those of white spruce on the basis of mean size. These provide evidence that white spruce, or a close ancestor such as *P. banksii*, was the link between North America and Asia, rather than *P. jezoensis* (Hills and Ogilvie 1970).

Radiocarbon evidence suggests that white spruce was likely found at least 280 km further north during the Climatic and Little Climatic Optima, 3 500 and 900 years ago (Sutton 1970). During the Pleistocene glaciation, a main eastern refugium extended further south into the Great Plains and perhaps as far as Lee County, Texas (Potzger and Tharp 1943; Graham and Heimsch 1960), and into North Carolina (Frey 1951). Meanwhile, western refugia are considered to have existed in the Yukon-Alaska and the lower eastern slopes of the Rockies, joined by a “fluctuating corridor” through Alberta (Nienstaedt and Teich 1972). It is considered that these east and west populations then followed the retreat of the ice sheet, meeting in the Great Lakes region (Halliday and Brown 1943; Löve 1959).

**Figure 1 The natural range of white spruce (from Fowells 1965)**



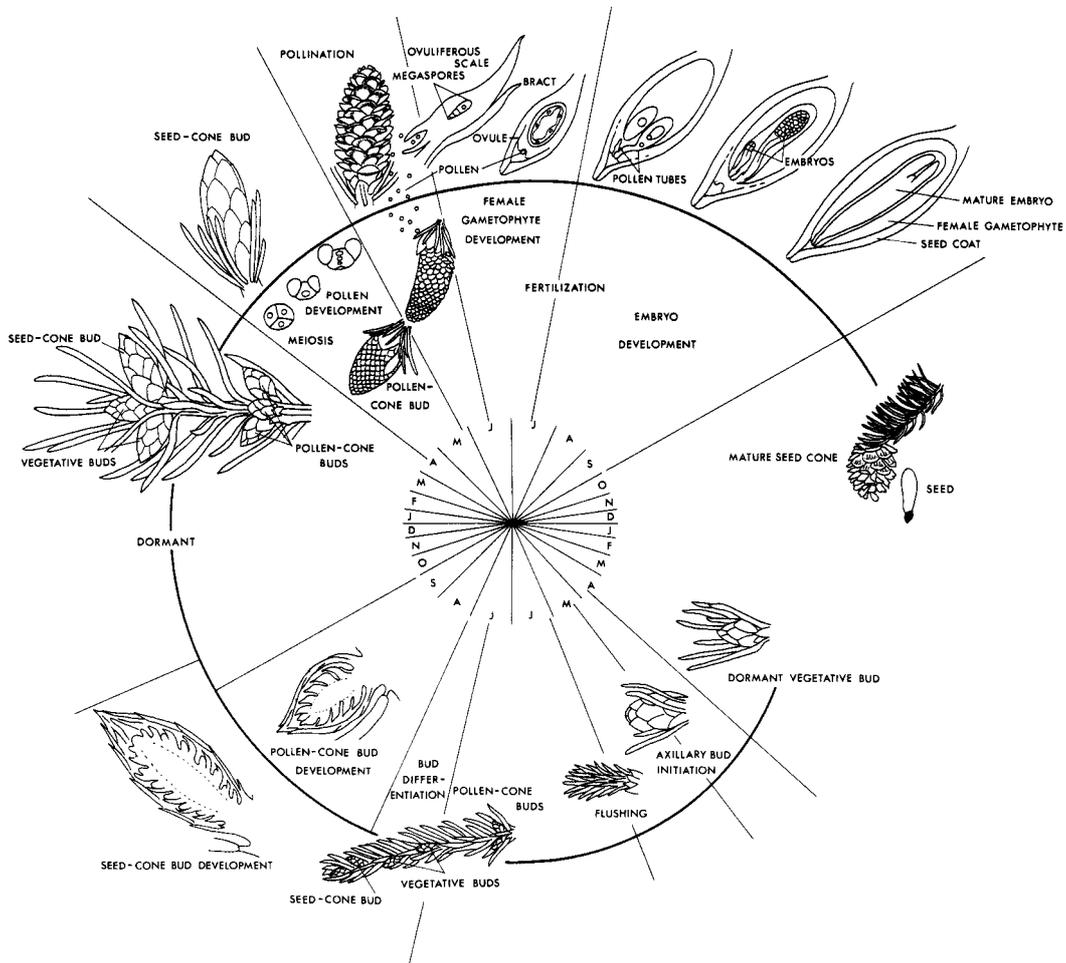
## Section IV - Reproductive Biology

### A. Reproductive development

White spruce is monoecious. Development of the reproductive structures follows a two-year cycle typical of most conifers in the northern hemisphere (Figure 2), 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 late April (Owens *et al.* 1977). Apices differentiate as vegetative, pollen cone or seed cone buds around mid-July, at the cessation of shoot elongation. The proportion of apices differentiating as reproductive buds may be increased by hot, dry weather at the time of differentiation, particularly if preceding cone crops have been poor (Owens and Blake 1985; Nienstaedt and Zasada 1990).

