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White Spruce: Taxonomy, Phylogeny, Biosystematics and Plant Geography

A Historical Review by Dr. Roy F. Sutton

Canadian Forest Service
Great Lakes Forestry Centre

Information Report
GLC-X-32

Canada

The Great Lakes Forestry Centre, Sault Ste. Marie, Ontario

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ACKNOWLEDGEMENT

This historical review of white spruce (*Picea glauca* [Moench] Voss), presented in three consecutive Information Reports, represents the lifetime of work and passion of the late Dr. Roy F. Sutton from the Canadian Forest Service (CFS), Great Lakes Forestry Centre (GLFC). Every effort was made to preserve the original work in its entirety.

In 2012, the late Dr. John Scarratt brought Dr. Sutton's manuscript to GLFC's editor Karen Jamieson (retired) for review. The manuscript was edited by Karen Jamieson, Brian Haddon, CFS Petawawa (retired) with the help of David Jamieson, CFS, GLFC. Karen and David made a concerted effort to confirm all the references in the manuscript. Unfortunately, some of the references could not be found due to the age of the material or the language it was published in, so a decision was made to remove these sections.

The document was not published at the time due to its size and the cost associated with French translation. As a result, a decision was made to publish portions of the document on Wikipedia (WIKI) and a GLFC intern was hired to complete this task. Karen matched sections of the manuscript with sections on WIKI so the content could be posted.

In 2022, the GLFC Knowledge Exchange Coordinator, Stan Phippen, received requests for the unpublished manuscript of Dr. Sutton, so he looked at the document to see if there was a way to publish it. A decision was made to split the manuscript, by chapters, into three consecutive in-house Information Reports and publish them over a few fiscal periods to spread out the financial costs associated with translation. The reports each contain two chapters of the original manuscript and follow the original chapter order. The references were separated to reflect only the citations within each report. Scientific names were updated to reflect the currently accepted terminology and an appendix is included in each report illustrating the changes made.

A thank-you goes out to all those people that have worked tirelessly to see this historical review and reports completed. Karen Jamieson, David Jamieson and Brian Haddon completed the monumental task of completing the initial edits to this work. Fiona Ortiz, Knowledge Transfer Forester, GLFC assisted with the final edits and pulling the sections together and preparing them for translation and publishing. Stan Phippen also completed the final edits to the reports, managed the translation and review process, made the reports accessible, laid them out, and sent them for publishing on the Canadian Forest Service publications website. Kim Chapman, GLFC Forest Ecologist, who assisted in updating the taxonomic information. Shelley Hanninen, Library Manager for Natural Resources Canada (NRCan) provided invaluable advice and information in finalizing the report. Drs. Arthur Groot (retired) and Rob Fleming, from the Canadian Wood Fibre Centre (CWFC) and the Canadian Forest Service wrote the foreword for the three reports to summarize and explain the purpose of Dr. Sutton's efforts. Art and Rob provided valuable guidance in preparation of the reports and assistance in understanding the terminology used by the author. Guy Smith, Regional Coordinator and Chief, Knowledge Transfer Policy for the CWFC in Sault Ste. Marie also provided leadership and coordination skills in pulling these reports together. A thank-you goes out to the 2 Billion Tree Commitment staff who provided some of the funding for the translation of these reports. A final thank-you goes

out to the CFS staff in Ottawa who reviewed and edited the French translation for accuracy as well as graphic design assistance. If I have left anyone out in my acknowledgements, my sincerest of apologies.

Thank you,

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FOREWORD

Roy Sutton completed a Ph.D. dissertation at Cornell University in 1968. He titled his 500-page thesis "Ecology of young white spruce (*Picea glauca* (Moench) Voss)".[1] Part of his thesis was a literature review nearly 50 pages long with the heading "Botanic-Ecologic Review of White Spruce". The Canadian federal Forestry Branch published the review the following year as a departmental report: "Silvics of White Spruce (*Picea glauca* (Moench) Voss)".[2]

Although Roy had been carrying out field research on white spruce regeneration prior to his Ph.D. work, his thesis established him as a prominent figure in Canadian silvicultural research. During his long and productive career, Roy continued to devote much of his energy to the problem of white spruce regeneration and to related topics involving root development, site preparation and vegetation management.

Roy nominally retired in 1993 at age 67, but his new status didn't change his work schedule. As an Emeritus Scientist, Roy had fewer administrative demands and more latitude in how he chose to spend his time. And what he chose to do was to follow his passion. The previous year he had stated that "White spruce is my love."[3] Roy now had the time to thoroughly explore all facets of his favourite tree species; he did this by picking up where he left off 25 years earlier.

Roy's work to update and expand his Ph.D. thesis literature review is contained in this series of three Information Reports. Several decades had passed since Roy completed his initial review, so a considerable body of white spruce research had been published in the meanwhile. Roy used his Ph.D. work as a foundation to incorporate the new material; in a number of instances, short sections of his original work appear in this current series of reports, either verbatim or slightly modified.

In addition to updating the review, Roy also expanded its scope. As a retired scientist he had more time than he had as a graduate student to work on a comprehensive treatment of knowledge about white spruce. Additionally, research topics that had received little or no attention up to 1968 (e.g., tissue culture) had subsequently emerged in the scientific literature. The first Information Report provides an overview of white spruce taxonomy, phylogeny, biosystematics and plant geography. While some sections are now dated given subsequent technological innovations (e.g., genomics), this report provides a thorough discussion of then-contemporary knowledge, including much relevant information on the ecology, biogeography and successional status of white spruce.

During the 1970s and 1980s, when Roy was highly active in reforestation research, white spruce was the most widely planted tree species in Canada, accounting for more than one-third of all

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[1] Sutton, R.F. 1968. Ecology of young white spruce (*Picea glauca* (Moench) Voss). Ph. D. thesis, Cornell Univ. 500 p.

[2] Sutton, R.F. 1969. Silvics of White Spruce (*Picea glauca* (Moench) Voss). Canada Department of Fisheries and Forestry, Forestry Branch Publication No. 1250.

[3] MacDonald H. 1992. Dr. Roy Sutton – Book Review Editor and Scientist. Forestry Chronicle 68(3): 379.

planted trees.[4] Much of that planting effort aimed to establish white spruce dominated plantations following clearcutting. As Roy pointed out in the third report of this series, “white spruce that are outplanted in the open in severe boreal climates without a modicum of protective ‘nursing’ can stagnate for decades” and “Regeneration of white spruce on clearcuts in the central boreal forest of Canada is hampered by late spring frosts, planting check, and vegetative competition…”. Nevertheless, white spruce research during that period, including Roy’s, concentrated on the clearcut, plant and tend model.

The focus on this silvicultural model becomes evident in the second Information Report of this series, with sections on vegetative reproduction (cuttings), tree improvement and tissue culture reflecting research to support planting stock production. Much of the material in the physiology section is drawn from research carried out on white spruce planting stock.

The third Information Report includes long sections on elements of the clearcut and plant model: planting stock, site preparation, tending and release. Alternative approaches (e.g., strip and group shelterwood silvicultural systems and mixed species management) are underrepresented in the silviculture section. Newer concepts such as emulation of natural disturbance and multi-cohort management are notably absent.

Roy had not completed this retirement project before he passed away in 2008. He may have never intended to produce a finished work, partly because he enjoyed tinkering, but also because he recognized that, with the continuous appearance of new research, a review is always incomplete. Roy was a meticulous scholar, firmly rooted in traditional approaches to research and publication. For many years, long after word processing software had become pervasive, passers-by could hear the clattering of typewriter keys as Roy sat in his office churning out reports, memos and reviews. So, it is a bit surprising that Roy sought an innovative information age approach to the issue of never-ending reviews.

Not long after Wikipedia (WIKI) was launched in 2001, Roy began to muse about incorporating his review material into a “WIKI”. He was early to recognize the advantages of an online collaborative effort: the product would be widely accessible, current, enduring, and would capture collective knowledge. Roy’s vision was realized posthumously in 2014, when a GLFC intern added a considerable amount of material from Roy’s review to the WIKI page for *Picea glauca*.

This series of Information Reports brings together a vast amount of information about white spruce, and it stands as a monument to Dr. Roy Sutton’s long and dedicated efforts. The value of the work is in no way diminished by the fact that it is not complete, or the fact that it reflects a silvicultural world view that prevailed during Roy’s working life.

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[4] Kuhnke, D.H. 1989. Silviculture statistics for Canada: an 11-year summary. For. Can., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-301.

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1.1 Introduction

A brief introductory overview of plant taxonomy and phylogeny will position white spruce within the plant kingdom and attempt to account for its evolutionary history. Taxonomy is the science dealing with identification, nomenclature, and classification (Porter 1967). Phylogeny deals with the origin and development of taxa, i.e., of any taxonomic entity or group without indicating the category to which it may belong (Lawrence 1955).

Aside from a few tree ferns and cycads that attain tree size, modern trees are either gymnosperms or angiosperms. Gymnosperms appeared in the late Palaeozoic, perhaps 250 million years ago (Spurr and Barnes 1980). By Mesozoic times, conifers had evolved into many forms, and genera had become much more widely distributed than modern genera by the late Jurassic or early Cretaceous period (Li 1953, Spurr and Barnes 1980). The late Miocene ended 13 million years ago, by which time coniferous forests were occupying large parts of the upland areas in Siberia and North America, while mesophytic hardwoods were retreating southwards in response to climatic cooling (Wolfe and Leopold 1967). For the first time, spruce-fir-hemlock (*Picea-Abies-Tsuga)* forest extended from the uplands of Oregon, northward through British Columbia and into Alaska (Spurr and Barnes 1980). Taxonomic repercussions continue from the Pleistocene glaciations, and will no doubt be generated by current global warming.

1.2 Gymnospermae

Plant taxonomists allocate spruces to the class *Gymnospermae* of the division Spermatophyta (seed plants) of the plant kingdom. The Gymnosperms ("naked-seeded plants") produce ovules that are not enclosed within an ovary. This feature separates the Gymnosperms from the other class of seed plants, the Angiosperms, in which ovules are enclosed within an ovary (Warming 1904, Abercrombie et al. 1962).

Many botanists have recognized five orders in classifying the living *Gymnospermae*: (1) Coniferales (or *Coniferae*), (2) Ginkgoales, (3) Taxales, (4) Cycadales, and (5) Gnetales. Dallimore and Jackson (1966) removed Coniferales from the family *Taxaceae* and placed it in a separate order, the Taxales, and divided the Coniferales into six families: (1) *Araucariaceae*, (2) *Cephalotaxaceae*, (3) *Cupressaceae*, (4) *Pinaceae*, (5) *Podocarpaceae*, and (6) *Taxodiaceae*. The Handbook also acknowledged the existence of conflicting views on the limits of the families and genera to be included in the Coniferales and that classification had not yet stabilized.

1.3 Pinaceae

The *Pinaceae* gradually became dominant during the later Miocene, and, in contrast with the *Taxodiaceae*, continued to expand through the Pliocene, and now extend up to the subarctic treeline, where severe continental climates have prevented the establishment of other, less resistant, species. This became possible with the evolution of genera with extreme winter hardiness and a short growing season. In interior Alaska, for instance, most trees cease growth as early as late July, at a 20-hour day length, and the growing season may be as short as 40-50 days (Sakai and Larcher 1987).

The most familiar North American and European representatives of the Gymnosperms belong to the family *Pinaceae* (Lawrence 1955, Dallimore and Jackson 1961, Welch 1991), which conventionally includes 10 genera: *Abies* Mill., *Cathaya* Chun & Kuang, *Cedrus* Trew, *Keteleeria* Carrière, *Larix* Mill., *Picea* A. Dietr., *Pinus* L., *Pseudolarix* Gordon & Glend., *Pseudotsuga* Carrière, and *Tsuga* (Endler) Carrière.

Members of the family *Pinaceae* are mostly evergreen trees and include the spruces (*Picea*). Their linear adult leaves are arranged spirally or, especially on lateral branches, apparently in two or more rows or, in some genera, tufts (Dallimore and Jackson 1961). Their buds are scaly, and male and female flowers are produced separately, either on the same tree or on different trees. Male flowers are long and catkin-like, with numerous stamens, each of which bears two oblong pollen sacs; pollen grains are usually globose with two bladder-like outgrowths that facilitate dissemination by wind. Female flowers are borne in cone-like structures, each flower usually consisting of a lower sterile bract and an upper ovuliferous scale, on the upper surface of which the seed lies “naked”, i.e., unenclosed in an ovary (Dallimore and Jackson 1961). Cones are mostly woody, with spirally arranged scales. Bracts separate from the scales, except at their base, and are generally small and relatively narrow, but sometimes longer than the scales (in *Pinus*, disappearing in the mature cone). Each fertile scale bears two seeds, inverted, and generally winged (Dallimore and Jackson 1966).

Some botanists recognize subfamilies and include the spruces in the *Abietoideae* (van Gelderen and van Hoey Smith 1986).

1.4 *Picea* A. Dietr. – The spruces

Picea, as a generic name, was first applied to the spruces in 1827, prior to which, and sometimes since, spruces have been variously allocated to the genera *Pinus* and *Abies*. Paradoxically, the term *Picea* has on occasion excluded the spruces (Hooker 1896, Welch 1991).

Early writers continually confused spruces with silver firs (Pacific Silver fir (*Abies amabilis* Dougl. ex J. Forbes), European silver fir (*Abies alba* Mill.) and even with pines (*Pinus*) (Edlin 1965). Brunet (1866b) observed that white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P) “have been imperfectly described and are almost always confounded”. Boucher (1664) recognized two kinds of Épinette, green and red; “L’Épinette rouge est d’un bois plus ferme & plus pesant ... elle se dépouille de ses feuilles en Automne”, a deciduous spruce!

As well as taxonomic confusion, aberrant nomenclature contributed its own puzzles. Loudon and Gordon classified spruces under *Abies* and silver firs under *Picea* (Dallimore and Jackson 1961). As if to clarify the matter, the ninth edition of the Encyclopaedia Britannica (Anon. 1879) noted that the classical *Picea* referred to Norway spruce (*Picea abies* (L.) Karst), “i.e., *Abies excelsa* ... evidently often confused by the Latin writers with their *Abies*, the *Picea pectinata* of modern botanists”.

The word “picea” may be derived from the Latin word for pitch pine (Oxford English Dictionary 1971), presumably maritime pine (*Pinus pinaster* Aiton), a native of the Mediterranean region and the mainstay of the European resin industry. Certainly, Hereman (1868) suggested that "picea" derived from "pix", or pitch. Interestingly, Evelyn (1664) inserted the marginal annotation "Pitch" alongside the textual statement that "The Picea is another sort of pine".

The name "spruce" is also very old and of obscure derivation, but perhaps derived from the German *Sprossen* meaning sprouts (Step 1940) or young shoots of the kind used in making spruce-beer (Hall 1949). Edlin (1949), however, suggested that the name derived from the Old French for Prussia or even (Edlin 1962) that it had been an English name for Prussia. The Oxford English Dictionary (1971) recorded such usage, "though now obsolete". Jacombe (1920) noted that Norway spruce became "spruce" by way of "spruce fir" after having been introduced into Britain as "pruce fir", i.e., Prussian fir.

The botanical features that characterize the spruces are: thin, scaly bark; mostly non-resinous buds; and solitary evergreen needles, each borne on a peg-like projection (pulvinus), which gives the spruce twig its diagnostic roughness once the needles have fallen.

1.5 Speciation

About 50 species of spruce have been described by van Gelderen and van Hoey Smith (1986). Dallimore and Jackson (1966) put the number of species described at 60, with "perhaps two-thirds of this number being accepted by most modern botanists, whilst the rest have been, or should be, reduced to synonymy".

Taxonomic difficulties presented by some of the Chinese species have been noted by Wright (1955) and Dallimore and Jackson (1961). Taxonomic uncertainties remain down to the species level in China and western parts of the *Picea range* in North America (Mitton 1995).

Yezo spruce (*Picea jezoensis* (Siebold & Zucc.) Carrière) may be the connecting link between the Old World and the western American spruces, including Engelmann (*Picea engelmannii* Engelmann). It is taxonomically similar to Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and Engelmann spruce, and crosses readily with white spruce (Wright 1955). But Fowler (1966) found that the cross Shrenk's spruce (*Picea schrenkiana* Fisch. & C. A. Mey.) × Yezo spruce was less successful than *Shrenk's* × *white spruce*, and argued that this would be contrary to expectations if Yezo spruce were the connecting link. Fowler considered white spruce to be the more likely link.

In practice, differentiation among species is normally based on one or more morphological characters, but biochemical differences are also useful differentiae, especially to investigate the complexities of hybridization.

Depending on the geographical area and environment in which a species first appeared, and within which its genetic constitution developed through natural selection, a species will exhibit more or less variation across its range. Differentiation into species occurs when divergent characters have evolved by natural selection to produce distinctive taxa. However, many factors contribute to the difficulty of separating botanical species one from another. Quite apart from the incompleteness of knowledge about the ranges of botanical characters within a supposed pure form of a species, especially of one distributed as widely and into such remote areas as white spruce (Daubenmire 1974), there are no objective criteria by which to determine the point at which distinctiveness of character warrants delineation of separate species. Limits on the amount of variation acceptable within a species are arbitrarily determined. Hybridization between species, and among hybrids and parent stocks, adds further complications.

The basic spruce type has changed relatively little during evolution into the present array of species. Although there are many variable characters in spruce, the range of variation in any single character is small, and each may be associated with almost any combination of other characters (Wright 1955). Taxonomically, the genus is more nearly comparable to a single species in pine (*Pinus*), maple (*Acer* L.), or ash (*Fraxinus* L.), than to any one of those whole genera. The excellent crossability suggests that differentiation has been rather small.

However, the “northern” species, including white, black, Engelmann, and Sitka spruces, are generally more variable than species, such as red spruce (*Picea rubens* Sarg.), further south on the migration routes. In each northern species, recognition of geographic races, taxonomic varieties, and taxonomic confusion suggest genetic diversity (Wright 1955). This view is supported by evidence from provenance experiments (e.g., Holst 1953, 1955, 1958a, b), and the profusion of botanical (Table 1.1) and common (Table 1.2) names that have been applied to white spruce.

Nomenclature for species, varieties, and formae is governed by rules laid down in the *International Code of Botanical Nomenclature*, the most recent version of which was adopted in 1993 by the Fifteenth International Botanical Congress, Yokohama, Japan, and published in 1994. The only way of referring to a plant unambiguously is to give the genus, the species, and the authority, i.e., the full or abbreviated name of the person or persons who first correctly described and published the name and description of the plant.

Without fully representative material to work with, taxonomists might easily have assumed greater homogeneity than warranted in describing the botanical characters of species such as white spruce and Engelmann spruce (Daubenmire 1974). Even after good botanical fingerprints have been ascertained, there are no objective criteria by which to determine the degree of variation warranting recognition of separate species.

Table 1. 1. Botanical synonyms for white spruce, Mitt. D.D.G. 14:93 (1908)

Botanical Synonyms
Abies alba Michaux[a] (Not Miller)
Abies alba Michaux fils[g]
Abies americana Du Mont de Courset[a]
Abies arctica Murray[e]
Abies canadensis Miller[a] (The hemlock spruce of Selby [1842] and others)
Abies curvifolia Salisbury[a]
Abies glauca a *curvifolia* Hort[c]
Abies laxa K. Koch[a]
Abies rubra Jaume St. Hilaire[a]
Picea alba Link[a]
Picea canadensis Britton, Sterns and Poggenberg[a]
Picea canadensis (Mill.) B.S.P. (Not (Michx.) Link)[d]
Picea canadensis Koehne[f]
Picea canadensis var. *glauca* (Moench) Sudw.[d]
Picea glauca Beisan.[d]
Picea glauca Voss[f]
Picea laxa Sargent[a]
Picea nigra var. *glauca* Carrière[a]
Picea rubra pusilla Peck[a]
Pinus abies laxa Muenchhausen[a]
Pinus alba Aiton[a]
Pinus alba Lambert[b]
Pinus americana a *alba* Castiglioni[a]
Pinus canadensis Du Roi (Not Linnaeus)[a]
Pinus glauca Moench[b]
Pinus laxa Ehrhart[a]
Pinus rubra var. *arctica* Lawson & Son[a]
Pinus rubra var. *arctica longifolia* Lawson & Son[a]
Pinus tetragona Moench[a]

[a] Sargent 1898
[b] Dallimore and Jackson 1961
[c] Nisbet 1905
[d] Little 1953a
[e] Murray 1867
[f] Lacassagne 1934
[g] Brunet 1866a.

Table 1. 2. Colloquial synonyms for white spruce, *P. glauca* (Moench) Voss

Synonym	References
Black Hills spruce	Little 1953a
Canadian spruce	Forestry Branch 1961
Cat spruce	Forestry Branch 1961
Double spruce[a]	Dallimore and Jackson 1961
Eastern spruce	Little 1953a
Eastern Canadian spruce	Streets 1962
Épinette blanche	Fernald 1950
Épinette verte	Boucher 1664
Field spruce	(author's personal observation)
Labrador spruce	Dame and Brooks 1901
Northern spruce	Forestry Branch 1961; in Labrador, McElhanney 1940
Pine	Forestry Branch 1961
Sapin blanc	McElhanney 1940
Sapinette blanche	in France, McElhanney 1940
Single spruce	Forestry Branch 1961
Skunk spruce	Forestry Branch 1961
Spruce pine	Dallimore and Jackson 1961
Upland spruce	Kenety 1917
Yellow spruce	Forestry Branch 1961

[a] Also applied to black spruce (Josselyn 1672, Forestry Branch 1961)

1.5.1 Chromosomes

The haploid chromosome number 12, found by Sax and Sax (1933) in two species of spruce, was confirmed by Santamour (1960) in 14 spruce species, including white, Engelmann, and red spruces. The basic number is 12 for most conifers. Natural polyploids, mostly 4n but some 3n and 8n, occurred at the rate of 0.007% in white spruce material examined by Winton (1964). In the spruces examined by Sax and Sax (1933), three of the chromosomes were clearly heterobrachial (arms of unequal length), the others "more or less isobrachial".

Conifer genomes are large, and white spruce has one of the smaller genomes, with 2C = 17 pg or 1.7×10^{10} bp (Dhillon 1987) and perhaps 75% of its DNA noncoding. Chromosome identification in white spruce is not possible on morphological features alone; as is commonly the case in conifer species, chromosomes are metacentric and of similar size (Khoshoo 1961, Brown et al. 1993). Nevertheless, Brown et al. (1993) go on to say that there are "sufficient morphological differences (e.g., length, arm ratios, and position of secondary constrictions) between the chromosomes of white spruce to identify 10 of 12 homologous pairs (chromosomes 6 and 7 being the exception, see below). The single B chromosome frequently observed in root tip cells is also readily distinguished, being half the length of the smallest white spruce chromosome".