Pollen cone bud development is complete by early October, when they become dormant. Completion of seed cone and vegetative bud development follows shortly thereafter. By the time buds become dormant, all microsporophylls, microsporangia, bracts and functional ovuliferous scales, and leaves have been initiated. Megaspore mother cells are present in the dormant seed cone buds, although meiosis has not begun (Owens and Molder 1977, 1984). Overwintering vegetative buds are small and dome-shaped. Reproductive buds, usually terminal or subterminal, may be identified by their larger size and ovate to obovate shape. Distinguishing between male and female buds may be difficult without dissection, but males are generally found in the middle to lower crown (Eis 1967a; Eis and Inkster 1972).

**Figure 2 The reproductive cycle of white spruce (from Owens and Molder 1984)**



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. The developmental morphology of reproductive structures was well-documented with colour photographs by Ho (1991). Flushing of reproductive buds precedes that of vegetative buds, and pollen is released over a one-week period. The pollen enters receptive seed cones and adheres to the sticky micropylar arms. When the cones close, a "pollination drop" draws the pollen into the ovule (Owens and Molder 1979; Ho 1984; Runions *et al.* 1995). Transport of the pollen to the micropyle may be facilitated by rainwater (Runions and Owens 1996). Fertilization occurs three to four weeks later, and embryo development is completed in early to late August (Owens and Molder 1979; Zasada 1988). Female gametophytes may abort at many stages of development, but most commonly at or shortly after meiosis (Owens and Molder 1984). Without fertilization, no embryo is formed and the megagametophyte tissue degenerates, leaving a normal-sized but empty seed (Owens and Molder 1979).

## B. Mating system and gene flow

White spruce is a wind-pollinated, monoecious species, and outcrossing is by far the most prevalent mating system. Self-pollination occurs to some degree, as the period of pollen release and female receptivity coincide for an individual tree (Nienstaedt 1958). Female strobili are concentrated in the top quarter of the crown, while males are more prevalent in the mid to lower crown, but the effectiveness of this zonation against selfing is questionable (Nienstaedt and Teich 1972). The two-step pollination mechanism, whereby pollen is collected in the sticky micropylar 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 fertilize any given ovule (Runions *et al.* 1995). Under controlled pollination, where large quantities of pollen are applied at one time, the micropylar arms become fully occupied and it is more likely that the first-on become first-in (Franklin 1974; Ho 1985). The nucellus itself can accommodate two or three pollen grains, and there is potential of some postzygotic selection to reduce the number of selfed embryos (Fowler 1987b). The incidence of selfing also varies greatly as a function of population size and structure. Selfing rates in a white spruce seed orchard varied from 0 to 22% (Denti and Schoen 1988). However, the presence of several ramets of the same clone might generate a pollen cloud quite unlike that in a natural stand. Although outcrossing pollen has no advantage over self-pollen prior to fertilization and self-fertilization, can occur, most selfed embryos fail to develop, likely as a result of homozygous lethal recessive genes (Mergen *et al.* 1965; Nienstaedt and Teich 1972).

Natural inbreeding among related trees is common in small populations. In two such stands in New Brunswick, the average inbreeding coefficient was estimated as  $F = 0.145$  (Coles and Fowler 1976; Park *et al.* 1984). An electrophoretic study of six stands near the limit of the range in subarctic Quebec displayed deficiencies of heterozygotes at 60% of the loci analysed and suggested rapid accumulation of inbreeding. Differences among these isolated populations were large ( $F_{st} = 0.113$ ), suggesting that genetic drift might be important (Tremblay and Simon 1989). Substantial deviations from random mating and high rates of inbreeding were also observed within stands in Newfoundland (Innes and Ringius 1990) and in a seed production area in Alberta (King *et al.* 1984). Another electrophoretic study of trees throughout a 19 ha stand in eastern Ontario demonstrated that, while selfing was not a major component of the mating system and there was an excess of heterozygotes in both the parental and filial populations, other forms of non-random mating among relatives and restricted transmission distances of effective pollen gametes were important (Cheliak *et al.* 1985).

Gene flow in *Picea* is mediated by small pollen grains, 70-85 nm 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, a substantial quantity may travel great distances; 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). 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  $5 \text{ m s}^{-1}$ , the authors calculated that spruce pollen reaching this altitude would drift about 47 km. Another study examined pollen contamination within a white spruce seed orchard that a forest fire had isolated from native stands by as much as 3 km upwind (Caron *et al.* 1994; Mercier *et al.* 1994). In a heavy pollen year, contamination levels within this well-isolated orchard were estimated at 93%.

### C. Seed production

Cones and seeds may be produced on white spruce as young as four years (Sutton 1970), but most trees do not produce seed until 10 to 15 years. Significant seed production normally occurs on trees that are at least 30 years of age (Nienstaedt and Teich 1972). Periodicity of seed production and crop size are extremely variable. Good cone crops are borne irregularly, but on average every four years (Stiell 1976). In a "heavy" crop year, Waldron (1965) estimated that a mature stand in Manitoba produced 13.8 million seeds/ha, but that only 59% were sound. In a "moderate" seed year, the stand produced 2.5 million seeds/ha. Maximum seed production over a 13-year period in a stand in Alaska was 40 million seeds/ha, and in three years exceeded 10 million seeds/ha (Nienstaedt and Zasada 1990).