After developing a fluorescence *in situ* hybridization (FISH) procedure for white spruce, using a biotinylated ribosomal DNA (rDNA) probe from soybean, Brown et al. (1993) localized the major rDNA loci on metaphase chromosomes and in interphase nuclei. Hybridization sites of the biotin-labelled rDNA probe were detected using antibody-fluorochrome conjugates and a confocal laser scanning microscope. Preparing suitable metaphase chromosome spreads is the most critical and difficult aspect of FISH experiments in white spruce; cell walls have to be digested completely, no hybridization being observed even when biotinylated genomic DNA was used as a probe (Brown et al. 1993). The rigidity of white spruce root tips and the "quite long" length of the chromosomes posed problems in obtaining metaphase preparations with well-separated chromosomes (Brown et al. 1993). The rDNA probe hybridization sites were detected as green fluorescence from the FITC conjugated antibodies, whereas non-hybridizing chromosomal sequences fluoresced red owing to the propidium iodide counterstain. White spruce was found to possess one of the highest numbers of rDNA loci yet reported among plant species, with at least 12 and possibly 14 rDNA sites, and with one site present on each of seven separate chromosome pairs. Of 17 metaphases observed, 19% revealed 11 rDNA loci, 60% revealed 12 loci, and 11% revealed 13 loci, but Brown et al. (1993) suspected that white spruce has 14 loci on seven homologous chromosome pairs. Both metaphases on which 13 hybridization sites were found were of better quality than the others analyzed in their study. Ten of the 13 hybridization sites observed were associated with secondary constrictions which distinguish pairs 2,3,4,5, and 10. The FItC signal on chromosome 2 was consistently the most intense, indicating a greater number of rDNA repeats at that locus. Two of the remaining hybridization sites were found on chromosomes 6 and 9, not associated with secondary constrictions. The last hybridization site was found on overlapping chromosomes; and since "all chromosome pairs that do not hybridize to the rDNA probe can be identified by morphology (chromosomes 1, 7, 8, 11, and 12), the overlapping chromosomes are, by the process of elimination, chromosomes 6 and 9" (Brown et al. 1993). One rDNA locus may have been inaccessible to the probe because of the overlapping of the chromosomes, or, alternatively, since a hybridization signal was only rarely observed on chromosome 9 in other metaphase preparations, and since the signal-to-noise ratio was consistently high, it is plausible that the number of rDNA repeats at the chromosome 9 locus may have been at the limits of Brown et al.'s (1993) detection system.

1.6 White spruce

White spruce is one of five species of spruce that are native to Canada, along with: red spruce, Sitka spruce, Engelmann spruce, and black spruce. Black and white spruces have immense boreal-wide distributions between which, because of differences in site preference and phenology, there is very little interaction. Sitka and white spruces, however, hybridize in the limited area where their ranges overlap. More massive interaction takes place between Engelmann and white spruces.

1.6.1 Genetic variation

Evolutionary theory predicts that species having large populations and broad geographic ranges will display high amounts of genetic variability, a consequence of the positive relationship between population size and both the occurrence and the accumulation of mutations (Mitton 1995). White spruce is an obvious candidate for encompassing great genetic variability. The theory is substantiated by evidence from electrophoretic analysis of multiple forms of enzymes, which has shown that conifers are one of the most genetically variable groups of plants, and that populations of most species store high levels of genetic variability. However, although having some distinct advantages over morphological markers for surveys of genetic variation in forest populations, enzyme electrophoresis has three major drawbacks: (1) about 27% of amino acid substitutions result in surface charge alteration, so causing a large percentage of substitutions to remain as hidden variation undetectable by the method, (2) electrophoretically detectable variations may not constitute a truly random sample of the genome because they represent primarily structural genes, and (3) the biological significance of enzyme variation observed in natural populations has not been unequivocally established (Boyle and Yeh 1988).

Patterns of genetic variation within a species will differ among genetic loci, due to the differential effects of evolutionary forces. Furnier and Stine (1992) examined variation at six nuclear allozyme loci and a chloroplast DNA (clDNA) locus in a range-wide sample of more than 400 white spruce trees from 22 populations. Chloroplasts are inherited paternally in white spruce. Greater differentiation among populations at the cpDNA locus than at the nuclear loci might be expected as a consequence of drift and gene flow. For certain sizes of populations, this difference in effective population size can result in drift acting to differentiate populations for an organelle locus while not acting on a nuclear locus. Also, gene flow by seeds will more effectively act to homogenize populations for nuclear loci than for organelle loci because every seed carries two copies of every nuclear gene for every one effective copy of an organelle gene. Furnier and Stine’s data showed significantly greater interpopulation differentiation for the cpDNA locus than for the allozyme loci, a result consistent with expectations. The mode of inheritance in interpreting observed patterns of genetic variation for genetic markers must therefore be taken into account.

The open wind-pollinated monoecious reproductive system, the longevity of individuals, and the lack of spatial discontinuity of large populations of most coniferous species are powerful factors predisposing conifers to the accumulation of variability (Hamrick et al. 1979, 1981; Mitton 1983; Tremblay and Simon 1989). This variability will develop under differential selective pressures generated by various environmental factors, including climatic heterogeneity and soil differences, which, together with the effects of isolation by distance, may lead to genetic substructuring and differentiation among populations (Mitton 1983).

Small and isolated populations at the margin of distribution, such as white spruce found at its northern limit at the treeline in eastern Canada, might be expected to be particularly subject to inbreeding and genetic drift, with less genetic variability compared with populations in the central parts of the range (Soulé 1973). But, as Tremblay and Simon (1989) pointed out, studies on the effect of marginality on populations of other coniferous species (Tigerstedt 1973, Lundkvist 1979, Yeh and Layton 1979, Guries and Ledig 1982) have given mixed results, and marginal populations of black spruce disclosed high levels of genetic variability (Desponts and Simon 1987), indicating that gene flow between those isolated populations remained sufficient to override the effect of geographic isolation.

Genetic variation is also promoted by the extension of immense geographical ranges into widely diverse natural environments (Mitton 1995). An incomplete appreciation of the botanical nature of a species complicates investigation and interpretation of speciation and hybridity. The handicap faced by taxonomists dealing with meagre collections of material for examination was cited by Wright (1955) as a major difficulty in taxonomic investigations.

Genetic variation can be divided into additive and non-additive components (Zobel and Talbert 1984). Additive variance arises from the cumulative effects of alleles at all gene loci influencing a characteristic or trait. Tree improvement work with northern conifers has emphasized additive genetic effects in random mating populations, usually within seed orchards. The assumption implicit in this approach, that other components of the genetic variation are not worth exploiting, was challenged by Boyle and Yeh (1988). Non-additive variance includes the effects of both the interaction of specific alleles at a gene locus (dominance) and the interaction among gene loci (epistasis). Significant levels of dominance deviation or specific combining ability will result in suboptimal genetic gains from purely additive strategies. Thus, non-additive genetic strategies must be exploited to maximize gains from tree improvement and to capitalize on advances in asexual reproduction, including micropropagation (Boyle and Yeh 1988).

Genetic variation can be examined by several techniques, including provenance studies, in which tree seedlings grown from seed collected from various sources and planted together in “common gardens” to yield estimates of heritability (the proportion of total phenotypic variation attributable to genetic variation) for virtually any measurable character. For example, white spruce seedlings from seed of 27 seed sources selected along latitudinal gradients in eastern and western Alberta, and along four elevational gradients in the foothills of western Alberta, were grown in each of two controlled environments simulating the photoperiod, temperatures, and humidities during a growing season in northern and southern Alberta (Dancik 1978). Even after one growing season, there were significant ($P < 0.01$) differences among sources in each environment. Such provenance studies enable differences among genotypes and the effects of environmental gradients to be detected, but do not allow causal genes to be identified.

Investigations initiated by Li et al. (1997) set out to determine the genetic structure of white spruce from Quebec and southeastern Ontario; to develop models describing patterns of genetic variation among provenances and their relationship with environmental variation; to test the validity of the models; and to guide seed transfer and delineation of breeding zones for white spruce in Quebec. Data collected from each of 63 provenances (composed of 263 separate families, 1-5 per provenance) included seedling heights at various ages, 1-year branch number, and 3-year bud burst and bud set. Significant differences were found for each trait among provenances, and among families within provenances. Provenances and families within provenances accounted for similar amounts of genetic variability. Regression models explained 19% to 65% (average 47%) of provenance variation and showed mainly a south-north cline pattern of variation and a lesser west-east cline. Li et al. (1997) concluded that within the area of study, white spruce provenances could be transferred 2°-3° in latitude from south to north and several degrees of longitude with little risk.

Whereas Li et al. (1993, 1997) found that white spruce provenances and families within provenances in Quebec and southeastern Ontario accounted for similar amounts of genetic variability for growth and phenology traits, Nienstaedt and Riemenschneider (1985) and

Tebbetts (1981) found 63%-75% of genetic variation in white spruce in the U.S. Lake States (Minnesota, Wisconsin, and Michigan) and Ottawa Valley (Ontario) white spruce planted in Maine attributable to differences among provenances.

No significant differences are detected among provenances for many traits in provenance samplings restricted to relatively small areas (2,000-60,000 km^2) in the eastern part of white spruce distribution (Dhir 1976; Pollard and Ying 1979a, b; Khalil 1985; Corriveau et al. 1991). This is an indication that white spruce provenances in much of the eastern distribution are only moderately differentiated despite the species' wide ecological amplitude.

Clonal variation in morphological variables, mineral nutrition, root growth capacity, net photosynthesis, tannin distribution, and cuticular and epicuticular wax features, were assessed within four families of white spruce obtained through controlled crosses among selected genotypes. For each family, plants were produced either from seeds (zygotic) or by somatic embryogenesis to produce three clones. Within a family and under similar growth conditions, several clones differed significantly from the zygotic seedlings in height, root collar diameter, needle dry mass, branch density, shoot dry mass, root dry mass, and length of needles. Branch density (the number of first-order branches per cm height) of zygotic seedlings and clones varied from 0.8 to 1.4, and from 0.6 to 1.3 branches/cm, respectively. Mean needle length of zygotic seedlings and clones ranged from 11 mm to 14 mm and from 11 mm to 17 mm, respectively. For many variables, e.g., height, dry mass of new roots, needle dry mass and branch density, differences among clones were significantly greater than differences among zygotic seedlings within a family. Tannins were more abundant in needles of clones than in needles of zygotic seedlings. In some clones, tannins occurred as a ribbon along the central vacuole, whereas in others they appeared as aggregates dispersed in the vacuole. Within a family, N, P, and K showed considerable variations in their use efficiency. Interclonal variations were observed in both root growth potential and net photosynthesis. Variations in growth and physiology reflect genetically determined differences among clones within a family (Lamhamedi et al. 2000).

Other techniques can identify specific genes or sequences of DNA from seeds and needles (cf. Tigerstedt 1973; Bergmann 1973; Lundkvist 1979; Adams 1981; King and Dancik 1983; Cheliak and Pitel 1984; Cheliak et al. 1987, 1988). Enzyme analysis, by various methods including electrophoresis and chromatography, has proved to be a powerful tool for characterizing enzymes, which are proteins that catalyze a great variety of chemical reactions. Enzymes that have the same catalytic function, but which originate from different organs or even different cell compartments of the same organ, can be separated into different enzyme proteins having the same specificity. Synonymous terms isoenzyme and isozyme (Markert and Möller 1959, Bergmeyer et al. 1963) are applied to an enzyme that differs in its protein structure, and therefore in the optimum conditions for its action, but has the same specificity as another enzyme. A set of isozyme variants are *allozymes*, i.e., they are coded by alleles at a locus (Brown and Moran 1981).

Paper chromatography has been used (Hanover and Wilkinson 1970) to evaluate phenols in needles of white and Sitka spruces, as well as suspected hybrids from the Skeena River area in

British Columbia, but assessments of genetic variation in forest trees have been particularly helped by the use of electrophoretic analyses, which can detect molecular differences in enzyme proteins (Copes and Beckwith 1977, Tobolski and Conkle 1977, Joly and Adams 1983). For instance, isoenzymes for a number of enzyme systems in germinants from seeds collected in pure stands of white spruce, Sitka spruce, and seeds from stands of spruce of uncertain genetic composition, were determined by Copes and Beckwith (1977) using electrophoretic apparatus similar to that described by Conkle (1972). Linhart et al. (1981) used the same method to investigate protein polymorphisms.

Monoterpene compositions were used by Wilkinson et al. (1971) to divide white spruce into two major groups, western and eastern, along the 95° W longitude separating Manitoba and Ontario, but a later range-wide study revealed no relationships between allozyme variation and geographic origins of populations (Furnier et al. 1991).

Isozyme surveys of natural populations offer a practical way of examining and quantifying genetic variation in conifers (Yeh and El-Kassaby 1980, King and Dancik 1983). Genetic variation, as measured by the number of alleles (i.e., either of a pair or series of alternative, contrasting Mendelian characters controlled by genes occurring at the same locus in homologous chromosomes) at a locus k, is $k = 4Nu + 1$, where N is the population size and u is the neutral mutation rate (Hartl and Clark 1989). Similarly, the predicted heterozygosity, H, also increases with population size:

$$H = 4Nu/(4Nu + 1).$$

A set of statistics devised by Nei (1973) enables the total genetic variability to be partitioned among and within subpopulations independently of genotype frequencies. As explained by Yeh and El-Kassaby (1980), HT measures the total genetic variation sampled over all populations and is a function of the overall allele frequencies. An allele is either one of a pair, or any of a group, of possible mutational forms of a gene at the same locus in homologous chromosomes (Ford-Robertson 1971). Hs is an estimate of the average amount of genetic variation within a subpopulation in terms of its average heterozygosity. If all subpopulations form a single panmictic unit (resulting from a general mingling of all manner of ancestral qualities and tendencies) and there is no essential differentiation among them, then all alleles will be equally distributed over the geographic range, and Hs will equal HT, an unusual circumstance in nature. Natural populations tend to differentiate into subpopulations by mutation, selection, random drift, or restricted gene flow.

Yeh and Arnott (1986) investigated enzyme patterns at 18 loci from a sample of nine seed lots that included two white spruce, three Sitka spruce, and four putative hybrid spruces from the coast-interior zone of reported introgression in British Columbia. Sufficient differentiation of allelic frequencies was found to separate the two species as well as the suspected hybrid seedlots. Of the 18 isozymes: seven (*Dia-1*, *Dia-3*, *Est*, *Mdh-1*, *Mdh-3*, *Pgm*, and *6pg-2*) exhibited no between-species variation; five (*Aat-1*, *Aat-2*, *Idh*, *Mdh-2*, and *Pgi*) exhibited moderate differentiation between the two species, and, with the exception of *Mdh-2*, possessed unique alleles that were species-specific albeit in low frequencies; and six (*Dia-2*, *Gdh*, *G6p*, *6pg-1*, *6pg-2*, and *Adh*) were highly differentiated between the two species, the latter having a unique allele (88) in high frequency in white spruce.

DNA probes have been used to analyze hybrid and mixed seedlots of spruce containing species mixes and hybrids of white × Engelmann spruce (known as interior spruce (*Picea glauca* var. *albertiana* S. Brown)), as well as Sitka spruce. Sutton et al. (1991) investigated the utility of chloroplast DNA (cpDNA) restriction fragment length polymorphisms for identification of the species composition of these seedlots. A BamHI library of Sitka spruce cpDNA was constructed in pUC8. Two clones were selected by hybridization with a 10.5 kb BamHI fragment of white spruce cpDNA, which is unique to interior spruce. One of these (pSS4) containing a 4.3 kb BamHI fragment was tested in screening of pure and mixed seedlots of Sitka and interior spruce. The probe was used successfully to screen total DNA samples to reliably identify and quantify the cpDNA composition of 2-week-old germinants using a sample size of 0.5 g and allows less than 5% species contamination to be detected. Analysis of seedlings from a hybrid seedlot showed that both chloroplast types could be found in some individuals, which suggests that chloroplasts can be biparentally inherited in *Picea* species.

Geographic variation of interior spruce (Jaquish 1982) was demonstrated by Roche (1969) in genecological studies of seedlings in the nursery stage and into the field. The dominant geographic variable determining genetic differentiation was the elevation of seed source, with high elevation sources completing shoot elongation and becoming dormant earlier, and producing less dry matter than low elevation sources. Clinal variation with latitude was weak although growth behaviour of northern sources was similar to that of high elevation sources. Similar responses to elevation source occurred in 13-year-old field provenance tests (Jaquish et al. 1984.)

Even material obtained by somatic embryogenesis, i.e., cloning by tissue culture techniques, cannot be assumed to be inherently homogeneous in genetic composition (Eastman et al. 1991). The term *somatic* indicates that the embryos develop asexually. Somaclonal variation reflecting genetic instability in tissue culture has been well documented (Lassner and Orton 1983). However, Eastman et al. (1991) monitored the integrity of the original interior spruce genotype during tissue culture and found a dearth of somaclonal variation in somatic embryogenesis; no somaclonal variation occurred during the initiation and throughout subsequent 2.5-year maintenance of the parent line cultures. Furthermore, each of the two interior spruce genotypes gave strongly similar ABA-dependent developmental profiles between the parent line and subclone cultures, which suggests that the morphology of a spruce embryogenic culture is primarily influenced by genotype rather than somaclonal variation (Webster et al. 1990, Eastman et al. 1991).

Early appreciation of the importance of provenance, such as Lyons' (1925) advocacy of using white spruce seed of local origin for plantation establishment, took a long time to mature into systematic and formal protocols. In time, however, provenance studies led to broad application of controls and standards for large-scale seed collection and distribution of seed and planting stock (Yeatman 1990). Further genetic improvement in productivity, quality, and uniformity of planted trees has been sought through diverse breeding programs within defined breeding zones or regions, programs that are founded on large genetic variation in economic traits found from tree to tree within selected regional populations. The strategies adopted reflect: differences among species in genetic, ecological, physiological, and silvicultural opportunities and constraints; economic factors of value and scale; and the wide range of institutional priorities, perceptions, and human resources (Yeatman 1990).

1.6.2 Variety (botanical variety)

A variety of a species is generally distinguished as the result of minor variations in such characters as length of leaves, number of leaves, and cone size. Especially within a widely distributed species, natural variation commonly leads to the development in a portion of the range of a visually distinguishable characteristic differing somewhat from that exhibited by individuals elsewhere in the range. If the differentiation is insufficient to have stimulated a taxonomist to register a claim for specific rank, the population could be described as a variety under the rules of the *International Code of Botanical Nomenclature*. A few varieties of white spruce have been described but, for many purposes, recognition of varieties of white spruce serves no useful purpose (Daubenmire 1974, Nienstaedt and Zasada 1990). As Huxley (1939) put it, "A name confers a false sense of importance on the named groups", while a false label is all too readily accepted as a guarantee of genetical uniformity to a greater extent than is justified by the character or characters offered as distinguishing a taxonomic unit (Langlet 1962).

Daubenmire's whole-range investigation, with samplings of seven populations of white spruce beyond the range of Engelmann spruce, 13 populations beyond the range of white spruce, and 13 populations within the area of sympatry, produced no evidence to support the recognition of the variety segregates that had been proposed for white spruce, "except insofar as the hybrid swarms may deserve nomenclatural recognition". However, the botanical varieties that have been described in the literature are mentioned for the sake of completeness.

The Black Hills spruce (*Picea glauca* var. *densata* Bailey) of South Dakota is typified by dense bright-green to bluish-green foliage and a somewhat compact growth form (Nienstaedt 1965). The Porsild spruce (*Picea glauca* var. *porsildii* Raup)[5], with rather smooth but resin-blistered bark similar to that of balsam fir (*Abies balsamea* (L.) Mill.) (Raup 1947, Farrar 1995) and a relatively broad crown, occurs widely in the Yukon Territory, northern Alberta, and Alaska (Little 1953a, Wright 1955, Nienstaedt 1965). Daubenmire (1974) pointed out that crown shape is "very subjective" and that smooth bark with resin blisters also occurs in Engelmann spruce.

1.6.2.1 Albertiana spruce

Stewardson Brown's *Picea albertiana* sp. nov. S. Brown (Brown 1907) never gained more than fleeting recognition as a new species but has been intermittently accorded varietal status, e.g., by Sargent (1922) and Rehder (1940). But although Elwes and Henry (1906-1913) also referred to *albertiana* as a variety they had the prescience to acknowledge the possibility of hybrid

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[5] Editor's note (Phippen 2022); this species is now accepted as Porsild spruce (*Picea glauca* (Moench) Voss) but the scientific name was left unchanged in the document as the author described it (https://data.canadensys.net/vascan/name/Porsild%20spruce?).

origin. However, Daubenmire (1974) has commented that Brown must have chosen "a most remarkable specimen" on which to base his description. Indeed, subsequent searches (e.g., by McKinnon [1938]) have found no evidence in support of Brown's *albertiana*, which now clearly seems to have been a product of introgression between white and Engelmann spruces in the region of overlap. Introgressive hybridization involves repeated backcrossing of the hybrids to one or both parents (Anderson 1949). The varietal name *albertiana* is now of historic interest only[6].

P. albertiana sp. nov. S. Brown, (Brown 1907) clouded the taxonomic picture during the early decades of the 20th century. Notwithstanding Brown's "two months' experience with the tree ... in the region from Banff, Alberta, to Field, B.C.", there is little doubt that Brown's new species was based on an individual—"a most remarkable specimen" (Daubenmire 1974)—of the hybrid swarm between white and Engelmann spruces (Wright 1955, Taylor 1959). Daubenmire also cited McKinnon's (1938) emphatic report that in extensive trips through the Canadian Rockies McKinnon and his team, which included A.B. Recknagel, Professor in Forest Management, Cornell University, and B.G. Griffith, Instructor in Forestry, University of British Columbia, had found no trace of *albertiana* during intensive sampling (19.6 km of strip in five areas and 119 ha in two additional areas) in the Upper Fraser River Valley. Recknagel (1939) commented that although it had always been supposed that Engelmann spruce was the prevailing species of spruce in the northern interior of British Columbia, in the so-called Cariboo Region, recent reconnaissance studies by McKinnon, Griffith, and himself had "definitely determined" that white, not Engelmann spruce is the prevailing species of spruce along the Prince Rupert Division of the Canadian National Railway, between Prince George and McBride, British Columbia, along latitude 54° N between 120° and 123° W longitude.

Although Brown (1907) stated that the cones of *albertiana* were shorter, broader, and darker than those of typical *Picea canadensis* Mill. B.S.P. [=*Picea glauca*], Horton (1956) found no evidence for this "either in a sample of white spruce specimens from the immediate area of the type specimen, or in an extensive comparison of western, eastern and far northern white spruce material at large".

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[6] See editor's note above.

1.6.3 Cultivar (horticultural variety)

The naming of a cultivated variety (cultivar) is governed by the 1962 *International Code for the Nomenclature of Cultivated Plants*. Cultivar names begin with a capital letter and are enclosed within single quotation marks, whereas the names of varieties and formae are written in lower case without quotation marks (Boom 1965). The hundreds of horticultural varieties (den Ouden and Boom 1965, Krüssmann 1985) are not considered further here.

Most of the taxonomic complications relating to the North American spruces occur in the western parts of the continent. The spruces in eastern North America present fewer problems. The black spruce/red spruce complex (Morgenstern and Farrar 1964) probably originated in a different group of more ancient migration from the morphologically distinct white spruce (Wright 1955). There are no confirmed hybrids of white and red spruce or the reciprocal (Gordon 1976).