Initiation and duration of seed dispersal are weather and site dependent (Zasada 1988). The mature cones open as they lose moisture and the scales flex in dry weather, reclosing during wet periods. Seed dispersal begins in mid- to late-August, with most seeds released in September (Crossley 1953; Waldron 1965; Dobbs 1976). The interval between seed ripening and beginning of dispersal can be less than two weeks, which creates problems in determining the best time to collect cones (Smith 1983; Mercier and Langlois 1992). At some northern sites, seed dispersal may begin before seeds are fully mature (Mercier 1994). In practice, cone collection can begin a couple of weeks earlier if seeds are allowed to "artificially ripen" by storing the cones under cool, moist conditions (Winston and Haddon 1981; Caron *et al.* 1990, 1993).

The seeds are winged and wind-dispersed. The actual distance reached from the source varies from site to site (Dobbs 1976), but in one study less than 5% of the seeds were dispersed more than 100 m from the source (Zasada and Lovig 1983). The seeds themselves are small, and average cleaned seed weight is about 2.0 g/1 000 seeds (Safford 1974).

### D. Natural regeneration

White spruce seeds exhibit varying degrees of dormancy that may be broken by exposure to low temperatures under moist conditions, i.e., cold stratification (Wang 1974). Dormancy results from inhibition of embryo development, induced by the seed coat and/or megagametophyte tissue (Downie and Bewley 1996). Seed dormancy may vary greatly among stands, individual trees and crop year (Hellum 1968; Wang 1976; Caron *et al.* 1990). In the wild, white spruce seeds normally germinate the following spring, as soon as soil surface temperatures are warm enough and provided there is adequate moisture (Nienstaedt and Zasada 1990).

Natural regeneration of white spruce can be difficult to predict and is not easily established under most harvesting systems. As a shade-tolerant species, white spruce is able to regenerate under mature stands of spruce and early successional species, but advance regeneration stocking is often poor (Jablanczy 1967, 1979; Krasny *et al.* 1984; Walker *et al.* 1986; Nienstaedt and Zasada 1990). Freshly disturbed areas with exposed mineral soils offer the best conditions for germination and establishment (Eis 1967b; Lees 1970; Dobbs 1976; Zasada *et al.* 1978). Thick organic layers are common under mature stands, but such surfaces restrict germination success and shallow root penetration leads to mortality if the canopy is opened suddenly (Jablanczy 1967). Where advance regeneration is established on thick moss, survival after logging is often poor and seedlings are soon replaced by other more aggressive species. Under the more open canopies of stands growing on alluvium sites, the sudden increase of competing vegetation after harvesting prevents seedling establishment and causes severe mortality to advance regeneration (Eis 1981). Advance regeneration that does establish under closed canopies will not survive

suppression as long as in other more tolerant species such as balsam fir (Jablanczy 1967, 1979). Allelopathic effects of *Cladonia* lichens may inhibit the establishment of regeneration (Fisher 1979).

#### **E. Vegetative reproduction in nature**

While vegetative reproduction is rare over much of the range of white spruce, layering is common at the northern limit where regeneration from seed is limited because of climatic conditions (Nienstaedt and Zasada 1990; Fayle and Scott 1995). Rooting occurs when lower branches of open-grown trees come in contact with the ground and are covered by soil or organic materials. Populations in these arctic areas likely originated from seed at a time when climatic conditions were warmer, and vegetative propagation is now the only possible means of regeneration (Elliott 1979).

## Section V - Genetics

### A. Cytology

Vegetative cells are normally diploid, with  $2n = 24$  chromosomes (Mehra and Khoshoo 1956; Santamour 1960). Aneuploidy and polyploidy are very rare (De Torok and White 1960); about 1 in 13 000 seedlings have been observed, mostly tetraploid, and most of them stunted (Winton 1964).

### B. Genetic variation

#### *B.1 Population-level variability*

White spruce was an early candidate for provenance research, and evidence of clinal variation for height growth related to latitude and elevation of origin appeared as early as 1950 (Morgenstern 1996). North-south adaptive variation has also been observed for such characters as cold hardiness of buds, foliage and stems (Simpson 1994), optimal and threshold germination temperature (Fraser 1971), germination rate (Roche 1969), seed quality (Khalil 1986), juvenile growth (Dunsworth and Dancik 1983; Khalil 1986), date of bud flush (Blum 1988), and various other seedling morphological and phenological traits (Nienstaedt and Teich 1972).

There is evidence of east-west variation patterns in such taxonomic characteristics as needle colour, number of stomata and branch pubescence (Nienstaedt and Teich 1972), cortical monoterpenes (Wilkinson *et al.* 1971), DNA content (Miksche 1968) and cpDNA allele frequencies (Furnier and Stine 1995). These data are consistent with the two-refugia theory of white spruce remigration, following the Pleistocene glaciation, with a major division at about 95°W, with latitudinal clines within each division (Nienstaedt and Teich 1972).

While white spruce generally exhibits clinal variation for adaptive traits, edaphic ecotypes have been identified in eastern Ontario that produce superior height growth on granitic and limestone sites (Teich and Holst 1974; Murray and Skeates 1985). White spruce populations from moist-warm habitats of the sub-boreal spruce biogeoclimatic zone in the interior of British Columbia have displayed greater resistance to white pine weevil (*Pissodes strobi*) attack (Alfaro *et al.* 1996). In a 20-year-old trial in the badly polluted industrial Erzgebirge region of East Germany, there was great variation in performance of 16 tested white spruce provenances. The best of these (from Sundridge, Ontario) was superior to the best of 17 tested provenances of Norway spruce (Weiss *et al.* 1988).