1.7 Hybridization

Hybridization, the crossing between populations having different adaptive gene complexes, is common in natural populations of many woody-plant groups (Spurr and Barnes 1980), including the *Pinaceae* (van Campo-Duplan and Gaussen 1950). Natural hybrids often occur in zones of contact or overlap between species (Remington 1968), as well as in disturbed habitats to which neither parent is well adapted (Anderson 1948, 1949). Hybridization between species of different genera, e.g., between Sitka spruce and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), has been reported (van Campo-Duplan and Gaussen 1950, Vabre 1954), but the literature is silent about intergeneric liaisons involving white spruce.

1.7.1 White x Sitka spruce

The discovery of natural hybrids between white spruce and Sitka spruce in exotic plantations in Denmark (Larsen 1934, Thaarup 1945, Bornebusch 1946) no doubt prompted searches for hybrids in the area of range overlap. Hybrids were subsequently found on the Kenai Peninsula and nearby Chugach Mountains, Alaska (Little 1953b, Copes and Beckwith 1977) and in the Skeena, Nass, and Bulkley River valleys of western north-central British Columbia (Roche 1969, Woods 1988). The hybrid is synonymously named *Picea* × *lutzii* Little, *Picea glauca* × *sitchensis*, or Lutz spruce. Introgressive hybridization occurs.

For white and Sitka spruces, an average crossability of greater than 50%, determined as:

$$\%\ \text{Crossability} = \frac{\text{No. of full seeds/cone white} \times \text{Sitka}}{\text{No. of full seeds/cone white} \times \text{white,}} \times 100$$

based on 7 years of experimentation, indicate a close relationship between the two spruces (Fowler 1987).

Sitka × Engelmann hybrids probably occur in southwestern British Columbia (Klinka et al. 1982). Hybridization might even have produced *P. glauca* × *engelmannii* × *sitchensis* spruce (Douglas 1975, Coupé et al. 1982, Coates et al. 1994).

1.7.2 White × black spruce

Evidence of natural hybridization between white and black spruces where their ranges overlap was reported by Little and Pauley (1958), Larsen (1965, 1989), Roche (1969), Dugle and Bols (1971), and Krajina et al. (1982). The hybrid origin of the "Rosendahl" spruce in Minnesota described by Little and Pauley (1958), was confirmed chromatographically by Riemenschneider and Mohn (1975), but other studies (Gordon 1976, Parker and McLachlan 1978) have cast doubt on the reality of white spruce × black spruce hybridization. Certainly, hybridization in the southern parts of the common range is rare, at least in part because female flowers of the two species are seldom concurrently receptive (Little and Pauley 1958, Riemenschneider and Mohn 1975, Nienstaedt and Zasada 1990). The two species here are readily separable by stable and distinctive features. Hybridization is apparently more common in the northern parts of the common range, e.g., north of 57° N along the Alaska Highway (Roche 1969) and along the northern treeline (Larsen 1965), which suggests that what might be called "season compression" might sometimes result in concurrent receptivity. Vegetation in the forest-tundra ecotone at Ennadai Lake, Northwest Territories, includes "Apparently intermediate forms between *P. mariana* and *P. glauca*… in abundance" (Larsen 1965). Comparison of the leaf oil composition of the Rosendahl spruce (*Picea glauca × mariana*) with the two parent species showed significant differences that reflected the hybrid origin of the Rosendahl spruce (von Rudloff and Holst 1968). Further chromatographic evidence of the hybrid origin was advanced by Riemenschneider and Mohn (1975), but Gordon (1976) remained unconvinced about the reality of the cross. And although spruce trees with characteristics superficially intermediate between those of white and black spruces are fairly common in wetland areas of central and northern British Columbia, Coates et al. (1994) commented that these trees are unlikely to be hybrids. Natural hybridization between these species in that area is believed to be rare or non-existent.

1.7.3 Introgression

Introgression or *introgressive* hybridization is the term applied to the process whereby hybrids between distinct species then hybridize with each other. Introgression refers to the gradual infiltration of germplasm of one species into that of another as a consequence of hybridization and repeated backcrossing, i.e., the crossing of a hybrid with either of its parents (Anderson 1949). Spurr and Barnes (1980) describe the probable process:

"Introgression is presumably achieved in three phases: (1) initial formation of F1 hybrids, (2) their backcrossing to one or other of the parental species, and (3) natural selection of certain favourable recombinant types (Davis and Heywood 1963). This is simply gene flow between species. If hybridization occurs between two closely related species, the probability of gene flow is higher than when the species have diverged sufficiently to have well-integrated, but different, gene pools. Genes from one population will be incorporated into the gene pool of the other (regardless of rank—species, subspecies, variety) if they improve the well-integrated harmony of the foreign gene pool. If they tend to disrupt the harmony, their frequency will be reduced; this is merely natural selection in action (Bigelow 1965). Not surprisingly, we find frequent reports of introgression between the closely related spruces of western Canada... and particularly white spruce and Engelmann spruce". (Nienstaedt and Teich 1972)

Introgression has been widely accepted as accounting for much of the variation found in some genera. However, Spurr and Barnes (1980) cautioned that such acceptance has probably been "more out of faith and intuition than from fact", and that "Commonly, introgression has been postulated or inferred rather than compellingly demonstrated". Often the range of variability of the parent species and F1 hybrid is not well known, and there is no easy way of distinguishing F1 hybrids from backcrosses (Dancik and Barnes 1972), or backcrosses from parents. The botanical characters of woody plant populations are immensely variable, and before the extent of hybridization and gene flow can be estimated with any degree of confidence detailed studies are needed of variation of both parents and hybrids using standardized collections and many characters. Gordon's (1976) detailed study of variation in black and red spruces and F1 hybrids found very little introgression and much less hybridization than had been reported previously.

Nevertheless, there is little doubt that introgression is the key factor controlling variation in the white spruce/Engelmann spruce complex in western Canada (Li et al. 1997). A hybridity index used by Wright (1955), for instance, provided evidence of widespread introgression between white and Engelmann spruces in the area bounded by latitudes 51° and 59° N and longitudes 109°and 124° W. Isozyme analyses have confirmed introgressive hybridization between white and Sitka spruces in the Skeena area of British Columbia (Copes and Beckwith 1977).

In range-wide provenance tests conducted in northeastern North America, western populations have been outperformed by eastern populations (Li et al. 1997).

1.7.4 White x Engelmann spruce

Interaction between white and Engelmann spruces occurs where their ranges overlap, i.e., through large parts of British Columbia, Montana, and Wyoming, with typical white spruce predominating at elevations lower than about 1,500 m, and typical Engelmann spruce predominating at elevations higher than about 1,800 m, both merging into introgressive hybrid swarms at intermediate elevations (Nienstaedt and Zasada 1990).

The taxonomic relationship between white and Engelmann spruces is very close (La Roi and Dugle 1968), even though "the pure forms of white and Engelmann spruce in British Columbia are distinct taxonomically and occupy quite distinct ecological niches" (Roche 1969). Hybridization takes place freely with introgression. Daubenmire (1974) has elaborated:

> "Although *P. glauca* spans the range from lowlands to alpine timberline in Alaska, in a southerly direction it becomes more and more restricted to lower altitudes. *P. engelmannii*, in contrast, is a tree principally characteristic of the subalpine forest belt throughout its range. However, slender peninsular extensions follow ravine bottoms kept cool by the downward flow of cold air and water, so that at the lower extremity of its total altitudinal spread, it overlapped the altitudinal range of *P. glauca*. Hybridization followed by backcrossing has produced populations of intermediate character with respect to physiology as well as morphology, so that there is strong continuity in a cline that extends from the foothills, where P. glauca has been altered little by introgression, to alpine timberline, where *P. engelmannii* exists in what appears to be nearly pure form."

In northern British Columbia and Alberta, white spruce occurs in its typical form, an obvious entity. Another obvious entity, Engelmann spruce, occurs in its typical form at higher altitudes in the southern interior of those provinces (Horton 1959, Taylor 1959). The plexus involving white and Engelmann spruces in their area of overlap has long exercised taxonomists.

Horton (1959) also commented on Brown's designation of the slender crown form of *albertiana* as characteristic: "In western Alberta both narrow and broad-crowned spruce can be seen growing together, although the former certainly predominate. Northwards in the [Canadian] Territories, however, far beyond the recorded range of Engelmann spruce, the white spruce [crown] is typically narrow."

Many similarities are apparent among the populations of inland spruce in western Canada. Taylor's (1959) view that "even such diagnostic features as mean cone length, and shape and character of the scales, are merely the extremes of a series of intermediates" led him to conclude that the phylogenetic relationship between white spruce and Engelmann spruce is best indicated by regarding them as subspecies of a single species. Hustich (1953) proposed an even broader amalgamation, with both white spruce and Norway spruce assuming subspecies status:

- *P. glauca*
  - ssp. *americana* (= *P. glauca* in the broad sense)
  - ssp. *abies* (= *P. abies* and *P. obovata*)
  - var. *europaea* (= *P. abies* of most authors)
  - var. *obovata* (= *P. obovata* of most authors)

Daubenmire (1974), who assumed that in such a scheme Engelmann spruce would rank as a subspecies or variety, suggested that "entrenched usage" would frustrate any proposal for such revision, albeit "perhaps theoretically desirable".

Recognition of the two species, white spruce and Engelmann spruce, and of hybrid swarms in the area of overlap, now seems to be generally accepted. This monograph on white spruce, therefore, includes information about Engelmann spruce and the white × Engelmann hybrid swarms that would seem to contribute to an understanding of white spruce.

Wright's (1955) index of hybridity confirmed postulated widespread introgression between white and Engelmann spruces in the area of overlap covering 8° of latitude and 15° of longitude. The process produces individuals that can vary morphologically from one typical extreme through any intermediate to the other typical extreme. In British Columbia and Alberta, the term "interior spruce" is commonly applied to such material.

Intermediate forms were studied by Taylor (1959) in the Banff, Upper Columbia Valley, and the Cranbrook–Moyie Lake areas of southeastern British Columbia and adjacent Alberta. He examined the variability between individual trees of certain mensural characteristics of needles and cones collected from about 70 "randomly selected" trees. There were no significant differences between samples taken from the north side of crowns vs. those from the south side, nor between needles from reproductive vs. those from vegetative twigs. Mean length of needles was 13.5 mm ± 2 mm, with coefficients of variability ranging from about 11 to 20. Needle lengths varied greatly on the same tree. Dimensions of cones, however, were less variable; mean diameter was 13.5 mm with a standard deviation of slightly more than 1 mm and coefficients of variability from 6 to 10. Cone lengths averaged about 42 mm ± 3.5 mm and similar coefficients of variability to those of cone length. The cone scale was found to be the most obvious difference between white and Engelmann spruces. Taylor described the scales of white spruce as obovate-triangular, somewhat stiff and with entire margins, with a rounded or somewhat flattened apex. The scales of Engelmann spruce were described as thin and somewhat papery, wedge-shaped, with wavy to erose (as if gnawed) margins, and commonly erose to truncate at the apex. He interpolated three classes of intermediates between these extremes (Taylor, 1959).

Needle length did not differ significantly among trees classed by cone type, but "Engelmann spruce needles tended to be straight and slender, acuminate and somewhat square in cross section, while those of white spruce were firmer, often curved and rounded at the apex, tending to be dorsiventrally flattened or triangular in section" (Taylor 1959). Needles with these characteristics in other combinations were classed as "intermediates".

Taylor (1959, table 3) also studied twig indumentum. He found that any of the five cone types could occur on trees with pubescent twigs, but the white spruce cone type occurred with equal frequency on both glabrous and pubescent twigs.

Wright (1955), using a hybridity index, found evidence of introgression between latitudes 51° and 58° N and longitudes 109° and 124° W. In Alberta, Horton (1956) found that only the shape of the cone scale and the nature of the shoot indumentum (any hairy covering or pubescence) were reliably diagnostic characters separating the two species. Horton suggested that those differences did not warrant separation into species. Taylor (1959), too, regarded white and Engelmann spruces as sub-species within a single highly variable species. Certainly, there is no discontinuity between the typical white spruce at low elevations and typical Engelmann spruce at high elevations; the variation is gradual and continuous (Roche 1969, Daubenmire 1974).

Cone scale morphology serves best to differentiate between white spruce and Engelmann spruce (Horton 1956, 1959; Taylor 1959). Shape, margin, texture, degree of roughness when wet, and phyllotaxy have been examined, but Daubenmire (1974) found the most definitive basis for separation to be the amount of scale extending beyond the seed wing. Quantification of these characters to judge degree of hybridity in the field is impracticable, but the amount of scale projecting beyond the seed wing (the "free scale") is both easily measured and highly reliable (Daubenmire 1974).

Determinations of "free scale" and "percentage of free scale" were made on a scale removed from the middle of water-soaked modal cones and pressed flat. Length and width of scale were measured and the length-width ratio calculated. Length of free scale is the distance from the imprint of the seed wing (disregarding the discoloured halo that often surrounds the actual imprint) to the tip of the cone scale; percentage of free scale is the length of free scale expressed as a percentage of the total length of the scale.

The more easily used field character, absolute length of free scale, obtainable from an open cone even without cutting, was found to be 99% reliable by Daubenmire (1974), who characterized the pure species thus:

White spruce	***Engelmann spruce***
Twigs usually glabrous; needles to 25 mm long; ovuliferous cones to 79 mm long, their phyllotaxy nearly always 3-5, never 5-8; ovuliferous scales to 16.9 mm long and 13.3 mm wide, 0.91-1.74 times as long as wide, scale extending beyond the seed wing 0.4-3.0 mm.	Twigs usually pubescent; needles to 50 mm long; ovuliferous cones to 79 mm long, their phyllotaxy variable, but often 5-8; ovuliferous scales to 21.0 mm long and 16.3 mm wide, 0.86-2.32 times as long as wide, scale extending beyond the seed wing 2.7-8.6 mm.

Differentiation between white and Engelmann spruce as described above is sufficiently clear to support the view that their phylogenetic relationship is that of separate species, especially when Pleistocene and Holocene evidence is taken into account. While the differences between white and Engelmann spruce are not large enough to invalidate Taylor's (1959) view that they are best regarded as subspecies of a single species, that there are two species seems now to be generally accepted.

1.7.5 White × Engelmann × Sitka spruce

Hybridization occurs between the white–Engelmann spruce complex and Sitka spruce where their ranges overlap in northwestern British Columbia, along river valleys, particularly those of the Nass and Skeena Rivers (Coates et al. 1994, Coates 2000). The situation is clearly depicted by a map presented by Coates (2000), modified from Krajina et al. (1982). In the middle Skeena–Nass transitional area, where most spruce appear to be a hybrid between white and Sitka and sometimes Engelmann spruce, all spruce are commonly referred to as "hybrid spruce" (LePage[7] 2001, personal communication).

1.8 Artificial hybrids

Verification of hybridity of some hybrids involving white spruce as the female is less difficult than many others; e.g., the combination white × Yezo spruce had one or two incomplete stomatal rows on the lower surface of needles and five to six rows on the upper surface, whereas the female parent normally has three to four rows on all surfaces while the male parent lacks stomata on the lower surface. Verification of hybridization is often much more difficult.

White spruce has been successfully crossed artificially with blue spruce (*Picea pungens* Engelm.) (Farrar 1995), Shrenk's spruce, Koyama's spruce (*Picea koyamai* Shirasawa*)*, Yezo spruce, and, more weakly, with dragon spruce (*Picea asperata* Masters), Serbian spruce (*Picea omorika* (Pančić) Purk.) (Farrar 1995) and Norway spruce (Fowler 1966, Santamour 1967, Ogilvie 1972). During the period 1946-1963, while the Genetics Project of the USDA Forest Service's Northeastern Forest Experiment Station was located at the Morris Arboretum in Philadelphia, Pennsylvania, the many spruce hybrids produced by Wright (1955) included crosses of white spruce as the female parent with *engelmannii*, *jezoensis*, *koyamai*, and *pungens*. The hybrid white × Engelmann spruce exhibited the branch pubescence of the male parent, especially on or near the sterigmata. And several characters of blue spruce, e.g., sharp needles, acute buds,

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loose bud scales, and lack of skunk odour, were expressed in white × blue spruce hybrids (Santamour 1967).

Of six interspecific crosses attempted by Fowler (1966), only Schrenk's × white spruce was reasonably successful. All five trees used as female parents produced some viable seed following pollination with white spruce, but the success of this cross differed markedly among the five parents, only one of which could be considered moderately cross-compatible, with 27.6 viable seeds per cone.

The hybrid Schrenk's × white spruce was described by Fowler (1966). At 6 weeks of age, hybrid Schrenk's × white spruce seedlings had red (Munsell Color Chart 2.5R 4/6) hypocotyls, similar to those of white spruce (2.5R 4/8), but differing from the yellow (5.0Y 7/8) hypocotyls of Schrenk's spruce, the female parent. The hybrid hypocotyls faded to a yellowish yellow-red (7.5 YR 6/6) at about 8-10 weeks of age. The hybrids were similar to the female parent in respect of cotyledon length and were slightly curved upwards, i.e., intermediate between the strongly upcurved cotyledons of Schrenk's spruce and the horizontal, almost straight cotyledons of white spruce. There was no significant difference in number of cotyledons between hybrids and parents. The terminal shoots of white spruce seedlings were strongly orthotropic (tending to form a vertical axis), those of Schrenk's spruce plagiotropic (with shoots tending to take positions at right angles to light rays), and the hybrids intermediate. In respect to total height at 9, 15, 18, and 22 weeks, the hybrids were clearly superior to either parent.

Though confined to the Ala-Tau and Thian Shan mountains of Turkestan in central Asia, Schrenk's spruce was judged by Fowler (1966) to be "fairly closely related" to white spruce.

Tri-hybrid crosses involving Lutz spruce have been made with Sakhalin spruce (*Picea glehnii* (F. Schmidt) Mast.) (2%), Lijiang spruce (*Picea likiangensis* (Franch.) Pritz.) (1%), Serbian spruce (6%), red spruce (0.04%), and black spruce (0.04%) (Gordon 1988). Progeny of Rosendahl spruce crossed successfully with red spruce (1%), and, depending on parent, backcrossed poorly with white spruce (0.08%) and well with one black spruce (10%).

Failure of Lutz spruce to backcross with Sitka spruce (Gordon 1988) gave added credence to Gordon's (1984) contention that backcrossing with several spruce hybrids was proving much less successful than expected.

1.9 Population studies

Genetic variation within populations has been estimated morphometrically and biochemically. Progeny tests or provenance tests in which individual tree progeny have been kept separate have commonly demonstrated high levels of within-population variation compared with variation among populations, including the white spruce–Engelmann spruce complex (Kiss 1986) and white spruce in Quebec (Corriveau et al. 1986).

1.9.1 Morphological separation of spruce species

Cone scale characters, especially length, width, length, i.e., width ratio, length of free scale (the distance from the imprint of the seed wing to the tip of the scale), and the percentage free scale (length of free scale expressed as a percentage of the total length of the scale), were found by Douglas (1975, cited by Coates et al. 1994) to be the most useful features for distinguishing among the spruces in British Columbia. Douglas's measurements agree closely with those taken by Daubenmire (1974) in samples from across the whole range of the species.

A summary of the taxonomic key devised by Douglas for identifying *Picea* species and their hybrids in British Columbia, published by Coupé et al. (1982), is given in Coates et al. (1994, table 3).

Scale samples should be taken from the middle of each of 10 cones from each of at least five single trees from a population and then averaged (Coupé et al. 1982).

For trees lacking cones, other characteristics are needed to distinguish among species and their hybrids. Yeh and Arnott (1986) examined nursery-grown seedlings and found that needle serration and the pattern of terminal budset with different day lengths were the most reliable characters for distinguishing between seedlots of white spruce, Sitka spruce and their hybrids in northwestern British Columbia. Hybrids with few or no needle serrations were grouped with Sitka spruce, and those with a high degree of serration were allied to white spruce.

Woods (1988) was able to categorize seedlots as Sitka spruce, interior spruce, or hybrids by comparing growth performance of containerized seedlings subjected to extended day length (interior spruce regime) with those receiving no supplemental light (Sitka spruce regime). Sitka spruce seedlings grown under extended photoperiod tend to become excessively tall, whereas interior spruce grown without extended photoperiod set bud early and did not reach target size. Hybrid seedlots are intermediate but tend to do better under the Sitka spruce regime (Coates et al. 1994).

Jeffers (1974) compiled a morphological key for identifying spruce seedlings in the United States.

1.9.2 Chemosystematic separation of spruce species

Biochemical methods, such as terpene and isoenzyme analysis have been used increasingly in recent times to distinguish among species and their hybrids. Analysis of isoenzymes (isozymes) has become an indispensable tool for genetic studies of inter-tree and inter-stand relationships and is becoming increasingly important for identifying seedlots (Coates et al. 1994).

Whereas morphological characters are controlled by many genes, each of which may have several different effects, often influenced strongly by environmental variation, terpenes and isozymes are controlled by relatively few genes and are not greatly influenced by environmental conditions. El-Kassaby and White (1985) published an annotated bibliography of work on the analysis and identification of isozymes and their utility in investigation of genetic variability.

The variation among spruce along an altitudinal gradient near Bow River, Alberta, was studied by Ogilvie and von Rudloff (1968) using needle terpene analysis. Terpenes differed between white spruce and Engelmann spruce, and there was an altitudinal gradient of intermediate forms. With blue and Engelmann spruces, at least, monoterpenes from mature trees were more useful than those from seedlings (Schaefer and Hanover 1986).

The existence of introgressive hybridization between white and Sitka spruces in the Skeena area has been confirmed by isozyme studies (Copes and Beckwith 1977, Yeh and Arnott 1986). Mitton and Andalora (1981) found no evidence of hybridization between Engelmann spruce and Colorado Spruce in the Rocky Mountains.

Isozyme studies have been used to establish the identity of seedlots in Alberta and British Columbia (King and Dancik 1983, King et al. 1984, Yeh and Arnott 1986). The seedlot classification presented by Yeh and Arnott (1986) differed enough from that of the British Columbia Ministry of Forests to raise questions about the accuracy of the criteria used by the province to classify hybrid spruce seedlots.

Mass screening and identification using terpenes and isozymes is simple and inexpensive, and while initial species identification of stands is more easily accomplished with traditional taxonomic methods based on morphology, the use of biochemical methods serves to clarify relationships where morphological identification leads to ambiguities (Copes and Beckwith 1977, Schaefer and Hanover 1986, Yeh and Arnott 1986).

1.9.3 Population genetic variation, structure, and evolution in Engelmann spruce, white spruce, and their natural hybrid complex in Alberta

Rajora and Dancik (2000) examined genetic variation, structure, and evolution of 12 populations of putative Engelmann spruce, white spruce, and Engelmann–white spruce natural hybrids from the sympatric areas and two populations of white spruce from the allopatric areas in Alberta using 23 allozyme loci coding for 13 enzymes in needles. Most of the alleles were widespread, but unique alleles were found in nine of the 14 populations. No species-specific allele was observed. However, allele frequency differences were observed between the putative Engelmann and white spruce populations at a number of loci. Frequencies of 13 alleles showed significant correlation with altitude, those of 11 alleles showed correlation with latitude, and those of three alleles showed correlation with longitude. On average, 66.2% (99% criterion) of the loci were polymorphic, the number of alleles per locus was 1.88, the number of alleles per polymorphic locus was 2.88, and the observed and expected heterozygosities were 0.063 and 0.184, respectively. Genetic variability of allopatric white spruce, putative Engelmann, sympatric white spruce, and hybrid populations was quite comparable. The mean FST estimate was 0.123 for the total populations. Canonical discriminant functions separated four putative Engelmann spruce populations from the fifth putative Engelmann spruce population, and from the allopatric and sympatric white spruce and sympatric putative hybrid populations. A cluster analysis from genetic distances generally separated allopatric and sympatric white spruce populations from the putative Engelmann spruce and hybrid populations. A Wagner tree of the 14 populations produced two main branches; one branch consisting of two allopatric and two sympatric white spruce and one putative hybrid populations, and another branch consisting of the remaining nine spruce populations representing putative Engelmann spruce, putative hybrids, and sympatric white spruce. Putative hybrids showed lower distances to white spruce from the canonical discriminant analysis, whereas they showed lower distances to putative Engelmann spruce from the genetic distance analysis. Rajora and Dancik (2000), citing high allozyme genetic identities between putative Engelmann and white spruce and allelic differentiation related to altitude in Alberta, suggested, as Horton (1956) and Taylor (1959) had done earlier, that Engelmann spruce might best be considered a subspecies of white spruce, with white spruce named as *Picea glauca* ssp. *glauca* and Engelmann spruce named as *Picea glauca* ssp. *engelmannii*.

Isozyme variation, reflecting gene diversity within and among populations, summarized from the literature by Boyle and Yeh (1988) was moderate to high for most species. The percentage of polymorphic loci ranged from 51% for Sitka spruce to almost 92% for both black spruce and Norway spruce. For white spruce, Cheliak and Pitel (1984) reported 85.7%, Yeh and Arnott (1986) 83.4%.

1.9.4 Provenance

The terms *provenance*, *geographic source*, and *geographic race* denote the original geographic area of origin occupied by individuals supplying seed or other propagules and, by extension, the provenance of the seed or propagules themselves (Callaham 1964, Jones and Burley 1973).

The woody-plant literature abounds in references to genetically mediated differences in morphological and physiological characters. Much of the information comes from provenance tests designed to find provenances suitable for planting in particular localities (Spurr and Barnes 1980). Major adaptive responses, primarily along latitudinal and altitudinal gradients have been found, with genetic differences demonstrated in such diverse characters as height growth, foliage color, dry-matter content of seedlings, stem form, rooting habit, resistance to insect attack, fruitfulness, tracheid length, and phenology. A clinal pattern is evident for most of these characters. Portions of a cline, sometimes designated as *ecotypes* or *varieties*, may be useful as a basis for selecting seed-collection zones, but the use of “varieties” in this regard, while convenient, may convey an unwarranted impression of uniformity within the named group (Spurr and Barnes 1980), and in any event conflicts with the definition sanctioned by the *International Code of Botanical Nomenclature*. Langlet (1962) observed trenchantly: “As regards the study of provenances, the study of ecological variability within species, the relation between this variability and the influence of the environment, and the reaction of different populations to transfer to an environment foreign to them, it is unnecessary and confusing to have the species crisscrossed by a jungle of taxonomical subspecific verbiage. It is sufficient to indicate the native locality”.

The determination of genecological norms and patterns of variation within and among populations is essential both for the sound genetic management of seed while conserving existing genetic diversity, and for the development and deployment of populations improved by breeding (Yeatman 1990).

White spruce provenances have differed widely in growth and survival in field tests covering a broad spectrum of sites in Canada and the United States, but, as shown by Dhir (1976), performance is highly site-dependent. Dhir tested 49 open-pollinated white spruce progenies from eight Upper Ottawa Valley stands at three sites within 16 km of each other and found almost a two-fold difference between the best and the poorest 10-year height growth and survival (6 years after planting). The dominating influence of site on progeny performance was very inconsistent from site to site.

Early provenance tests established in the late 1950s through the mid 1960s identified very productive seed sources in southeastern Ontario, including Beachburg (45.7°N, 76.8°W) and Peterborough (44.1°N, 78.0°W) (Nienstaedt 1969, Teich 1973, Teich et al. 1975, Khalil 1974). Some of these provenances performed well far from their source, e.g., in three experiments in Nova Scotia, Ottawa Valley provenances were in top rank at 5 years (Morgenstern et al. 1988) but were less successful in Newfoundland (Hall 1986). Nevertheless, in Newfoundland trials involving 31 white spruce provenances, results 25 years from seed and planted as 2+2 stock, provinces from the Ottawa Valley and Quebec were consistently superior to others that ranged from New Brunswick to northwest Ontario and south to Michigan (Hall 1986).

Provenances from southeastern Ontario have performed particularly well in regional trials in the Lake States and eastern Canada (Nienstaedt 1969, Teich 1970, Hall 1986). In British Columbia, too, fast-growing provenances that have performed well in a variety of environments have been identified in the “wet-belt transition zone”, extending from east of Williams Lake southwards to Shuswap Lake. The Birch Island provenance is one of the superior provenances appearing to show promise for extensive planting throughout interior British Columbia, south of latitude 55° N (Lester et al. 1990). Trials at Dryden Nursery, northwestern Ontario, examined 3-year height growth of white spruce raised from seed collections of 74 sources (including Beachburg) from southern Manitoba through eastern Ontario, with seed from Birch Island, British Columbia included in the trial (Skeates and Irving 1988). Birch Island and Beachburg provenances placed first and second in the trial with mean heights of 134% and 114% of those of local provenances. Performance of trees of different origins in older Ontario trials has been found to be highly correlated with early plantation performance (Murray and Skeates 1985).

Larger regional and range-wide studies were subsequently established (Ying 1980, Murray and Cheliak 1985). Some 49.1 ha of white spruce provenance tests were established between 1958 and 1987 in Canada (Ying and Morgenstern 1988).

Evidence from chemosystematics, cone morphology, and seedling phenology suggests a major east-west division of the range at about 95° W, which would accord with an assumption of glacial refugia in Yukon and Appalachia (Ying and Morgenstern 1988). Variation within each division is clinal along latitudinal gradients (Nienstaedt and Teich 1972). Hierarchical sampling within limited geographic areas showed high variation tree-to-tree, and low variation stand-to-stand in growth (Dhir 1976), seedling phenology (Pollard and Ying 1979a, b) and cone morphology (Khalil 1975).

Provenances of white spruce have been found to differ in a considerable number of genetically determined characteristics, including rate of height growth (Holst 1960, 1962 , Genys 1965, Nienstaedt 1969), wood density (Holst 1960, 1962), branch angle (Holst 1962), response to soil calcium ion concentration (Farrar and Nicholson 1967, Cunningham 1971), germination temperature thresholds (Fraser 1971), nuclear volumes and DNA content (Mergen and Thielges 1967, Miksche 1968), and needle, branch, and bud characteristics (Nienstaedt and Teich 1972).

Highly significant differences between provenances were found in a 25-year provenance trial that examined dry mass productivity and wood density variation (Corriveau et al. 1988). Of the total wood density variation, 20% was attributable to provenance, while 80% was due to tree-to-tree variation within sources and to experimental error, results that were confirmed by a second study conducted in natural forests. No geographic trend in wood density was found within the sampled portion of the natural range of white spruce in Quebec, but it was observed that provenances of some regions produce a wood of higher density than the average. Several fast-growing populations with high wood density were recorded. Substantial gains in dry mass production could be expected by selecting rapid-growing populations then selecting within those populations for trees producing wood of greater than average density.

Of 36 characteristics measured on seedling white spruce from 28 range-wide provenances, only four were without significant (mostly $P < 0.01$) variation among provenances (Nienstaedt and Teich 1972). Patterns of variation suggest clinal trends and adaptive responses to selective pressures imposed by variation in precipitation, photoperiod, and temperature regimes (Farmer et al. 1983). Local provenances are not necessarily the most productive (Holst 1969, Teich 1969), but in the absence of reliable information about seed of non-local provenance, local seed from desirable phenotypes is recommended (Jeffers 1968, Holst and Teich 1969, Roche et al. 1969).

Analysis of the 10-year height data for white spruce progeny trials for the East Kootenay and Prince Rupert selection unit (Kiss 1988) confirmed results from the Prince George selection unit trials (Kiss 1986) in British Columbia. The major conclusions from the Prince George selection unit were summarized as follows:

1. Differences in height and survival among families were highly significant. Mean height of the best 25% (44) of the families was 10.7% greater than the mean for all the progenies, which can be characterized as realized gain. The difference in survival between the best and poorest 25% of the families was 5.8%, a substantial difference considering the high overall survival rate of 93%.
2. For height growth, family heritability was 0.68 ± 0.40, while individual heritability was 0.26 ± 0.19.
3. The best and poorest performing families can be identified at an early age. Over 80% of the families identified as being in the top 25% at age 3 were still in the same group at age 10. Correlation between 3- and 10-year family heights was $r = 0.8466$.
4. Genotype-environment interactions were non-significant.

At Prince Rupert, realized gain using the top 25% of families was 8%. At East Kootenay, realized gain was 16% (Kiss 1988). As at Prince George, most of the good general combiners were identifiable at plantation age 3 (6 years from seed), and genotype – environment interactions were small.

In the United States, the term *seed source* has been used synonymously with provenance (Schopmeyer 1974, p.867), but failure to recognize the difference between provenance and seed source can be costly (Zobel and Talbert 1984). The terms *seed source* or *origin* should be used to refer to the locality of collection of a seed lot, as distinct from the original geographic area of origin.

1.9.5 Race

Geographic race is a subdivision of a species consisting of genetically similar individuals, related to a common descent, and occupying a particular territory to which it has become adapted through natural selection (Wakeley 1959, cited by Zobel and Talbert 1984). Race denotes within-species variation, which has evolved naturally in different parts of the natural range of a species under the influence of differences in latitude, altitude, rainfall patterns, or other environmentally induced variation of consequence in temperature, moisture, soil, or day length (Holzer 1965). Racial variation is exhibited within populations that have developed when grown together in a uniform environment.

Zobel and Talbert (1984) also cautioned against using "race" to mean anything but provenance. They suggested that terms such as *altitudinal race*, *climatic race*, *physiological race*, *physiographic race*, and *edaphic race* may confuse by wrongly implying a singular cause of variation.

1.9.6 Land race

A land race is a population of individuals that, through natural selection, has become adapted to a specific environment to which it was introduced and not formerly native. The concept is important in relation to the use of provenances outside their native environments. Regeneration in the new environment uses seed or other propagules from introduced trees that have been successful there. The greater the number of generations of growth and selection, the better will be the land race developed. According to Zobel and Talbert (1984), "The group of best-adapted individuals with desirable growth and form are collectively referred to as a *land race*."

1.9.7 Ecotype

An *ecotype* is a group of plants of similar genotype that occupies a specific ecological niche. Edaphic ecotypes occur in white spruce in eastern Canada (Murray and Skeates 1985). Limestone ecotypes have been demonstrated in both the laboratory (Farrar and Nicholson 1967) and the field (Teich and Holst 1974). White spruce of provenances from soils of limestone and granitic parent material and planted on calcareous and granitic soils were taller 15 years after planting on soils consistent with their provenance, than when provenance and planting site soils differed. At the limestone site the limestone provenances were 10% taller than the granitic provenances, and at the granitic site the granitic provenances were 9% taller than the limestone provenances. This interaction was significant ($P < 0.001$) and the superior growth of limestone provenances on limestone soil and of granitic provenances on granitic soil supports the hypothesis that there are white spruce limestone ecotypes (Teich and Holst 1974).

1.9.8 Cline

A cline is a gradient in a measurable characteristic (Huxley 1938), especially one associated with an environmental gradient. Each cline is based on a single characteristic, and there may be many different clines within a given population. Zobel and Talbert (1984) presented a useful tabular comparison of clines and ecotypes.

2. PLANT GEOGRAPHY

The historical and present-day distribution of plant taxa, the location of their origins, studies of dispersal and migration, and the evolution and present distribution of flora are grist for the mill of plant geography (Spurr and Barnes 1980) or "ecologic plant geography" (Daubenmire 1978), which aims to record and explain how plant taxa have come to be distributed as they are (Good 1964). Essentially geographical, plant geography is concerned primarily with the correlation between plants and the distribution of external conditions of their habitat; while plant ecology is essentially physiological and is concerned particularly with the interrelationships among plants and with their habitat (Good 1964).

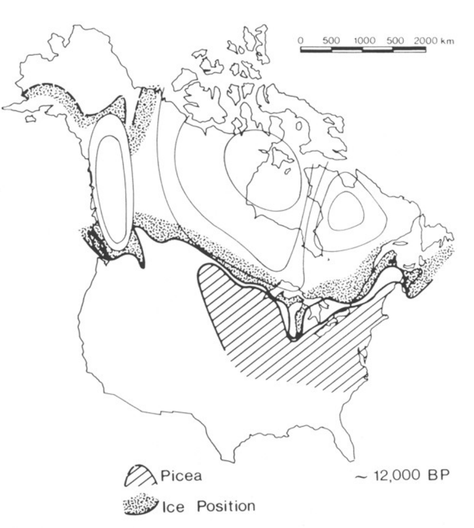

Figure 2. 1 The approximate extent of *Picea glauca* at 12,000 BP with the ice front position, after Prest (1970).

White spruce probably survived the most recent glaciation in two widely separated refugia: one in the northwest of the continent, the other in the east (Nienstaedt and Teich 1972). It is now "well established that *Picea*, including *P. glauca*, persisted during the latest glacial epoch, centred in 18,000 BP, in a wide belt of the United States, between latitudes 40° and 35°, and extending from northern Kansas through Missouri, Iowa, Illinois, Pennsylvania, and North Carolina (Wright 1981, Baker et al. 1982, Watts 1983, Dort et al. 1985)", (Ritchie and MacDonald 1986).

The taxonomically recognized interior spruce may well have survived in the Yukon refugium and spread from there to meet the typical element in Manitoba (Halliday and Brown 1943). Genetic evidence based on monoterpene analysis (Wilkinson et al. 1971) and DNA content (Miksche 1968) support the idea of two founding populations (Nienstaedt and Teich 1972, Farmer et al. 1983). Comparison of isoenzymes of formic (FDH), glutamic (GDH), and lactic (LDH) dehydrogenases and cationic peroxidases in seeds from southwest Yukon, including glaciated and non-glaciated regions, and from a glaciated part of similar area in southern Ontario, supported the conclusion that the Yukon refugium was a centre of genetic diversity. However, white spruce in both of the two Yukon regions were genetically more diverse than were those in southern Ontario (Tsay and Taylor 1978). The northward post-glacial spread of white spruce was steady in eastern and mid-western parts of North America (Watts 1983); the northeastern spread from full-glacial centres in Pennsylvania and adjacent states into maritime Canada began about 14,000 BP and reached the Atlantic coast of central Labrador by about 7,000 BP, at an average annual rate of advance of 200-300 m (Ritchie and MacDonald 1986). The northernmost extension of white spruce in eastern Canada reached a maximum 3,000-4,000 BP, and has subsequently retreated.

In the Great Lakes region, there is good evidence that the treeline advanced northward as the ice front retreated, at an annual rate of about 200 m. Ritchie and MacDonald (1986) gave an excellent detailed synthesis of the evidence.

A study of pollen and macrofossil stratigraphies in three lakes situated along a transect across the boreal forest and Great Lakes–St. Lawrence forest ecotone in northern Ontario determined that the palaeoecology of the early postglacial boreal forest was dominated by white spruce, and found hypsithermal ecotonal movements within the region, with species showing individualistic responses to climate change and soil development, and contrasting vegetation histories between Clay Belt and upland Shield controlled by complex climatic/edaphic functions (Liu 1990).

Ritchie and Macdonald's account of the anomalous western region merits extended quotation:

> "White spruce was recorded at the Rosebud site in Nebraska, outside the area occupied by Laurentide Ice, by Watts and Wright (1966). It dominated the site at 12,600 BP, as it did elsewhere in the northern prairie region during the late-glacial, and its northwesternmost record, as macrofossils, is from the Hafichuk site in southern Saskatchewan (Ritchie and De Vries 1964). Its northern range at about 12,000 BP is shown in (Ritchie and MacDonald's 1986) Figure 2.1. About 11,000 BP it reached the Riding Mountain upland in Manitoba, recorded there as macrofossils and pollen (Ritchie 1964). A very similar chronology of arrival and expansion was recorded by Mott (1973) from adjacent sites in south-central Saskatchewan... By 11,000 BP *Picea* had reached the Lofty Lake site in central Alberta, and we assume that at least some of the pollen recorded there by Lichti-Federovich (1970) is of white spruce. A white spruce cone dated 10,400 BP was recorded at Wedge Lake near Calgary, Alberta, by MacDonald (1982).
>
> The recent investigation of a set of sites between northern Alberta and the vicinity of Great Bear Lake has provided the basis for tracing the fossil record of white spruce from its limit in central Alberta at 11,000 BP to its modern configuration (MacDonald 1984). Ice retreated rapidly in the region (Andrews 1973) and by 10,000 BP a broad tract of land extending from central Alberta to the Mackenzie Delta (Denton and Hughes 1981) was available for occupancy by plants. At Lone Fox Lake in north-central Alberta the white spruce percentage curve rises sharply after 10,000 BP and reaches its maximum value (30%) at about 8,500 BP. The nearby site, designated Yesterday Lake, was sampled at wider intervals and the pollen of the spruce species was not distinguished, but the *Picea* curve rises to its maximum at about 9,500 BP. The Snowshoe Lake site in northeastern British Columbia yielded a collective *Picea* curve with an abrupt rise from 0% to 60% at roughly 9,900 BP. The white spruce rise at the Wild Spear Lake site in the Caribou Mountains near the northern border of Alberta could not be dated precisely because the sediments at that level are marly. However, radiocarbon dates on organic matter above and below the white spruce rise indicate that it occurred at approximately 9,000 BP. The Lac Ciel Blanc site near the northern border of British Columbia yielded a spruce percentage curve rise between 9,910 and 9,350 BP. The white spruce rise occurred at 9,050 BP at Lac Mélèze, Northwest Territories. A recent report by Slater (1985) shows a steep spruce curve from 0% to 40% at a level in the sediment dated as younger than 10,300 and older than 7,510 BP.

> A collation of the pertinent data for the Lower Mackenzie River Region had shown that the mean arrival date for *Picea* at 22 sites is 9,095 BP, and white spruce has been distinguished as the dominant spruce at most of these sites (Ritchie 1984a). Recent additions to the Mackenzie Delta region sites, by Ritchie (1984b and one unpublished site), confirm the finding that the registration of white spruce pollen began shortly before 9,500 BP and increased rapidly to maximum values by about 8,500 BP.
>
> We conclude that there is no evidence for a steady, time-transgressive spreading of spruce along the broad 2,000 km long tract that became ice free between the Cordillera and the Laurentide ice, from central Alberta to the Beaufort Sea. Rather, spruce expanded rapidly during only a few centuries following roughly 9,500 BP.
>
> By contrast with the above pattern, recent investigations in Alaska show that spruce spread into eastern Alaska from the north-west Yukon at about 9,500 BP (Ager 1975; the Tanana Valley sites) and subsequently spread slowly westward across the Interior and into the Brooks Range, reaching western Alaska only at 5,000 BP (Ager 1983, Brubaker et al. 1983, Anderson 1985, Edwards et al. 1985). White spruce pollen has been distinguished in several of these investigations, and in each instance it is the first of the spruces to be registered and to increase.
>
> In summary, the pollen data indicate that the chronological pattern of white spruce registration followed by rapid increase is anomalous in the Western Interior of Canada and requires some particular explanation. Elsewhere, as others have either noted or implied, an explanation in terms of a gradual, time-transgressive spreading from a wide, southern, full-glacial refugium appears to be adequate.” (Ritchie and MacDonald 1986).

Nevertheless, the hypothesis that white spruce spread from a full-glacial northwestern, Beringian refugium, in addition to the southern area, and that the modern populations of white spruce result from convergent spreading and mixing of Beringian and southern populations (Raup and Argus 1982) is not supported by secure fossil evidence that would establish the presence in northwestern Canada and adjacent Alaska of white spruce between 10,000 and 25,000 BP (Ritchie and MacDonald 1986).

Another hypothesis, which would account for an explosive surge of white spruce populations along the length of the western interior corridor by virtue of small, low-pollen-producing populations of white spruce in isolated salubrious localities, also appears unlikely (Ritchie and MacDonald 1986). The hypothesis proposed by Ritchie and MacDonald (1986) is that strong and persistent southeasterly winds along the retreating ice front, beginning about 10,000 BP, facilitated dispersal of seed, some of which could have skittered long distances over snowpack or ice during the winter after seedfall. Such dispersal would supplement aerial dispersal. This hypothesis is supported by the discovery of fossil dunes in northwestern Saskatchewan that are interpreted as primary parabolic dunes developed under the influence of essentially unidirectional and probably strong southeasterly winds of adiabatic origin (David 1981). Significant quantities of seed are dispersed under the influence of high winds (Dobbs 1976). If the rate of fall of white spruce seed is about 1.2 m/sec, as determined for red spruce seed (Siggins 1933), then seed from the top of a white spruce 25 m tall could theoretically be carried almost 360 m by a 65 km/h wind, and perhaps considerably further by turbulence and convection currents (Rowe 1955); and seed that falls late onto crusted snowpack might progress by saltation for very long distances under the influence of strong winds (Dobbs 1976). The basic proposition, further supported by General Circulation Model reconstructions of global climates (Kutzbach and Guetter 1986), is that the ice mass, up to 1 km thick around 10,000-9,000 BP, was conducive to the generation of strong adiabatic winds, particularly in winter (Ritchie and MacDonald 1986). Insolation at those latitudes at that time is estimated to have been about 10% higher than current levels; seed production would be promoted by hot summer weather, and even though the growing season might have been short, there would presumably be sufficient summer warmth to enable seedlings to become established. The hypothesis is plausible.

Climate has continued to influence vegetation dynamics, and climate change has continued to have repercussions on the vegetation. The response of local vegetation to a large-scale air-mass circulation change depends on many factors, including the kind and condition of pre-existing vegetation, topographic diversity, local hydrology, local disturbance, and chance variation. Also, the changes in local climate (e.g., in temperature, precipitation, or radiation) due to a uniform regional change in large-scale circulation patterns, vary from place to place. Thus, rather than focussing on the palynology of individual lakes, Gajewski (1987) determined tree pollen diagrams (genera only) for the last 1,000-2,000 years from seven lakes along a transect from Maine to Minnesota and subjected the data to principal component analysis to determine long-term trends, medium-frequency oscillations, and higher-frequency fluctuations. The analysis was predicated on the large-scale nature of climatic anomalies and changes. To identify the large-scale changes, Gajewski (1987) ignored individual species responses to climate by calculating the principal components of correlation between species and then comparing the community change of several diagrams through time. At the three easternmost lakes, the first component recorded a long-term increase in boreal forest taxa (i.e., “some combination of *Picea*, *Abies*, *Alnus*”) at the expense of *Tsuga*, *Fagus* L., and *Acer*. The first major increase in Picea pollen percentages occurred 1,300 years ago at Clear Pond, New York but not until 300 years later at Conroy and Basin Ponds, Maine. At the westernmost lake, Lake of the Clouds, Minnesota, the long-term trend is also an expansion of the boreal forest species at the expense of more southerly species, which accords with the results of several local studies, e.g., by Wright (1971), Bernabo and Webb (1977), and Davis (1983). All of the pollen diagrams show a long-term trend that can be explained by the changes in atmospheric circulation associated with the final phases of the gradual “Milankovitch cooling” of the past several thousand years as summer temperatures have steadily declined with decreased summer insolation (Kutzbach 1981).