Local provenances are generally well-adapted and grow well, but it is not uncommon for provenances from more southerly locations to exhibit better growth (Nienstaedt and Teich 1972). Some particular sources have demonstrated superior performance over a wide range of sites. A provenance from Birch Island, British Columbia, has proven exceptional and in coastal nurseries will match the growth of

Sitka spruce (Nienstaedt and Zasada 1990). Provenances from the Ottawa Valley have performed well at many locations from the Lakes States through to Newfoundland (Nienstaedt 1969; Corriveau and Boudoux 1971; Teich *et al.* 1975; Fowler and Coles 1977; Radsliff *et al.* 1983; Khalil 1985). Although these sources grew well in Newfoundland, survival was sometimes poor (Hall 1986). In Nova Scotia, Ottawa Valley sources were surpassed in height growth by provenances from Prince Edward Island (Bailey 1987). In a range-wide provenance test in Alberta, the 10 best provenances included sources from Saskatchewan, Manitoba, Ontario and Quebec, and had 15% greater height and only slightly lower survival after 15 years than did the local seed sources (Hansen *et al.* 1995).

When provenances of diverse geographic origin are tested, population differences may explain 10 to 15% of the phenotypic variation in wood relative density (Stellrecht *et al.* 1974; Beaulieu and Corriveau 1985; Corriveau *et al.* 1987). However, population differences within a smaller geographic area can be negligible, even while family differences within stands can account for 16% of the variation in relative density of outer wood (Corriveau *et al.* 1991).

In contrast to many other characters, geographic variation at polymorphic allozyme loci appears to be weak. A 19-year-old test in Minnesota of 22 provenances from across the range of white spruce demonstrated that while 48.0% and 54.1% of the variation in height at ages nine and 19, respectively, was due to differences among populations, an average of only 3.8% of the allozyme variation was due to population differences (Furnier *et al.* 1991). The variance among enzyme systems at 13 loci in four populations in Alaska, on an altitudinal gradient from 120 to 750 m, was such that only 2% of the variance was among populations, while 97% of the genetic diversity was within-stand, suggesting that the allozyme systems studied were selectively neutral (Alden and Loopstra 1987).

## ***B.2 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. The partitioning of genetic variance among and within populations is greatly influenced by the range of adaptive variation sampled by the tested provenances. A wide-range sample of provenances tested in Wisconsin estimated population variance to be two to three times the family-within-population variance for height at nine and 15 years (Nienstaedt and Riemenschneider 1985). Another sample drawn from across Quebec and Ontario indicated that population variance was as large as that of families-within-populations (Li *et al.* 1993). Field trials using hierarchal sampling over a limited area of southeastern Ontario showed high within-stand variation for height growth and phenology, while variation among stands was low (Dhir 1976; Pollard and Ying 1979a, b).

The oldest white spruce progeny tests were established on four sites at the Petawawa Forest Experiment Station in 1958 (Holst and Teich 1969). Narrow-sense heritabilities for this material were reported at age eight to 11 years in the range of 0.15 to 0.35 for height, and at three of the four sites was similar at age 22 (Ying and Morgenstern 1979). A similar progeny test in Minnesota produced heritability estimates for height of 0.27 at age nine, increasing to 0.35 at age 12 (Mohn *et al.* 1976), and another in Wisconsin produced estimates of 0.16 and 0.25 at ages nine and 15, respectively (Nienstaedt and Riemenschneider 1985).

Heritability estimates for diameter have typically been lower: from 0.05 to 0.10 at age 22 in the Ontario test (Ying and Morgenstern 1979), and 0.14 in the Minnesota test (Merrill and Mohn 1985).

The Petawawa trial was revisited by Magnussen (1993), who found that heritability estimates were much higher when only the "crop" trees were considered, as would be the case during selection in older stands. Stem analysis of almost 300 trees from 18 open-pollinated families at 36 years of age showed strong heritability of height growth, in the range of 0.3 to 0.6. Heritability for volume was also moderately strong, peaking at about 0.3 at age 20 and declining rapidly thereafter.

White spruce in the western part of the range is frequently deformed by the white pine weevil (*Pissodes strobi*). Resistance to this pest varies substantially among individuals within a population, and the genetic basis has been demonstrated (Kiss and Yanchuk 1991; Alfaro *et al.* 1996).

While significant variation in wood specific gravity exists among populations, there are few correlations with environmental gradients or growth, and most of the variability exists among individuals within stands (Beaulieu and Corriveau 1985). Corriveau *et al.* (1991) studied the variation of wood quality characters in 19-year-old open-pollinated progenies from eight populations of white spruce in the Upper Ottawa Valley. Their results indicated that the relative density of outer wood in white spruce is under strong genetic control, with 16% of the variation explained by family differences and narrow-sense heritability estimated to be 0.63. An open-pollinated family test in British Columbia produced a similarly high estimate of heritability for wood specific gravity, 0.47, at age 15 (Yanchuk and Kiss 1993).