The Milankovitch hypothesis of global climate change states that maximum summer solar radiation at high latitudes in the northern hemisphere occurred at about 10,000 BP (Ritchie et al. 1983). Preliminary climatic simulation experiments confirmed the hypothesis, but a large amount of evidence from North American determinations of fossil pollen indicates a maximum Holocene warmth at 7,000-6,000, or 9,000-5,000 BP. Ritchie et al. (1983) reported data from four sites in northern Yukon centred on the Mackenzie River delta (two of the sites beyond the modern treeline), which support the Milankovitch hypothesis. Pollen influx data from around 10,000 BP indicated a transition from tundra to boreal forest, and "particularly convincing data" for a spruce influx were obtained from one of the sites beyond the modern treeline, which Ritchie et al. (1983) took to indicate an early Holocene maximum treeline advance. Furthermore, pollen of certain indicator taxa (cattail and bog myrtle) were restricted to the period around 10,000 BP, as were amounts of poplar (*Populus* L.) pollen reaching 20-30% of the total sample.

The influence of characteristic seasonal patterns of climatic dominance by different air masses in determining the major vegetation zones of eastern North America has been pointed out by Bryson (1966); e.g., domination of the boreal forest by continental polar air masses in winter and spring, and by Pacific or tropical air masses in summer. The medium-frequency changes in Gajewski's (1987) study are coherent among lakes; changes at all of the lakes, at 1,700-1,500, 1,200-1,000, 600-500, and 200 BP, coincide with the Medieval Warm Period from 1,000-1,200 AD and the Little Ice Age from 1,450-1,850 AD (Lamb 1977). Gajewski (1987) concluded that temporal variability in forests occurs on a scale important for interpreting the modern landscape. His study, in a 25°-longitude transect of the Hemlock–White Pine–Northern Hardwoods Region of the Eastern Deciduous Forest Formation (Braun 1950), demonstrated that the search for vegetation response to climatic change need not be limited to ecotones or "sensitive" sites. The increase in *Picea* across the whole area and the east–west shift in *Tsuga* and *Fagus* are examples of quite rapid major changes in this forest region.

Spruces are an important and characteristic component of the circumpolar boreal forest. The genus is widely represented through the cool temperate and boreal regions of the northern hemisphere (Sargent 1922, Scoggan 1957). Southward extensions at high elevations occur in northern Mexico, southern Europe, Asia Minor, the Himalayas, and Taiwan (Fowells 1965), for, as Bell (1881) noted, "The appropriate temperature for the growth of a number of species is carried far to the south of their normal latitudes, along the elevated parts of the continent, especially the Alleghanies and the Rocky Mountains."

2.1 Evolution

Much earlier than the Angiosperms, conifers first appear in the fossil record in the Upper Carboniferous period about 300 million BP in late Paleozoic times (Porter 1967). Some prototype conifers had leaves and branches much like those of modern species of *Araucaria*, but seed ferns, horsetails, club mosses, and "an extinct line of primitive conifers (Cordaites)", the ancestral order *Cordaitales*, formed the dominant Paleozoic tree flora (Spurr and Barnes 1980).

Conifers evolved steadily through the latter part of the Palaeozoic era and the first half of the Mesozoic era. Forms essentially similar to modern genera appeared in the Jurassic period (180–135 million BP), and by the end of the Mesozoic era (about 63 million BP) the coniferous flora of the world did not differ materially from that of modern times (Florin 1944a, b, cited by Stebbins 1950). Subsequent evolutionary changes have mostly been variations on a pre-existing series of complex architectural patterns (Stebbins 1950).

In Mesozoic times, conifers proliferated in form and abundance, probably achieving their widest distribution in the Jurassic and early Cretaceous Periods, roughly 180-100 million BP (Spurr and Barnes 1980).

Tropical trees formed the dominant vegetation in Cretaceous times, when the land mass occupied rather low latitudes. Since Cretaceous times about 100 million years ago, the single tectonic plate, of which most of North America (including virtually the whole of the boreal forest zone) is part, has been drifting northwestwards away from Europe.

Most modern plant genera had evolved by the Miocene time, 25–13 million BP. *Pinaceae* gradually became dominant during the later Miocene. Fossils of the spruce *Picea banksii* n. sp. appear in sediments of late Miocene to Early Pliocene age (Hills and Ogilvie 1970). *P. banksii*, which has morphological affinities with both Norway spruce and, especially, white spruce, is thought to have spread into North America via the Bering land-bridge and to have given rise first to the black spruce complex and subsequently to the white spruce complex (Ogilvie 1972). The *Pinaceae*, in contrast with the *Taxodiaceae*, continued to expand through the Pliocene, and now extend as far as the subarctic tree line, where severe continental climates have prevented the establishment of other, less resistant species. This became possible because genera with extreme winter hardiness and a short growing period were evolved. In interior Alaska, most trees cease their growth as early as late July, at a 20 hour day length, and the growing season may be as brief as 40-50 days (Sakai and Larcher 1987) or even, exceptionally, 20 days (Nienstaedt and Zasada 1990).

Most modern species were already in existence at the start of the Pliocene 13 million years ago. The drift to higher latitudes brought climatic changes as did the uplift of major north–south mountain ranges in the west, which reduced the influence of winds from the Pacific Ocean and thereby decreased precipitation and increased temperature extremes over much of the west-central parts of the continent. Some genera were able to accommodate increasing climatic rigors by developing dormancy strategies; other genera retreated to more salubrious climates.

A trend to climatic cooling through the Miocene and Pliocene culminated in the ice ages of the Pleistocene. In much of the northern hemisphere, sub-tropical and warm-temperate vegetation gave way to temperate mesophytic vegetation, and before the end of the Miocene coniferous forests were occupying vast areas of Siberia and North America formerly occupied by mesophytic hardwoods (Wolfe and Leopold 1967); forests of spruce, fir, and hemlock, “for the first time extended from the uplands of [what is now] Oregon northward through [what is now] British Columbia and into [what is now] Alaska” (Spurr and Barnes 1980).

In the Pliocene Epoch, about 10 million years ago, the western part of North America became too cool in the wet coastal regions and too dry in the warmer parts for many of the broadleaved angiosperm trees to persist. Conifers, which had earlier occupied cool sites at high elevation, became more prominent because they adapted to moisture stresses which, for trees, are fully as much the result of low temperature as they are of deficiencies of precipitation. Meanwhile, angiosperms persisted in the eastern part of the continent, which remained more hospitable because of the influence of the warmth and moisture supplied by Caribbean and Atlantic air masses.

About 2 million years ago, the Pleistocene Epoch ushered in episodic ice ages. Ensuing glaciations have wrought great changes, both direct and indirect, to vegetation, drainage, and soils. As continental ice masses grew, and as sea level dropped in consequence, broad areas of newly exposed continental shelf became available for southward colonization by northern species. Smith noted that:

> There is evidence that spruce grew in Texas during the glacial stages…
>
> Severe climatic conditions have undoubtedly eliminated many species, and the modern forests of any locality are simpler because of such losses. On the other hand, the climatic contrasts between various regions are greater than in most geologic ages, and more forested regions are isolated from one another. In North America, had there been an east – west mountain range from the Carolinas to California, like the Alps of Europe, most of the forest species of preglacial North America would have been herded to extinction against an insurmountable barrier as they were in most of Europe. The forest was pushed into several separate north–south avenues of retreat, however, and a number of combinations of species appear to have relatively recent common ancestry. It takes no stretch of imagination to believe that eastern and western white pine, eastern and western hemlock, jack and lodgepole pine, white and Engelmann spruce[s], and some other combinations within genera were once the same and have become different by separation into regions with dissimilar environment. (Smith 1980).

During the Quaternary Period the forests with which we are familiar seldom maintained a constant species composition for more than 2,000 or 3,000 years at a time (Davis 1981). Davis presented evidence suggesting that forest communities in temperate regions are chance combinations of species, without an evolutionary history, a view influenced by the then newly ascendant recognition that interglacial intervals during the Quaternary Period, when modern flora evolved, were much shorter than previously believed. Rather than lasting hundreds of thousands of years, interglacial intervals were brief interruptions of 10,000-20,000 years, with at least 16 glaciations lasting 50,000-100,000 years (Hays et al. 1969, Emiliani 1972, Kukla et al. 1972). The last glaciation, the Wisconsin, began about 100,000 BP; with glaciers expanding to reach their maximum 18,000-20,000 BP. The Wisconsin glaciation terminated with a sudden warming that melted the ice sheets in just a few thousand years (Broecker and van Donk 1970). The rapid climatic changes terminating glaciations appear to have been more disruptive to vegetation than the more gradual changes that caused their growth.

The last glacial maximum began its fluctuating retreat about 18,000 (16,000 or 20,000) BP and ended about 8,000 BP. Once freed of ice, land was quickly colonized by vegetation, notably sedges, but also including boreal trees. In the Great Lakes region about 11,850 years ago, the readvancing ice front extended southward to the central part of the Lake Michigan basin, prolonging the spruce period in the forests of the surrounding area, but having little effect on revegetation patterns in New England to the east and in Minnesota and the Great Plains to the west (Spurr and Barnes 1980). This readvance seems to have been a local event and not the result of a major climatic change (Spurr and Barnes 1980).

Regional climatic variation will inevitably affect the dynamics of the ice sheet, including the position of the ice front.

As envisioned by Spurr and Barnes (1980), the course of late-glacial and post-glacial forest vegetation and climatic change produced sequentially in New England a relative dominance of spruce, then of pine, and subsequently of hardwoods (Deevey 1949). Interpretation of determinations of pollen deposits in peat and pond sediments suggest that tundra developed in southern New England during the period of increasing warmth following the retreat of the Wisconsin ice front until about 12,000 BP, then giving way to transitional open spruce – hardwood woodland, which was replaced first by open spruce woodland and then rather abruptly, about 9,500 BP, by mixed deciduous–coniferous forest (Davis 1967, 1969). Pollen deposits in Cape Breton, Nova Scotia, indicate that white spruce and black spruce, absent from present-day forest in the area, were present during an interstadial interval, cooler than the present climate (Mott and Prest 1967).

The hypothesis that white spruce might have survived the latest ice age in the northwest remains open to question in the absence of incontrovertible supporting fossil evidence (Raup and Argus 1982, Ritchie 1987).

Tundra is thought not to have been widespread in late-glacial times in much of the western Great Lakes region, though evidence of its occurrence has been found in northeastern Minnesota and Michigan (Spurr and Barnes 1980). Further south, “spruce forest apparently extended to the edge of the ice” (Wright 1971). Dense post-glacial spruce forests in what is now Ohio began to give way to oak about 11,000-10,500 BP (Ogden 1966); and hardwoods, such as elm and oak, reached what is now southern Minnesota about 9500 BP. Following the warmer, drier hypsithermal period, perhaps 8,000-4,000 BP, spruce, larch (*Larix*), and ericaceous vegetation increased on lowland areas in Minnesota in a cooler, wetter climate.

In what is now northern Montana, Engelmann spruce was present in the earliest post-glacial forest, but decreased during warmer, drier conditions dating from about 6,600 years ago, thereafter, along with alpine fir and western white pine, increasing with subsequent cooler and more humid conditions.

Spruce, birch, and arctic tundra species are believed to have survived through glacial times in an extensive refugium in unglaciated interior Alaska (Spurr and Barnes 1980, citing Hansen 1947, 1955 and Heusser 1960, 1965).

Climates continue to change. Recent climatic variations in the Northern Hemisphere, as expressed by near-surface air temperatures measured at land-based weather stations, show general trends of warming to about 1940, cooling to the mid-1960s, and warming from about 1970 (Jäger 1988, Kalma et al. 1992). Climate oscillations can be abrupt (Yu and Wright 2001). Global warming of 0.3°-0.7°C in the last 100 years has occurred, while atmospheric concentrations of CO_2 have increased from 280 to 350 ppm (Kalma et al. 1992). Most current general circulation models (GCMs) simulate the climate at a global scale remarkably well, though no model yet gives a realistic simulation of climate on a subcontinental scale. Topographic effects still have to be accommodated to the resolution of the model, while realistic parameterization of the land surface remains unsolved (Kalma et al. 1992). The effects of global warming on vegetation would include: increase in growth rate, increase in transpiration, lengthening of the growing season, shortening of the required growing period, and generally an increase in crop yield, except where moisture is limiting. Warming is likely to be greater at higher latitudes and in winters, and this would inevitably affect regeneration success and growth rates throughout the range of white spruce, not only at high latitudes and high elevations, but also, because of white spruce's cold requirement, in the southern parts of the range.

Evidence for continuing changes in climate since the end of the last ice age is irrefutable. Documented advances and retreats of the toe of valley glaciers, for instance, are thought to reflect cooling and warming climates respectively. Mild post-glacial conditions lasted until about AD 1,300, after which North American and European climates became increasingly frigid until about AD 1,800. Increases of the order of 20% in the level of atmospheric carbon dioxide and other greenhouse gases since the onset of the Industrial Revolution are widely thought to presage substantial global warming (Pollard 1987).

The primary impact of increasing levels of greenhouse gases on global climate will be to disturb the Earth's energy balance, with first-order repercussions on evaporation, humidity, cloudiness, and precipitation. Second-order geographical effects on weather patterns, storm tracks, drought zones, etc., are probably inevitable:

> "The best numerical models of the global atmosphere consistently predict a 1°–4.5°C rise in the mean temperature of the lower atmosphere with a doubling of atmospheric CO_2 (Manabe and Wetherald 1975, Manabe and Stouffer 1980, Newell and Weare 1976, Hansen et al. 1981, Broecker 1975, and Schlesinger 1984)" (Harrington 1987).

The upper half of this range is more likely (Pollard 1987), and although the predicted mean global temperature rise appears small, a rise of 2.5°C might be sufficient to complete the melting of the Northern Hemisphere ice pack. Furthermore, as pointed out by Cronin et al. (1981), if the Ross ice shelf in Antarctica were to be dislodged by still warmer temperatures, sea levels would be raised 7 m, inundating many of the major cities of the world (Harrington 1987). Climatic change of such magnitude could drastically affect forests (Winget 1987) through significant displacement of climate regions in relation to current forest regions (Pollard 1987).

Future global climatic change will influence patterns of precipitation as well as temperature regimes. Where temperature is currently limiting to forest growth, as in northern boreal regions, changes in temperature will be much more significant than in the tropics (Warrick et al. 1986). Changes in precipitation will be more important in low-latitude, semi-arid regions than at high latitudes. However, the situation will be much less clear cut at mid-latitudes, where much of Canada's productive land is located (Pollard 1987).

In northern Canada, warming would lead to earlier loss of snow cover and reduced albedo. The effect of this on soil moisture has been debated, not least because of indeterminate interrelationships between precipitation and temperature during global warming.

Pollard (1987) has noted that quite apart from any absolute change that might occur in precipitation, the dependency of form of precipitation (i.e., rain, freezing rain, hail, wet snow, dry snow, etc.) on temperature may be consequential for forest vegetation, both directly through mechanical injury and indirectly through freeze – thaw phenomena, including frost heaving and effects on soil moisture, snow accumulation, and run-off. A minor shift in climatic pattern would have the potential to effect dramatic changes in the forest environment in Canada.

Regeneration policies and options might be influenced by global warming, as a warmer and drier climate would hinder conifer production and encourage the domination by hardwoods (Navratil et al. 1991). Any shifts in temperature and snow cover will inevitably affect northern ecosystems, not least through their influence on permafrost. As Keeling (1983) stated, one of the more reliable expectations of the effects of global warming is that northern latitudes will experience significantly greater changes than mid latitudes because of a feedback involving snow cover that might at least double or triple the effects of the global mean change in temperature. Ultimately, the productivity of the far northern forests may increase.

2.2 Climate

White spruce tolerates a tremendously wide range of climates. Across the northern reaches of the species' distribution, climatic extremes are commonplace. In one study area, for instance, temperatures of -54°C and 34°C were recorded in January and July, respectively (Maini 1966, Van Cleve et al. 1986). Mean daily temperatures of -29°C for January occur throughout the range in Alaska, Yukon, and the Northwest Territories; but it has long been known that winter minimum temperatures do not have much effect on the formation of timberlines, for hardy conifers survive without injury in the coldest winter climates in North America and Siberia, where official minima have reached -62°C and -67°C, respectively (Arno 1984). Mean daily July temperatures range from 21°C in the extreme southeastern area of distribution to 13°C throughout much of the rest of the range (Nienstaedt and Zasada 1990). Maximum temperatures have reached 43°C within the range in Manitoba.

Mean annual precipitation generally decreases westwards from 1,270 mm in eastern parts of the species' distribution, to 250 mm through the Northwest Territories, Yukon, and parts of Alaska. However, moisture stresses are greatest along the southern edge of distribution through Alberta, Saskatchewan, and Manitoba, where a mean annual precipitation of 380-510 mm coincides with mean July daily temperature maxima of 24°C (Nienstaedt and Zasada 1990).

Snow accumulates in considerable quantities at most alpine timberlines in North America and has both beneficial and detrimental effects on tree growth and survival. At the arctic timberline and at most lower timberlines, snow depths are modest, and snow is not a major factor influencing tree growth (Arno 1984).

Biologists and climatologists have long noted the general correspondence of the arctic and alpine limits of tree growth with the location of the 10°C isotherm for the warmest month (Arno 1984). Other climatic factors have been suggested as having a role in determining the position of the northern treeline, include cumulative summer degree days, position of the Arctic front in July, mean net radiation (especially during the growing season), and low light intensities (Elliott 1979a). None of these factors absolutely define the northern limit of spruce, and climatic relationships are complicated by mountainous topography in northern Alaska (Densmore 1980). In any event, factors other than climatic, especially edaphic factors, also exert considerable influence on species' distribution.

Jacoby and Ulan (1982) used tree-ring chronology extending back to 1686 AD based on increment cores from seven white spruce growing on flat, poorly drained muskeg overlying permafrost, near Churchill, Manitoba, to reconstruct past ice conditions in a Hudson Bay estuary.

Relationships between white spruce growth and climate were studied by Jozsa et al. (1984) using ring-width and ring-density data from X-ray densitometry. Strong cross-dating between randomly selected individual cores and site summary chronologies, and by high correlations between tree-ring chronologies for sites hundreds of kilometres apart, revealed strong climate – tree growth relationships. Other, non-climatic, factors also affected relationships, including local fire history, ecological succession, soil, and human activities.

By principal-component analysis, the relative abundance of many plant species, including white spruce, in seven communities in central northern Canada was investigated by Larsen (1971). The distribution and frequency of at least some species were correlated with air mass frequencies.

Since the 1970s investigations of physiological responses of trees to limiting conditions in the field have promoted and accompanied the development of a variety of portable, ecophysiological instrumentation. Most of such investigations have been conducted at alpine tree lines in temperate latitudes rather than at less accessible high latitude sites (Goldstein et al. 1985). Evidence from studies such as those by Garfinkel and Brubaker (1980), Goldstein (1981), and Ugolini et al. (1981), pointed increasingly to the principal role of growing-season conditions in determining tree line locations. Foliage was not damaged by winter desiccation or frost (Goldstein 1981), and factors related to the water balance of trees, e.g., vapour pressure deficit and soil temperature, may be the major controlling factor by which environmental temperatures limit growth (Goldstein et al. 1985). White spruce stomata were found to close in response to evaporative demand and low soil temperature. Soil temperature seems to be an important component of tree line water relations, since stomata close under conditions of low soil temperature, even when there is ample soil moisture and low or moderate demand (Goldstein et al. 1985).

The great sensitivity of white spruce stomata to vapour pressure deficit (Hinckley et al. 1978), soil temperature, and xylem pressure potential indicates a strong ability to avoid low water potentials (Goldstein et al. 1985). This may largely explain the ability of white spruce to avoid winter desiccation damage by preventing transpiration when the soil is frozen.

Different biological processes (e.g., germination, growth, and photosynthesis) have different temperature minima and optima (Tranquillini 1979). Arno (1984) cited unnamed Russian scientists as having determined that while degree days greater than 10°C of 600°-700°C and 200°-300°C correlated, respectively, with polar and alpine timber lines, the annual sums of daily leaf temperatures greater than 10°C reach about 800°C in both cases. The cooler mountain air temperatures at alpine timberlines are apparently compensated for by marked increases in leaf temperature. This increase is a consequence of the greater intensity of solar radiation at alpine than at polar timberlines (Arno 1984).

Wind undeniably influences the positioning of timberlines, and is thought to be the chief cause of dwarfing and krummholz formation at most alpine timberlines. Trees are damaged mechanically by ice pellets and their own flailing branches. But while warm, dry winter winds, especially those downslope of elevated topography, certainly account for major occurrences of "red-belt" damage, tree species at continental alpine timberlines appear to be resistant to such damage, provided that new growth has ripened fully (Arno 1984). Still air and bright sunlight at similar temperatures and relative humidity cause much more pronounced drying of hardy conifers (Marchand and Chabot 1978, Tranquillini 1979). Drought-resistant conifers are able to close their stomata during high winds. Moreover, wind cools the leaves, which therefore remain at about air temperature. Leaf vapour pressure does not rise, and the tendency for water to evaporate is not increased. Conversely, severe loss of water can occur in spring when trees are bathed in bright sunshine reflecting off snow, the air is still and relatively warm, and the roots and lower stems are frozen. Under those conditions, leaf temperatures may be 10°C greater than air temperature, and water loss increases (Marchand and Chabot 1978, Richards 1981).

Abrasion of exposed krummholz foliage by ice-blasting winter winds increases desiccation damage (Hadley and Smith 1983).

2.2.1 Climate change / periodicity (effect on future distribution)

Increasing concentrations of greenhouse gases in the atmosphere are expected to raise temperatures globally, with greatest warming at high latitudes, and with substantial northerly displacement of the boreal forest zone in the northern hemisphere (Prentice et al. 1991). Using a forest succession model that includes a generalized disturbance regime and realistic climatic effects on species regeneration and growth, implications of such a shift were analysed for forest composition and biomass dynamics across the present-day boreonemoral zone in Scandinavia. Temperature increases in the range of 2°-4°C in summer and 5°-6°C in winter, typical of simulated CO_2 doubling effects, would force the boreonemoral zone more than 1,000 km northwards from central Sweden, where dominance would pass from Norway spruce to beech, oak (*Quercus* L.), and pine over 150-200 years. Simulated increases of 175-250 mm in annual precipitation are required to counteract drought, which would otherwise reduce forest biomass and increase the representation of more drought-tolerant species. The simulated forest dynamics are the net result of individual responses of species to different aspects of climate, modulated by successional processes that are on the same scale as human effects on climate.