Substantial genetic variation has also been demonstrated in the initiation, maturation and germination of somatic white spruce embryos from zygotic embryonic tissue (Park *et al.* 1993, 1994). Of particular concern to clonal selection programmes, a substantial portion of the genetic variance in the response to cultural treatments and the maturation and germination of somatic embryos was due to non-additive genetic variance.

### **C. Inbreeding depression and genetic load**

Strong inbreeding depression has been reported in white spruce (Mergen *et al.* 1965; Fowler and Park 1983; Park *et al.* 1984), and height growth losses as great as 33% have been reported (Ying 1978). Compared with other conifers, the number of lethal equivalents per zygote, 12.6, is high, and selfing has severe effects on seed set, early growth and survival (Fowler and Park 1983). Selection likely acts to remove selfed and highly inbred individuals early in the life-cycle, prior to the age of reproduction (Furnier *et al.* 1991). Nevertheless, natural inbreeding among related trees is common in small populations. In two such stands in New Brunswick, the average inbreeding coefficient was estimated as  $F = 0.145$  (Coles and Fowler 1976; Park *et al.* 1984).

## **Section VI - Crosses**

Potential crosses with white spruce are summarised in Table 1 (modified from Nienstaedt and Teich 1972). Introgressive hybridisation between white and Englemann spruce is widespread where the species are sympatric over large areas of British Columbia and Alberta (Nienstaedt and Teich 1972). In these areas breeding programmes simply treat the hybrid complex as a single species, "interior spruce".

**Table 1 Species cross compatibility with white spruce (modified from Nienstaedt and Teich 1972)**

Species	References
<b><i>Commonly occurring in sympatric range</i></b>	
<i>P. englemannii</i> Parry ex Engelm. = <i>P. glauca</i> var. <i>albertiana</i> (S. Brown) Sarg.	Roche 1969; Daubenmire 1974
<i>P. sitchensis</i> (Bong.) Carr. = <i>Picea</i> × <i>lutzii</i> Little	Roche 1969; Fowler 1987a
<b><i>Successful crosses; hybridity verified</i></b>	
<i>P. jezoensis</i> var <i>hondoensis</i> (Mayr.) Rehder	Wright 1955
<i>P. koyamai</i> Shirasawa	Wright 1955
<i>P. omorika</i> (Pancic) Purkyne	Jeffers 1971; Gordon 1980
<i>P. pungens</i> Engelm.	Hanover and Wilkinson 1969; Bongarten and Hanover 1982; Gordon 1980
<i>P. schrenkiana</i> Fisch. & Mey.	Fowler 1966; Gordon 1980
<b><i>Limited crossibility; hybridity verified</i></b>	
<i>P. likiangensis</i> (Franch.) Pritz.	Jeffers 1971; Gordon 1986
<i>P. maximowiczii</i> Reg.	Jeffers 1971
<i>P. mexicana</i> Martinez	Gordon 1980
<i>P. mariana</i> (Mill.) B.S.P.	Gordon 1986; Little and Pauley 1958; Parker and McLachlan 1978
<i>P. smithiana</i> Boiss.	Mergen <i>et al.</i> 1965; Nienstaedt and Fowler 1982
<b><i>Possible crossibility; hybrids not verified</i></b>	
<i>P. abies</i> (L.) Karst.	Jeffers 1971
<i>P. asperata</i> Mast.	Mergen <i>et al.</i> 1965
<i>P. chihuahuana</i> Martinez	Gordon 1980
<i>P. glehnii</i> (Fr. Schmidt) Mast.	Anonymous 1962
<i>P. montigena</i> Mast.	Jeffers 1971
<i>P. orientalis</i> (L.) Link	Mergen <i>et al.</i> 1965
<i>P. retroflexa</i> Mast.	Jeffers 1971
<i>P. rubens</i> Sarg.	Gordon 1980; Bongarten and Hanover 1982

## Section VII - Ecology and Associated Species

Much of the information in this section has been derived from the excellent chapter on the silvics of white spruce by Hans Nienstaedt and John Zasada, in USDA Forest Service Agricultural Handbook 654 (Nienstaedt and Zasada 1990). Other citations are given as appropriate when specific information is attributable to other sources.

### A. Habitat

Having repopulated a tremendous area following glaciation, white spruce can grow under a great variety of conditions, including extreme climates and soils, and is regarded as a "plastic" species. It is tolerant of shade, but recovers well after release from suppression and exposure to more light (Farrar 1995). Although it is a climax species in succession, it not only succeeded in establishing itself soon after glaciation, but also demonstrated an ability to invade abandoned farmland throughout eastern Canada, occupying about 200 000 ha of old fields in Nova Scotia alone (Drinkwater 1957).

#### A.1 Climate

The northern limit of the white spruce is likely determined by a number of climatic, biotic and abiotic factors. What is clear is that climatic extremes in this area are significant. Mean daily temperatures for January throughout much of the species range in Alaska, the Yukon and the Northwest Territories are in the vicinity of -29°C, whereas those in July reach only 13°C. Moisture is also limited in this area, with mean annual precipitation of only 250 mm. While photoperiod north of the Arctic Circle is 24 hours at the summer solstice, the length of the growing season at the northern limit is only about 60 days and may be as short as 20 days.