A change in climate has great potential for affecting tree growth. The greatest initial impact, however, is likely to be on regeneration rather than on growth rate. The interrelationships between trees and pests and diseases will also be affected, and may become critically important.

Past changes in climate have also clearly affected the distribution of plant species, including white spruce. Forests in north-central Wisconsin, for instance, were preceded by a boreal forest composed largely of white spruce before hickory (*Carya* Nuttall) and butternut (*Juglans cinerea* L.) made a temporary appearance, during a surmised warmer period of climate in late post-glacial time (Wilson and Webster 1942).

Vilks and Mudie (1983) reported evidence for postglacial paleoceanographic and paleoclimatic changes in Lake Melville, Labrador. A piston core collected in August 1979 was 14C-dated, and contents of foraminifera, dinoflagellates, and pollen were used to reconstruct a postglacial history of the fiord oceanography and regional climate. Pollen assemblages indicated a succession of four major vegetation types: low arctic tundra with alder, dwarf birch (*Betula nana* L.), and willow(*Salix* L.); then, from about 8,000 BP to 7500 BP, shrub/woodland tundra, with fir , alder (*Alnus* Mill.), and both tree and dwarf birch; followed, about 6,000 BP, by spruce woodland; and, beginning about 5,000 BP, a final boreal forest phase, dominated by spruce, but with significant amounts of pine, fir, and birch.

The boreal forests of the world, occupying some 15 million km^2 over North America and Eurasia, are a major source of softwood timber and are expected to play a significant role in the response of vegetation to global climate change. A systems analysis, developed by Shugart et al. (1992), provides a synthesis of the important patterns and processes that occur in boreal forests and reviews the principal mechanisms that control the forests' pattern in space and time. The effects of low temperatures, soil ice, insects, plant competition, wildfires, and climatic change on boreal forests are discussed as a basis for the development of the first global scale computer model of the dynamical change of a biome, able to project the change of the boreal forest over timescales of decades to millennia, and over the global extent of this forest.

A gap model of environmental processes and vegetation patterns was used to examine the sensitivity of permafrost and permafrost-free forests at Fairbanks, interior Alaska, to changes in air temperature and precipitation predicted to result from CO_2-induced climate change (Bonan et al. 1990). Current predictions are for changes to be most pronounced at high latitudes, with 6°-12°C in winter, and 2°-6°C in summer. Forest dynamics and stand structure were simulated for two forest types, including a white spruce/paper birch/trembling aspen forest on a well-drained permafrost-free site at 133 m elevation, on a south-facing terrace slope. The analysis indicated that in the uplands of interior Alaska, the effect of climatic warming on boreal forest ecology may be more a response to increased potential evapotranspirational demands than a direct response to increased air temperature.

Selection of white spruce families in the context of climate change and heat tolerance was studied by Bigras (2000). To assess the responses and plasticity of white spruce seedlings to high temperatures, 12 open-pollinated families differing in growth performance were exposed to a 30-minute heat treatment of 42°, 44°, 46°, 48° or 50°C, with or without heat preconditioning, at 38°C for 5 hours. Damage was evaluated based on chlorophyll fluorescence parameters after heat preconditioning, after the heat treatments and during a 7-day recovery period. Visible needle damage was also evaluated after the heat treatments and 14 days later. Chlorophyll fluorescence parameters indicated that seedlings subjected to a heat treatment of

42°-43°C lost the ability to phosphorylate and donate water to photosystem II. A heat treatment of 44°-46°C severely limited the ability of the seedlings to use NADPH and ATP in the Calvin cycle. Based on visible needle damage, families with superior height growth performance were more sensitive to heat stress than were families with intermediate or inferior height growth performance. Moreover, families with superior height growth performance had low photochemical efficiencies in the light (DELTAF/Fm') after heat treatment. Heat preconditioning increased the thermotolerance of the seedlings. Bigras concluded that white spruce seedlings exhibiting fast-growing characteristics under present conditions may not grow as well at higher temperatures, such as might develop with global warming.

Barber et al. (2000) noted reduced growth of Alaskan white spruce in the 20th century from temperature-induced drought stress, and observed that the extension of growing season at high northern latitudes seems increasingly clear from satellite observations of vegetation extent and duration. This extension is also thought to explain the observed increase in amplitude of seasonal variations in atmospheric CO_2 concentration. Increased plant respiration and photosynthesis both correlate well with increases in temperature this century and are therefore the most probable link between the vegetation and CO_2 observations. From these observations, it has been suggested that increases in temperature have stimulated carbon uptake in high latitudes and for the boreal forest system as a whole. Multi-proxy tree-ring data (ring width, maximum late-wood density and carbon-isotope composition) from 20 productive stands of white spruce in interior Alaska show a strong and consistent relationship over the past 90 years and indicate that, in contrast with earlier predictions, radial growth has decreased with increasing temperature. Temperature-induced drought stress has disproportionately affected the most rapidly growing white spruce, suggesting that under recent climate warming, drought may have limited carbon uptake in a large portion of the North American boreal forest.

Ecosystem boundaries based in whole or in part on climate and vegetation will change in response to temperature and humidity regimes and the different metabolic response of species to changing thermal regimes (Root and Hughes 2005). Large sub-continental ecosystem boundaries based on north–south variations in temperature and east–west variations in humidity, such as the site regions (ecoregions) described by Hills (1961) and Crins (2002) for Ontario, will shift in response to changes in the controlling factors. The most consequential changes in ecosystem composition, structure, and function, are likely to occur at northern latitudes and higher altitudes, such as boreal forest ecosystems, where changes in weather-related disturbance regimes, e.g., fire, and nutrient cycling, are primary controls on productivity. Examples of probable climate-induced ecosystem change include: loss of alpine forest, boreal forest to wetland, boreal forest to Great Lakes–St. Lawrence forest, treeline to boreal grassland steppe, and boreal forest to aspen parkland.

Beaulieu and Rainville (2005) proposed a methodology combining a biophysical site index and a seed source transfer model based on both temperature and precipitation to estimate white spruce plantation yield under current conditions and future global warming. The biophysical site index model predicts dominant height at 25 years, which is further used to estimate plantation yield using yield tables. The transfer model shows that, on average, seed sources are best adapted to the temperature conditions at their present location and exhibit their maximum yield there, though transfer of seed sources to drier sites could improve plantation yield. Beaulieu and Rainville's simulation predicted that global warming should favour a slight increase in plantation yield of white spruce in southern Quebec, but one cannot expect to obtain similar yields from a seed source rapidly exposed to warmer conditions, compared with a seed source established in growing conditions to which it is adapted.

2.2.2 Ecoclimatic regions

Climatic factors govern the incoming energy available to plants and largely determine the amount of moisture available, although climate cannot be completely separated from either time or topography (Viereck et al. 1986). Regions vary in ecoclimatic characteristics important to species distribution and plant growth (Ecoregions Working Group 1989). Groupings of ecoclimatic regions form ecoclimatic provinces. For example, the Boreal Ecoclimatic Province supports close-canopied forests of conifer or mixed conifer–hardwood, and the Cool Temperate Ecoclimatic Province supports mixed forests of shade-tolerant hardwoods and conifers. White spruce is a characteristic component of the Boreal Ecoclimatic Province, and also occurs in the Cool Temperate and Subarctic Ecoclimatic Provinces.

Twenty-four ecoclimatic regions within the Canadian Boreal Ecoclimatic Province were recognized by the Ecoregions Working Group (1989). White spruce is absent from only seven or eight of these, mostly in Newfoundland and Labrador and in neighbouring parts of Quebec and New Brunswick. In some regions, white spruce occurs mainly on sites that differ from "normal" in being moister (e.g., HBo region), warmer and moister (e.g., HBs region), or cooler and drier (e.g., LBt region).

In the High Subarctic Ecoclimatic Region (HS), where summers are cool, frost is common except in July and August, and the mean annual temperature ranges from -5° to -20°C, with mean annual precipitation of 250-350 mm, "normal sites are characterized by stunted and very open-growing stands of black spruce and tamarack, with secondary quantities of white spruce" (Ecoregions Working Group 1989). At Inuvik Airport, the mean monthly temperature of the coldest month is -34.4°C, and the lowest temperature on record stands at -56.7°C. Dry sites often support open stands of white spruce, and white spruce, balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.) are common along rivers.

With somewhat less frigid conditions and considerably greater precipitation, trees grow to a larger size and in denser stands in the Low Subarctic Ecoclimatic Region [LS] than in the High Subarctic Ecoclimatic Region. Open stands of white spruce and paper birch can dominate drier sites and, with trembling aspen (*Populus tremuloides* Michx.), also occur on warm, protected sites.

In the Atlantic Low Subarctic Ecoclimate Region (LSa), "normal sites are commonly dominated by forests of white spruce with a moss understory. Drier sites also have forests of white spruce, but with a lichen understory" (Ecoregions Working Group 1989). Mean monthly temperatures are above freezing from June through September; winters are cold but are somewhat ameliorated by maritime influences compared with adjacent inland locations.

In the Boreal region, white spruce and red spruce are mentioned by the Ecoregions Working Group (1989) as co-occurring species only in the Transitional Low Boreal Ecoclimate Region (LBt), in southern New Brunswick.

In the coastal portions of Oceanic Low Boreal Ecoclimate Region (LBn) in Nova Scotia and New Brunswick, the conspicuous presence of white spruce and absence of black spruce is attributed to the tolerance of white spruce to salt spray, which “tends to limit the growth of black spruce” (Ecoregions Working Group 1989). White spruce achieves better form and growth along the coast than either Black spruce or balsam fir (Loucks 1962).

White spruce also occurs in the Cool Temperate Ecoclimatic Province that stretches eastwards, south of boreal regions, from the Sault Ste. Marie area of Ontario to Prince Edward Island and parts of Nova Scotia and New Brunswick. In the Humid High Cool Temperate Ecoclimatic Region (HCTh), white spruce occurs on sites that are moister than “normal”. Valleys in the Transitional High Cool Temperate Ecoclimatic Region (HCTt) support conifers, including white spruce, while hardwoods dominate the ridges. White spruce, black spruce, and balsam fir occur on colder and wetter sites in the Humid Mid-Cool Temperate Ecoclimatic Region (MCTh) of southern Ontario.

Mostly in Yukon Territory, the Subalpine Northern Subarctic Cordilleran Ecoclimatic Region (NSCs), on “normal” sites at lower elevations, supports discontinuous open stands of stunted white spruce in a matrix of willow, dwarf birch) (0.5 – 1.5 m tall), and northern Labrador tea (*Rhododendron tomentosum* Harmaja). South- and west-facing scree slopes are sparsely vegetated with white spruce, shrubs, and moss.

In the Subalpine Northern Cordilleran Ecoclimatic Region (NCs), also mainly in Yukon Territory, a scattered cover of stunted trees includes white spruce together with alpine fir and lodgepole pine. At lower elevations, white spruce “is prominent throughout”. Normal sites in the Boreal Northern Cordilleran Ecoclimatic Region (NCb), south of NCs, carry communities of white spruce and feathermoss, “which constitute the climax vegetation of the area” (Ecoregions Working Group 1989); alluvial sites support white spruce and balsam poplar.

Normal sites in the Subalpine Mid-Cordilleran Ecoclimatic Region (MCa) are dominated by white spruce and alpine fir in a matrix of dwarf birch and willow (Ecoregions Working Group 1989). In the Boreal Mid-Cordilleran Ecoclimatic Region (MCb) “white spruce (cross Engelmann), and to a limited extent black spruce, with an understory of feathermoss, represent the climatic climax vegetation”, though “normal sites are characterized by closed-canopied forests of lodgepole pine”. Poorly drained sites carry black spruce and white spruce with understories of Labrador tea, horsetail, and moss.

Engelmann spruce and alpine fir “the climatic climax species”—are most common in late-successional stands of the Subalpine Southern Cordilleran Ecoclimatic Region (SCs), but normal sites are characterized by closed-canopied lodgepole pine of fire origin (Ecoregions Working Group 1989).

The transition between boreal and Cordilleran vegetation on the lower slopes of the Rocky Mountains and eastern slopes of the Coast Mountains is represented by the Boreal Southern Cordilleran Ecoclimatic Region (SCb), where “Mixed forests of trembling aspen, balsam poplar, paper birch, lodgepole pine (*Pinus contorta* Dougl. ex Loud), white spruce, black spruce, and balsam fir occur on normal sites" (Ecoregions Working Group 1989). Closed forest of lodgepole pine and white spruce occur at higher elevations. White spruce, black spruce, and balsam fir are climatic climax species on upland sites, black spruce and balsam fir on poorly drained sites. The Ecoregions Working Group (1989) noted that both white spruce and Engelmann spruce occur in the Montane Southern Cordilleran Ecoclimatic Region (SCm), but did not describe patterns of distribution.

In the Boreal Interior Cordilleran Ecoclimatic Region (ICb), white spruce and alpine fir are the climatic climax species, but only on sites wetter than normal, which are presumably less subject to forest fire than are normal sites, is the climatic climax vegetation developed.

Extensive vertical stratification of vegetation occurs in south-central British Columbia. The Ecoregions Working Group (l989) designated this area as a complex of several ecoclimatic regions rather than attempt to map the regions separately. The Subalpine Interior Cordilleran Ecoclimatic Region (ICs) typically supports Engelmann spruce, subalpine fir, and lodgepole pine on "normal" sites, while wet sites are commonly dominated by "spruce and fir". In the Subalpine Transitional Interior Cordilleran Ecoclimatic region (ICn), late successional and mature stands of white spruce × Engelmann spruce, subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine, and Douglas-fir (*Pseudotsgua menziesii* (Mirb.) Franco) can develop on normal sites. And, as in ICs, "spruce and fir" occur on poorly drained sites. Moister than normal sites in the Montane Interior Cordilleran Ecoclimatic Region (ICm) develop mixed stands of white spruce, Douglas-fir, and Douglas maple (*Acer glabrum* var. *douglasii* (Hook.) Dippel).

The manner and extent to which the distribution of white spruce and other species are influenced by various ecoregional components are not discussed by the Ecoregions Working Group (1989), but for each ecoclimatic region a detailed climate diagram was presented for a station "chosen to be as representative as possible" for that region.

2.2.2.1 Subdivisions of the boreal

The North American boreal zone has commonly been divided into two or three subzones (Hare 1950, Hare and Ritchie 1972, Rowe 1972, Viereck 1975). In northwestern Europe four boreal subzones have been distinguished: northern, middle, southern, and hemiboreal (Ahti et al. 1968). Largely based on the well-defined forest vegetation zones in Finland, the subzones differ not only in their flora and plant communities but also in their productivity (Koivisto 1970, Bazilevich and Rodin 1971) and several other related biological phenomena (Hamet-Ahti 1976, 1981; Norokorpi 1986).

2.3 Soils

White spruce occurs on a wide variety of soils, including soils of glacial, lacustrine, marine, and alluvial origins; overlying basic dolomites, limestones and acidic Precambrian and Devonian granites and gneisses; and Silurian sedimentary schists, shales, slates, and conglomerates (Halliday 1937). The wide range of textures accommodated includes clays (Wilde et al. 1949, 1954; Nienstaedt 1957, Rowe 1972), even those that are massive when wet and columnar when dry (Jameson 1963), and sand flats, and coarse soils (Forest Section L. 4d, Rowe 1972). Very large white spruce are found on soils consisting of layers of rich silts interspersed with layers of organic matter, the result of periodic spring floods (J.M. Robinson[8] , personal communication, 17 Sept. 1969). Its occurrence on some organic soils is not characteristic, except perhaps on shallow mesic organic soils in Saskatchewan and in association with black spruce on organic soils in central Yukon (Nienstaedt and Zasada 1990).

Podzolized, brunisolic, luvisolic, gleysolic, and regosolic (immature) soils are typical of those supporting white spruce throughout the range of the species (Nienstaedt 1957). Soils supporting white spruce are most commonly Alfisols or Inceptisols (Nienstaedt and Zasada 1990). In the podzol region of Wisconsin, white spruce occurs on loam podzols, podzolized gley loams, strongly podzolized clays, gley-podzol clays, stream-bottom soils, and wood peat (Wilde et al. 1949). Moist sandy loams also support good growth (Harlow and Harrar 1950). On sandy podzols (Wilde et al. 1949), it is usually a minor species (Nienstaedt and Zasada 1990). Good development occurs on moist alluvium (Seeley, cited by Nienstaedt 1957; Jeffrey 1961, 1964; Lacate et al. 1965; Viereck 1973) on the banks of streams and borders of swamps (Sargent 1898, Kenety 1917, Rowe 1972). White spruce makes good growth on well-drained lacustrine soils in Alberta Mixedwoods (Heger 1971), on moderately-well-drained clay loams in Saskatchewan (Kabzems 1971), and on melanized loams and clays (with sparse litter and a dark-coloured organically-enriched mineral horizon) in the Algoma district of Ontario (Wilde et al. 1954).

White spruce becomes less accommodating of soil with increasing severity of climate. The distribution of white spruce in Labrador seems to depend almost entirely on the character of the soil (Sargent 1898), and between the southwestern shores of Hudson Bay and the northeastern regions of Saskatchewan, white spruce is confined to very local physiographic features, characterized by well-drained or fertile soils (Ritchie 1956). Robinson[9] (personal communication 17 Sept. 1969) called white spruce the black walnut of the north where “it only does well on the very best sites”, yet “white spruce near the mouth of the Mackenzie River can be found growing very well on not more than 12 inches [30 cm] of active soil over permafrost, provided there is no moss cover and the soil surface is warm. If it is covered with an insulating layer of mosses, especially sphagnum, the tree growth practically ceases”.

On dry, deep, outwash deposits in northern Ontario, both white spruce and aspen grow slowly (MacLean 1960). But, broadly, white spruce is able to tolerate considerable droughtiness of sites that are fertile, and no fertile site is too moist unless soil moisture is stagnant (Sutton 1968). Soil fertility holds the key not just to white spruce growth but to the distribution of the species. At least moderate fertility is needed for good growth, but white spruce occurs on many sites where nutrient deficiencies depress its growth more than that of black spruce, red spruce, Norway spruce, and the pines generally (Heiberg and White 1951, Lafond 1954, McLeod 1956, MacArthur 1957, Paine 1960, Swan 1960). White spruce performed much more poorly than Japanese larch in an afforestation trial on abandoned, hill-top farmland in New York State, an “adverse” site (Cook and Schierbaum 1948). Minimum soil-fertility standards recommended for

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[8] Canadian Forest Service, Ottawa, Ontario.

[9] Canadian Forest Service, Ottawa, Ontario.

white spruce sufficient to produce 126-157 m^3/ha of wood at 40 years are much higher than for pine species commonly planted in the Lake States (Wilde 1966): 3.5% organic matter, 12.0 meq/100 g exchange capacity, 0.12% total N, 44.8 kg/ha available P, 145.7 kg/ha available K, 3.00 meq/100 g exchangeable Ca, and 0.70 meq/100 g exchangeable Mg.

Forest floors under stands dominated by white spruce respond in ways that vary with site conditions, including the disturbance history of the site (Nienstaedt and Zasada 1990). Composition, biomass, and mineral soil physical and chemical properties are affected. In Alaska, the accumulation of organic layers (to greater thicknesses in mature stands of spruce than those in hardwood stands on similar sites) leads to decreased soil temperatures, in some cases leading to the development of permafrost (Viereck 1970a, b), Viereck et al. 1983). “Along the Canol Road in the Yukon many of the white spruce had litter accumulation of as much as 12 inches [30 cm] near the tree trunks... but the pH of that litter was no higher than that of aspen [litter]” (Robinson, J.M.[10] personal communication 17 Sept. 1969). Acidity of the mineral soil sampled at an average depth of 17 cm in 13 white spruce stands on abandoned farmland in Ontario increased by 1.2 pH units over a period of 46 years (Brand et al. 1986).

A considerable range of soil pH is tolerated by white spruce (Nienstaedt 1957). Stone, in personal communication with Nienstaedt[11] (1957), reported white spruce on some soils as acid as pH 4.5 and on others as alkaline as pH 7.5 in the surface layers. Thrifty stands of white spruce in Manitoba have developed on soils of pH 7.6 at only 10 cm below the surface, and pH 8.4 at 43 cm below the surface (Stoeckeler 1938, USDA Forest Service 1938); rooting depth in those soils was at least 81 cm. An abundant calcium supply is common to most white spruce locations in New York State (Nienstaedt and Zasada 1990). Chlorosis was observed in young white spruce in heavily-limed nursery soils at about pH 8.3 (Stone, cited by Nienstaedt 1957). Wilde (1966) gave 4.7-6.5 as the approximate optimum range of pH for white spruce in Wisconsin, but optimum growth seems possible at pH levels up to 7.0 and perhaps higher (Sutton 1968). Alluvium on the floodplains of northern rivers shows pH levels from 5.0 to 8.2 (Zasada et al. 1977). High-lime ecotypes may exist (Pelletier 1966), and in Canada Forest Section B8 the presence of balsam poplar and white spruce on some of the moulded moraines and clays seems to be correlated with the considerable lime content of these materials (Rowe 1972, Stiell 1976), while calcareous soils are favourable sites for northern outliers of white spruce (Hustich 1953).

Mature stands of white spruce in boreal regions often have well-developed moss layers dominated by feather mosses, e.g., stairstep moss (*Hylocomium splendens* (Hedw.) B.S.G.), red-stemmed feathermoss (*Pleurozium schreberi* (Brid.) Mitt.), knight’s plume moss (*Ptilium crista-castrensis* (Hedw.) De Not.) and broom mosses (*Dicranum* Hedw. spp.) rather than peat mosses (*Sphagnum* Dill. spp.). (La Roi and Stringer 1976, Viereck 1987). The thickness of the moss – organic layer commonly exceeds 25 cm in the far north and may approach twice that figure. The mosses compete for nutrients and have a major influence on soil temperatures in the

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[10] J.M. Robinson, Can. Dep. For., For. Res. Branch, Ottawa, Ontario; notes in File Project H-123 on Symposium on the management of black spruce in Ontario, March 1962.

[11] H. Nienstaedt, For. Serv., Lake States For. Exp. Sta., St. Paul MN.

rooting zone. Permafrost development in parts of Alaska, Yukon, and the Northwest Territories is facilitated by the insulative organic layer (Viereck 1970a, b, Gill 1975, Van Cleve and Yarie 1986). The role of windthrow in maintaining diversification of the bryophyte flora in boreal spruce forests has been described by Jonsson et al. (1990) and Jonsson and Dynesius (1993).

The interaction among permafrost, fire, and white spruce was described by Jack Robinson[12] (1962):

> "At Norman Wells there are excellent white spruce stands on the islands of the Mackenzie River and a narrow band of good [white] spruce near the river banks. Behind this, the forest changes to a muskeg-type black spruce with a deep moss cover and permafrost close to the surface of the mineral soil. Up the slopes of the Franklin Mountains a similar condition was found until an area covered by a recent severe fire was reached. This had burnt all of the moss cover to the mineral soil surface and there was no permafrost [here] at the end of July at a depth of 42 inches [107 cm]. Farther up the slope and above the burnt area the sphagnum, scrub black spruce and permafrost was again found…A gravel bar on the hillside caused most probably by an old beach line bore fast growing white spruce. This good stand probably resulted from a previous fire..."