The southern limit of white spruce's dominance as a species in forest stands roughly follows the 18°C July isotherm, except in the Prairie Provinces where it swings somewhat north. Maximum summer temperatures as high as 43°C have been recorded within the range in Manitoba, and mean annual precipitation can be as high as 1 270 mm in Nova Scotia and Newfoundland. Low mean annual precipitation in the range of 380 to 510 mm combines with mean high temperatures in July of over 24°C to produce the most severe conditions along the southern edge of the range in the Prairie Provinces.

#### A.2 Soils and site type

A wide range of soils and site conditions support white spruce, although the diversity of sites becomes more limited in northern areas with increasing severity of climate (Sutton 1970). Within its range, it is found on soils of glacial, lacustrine, marine and alluvial origin derived from geologically diverse substrata, including granites, gneisses, sedimentaries, slates, schists, shales and conglomerates.

Podzolic soils are most common, but white spruce also grows on brunisolic, luvisolic, gleysolic and regisolic soils. It can also be found as a minor species on sand flats and other coarse-textured soils, on shallow mesic organic soils in Saskatchewan, and on organic soils with black spruce in the central Yukon.

While white spruce can occupy extremely harsh site conditions, it is generally regarded as more demanding than other associated conifers, requiring higher moisture and fertility to achieve best development on moderately well-drained soils. Optimum pH values are probably in the range of 4.7 to 7.0 (Sutton 1970; Stiell 1976), but white spruce stands are found on strongly acidic soils at pH 4.0, as well as alkaline soils as high as pH 8.0. Ecotypic variation has been observed in white spruce, with some ecotypes adapted to limestone sites (Teich and Holst 1974; Murray and Skeates 1985). White spruce stand development itself can have an impact on organic layers and on properties of the mineral soil. Brand *et al.* (1986) found that soil pH decreased by 1.2 units in plantations established on abandoned farmland in Ontario.

## B. Synecology and associated species

Distributed over such a wide range, it is no surprise that white spruce is an important component of several different forest types. In the eastern part of its range, it occurs in pure stands on abandoned fields in New England and the Maritime Provinces (Drinkwater 1957; Sutton 1970) and in moist boreal regions in the north. It more commonly occurs as a major stand component in association with black spruce (*Picea mariana*), red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*), and to a lesser extent with yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*). When white spruce occurs in communities with intolerant species such as trembling aspen, white birch or red pine (*Pinus resinosa*), its greater shade tolerance leads to its assuming increasing importance as succession progresses. In northern Quebec, white spruce is associated with lichen (*Cladonia*), feathermosses (e.g., *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium cristacastrensis*, and *Dicranum* spp.), dwarf birch (*Betula nana*) and many ericaceous plants.

Pure stands are more common in the western part of the range. Associated species in such stands in Alaska include white birch, trembling aspen, black spruce and balsam poplar (*Populus balsamifera*), whereas in western Canada the pure white spruce type is associated with subalpine fir (*Abies lasiocarpa*), balsam fir, Douglas fir (*Pseudotsuga menziesii*), jack pine (*Pinus banksiana*) and lodgepole pine (*P. contorta*). In northwestern Canada and Alaska, closed white spruce stands occur in communities with willows (*Salix* spp.) and buffalo berry (*Shepherdia* spp.), combined either with northern goldenrod (*Solidago multiradiata*) and crowberry (*Empetrum* spp.), or with huckleberry (*Gaylussacia* spp.), dewberry (*Rubus* spp.) and peavine (*Lathyrus* spp.).

In low elevations of western Canada and throughout interior Alaska, white spruce is found in mixed-wood stands with trembling aspen. Common understorey shrubs found under such canopies in Alaska include green alder (*Alnus crispa*), willows, common bearberry (*Arctostaphylos uva-ursi*), highbush cranberry (*Viburnum edule*) and mountain cranberry (*Vaccinium vitis-idaea*). In the Prairie Provinces, the white spruce-aspen type is associated with common snowberry (*Symphoricarpos albus*), red osier dogwood (*Cornus stolonifera*), western serviceberry (*Amelanchier alnifolia*) and western chokecherry (*Prunus virginiana* var. *demissa*).

Mixed white spruce-paper birch stands are also common in western Canada and parts of Alaska. In this stand type, the understorey vegetation usually includes willows, green alder, highbush cranberry,

prickly rose (*Rosa acicularis*), mountain cranberry, bunchberry (*Cornus canadensis*) and Labrador-tea (*Ledum groenlandicum*).

Both the white spruce-aspen and white spruce-white birch stand types are successional stages leading to the pure white spruce type or, in alpine treeline communities, the black spruce-white spruce type. The latter occurs as open stands that, depending on moisture availability, may also support resin birch (*Betula glandulosa*), alders, willows, feathermosses and *Cladonia* lichens, together with Labrador-tea, bog blueberry (*Vaccinium uliginosum*), mountain cranberry and black crowberry (*Empetrum nigrum*).