Viereck et al. (1983) studied the vegetation, soils, and forest productivity in a range of forest stands in the taiga of interior Alaska. The stands were arranged on an environmental gradient from a trembling aspen stand on a dry, steep, south-facing bluff, to open black spruce stands underlain by permafrost on north-facing slopes. The coldest site was a mixed white spruce and black spruce woodland at the treeline. Mesic upland were represented by successional stands of white birch, trembling aspen, and highly productive stands of white spruce. Several floodplain stands represented the successional sequence from productive balsam poplar and white spruce to black spruce stands underlain by permafrost on the older terraces. Viereck et al. (1983) described the environmental gradient by using two soil factors, soil moisture and annual accumulated soil degree days (SDD), which ranged from 2217 SDD for the warmest trembling aspen stand to 480 SDD for the coldest permafrost-dominated black spruce site. Oils varied from alfic cryochrepts on most of the mesic sites to histic pergelic cryochrepts on the colder sites underlain by permafrost. A black spruce stand on permafrost has the lowest tree standing crop (1,586 g/m^2) and annual productivity (56 g/m^2) whereas a mature white spruce stand had the greatest tree standing crop (24,577 g/m^2) and an annual productivity of 540 g/m^2, little more than half that of the successional balsam poplar stand on floodplain alluvium.

The depth of freezing and speed of thawing of soil under dense stands of Norway spruce in boreal Komi (one of the federated republics of Russia), west of the Urals, were studied by Deryugin (1989) on fresh and moist sites. The soil froze deepest (average 47 cm) on the fresh site, but on the moist site averaged only 7 cm in depth of freezing. Nearby arable land froze to a depth of 12 cm, birch forest to 32 cm. Snow depth and soil moisture content were the most influential factors governing depth of freezing. In birch forest, soil thawed mostly before the

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[12] J.M. Robinson, Can. Dep. For., For. Res. Branch, Ottawa, Ontario; notes in File Project H-123 on Symposium on the management of black spruce in Ontario, March 1962.

snow melted, whereas in the spruce forest the soil thawed mostly after snowmelt. In dense spruce forest, the rate of soil thawing averaged 1.8 cm per day, which was 1.1 cm per day less than in birch forest, where thawing was completed 27 days earlier than in spruce forest.

2.3.1 Fertility requirements in nurseries

Fertility requirements for white spruce based on foliar concentrations and determined by Swan (1971) in sand-culture experiments were: nitrogen 1.50 – 2.50; phosphorus 0.18 – 0.32; potassium 0.45 – 0.80; magnesium 0.10 – 0.20; and calcium 0.15 – 0.40, all percent of dry matter. Nienstaedt and Zasada (1990) noted that these values, other than those for calcium, are in line with values published by Iyer (1977) for 3-year-old white spruce nursery seedlings. Values published by Armson and Sadreika (1979) for white spruce in Ontario varied by stock type and between northern and southern nurseries (Table 2.1).

Of course, the concentrations of nutrient in plant tissues depend on many factors, including growing conditions. Interpretation of concentrations determined by analysis is easy only when a nutrient occurs in excessively low or, occasionally, excessively high concentration. Values are influenced by environmental factors and interactions among the 16 nutrient elements known to be essential to plants, 13 of which are obtained from the soil and are used in relatively large amounts, including nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur (Buckman and Brady 1969). Nutrient concentrations in conifers also vary with season, age, kind of tissue sampled, and analytical technique. The ranges of concentrations occurring in well-grown plants (Table 2.1 and 2.2) provide a useful guide by which to assess the adequacy of particular nutrients, and the ratios among the major nutrients are helpful guides to nutritional imbalances. The variability of the data in Table 2.2 is typical, with the extremes contributing little more than a note of caution to the results. The nutrient minima average 45% less than the means, and the maxima average 567% more.

Individual determinations provide data of some interest, but, unless they are related to obvious imbalances, are not compelling.

Table 2. 1. Ranges of nutrient concentrations occurring in bareroot white spruce foliage, by geographical location of nursery and stock type, in percent dry weight (after Armson and Sadreika 1979).

	Northern Ontario stock type					Southern Ontario stock type						
Nutrient	**1+0**	**2+0**	**3+0**	**1+1**	**2+1**	**1+0**	**2+0**	**3+0**	**1+1**	**2+1**	**1+2**	**2+2**
N	1.25 to 3.08	1.81 to 2.27	1.62 to 2.07	1.40 to 1.48	2.11 to 2.42	2.32 to 2.77	1.76 to 2.78	1.51 to 2.12	2.22 to 2.58	1.98 to 2.50	1.39 to 2.22	1.56 to 2.75
P	0.23 to 0.37	0.11 to 0.22	0.15 to 0.25	0.11 to 0.14	0.18 to 0.25	0.26 to 0.34	0.21 to 0.31	0.10 to 0.23	0.15 to 0.24	0.12 to 0.19	0.18 to 0.19	0.12 to 0.16
K	0.28 to 2.63	0.54 to 1.92	0.50 to 1.25	1.41 to 1.69	0.58 to 0.82	0.67 to 2.10	0.42 to 0.63	0.59 to 1.20	0.55 to 0.64	0.53 to 1.14	0.45 to 0.67	0.18 to 1.15
Ca	0.47 to 0.92	0.57 to 0.83	0.07 to 0.99	0.31 to 0.50	1.04 to 1.18	0.30 to 1.07	0.70 to 1.63	0.63 to 0.81	0.31 to 0.81	0.29 to 2.04	0.20 to 0.83	0.81 to 1.70
Mg	0.10 to 0.13	0.08 to 0.10	0.07 to 0.11	0.08 to 0.09	0.10 to 0.11	0.08 to 0.14	0.09 to 0.13	0.09 to 0.11	0.06 to 0.10	0.06 to 0.12	0.07 to 0.10	0.06 to 0.21

Table 2. 2. Means and ranges of morphological and nutrient concentration values for samples of 80 white spruce 1+0 seedlings collected annually in a British Columbia nursery on 15 October 1968–1978. (after Duryea and Landis 1984).

Variable	Mean	Minimum	Maximum	50% range[a]
Seedling dry weight (g)	0.18	0.03	0.60	
Shoot length (cm)	3.90	1.70	9.20	
Shoot:Root ratio	0.57	0.24	0.97	
N (%)	2.59	0.24	3.50	2.28 – 2.91
P (%)	0.32	0.22	0.42	0.30 – 0.35
K (%)	0.90	0.52	1.26	0.83 – 0.98
Ca (%)	0.49	0.12	0.87	0.39 – 0.59
Mg (%)	0.15	0.10	0.22	0.14 – 0.17

[a] Range for 50% of observations; calculated as mean ± standard deviation.

2.4 Limits of present distribution

White spruce has a transcontinental range in North America. In Canada, its contiguous distribution encompasses virtually the whole of the Boreal, Subalpine, Montane, Columbia, Great Lakes–St. Lawrence, and Acadian Forest Regions (Rowe 1972), extending into every province and territory (Forestry Branch 1961). On the west coast of Hudson Bay, it extends to Seal River, about 59°N, "from which the northward limit runs apparently almost directly north-west to near the mouth of the Mackenzie River, or about latitude 68°" (Bell 1881). Collins and

Sumner (1953) reported finding white spruce within 13 km of the Arctic coast in the Firth Valley, Yukon, at about 69°30´ N, 139°30´ W. It reaches within 100 km of the Pacific Ocean in the Skeena Valley, overlapping with the range of Sitka spruce, and almost reaching the Arctic Ocean at latitude 69° N in the District of Mackenzie, with white spruce up to 15 m high occurring on some of the islands in the Delta near Inuvik. The wide variety of ecological conditions in which four Quebec conifers, including white spruce, are able to establish themselves, was noted by Lafond (1966), but white spruce was more exacting than black spruce. In the United States, the range of white spruce extends into Maine, Vermont, New Hampshire, New York, Michigan, Wisconsin, Minnesota, and Alaska (Sargent 1922, Harlow and Harrar 1950), where it reaches the Bering Strait in 66°44´ N" at Norton Bay and the Gulf of Alaska at Cook Inlet (Nienstaedt and Zasada 1990).

Southern outliers have been reported in southern Saskatchewan and the Cypress Hills of southwestern Saskatchewan (Scoggan 1957, Nienstaedt and Zasada 1990) and southeastern Alberta (Cypress Hills Interprovincial Park Web site -- http://www.cypresshills.com/), northwestern Montana (Munns 1938, Harlow and Harrar 1950), south-central Montana (Munns 1938), in the Black Hills on the Wyoming – South Dakota boundary (Munns 1938, Fernald 1950), on the Manitoba – North Dakota boundary (Munns 1938), and at Shushan, New York (Cook and Smith 1959).

An extensive survey of spruce types in interior British Columbia evaluated specimens individually in terms of a morphological index that was used to assign each sample to white spruce, Engelmann spruce, or Intermediate groups (Garman 1957). The survey showed that white spruce occurs in the Liard and Peace River drainages of the northern and northeastern part of British Columbia, and that another block of white spruce occurs on the plateau between the Coast Mountains and Rocky Mountains to the west and east, and between latitudes 51° and 55° N. On the lower slope of the mountains to the east of this block occur the variant or Intermediate types, which form a corridor across the northern part of the Nechako Plateau between the two blocks of white spruce. The elements of this type appear in various combinations with Sitka spruce of the Nass Basin, south of Cedarvale on the Skeena River. The Intermediate type appears again in the southern part of the Rocky Mountain Trench, but, except for this, the area south of Bonaparte River, and south of the North Thompson River at Birch Island, Engelmann spruce occurs, mostly at elevations above 1,200 m.

A hypothesis was advanced by Garman (1957) to account for the distribution of white and Engelmann spruces in British Columbia as follows:

> The extent of glaciation from Idaho to the Yukon was about 2,100 km. At the estimated rate of disintegration of the ice sheet (Coleman 1926) the area now known as British Columbia would be free of ice about 10,000 years ago. This allows for the geographical centre of the area at about latitude 56° N. to have been occupied by many generations of spruce since the last glacial period ended. Boreal spruce apparently migrated at low level from a refugium in the north, and a Montane type spread northward from a large residual reservoir to the south of maximum glaciation. The two overlap in geographical range and now present a complex of variable types made up of the migrant species and variants

> produced by their contact with each other. Thus, white spruce is found extending from the northeastern part of the province southward into the Interior Plateau and possibly south through the Rocky Mountain Trench into the East and West Kootenay Valleys. Engelmann spruce, on the other hand, extends northward at higher elevations in the Cascade, Monashee, Selkirk, and possibly the Rocky Mountains, as well as the highlands surrounding the Interior Plateau.

Climatic change is of particular significance at the northern and southern limits of the boreal forest and along the outlier peripheries (Jozsa et al. 1984).

2.4.1 Arctic limits

One of the hardiest conifers, white spruce in parts of its range withstands mean daily January temperature of -6.7°C and extreme minimum temperatures as low as -56.5°C; minimum temperatures of -50°C are general throughout much of the range except the southernmost and southeasternmost parts (Fowells 1965). By itself, or with black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch), white spruce forms the northern boundary of tree-form growth (Sutton 1969). White spruce up to 15 m in height occur at 69°N on islands in the Mackenzie Delta near Inuvik in the Northwest Territories. Hustich (1966) depicted *Picea* spp. as forming the northernmost limit of tree growth in North America.

The arctic or northern timberline in North America forms a broad transition zone from Labrador to northern Alaska. In Labrador, white spruce is not abundant and constitutes less than 5% of the forest, with a range that coincides very closely with that of black spruce but extending slightly further north (Wilton 1964).

Determination of the northern limit of trees in Labrador has generated considerable confusion, reports based on observations from the air and lake often lacking verification by field checks. Thorough investigations by Elliott and Short (1979) led them to propose Napaktok (Black Duck) Bay as the true northern tree limit. Dense forests of white spruce were found on the glacio-fluvial terraces and lower slopes of the southern part of the bay. These forests appeared to be very old and contained many fallen trees. Reproduction was taking place, “with a wide variety of age classes of trees present”. Scattered dwarf white spruce were found up-valley and along the higher lake shores forming a stressed altitudinal tree line at about 140 m. These stunted white spruce were not producing cones, and no seedlings were found.

Unlike alpine timberlines, the northern timberline occurs at low elevations. The arctic forest–tundra transition zone in northwestern Canada varies in width, perhaps averaging 145 km, and widening markedly from west to east (Timoney et al. 1992), in contrast with the telescoped alpine timberlines (Arno 1984). North of the arctic timberline lies the low-growing tundra, and southwards lies the boreal forest.

Two zones can be distinguished in the arctic timberline (Löve 1970, Hare and Ritchie 1972): a forest–tundra zone of scattered patches of krummholz or stunted trees, with larger trees along rivers and on sheltered sites set in a matrix of tundra; and “open boreal forest” or “lichen woodland”, consisting of open groves of erect trees underlain by carpet of *Cladonia* spp. lichens

(Löve 1970). The proportion of trees to lichen mat increases southwards towards the "forest line", where trees cover 50% or more of the landscape (Black and Bliss 1978, Arno 1984).

The influence of plants on soil frost near Fort Yukon is typical of permafrost conditions on wooded floodplains in northern interior Alaska (Benninghoff 1952): "Erosion and thawing by a meandering stream cause the permafrost table to retreat far below the stream bottom level, but it rises under deposits on the slip-off side (Péwé 1947). The permafrost table rises several feet more in the new alluvium during maturation of the initial balsam poplar forest, and rises still more as that forest is replaced by a dense stand of white spruce". The range of white spruce extends well into the zone of continuous permafrost (">80% of area underlain by permafrost") as illustrated by Shilts et al. (1987).

The range extends westwards from Newfoundland and Labrador, and along the northern limit of trees to Hudson Bay, Northwest Territories, Yukon, and into northwestern Alaska (Fowells 1965). Although Bell (1881) was emphatic that it "nowhere reaches the Atlantic coast [from which it recedes] further and further in going north", Payette (1980) has noted that "white spruce forms pure stands near the seaboard, within the fog belt" in northern Quebec and Labrador, and is "relatively abundant along the maritime fringe" of Newfoundland (Payette 1980). On the south coast of Ungava Bay, white spruce at the mouths of the Whale, George's and Ungava Rivers is "large enough for building boats, but the trunks are short and apt to be knotty" (Bell 1881). On the east coast of Hudson Bay, white spruce extends north to "about latitude 57°", or a few miles above Richmond Gulf, but is said to extend further north at a distance inland. According to both Hearne and Sir John Richardson, it is found on the Coppermine River to within 20 or 30 miles of the sea. Around James' Bay, and between this bay and Lakes Huron, Superior and Winnipeg, it attains a good size for lumber, and even on the Hayes and Nelson Rivers I have seen good, sound logs cut upwards of 2 feet in diameter, and showing from 100 to 140 lines of growth. Across western Canada and Alaska, white spruce occurs further north than black spruce, and, while poplar (*Populus*), willow, and birch may occur along streams well into the tundra beyond the limits of spruce, the hardwoods are usually no more than scrub (Hustich 1953). Spruce characteristically occurs in fingers of tree-form forest, extending far down the northern rivers and as scattered clumps of dwarfed "bush" spruce on intervening lands (Munns 1938, Halliday and Brown 1943). In Manitoba, Scoggan (1957, citing a 1951 but otherwise unreferenced report by Baldwin) noted that the northernmost collection of white spruce was at latitude 59°48'N, but Bryson et al. (1965) found white spruce in the northern edge of continuous forest in central Canada at Ennadai Lake, about 60°45' N, 101°'W, just north of the northwest corner of Manitoba. Bryson et al. (1965) noted that the forest retained "the same general characteristics as when it was first described [by Tyrrell (1897)] in 1896". Collins and Sumner (1953) reported finding white spruce within 13 km of the Arctic coast in the Firth valley, Yukon, at about 69°30' N, 139°30' W, and Sargent (1922) noted that white spruce in Alaska "reached Behring Strait in 66°44' N".

Climate, especially temperature, is obviously a factor in determining distributions of northern flora. Halliday and Brown (1943) suggested that white spruce's northern limit corresponds "very closely" with the July mean monthly isotherm of 10°C in Ungava, but that the northern limit west of Hudson Bay was south of that isotherm. Other climatic factors that have been suggested as affecting the northern limit of white spruce include: cumulative summer degree days, position of the Arctic front in July, mean net radiation especially during the growing season, and low light intensities (Nienstaedt and Zasada 1990). Topography, soil conditions, and glaciation may also be important in controlling northern limits of spruce (Drew and Shanks 1965).

The possibility that at least some northern Canadian trees are relicts that were established during former warmer climates has been raised by several researchers, including Payette (1975, 1976) and Elliott (1979b). The Hypsithermal treeline was further north in Quebec until approximately 3,500 BP. Elliott's (1979b) investigations in a 140-km transect of nine study sites from the northern boreal forest (Kasba Lake, Keewatin, N.W.T.) through the forest–tundra ecotone at the northern end of Ennadai Lake, supported the hypothesis that the northern trees are relicts out of phase with the current climate. She found zero viability of pollen and seed at tree line and in the frost–tundra ecotone, a lack of buried conifer seed store for ecotonal tree stands, and an almost total lack of either sexually or asexually produced tree juveniles in the ecotone. This was true for all species: white spruce, black spruce, and tamarack.

Further comments by Elliott (1979b) bear repeating at length:

> The production of female cones does not imply the production of viable seeds. Many northern workers refer to the episodic production of cones as evidence that occasional good seed years do occur in the ecotone (Nichols 1976). All three tree species in the Ennadai Lake region were abundantly producing cones, yet none of the seeds produced were viable, many of the seeds even being unfilled.
>
> The general absence of juvenile trees in the forest–tundra ecotone corresponds to the global cooling since the 1940s. The minor warming of 0.5°-0.6°C from 1880 to 1940 (Mitchell 1961, Lamb 1966, Miles 1978) apparently was also of insufficient magnitude for sexual reproduction in most of the ecotonal stands, though a concrete verification of this statement awaits the completion of dendrochronological studies...
>
> Palynological and paleosol studies in Keewatin have shown that tree line was a minimum of 280 km north of its present position for at least part of the Hypsithermal, retreating south of its current locale by ca. 3,500 BP ... Climatic fluctuations following the Hypsithermal were apparently of a sufficient magnitude and duration to again move north at least two more times.
>
> The above studies [cited by Elliott 1979b] show forest was present at Dimma Lake, just north of Ennadai Lake during the secondary "Climatic Optimum". Larsen has collected buried forest fire charcoal over a podzol (spodosol) from, Dimma Lake (61°33′ N, 100°38′ W) which was radiocarbon dated at 1050 ± 180 BP (WIS-17: Bender et al. 1965). It then appears that the ecotonal tree stands were once part of the above-mentioned northern forest, being left on favourable sites when the forest retreated southward, as evidenced by dead trees, paleosols, and peat banks with forest deposits in the interoutlier areas. There stands have continued to survive in the ecotone because of their ability to

> vegetatively reproduce, with the warm summer temperatures necessary for sexual regeneration not being required.
>
> For a retreat of tree line to occur, it appears that a severe climatic cooling must occur, or more likely, a more minor cooling accompanied by a decrease in precipitation and hence, widespread forest fires (Nichols 1975). The northern trees in Keewatin may then be thought to be in a perilous situation, either barely maintaining their position through asexual reproduction or in a retreat. In contrast, it appears that the northern trees in Labrador–Ungava are in a healthier position, with abundant sexual regeneration occurring in and surrounding the northernmost trees on the Labrador coast at Napaktok Bay (57°56′N, 62°35′W) and in an ecotonal stand above the Koroc River in northeastern Quebec (58°41′N, 65°23′W) (Elliott and Short 1979).

A Black Spruce/White Spruce Cover Type, with the two spruces present in nearly equal proportions, occurs commonly as open lichen – woodland near the northern and western limits of tree growth between Hudson Bay and northwestern Alaska, and in open stands at the alpine treeline throughout Alaska and western Canada (Viereck 1980). It is also found in other areas of the northern conifer forest on sites that are intermediate with respect to both species, e.g., old terraces and at the base of south-facing slopes. The type occurs on various soils, often underlain by permafrost. Open stands near treeline have a more or less continuous shrub layer of glandular birch (*Betula glandulosa* Michaux), alder, and willow spp.; feathermosses are common, and *Cladonia* lichens form extensive mats on drier sites. Common Labrador tea, mountain cranberry (*Vaccinium vitis-idaea* L.), and black crowberry (*Empetrum nigrum* L.) are common. Closed stands on floodplains have a continuous ground cover of feathermosses and occasionally sphagnum.

In order to evaluate the relationships between white spruce expansion and climate, Payette and Filion (1985) determined the age structure of populations at different sites at the treeline along the east coast of Hudson Bay, Quebec. Increment cores were taken from stems at 30 cm above ground level, and stem diameters were measured at that point and at the stem base. The spatial distribution pattern of white spruce was studied in a transect taken across a small circular grove at an exposed site near the treeline. Occurrence, age at collar, and diameter at stem base were recorded. Variation in white spruce age with altitude above treeline was measured in two altitudinal transects in which black spruce and tamarack of seed origin were also sampled. The influence of fire on regeneration in the northernmost white spruce forest was assessed from age structure and mapping of charcoal sites, charred black spruce subfossils and black spruce krummholz. Charcoal and subfossils were aged by 14C determination, and fire scars and ages of post-fire trees were used for absolute and relative dating of recent burns. The results showed that white spruce populations at this northern limit have expanded significantly during climatic warming of the last 100 years. Expansion began around AD 1880 but was more important during the 20th century, especially between 1920 and 1965. Although no major change in the position of the forest limit and the latitudinal treeline occurred, local altitudinal tree lines rose a few tens of metres. The seed regeneration line increased to about 100 m above the present altitudinal treeline during the same period. Tree density increased below the local treeline at many sites. There, spruce expansion was stepwise, as indicated by widely distributed clustered cohorts belonging to the 10–29, 50–59, and 70–89 age class groups. Although the expansion process was stimulated by nearby old seed bearers, long-distance seed dispersal also occurred. The development of contagious dispersion during the formation of white spruce groves or forests caused local ecological changes, particularly in snow patterns and tree growth. Fire selectivity influenced tree regeneration during the past centuries. Vigorous post-fire white spruce regeneration was stimulated by favourable climatic conditions 100 years ago in the northernmost forest site. Payette and Filion (1985) concluded that Holocene treeline displacements were of low magnitude in northern Quebec and that climatic change primarily affected tree density.

Studies on recruitment of white spruce populations from 1785 to the present day, as well as responses to climatic change at the treeline near Churchill, Manitoba, were conducted by Scott et al. (1987). Open forest and forest/tundra are distinguished by seedling establishment, crown form and growth patterns of the trees. Forest/tundra plots were found to show transitions to open forest. Where the two systems were established before the major climatic warming of the 20th century, they are resistant to invasion and there is little change in the position of the treeline. Once begun, population growth within the open forest tends to become self-generating and seems to be little affected by subsequent climatic cooling. Seedling establishment in the mature open forest established before 1,800 AD has declined during the climatic warming.