Where white spruce occurs as an important component of the boreal spruce-fir forest, green alder is the most commonly associated tall shrub, with willows important in western areas, and mountain maple (*Acer spicatum*), showy mountain ash (*Sorbus decora*) and American mountain ash (*S. americana*) important in the east. Common medium to low shrubs are highbush cranberry, red currant (*Ribes triste*), prickly rose and raspberry (*Rubus idaeus*). Ground vegetation commonly includes fireweed (*Epilobium angustifolium*), one-sided wintergreen (*Pyrola secunda*), one-flowered wintergreen (*Moneses uniflora*), northern twinflower (*Linnaea borealis*), naked bishop's cap (*Mitella nuda*), bunchberry, dwarf rattlesnake plantain (*Goodyera repens*), stiff club moss (*Lycopodium annotinum*) and horsetail (*Equisetum* spp.) (la Roi 1967). Many bryophytes occur in these boreal spruce-fir stands. The most common mosses are *Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium cristacastrensis*, *Dicranum fuscescens* and *Drepanocladus uncinatus*. Common liverworts are *Ptilidium pulcherrimum*, *P. ciliare*, *Lophozia* spp. and *Blepharostoma trichophyllum*. Common lichens include *Peltigera apthosa*, *P. canina*, *Cladonia rangiferina*, *C. sylvatica*, *C. alpestris*, *C. gracilis* and *Cetraria islandica* (la Roi and Stringer 1976).

### C. Competition and stand structure

White spruce can exist in various stand types and various stages of succession. Under shade, it is classified as intermediate to tolerant (Nienstaedt and Zasada 1990; Farrar 1995). It will compete with, but not necessarily outperform, other shade-tolerant conifers such as hemlock, black and red spruce, balsam fir, sugar maple and beech. In association with less tolerant early-successional species such as aspen, white birch and lodgepole pine, it may remain a suppressed, understory component, becoming more prominent at later successional stages. White spruce competes poorly against the dense growth of perennials, bracken fern and understory shrubs (Fowells 1965).

While white spruce can form pure stands, particularly in the northwestern part of its range and in the New England States and Maritime Provinces, these stands are not always self-sustaining climax types. Where white spruce pioneers to form even-aged stands on old fields in the Maritimes, advance regeneration is often outnumbered and outperformed by balsam fir seedlings that become a larger component after release (Jablanczy 1979). In mixtures, particularly with less tolerant species, the response to release by disturbance or cutting can be much more successful (Crossley 1976; Berry 1982; Nienstaedt and Zasada 1990).

White spruce can be a component of multi-aged stands, either as pure stands or mixed with other tolerant late-successional conifers and hardwoods. Older age classes in such stands can be as high as 200 to 250 years in Alberta (Day 1972; Nienstaedt and Zasada 1990). As establishment is facilitated by disturbance, the age distribution in such stands is not continuous, but rather grouped according to periods of successful establishment.

#### D. Ecosystem dynamics

Many abiotic factors interact with white spruce in forest ecosystems; some pose a direct threat to the species or cause significant damage. Wild fires can eliminate seed supply and leave a seedbed that is more conducive to the establishment of other species such as lodgepole pine, intolerant hardwoods and even black spruce. Stands established on flood plains may benefit from deposit of seedbed materials or suffer from disturbance to young regeneration. Frost heaving can cause severe damage, particularly to container seedlings planted on finer-textured soils. Root form and depth of white spruce can vary greatly depending on site conditions (Strong and la Roi 1983), and shallow-rooted stands may be prone to windthrow. Periodic storms may cause considerable damage from hail, ice and snow (Dobbs and McMinn 1973; Gill 1974; Sampson and Wurtz 1994). Late-spring frosts can cause significant damage to flushing vegetative and reproductive buds.

While a great number of insects are a natural component of white spruce forest types, few are responsible for large losses. Of these, the eastern spruce budworm (*Choristoneura fumiferana*) is the most destructive. Massive epidemics of this defoliator occur periodically, resulting in heavy mortality and loss of growth, particularly where white spruce is associated with balsam fir (Rose *et al.* 1994). Several other defoliators cause damage or weaken trees on a smaller scale, including the yellow-headed spruce sawfly (*Pikonema alaskensis*), European spruce sawfly (*Diprion hercyniae*), needleminers, needleworms, loopers, tussock moths and the spruce harlequin. Other groups of insects attack buds and shoots of white spruce, including gall-forming adelgids (*Adelges* spp.), spruce bud moths (*Zeiraphera* spp.) and the white pine weevil (*Pissodes strobi*).

Several species of bark beetles, *Scolytidae*, feed and breed in galleries between the bark and wood. The spruce beetle (*Dendroctonus rufipennis*) may attack trees of normal vigour, particularly those which are large-diameter and slow-growing, and has killed large areas (Ostaff and Newell 1981; Hard *et al.* 1983; Werner and Holsten 1984). Generally, though, bark beetles are considered secondary pests, attacking trees weakened by other means such as budworm epidemics, and may be thought of as beneficial in that their feeding hastens the return of wood to the humus (Rose *et al.* 1994).

Warren's collar weevil (*Hylobius warreni*) causes significant damage in scattered areas, girdling smaller trees and making larger trees susceptible to root rots such as *Inonotus tomentosus* (Merler and van der Kamp 1984; Rose *et al.* 1994). The strawberry root weevil (*Otiorhynchus ovatus*) can cause injury to young seedlings, and the root-collar weevil *Hylobius congener* can cause significant mortality to white spruce seedlings planted on recently cut softwood sites (Pendrel 1990; Eidt and Weaver 1993).

Many insect species inhabit or feed on spruce cones and seed, as part of their life-cycle. Significant losses in natural stands and seed orchards are caused in particular by the white spruce cone maggot (*Strobilomyia neanthracina*) and the spruce seed moth (*Cydia strobilella*), and to a lesser extent by the spruce budworm and spruce coneworm (*Dioryctria reniculelloides*), among others (Hedlin *et al.* 1980; Turgeon 1994). Only a few pathogens cause problems with cone and seed production. The spruce cone rust (*Chrysomyxa pirolata*) can cause abnormal development of the cones, reduced seed production, and decreased viability of seeds (Sutherland *et al.* 1987; Myren *et al.* 1994).

Emerging seedlings, particularly in bareroot nurseries, are commonly affected by damping-off fungi, primarily *Fusarium* but also *Pythium*, *Rhizoctonia*, *Phytophthora* and *Cylindrocladium* (Filer and Peterson 1975). Young seedlings may also suffer from Sirococcus blight (*Sirococcus strobilinus*) and infestation by the nematode *Xiphinema bakeri* (Sutherland and Van Eerden 1980).

Spruce needle rust (*Chrysomyxa ledi* and *C. ledicola*) is common wherever the alternate host, Labrador-tea, is found, but extensive damage from the fungus is rare. Spruce broom rust is common, causing abnormal proliferation of shoots to form "witches'-broom", but rarely causes death. Witches'-broom on white spruce is sometimes caused by eastern dwarf mistletoe (*Arceuthobium pusillum*), although black spruce is more susceptible to this parasite. Scleroderris canker (*Gremmeniella abietina*) and cytospora canker (*Leucostoma kunzei*) both affect white spruce, but cause little damage (Myren *et al.* 1994). Massive tumour-like growths are commonly observed on stems and branches in some white spruce populations, particularly near coastal areas, but their etiology is not known (De Torok and White 1960).

Many rot fungi produce stem, butt and root rot in white spruce, including red ring rot (*Phellinus pini*), red belt fungus (*Fomitopsis pinicola*) and Armillaria root rot (*Armillaria mellea* complex). Tomentosus root rot (*Inonotus tomentosus*) and brown cubical rot (*Phaeolus schweinitzii*) infect root systems and can reduce quality and growth, even if direct mortality is often light (Myren *et al.* 1994).

White spruce forest stands commonly provide cover for many species of animals. Some, like moose, deer, black bear and many other fur-bearers, seek shelter in forest habitats but rarely feed on white spruce. Porcupines (*Erethizon dorsatum*) also seek shelter in white spruce forests and may kill small numbers of trees by feeding on the bark (Rose *et al.* 1994). Snowshoe hares (*Lepus americanus*), which commonly feed on foliage of young trees, tend to favour many other conifer species over white spruce (Bergeron and Tardif 1988; Rangen *et al.* 1994), although planted white spruce seedlings are preferred over natural regeneration (Sampson and Wurtz 1994). Many small mammals such as squirrels, mice, voles, chipmunks and shrews are heavy consumers of white spruce seed and can have a major impact on regeneration, while the impact of seed-eating birds, including chickadees, grossbeaks, crossbills, juncos and sparrows, is relatively small (Radvanyi 1974). Many more bird species feed on the many species of insects that inhabit or feed on white spruce trees and associated species.

The hybrid between white and Sitka spruce, *Picea* × *lutzi*, also occurs naturally where these species are sympatric. The hybrid has frequently been made artificially with parents from outside the sympatric area (Fowler 1987a), often in the hope of imparting the resistance of white spruce to the white pine weevil (*Pissodes strobi* Peck). 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).

Many other artificial hybrids have been made successfully (e.g. Wright 1955; Jeffers 1971; Bongarten and Hanover 1982). The hybrid with Himalayan spruce (*P. smithiana*) was inferior to native white spruce when field tested in New Brunswick, but superior in Wisconsin (Nienstaedt and Fowler 1982). Generally speaking, few of these hybrids have shown promise and none has achieved commercial importance (Nienstaedt and Zasada 1990).

## **Section VIII - Summary**

White spruce is an enormously important tree species in North America. It occupies a dominant role in several forest types that span the breadth of the continent, from the northern tree limit south to the Lake States and New England. The species has been successful as both a pioneering and climax type, and is genetically broadly adapted and highly variable. It is an outcrossing, wind-pollinated species that can transfer genes rapidly, and yet it tolerates higher levels of inbreeding when found in small populations.

The ecology of white spruce is extremely diverse, given its tremendous geographic distribution and its genetic plasticity. The typical white spruce ecosystem has a diverse mixture of associated tree species, vascular flora, bryophytes, insects, fungi, birds and animals. Only a very small number of these associated species pose a major threat by competition or direct damage, and white spruce is well-adapted to this complex coexistence.

White spruce is well-suited to artificial regeneration. It is the most commonly planted forest species throughout its natural range. Tree breeding programmes have a long history, and improved material from seed orchards now constitutes a significant portion of deployed reforestation material in some areas. While white 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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