2.4.2 Alpine limits

Mountains that are sufficiently high exhibit an alpine timberline, at which trees reach their upper elevational limits (Arno 1984). The boundary, seldom abrupt, usually forms a transition zone between closed forest below and treeless alpine tundra above. This zone of transition occurs “near the top of the tallest peaks in the northeastern United States, high up on the giant volcanoes in central Mexico, and on mountains in each of the 11 western states and throughout much of Canada and Alaska” (Arno 1984). Environmentally dwarfed scrub (krummholz) commonly forms the upper limit.

Alpine timberlines reflect topographically modified regional climates. Air temperatures usually decrease with increasing elevation. For interior mountains in the western United States, Arno (1984) estimated an average lapse rate of 3.5°F (1.9°C) per 1,000-foot (305 m) gain in elevation, only about two-thirds of the dry-adiabatic lapse rate of 9.8°C per km or about 5.4°F per thousand feet (Huschke 1959). For maritime mountains in the western United States, Baker (1944) estimated an average lapse rate of 1.4°F (0.8°C) per 1,000 (305 m) feet. Geiger (1950), in chapters on the skin of air on mountain slopes and the influence of topography, discussed the interacting variables that control the microclimates created.

Compared with arctic timberlines, alpine timberlines may receive fewer than half of the number of degree days (>10°C) based on air temperature because solar radiation intensities are greater at alpine than at arctic timberlines. However, the number of degree days calculated from leaf temperatures may be very similar in the two kinds of timberlines (Arno 1984).

Summer warmth generally sets the limit to which tree growth can occur, for while timberline conifers are very frost hardy during most of the year, they become sensitive to just 1 or 2 degrees of frost in mid-summer (Tranquillini 1979). A series of warm summers in the 1940s seems to have permitted the establishment of “significant numbers” of spruce seedlings above the previous treeline in the hills near Fairbanks, Alaska (Viereck 1979, Viereck et al. 1986). Survival depends on a sufficiency of new growth to support the tree. The windiness of high-elevation sites is also a potent determinant of the distribution of tree growth. Wind can mechanically damage tree tissues directly, including blasting with wind-borne particles, and may also contribute to the desiccation of foliage, especially of shoots that project above snow cover.

At the alpine timberline, tree growth is inhibited when excessive snow lingers and shortens the growing season to the point where new growth would not have time to harden before the onset of fall frost. Moderate snowpack, however, may promote tree growth by insulating the trees from extreme cold during the winter, curtailing water loss (Sowell et al. 1996), and prolonging a supply of moisture through the early part of the growing season. However, snow accumulation in sheltered gullies in the Selkirk Mountains of southeastern British Columbia was adduced by Shaw (1909) to explain why the timberline (formed of Engelmann spruce and subalpine fir) was 400 m lower there than on exposed intervening shoulders.

White spruce is found at elevations up to 610 m on the central tableland of Labrador north of latitude 52°N (Nienstaedt 1965) and up to 910 m on the south slope of the Brooks Range in the Dietrich River Valley, Alaska, at about latitude 68°N (Densmore 1980). Along with lodgepole pine, black spruce, alpine fir, and tamarack, white spruce is a component of the timberline forest at latitude 61°N on the Liard Range, Northwest Territories, and occupies elevations of up to 1160 m (Jeffrey 1964). The trees, seldom exceeding 5 m in height, display pronounced flagging from desiccating westerly winds.

Engelmann spruce rather than white spruce occupies high-elevation sites in western North America, but because of the relationship between the two species, and in particular because of the existence of hybrid swarms, Engelmann spruce must be considered at least to the extent that this illuminates any aspect of white spruce.

Both water uptake and water stored in roots appear to be critical for the survival of subalpine Engelmann spruce saplings that are exposed above the snowpack in later winter-early spring (Boyce and Lucero 1999). Transpiration is greatly reduced in small saplings while engulfed in snowpack. For exposed trees, the availability of soil water may be critical in late winter, when transpirational demands increase. Increased rates of transpiration in response to loss of snowpack, coupled with low sapwood water reserves and an extended period of soil frost in windswept areas, may prevent Engelmann spruce from regenerating in open areas both above and below the tree line. Cuticular damage by windblown ice is probably more important at the tree line (Hadley and Smith 1983, 1986), but damage caused by desiccation is likely to be more important at lower elevations (Boyce and Lucero 1999).

2.4.3 Lower limits

Valley bottoms in mountainous areas (e.g., in southern Yukon) can experience much lower temperatures than do the slopes above because of temperature inversions caused by strong radiational winter cooling (Senyk 1983). The effect is strong enough to produce subalpine, alpine, or arctic tundra on the valley floor, and yet support closed spruce or spruce fir forests from as little as 50 m upslope up to the upper timberline.

In semi-arid climates, the lower slopes of some mountains develop a lower timberline downslope of forest, where trees give way to dry grassland, sagebrush, or tall shrubs (Arno 1984). Drought is the main determinant. In interior British Columbia, white spruce grows at elevations as low as 760 m in the east Kootenay Valley (Roche 1969).

2.4.4 Southern limits

The southern limit of distribution of white spruce is more complex. From east of the main range of coastal mountains in British Columbia, the southern continuous limit of white spruce is the forest/prairie interface through Alberta, Saskatchewan, Manitoba, the northern parts of Minnesota and Wisconsin, central Michigan, northeastern New York, and Maine (Fowells 1965). Sargent (1922) and Harlow and Harrar (1950) also included Vermont and New Hampshire; and, while Dame and Brooks (1901) excluded New York and states further west, they included Massachusetts as far south as Amherst and Northampton, “probably the southern limit of the species” in that area. Nisbet (1905) gave the range of white spruce as extending to “Carolina”, but he did not recognize red spruce as a species and presumably included it with white spruce.

Climatologist Hare (1950) considered the boundary between the boreal forest formation in eastern Canada and the mixed forest formation to the south to be “readily determinable in climatological terms”, though Hare recognized a “Southern transition” ecotone between the boreal and Great Lakes–St. Lawrence forests, and admitted that the “ecotone between these two formations is less easy to define than the forest–tundra [boundary]”. Species proper to the Great Lakes–St. Lawrence mixed forest formation penetrate the southern margins of the boreal forest; eastern white cedar (*Thuja occidentalis* L.), black ash (*Fraxinus nigra* Marsh.), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), yellow birch (*Betula alleghaniensis* Britt.), and large-toothed aspen (*Populus grandidentata* Michx.) all occur as individuals or groves in penetrations into the boreal forest from the south (Hare 1950).

Towards the southern parts of its range, white spruce encounters increasingly effective ecological competition from hardwoods, some of which may reinforce their growth-rate/sprouting competitiveness with allelopathic depredation of coniferous regeneration (Tubbs 1976). Further southward extension of the distribution is inhibited by white spruce’s cold requirement.

The southern limit of the western Canadian boreal forest was found to show a "surprisingly close" relationship with the zero isoline of the P-PET climatic moisture index (Hogg 1994). That index was calculated by subtracting monthly potential evapotranspiration (PET) from mean monthly precipitation (P), with units in centimetres. Potential evapotranspiration was determined using the method of Jensen-Haise (Bonan 1989, Jensen et al. 1990):

$$PET = C_T(T - T_x)(R_s/\lambda) ,$$

where T is the mean monthly air temperature (°C), Rs is the mean monthly global solar radiation (megajoules per square meter), and λ is the latent heat of vaporization ($24.54\ \mathrm{MJ \cdot m^{-2} \cdot cm^{-1}}$ at 20°C). The parameters, C_T and T_x, were calculated as:

$$C_T = \frac{1}{(38 - (A/152.5) + 38/(e2 - e1)} ,$$

and

$$T_x = - 2.5 - 1.4/(e_2 - e_1) - A/550 ,$$

where A is the station's altitude above sea level (m), e_2 and e_1 are the saturation vapour pressures (kilopascals) at the mean minimum and mean maximum July temperatures, respectively. The annual climatic moisture index, P-PET, was determined as the sum of the monthly moisture indices (Hogg 1994).

The goodness of fit between the values of climatic indices and the distribution of the boreal forest was examined for the area 49°-54°N latitude, and from 92°-120°W longitude (excluding the Cordilleran Forest and major lakes). This area encompasses 407,000 km^2 of boreal forest and 470,000 km^2 of grassland, including aspen parkland. Goodness of fit was assessed by measuring the areas of boreal and grassland that were each correctly classified by the climate isoline corresponding most closely to the southern limit of the boreal forest. Two methods were used: overall accuracy, based on the total percentage area correctly classified; and KHAT accuracy using K-analysis (Congalton 1991). The KHAT statistic takes a value of 0% when the classification is no better than that given by chance, a value of 100% when there is a perfect fit. The KHAT value of 87% was gratifyingly high (Table 2.3).

Table 2. 3. Accuracy of different climate measurements in delineating the southern boundary of the boreal forest in western Canada.

Climatic measurement	**Isoline value**	**Overall accuracy %**	**KHAT accuracy %**
P – PET moisture index cm	0	94	87
Thornthwaite moisture index	–5	87	74
Growing degree – days	1,300	68	33
>5°C	to	to	to
	1,400	77	52
Mean July temp. °C	18	64	27
Mean annual temp. °C	1	86	71

In western Canada, the southern limits of distribution of the major boreal conifer species differ by as little as 3 km and up to 107 km (Zoltai 1975). The range of white spruce generally extends farther into dry climate regions than the other conifers, particularly along the valleys of the Bow, Red Deer, Battle, and North Saskatchewan Rivers. In these situations, white spruce predominates in valley bottoms and on north-facing slopes, where the reduced solar radiation would be expected to reduce PET and contribute to moister soils than on the adjacent plains (Hogg 1994).

Past fire regimes have probably played a role in determining the southern limit of conifers. Vast conflagrations repeatedly sweeping across the Canadian prairies and aspen parkland (Bird 1961, Heinselman 1981) would have eliminated conifers (Axelrod 1985).

The results of Hogg's (1994) study suggest that the distribution of forest in the Prairie Provinces is strongly affected by altitude, even in areas with modest topographic relief. The P-PET moisture index showed a strong increase with increasing altitude because of strong reductions in maximum daily temperatures, coupled with increases in precipitation. This, suggested Hogg (1994), can explain the presence of white spruce–lodgepole pine forest in the Cypress Hills on the southern Alberta–Saskatchewan border, an otherwise arid region dominated by short-grass prairie. A similar effect of altitude on the climatic moisture index is evident at Riding Mountain in southwestern Manitoba, which can account for the southern extension of boreal forest into this region.

Exploitation of the forest cover in the 78 townships in the southeast corner of the South-Eastern Administrative Region of the Manitoba Department of Mines and Natural Resources began with settlement in the agricultural area to the west in the 1870s. White and red pines were most important, but some white spruce was harvested too. The gross merchantable volume of wood on Crown land, constituting 85% of the area, was only 0.9% white spruce (Jameson and Cayford 1964).

Nienstaedt and Zasada (1990) stated that the southern limit of the forest belt in which white spruce forms "more than 60% of the total stand" roughly follows the 18°C July isotherm, the relationship being "particularly close northeast of Lake Superior", and the limit swinging north of the isotherm in the prairie provinces. However, no data are adduced, partly perhaps because of the difficulty in establishing the line of 60% white spruce content, which in any event would seem to be more applicable to the western part of the distribution than of central and eastern parts.

2.4.5 Outliers

Outlying populations of white spruce south of the main distribution occur in southern and southwestern Saskatchewan (Scoggan 1957), northwestern Montana (Munns 1938, Harlow and Harrar 1950), south central Montana (Munns 1938), on the Wyoming–South Dakota boundary (Munns 1938, Fernald 1950, Harlow and Harrar 1950), and at Shushan, New York (Cook and Smith 1959). Bell (1881) referred to the spruce in the Black Hills of South Dakota and in Montana, and to Wyoming outliers as Engelmann. Orr (1975) described the climate, geology, soils, vegetation, and water yields in the 5,150-square-mile (13,338 km^2) Black Hills on SW South Dakota and NE Wyoming. The forests are coniferous, mainly ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. & C. Laws.) and also white spruce var. *densata*.

The map by Munns (1938) erroneously showed an outlier straddling the Manitoba–North Dakota boundary. White spruce is present in the Spruce Woods in south-central Manitoba

(Jameson 1956), but is absent from the native flora of the Turtle Mountains, at least in Manitoban territory (Bella 1968) and probably also from the North Dakotan portion (Cayford[13] personal communication, 1968). Cayford referred to a 1964 booklet "Common Trees and Shrubs of North Dakota" by J.M. Molberg (1964) of the North Dakota School of Forestry at Bottineau, and noted that white spruce was not among the flora listed for the Turtle Mountains.

2.4.6 Exotics

As an exotic, white spruce is widespread but uncommon. It was introduced into England (Hereman 1868) and parts of continental Europe (Nisbet 1905, Jackson 1948) in or soon after the year 1700, into Denmark about 1790 (Sabroe 1954), and into Tasmania and Ceylon shortly before 1932 (Troup 1932).

Figure 2. 2 A windscreen of *Picea alba* Link [white spruce] (upright trees) and mugo pine (*Pinus mugo* (Turra)) (bent trees) near Viborg in Jutland, Denmark.

In Denmark, white spruce has been used widely in shelterbelts on sandy soils. Nisbet (1905) noted that: "On the heaths of Denmark and the dunes of Jutland, it is largely used as a protective fringe..., and is considered the best of trees for this purpose." Van der Linde's (1962) Figure 2.2 is a photograph of just such white spruce in Jutland, while Sabroe's (1954) aerial oblique photograph is of a whole landscape dominated by shelter hedges of white spruce. The heathlands of western Jutland underwent economic transformation through the establishment of a network of primarily coniferous shelterbelts, notably through the work of the Danske Hedeselkab, founded in 1866, as well as the cooperative associations for shelterbelt planting dating from 1938 (Guyot 1968). Nisbet (1905) also noted that firmly-rooted white spruce served very well to stabilize windswept edges of woods in Germany. In a narrow belt of mixed Norway and white spruces over an extremely exposed hilltop crest at high elevation in northern England, the Norway spruce were "completely dwarfed" whereas the white spruce had reached heights of between 3 and 4.3 m (Guillebaud et al. 1920). The age of the belt was not recorded, but adjoining 66-year-old stands may have been of the same vintage.

Iceland, with soil and climate similar in many respects to northern Norway and Alaska, also sought exotic forest trees to supplement the limited native forest flora. Between 1899 and 1913, seed and seedlings of several coniferous species (all from places having a milder climate), including Engelmann spruce and Norway spruce, were introduced and planted in the south, north, and northwest of Iceland (Bjarnason 1951). The spruces successfully ripened seed. Since 1936, further imports included white spruce seed from Alaska and Engelmann spruce plants from Norway from seed 2,800 m above sea level. Bjarnason (1951) described the results as promising.

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White spruce has also been used as a minor plantation species in England (Selby 1842, Anon. 1879). In Scotland, at Corrour, Inverness-shire, Sir John Stirling Maxwell in 1907 began using white spruce in his pioneering plantations at high elevations on deep peat. However, plantations in Britain have generally been unsatisfactory (Edlin 1962), mainly because of damage by spring frosts after mild weather had induced flushing earlier in the season. However, the species is held in high regard in the Belgian peat region, where it grows better than do the other spruces (Fraser 1933).

Paterson (1958) evaluated interior spruce (white, Engelmann, hybrid) in British Columbia for possible use in British forestation.

In northern Sweden, to determine the possibilities of growing forest on the higher fells, Stefansson (1957) established plots at elevations of 350 m to 725 m at Frostviken (64°30′ N) with 2- to 3-year-old seedlings of native and introduced conifers, including white spruce. Examinations at intervals during the first 20 years after planting showed that while white spruce grew rapidly at first, its growth slowed down and did not prove altogether wind-resistant.

White spruce is growing well in the world's most northern arboretum at Trondheim, Norway (Wentzel 1961), and at many arboreta in the United Kingdom, including Batsford Park, Gloucestershire (Leathart 1967a) and Tubney, Oxfordshire (Leathart 1967b).

2.5 Vegetation associations

The range of white spruce encompasses a great variety of boreal and sub-boreal climates and soils, and in different parts of the range, white and allied spruces associate with a great number of other species. An overview of the boreal home base of white spruce will serve to introduce an account of vegetation associations.

The boreal forest region covers a wide belt from Alaska/Yukon in the west to Newfoundland in the east. Wherever fire or other major disturbance has long been absent from reasonably productive upland habitats, there have developed coniferous forest ecosystems dominated by white spruce, black spruce, balsam fir, or subalpine fir, or various mixtures of these (La Roi 1967), often with an admixture of white birch, trembling aspen, or balsam poplar.

The boreal zone is distinguished climatically from the arctic by the replacement in summer of arctic airstreams by air masses originating primarily from the Pacific (Ritchie 1987). The earlier occurrence of the spring changeover in the west than in the east, and the influence of Hudson Bay, account for the southerly extension of the boreal and arctic zones in eastern Canada.

The boreal forest zone consists of closed-crown conifer forests with a conspicuous deciduous element (Ritchie 1987). The proportions of the dominant conifers (white and black spruces, jack pine (*Pinus banksiana* Lamb.), tamarack, and balsam fir) vary greatly in response to interactions among climate, topography, soil, fire, pests, and perhaps other factors.

Boreal vegetation never attains stability because of interactions among fire, vegetation, soil–water relationships, frost action, and permafrost (Churchill and Hanson 1958, Spurr and Barnes 1980). Wildfires produce a vegetation mosaic supporting an ever-changing diversity of plant and animal populations (Viereck 1973). In the absence of fire, the accumulation of sphagnum peat on level upland sites would eventually oust coniferous vegetation and produce muskeg.

Mixedwood cover types occur over a wide range of moisture regimes, soil texture and thicknesses of organic matter (Navratil et al. 1991). Historically, white spruce has been considered the most useful and desirable species in the mixedwood zone because of its large size, high yield, and valuable wood (Navratil et al. 1991).

Nearly every successional pathway in the boreal forest includes a mixedwood phase (DeLong 1991). All species regenerate after disturbance, but the level of disturbance and presence or absence of an adjacent undisturbed seed source controls the resultant species composition. Disturbances that do not expose mineral soil favour deciduous species that regenerate by suckering from disturbed root or stem sections. All species regenerate well after disturbances that expose large areas of mineral soil. Lodgepole pine and black spruce will generally regenerate after fire, if enough cones are present and unconsumed. Seed subsequently released will typically fall onto a receptive seedbed on the burned-over forest floor. In the case of white spruce, the presence of an adjacent undisturbed seed source is required, as seed from the disturbed stand is usually destroyed during the disturbance. This would suggest that white spruce would have difficulty in getting established, yet it is one of the more dominant species in the boreal forest, at least in part because it can regenerate under a canopy (DeLong 1991).

Regeneration, however, may not be the most difficult obstacle facing spruces. Regional malaise, called “die-back” or “decline” when the cause is obscure, is well known in Norway spruce in Europe, red spruce in eastern North America, and, somewhat less obviously, in black and white spruces in boreal Canada. Pastor et al. (1987) examined the hypothesis that litter from black and white spruces reduces the availability of soil nitrogen and may either cause spruce decline directly or predispose the forest to dieback from other causes. Certainly, spruce litter is poor in nitrogen and rich in recalcitrant compounds. Simulations with the model LINKAGES showed the importance of this factor to cycles of boreal forest decline in the absence of air pollution or other disturbance.

DeLong (1991) tabled some of the autecological characteristics of the main boreal tree species: aspen, balsam poplar, white spruce, lodgepole pine, and black spruce (Table 2.4). The autecology of the component species determines the dynamics of the boreal mixedwoods.

The boreal forest “is by no means uniform within the North American part of its range” (La Roi 1967), a view obviously held by Rowe (1972) who expanded the 27 sections of Halliday’s (1937) classification into 45 sections and subsections of the Canadian Boreal Forest Region, none of them internally homogeneous. Three additional sections to accommodate Alaskan variation were recognized by La Roi (1967).

Table 2. 4. Some autecological characteristics of the main tree species occurring in boreal mixedwood forests. (after DeLong 1991).

Characteristic	Aspen	Balsam poplar	White spruce	Lodgepole pine	Black spruce
Regeneration ability under canopy	Low	Low	High	Low	Low
Regeneration ability after light disturbance	High	High	Low	Low	Low
Regeneration ability after heavy disturbance	High	High	High	High	High
Susceptibility to damage by fire	High	Low	High	High	High
Nutrient content of leaf litter	High	High	Low	Low	Low
Juvenile growth	High	High	Low	Mod	Low
Palatability	High	High	Low	Mod	Low

In many ways, the spruce–fir ecosystem types may be considered dominant in the boreal forest (Whittaker 1962). A problem program analysis, prepared in 1970 in the Canadian Forestry Service, noted that the spruce–fir forests are “difficult to define although they have been recognized as a ‘type’ by foresters for many years.” A tentative definition was advanced: this type is essentially a mixedwood forest type averaging, by volume, approximately 60% conifer (essentially white spruce and balsam fir) and 40% hardwood (essentially white birch and poplar in a 50:50 ratio), occupying 3.4 million ha (8.4 million acres).

La Roi (1967) presented a useful range-wide survey of the White Spruce–Fir and Black Spruce ecosystem types. The criteria for selection of white spruce–fir stands were: white spruce or fir, separately or jointly, making up more than 50% of the living basal area of trees, with similar composition contributing more than 50% to the dominant overstorey; and trees to be larger than 30 cm dbh. Vegetation in five vascular strata (Tree, Low Tree–Sapling, Tall Shrub–Transgressive, Medium and Low Shrub–Transgressive, and Herb–Dwarf Shrub–Seedling) were recorded in 34 white spruce–fir stands spread across 24 boreal forest sections, plus five more stands in the Great Lakes–St. Lawrence and Acadian Regions, and one stand in the boreal–subalpine transition (Figure 2.3). The vascular flora consisted of 291 species in 147 genera and 47 families. That this amounted to only about one-quarter of the potential number of species was attributed to low sampling intensity, size of sampling unit, and the exclusion from the closed coniferous forest habitat defined by the selection criteria of the tolerance limits or synecological amplitudes of many plants found in other boreal ecosystems. The flora of the 34 white spruce–fir stands were richer in species than that of the 26 black spruce stands, especially in the lowest stratum. Floristic similarity between the two ecosystem types was least in the lowest stratum, and highest in the tree layer. In Alaska and western Yukon Territory, the White Spruce–Fir stands included no fir; in southeastern Newfoundland, no white spruce occurred with the balsam fir; and stands located between those areas generally contained both white spruce and balsam fir (as far west as Prince Albert National Park, Saskatchewan) or subalpine fir further west. White birch was present in every stand southeast of Great Slave Lake, mostly absent from mountain and foothill stands in northwestern Canada, and present in the Alaska interior. Trembling aspen and balsam poplar were present in about two-thirds of the stands westwards from the Ontario Clay Belt south of James Bay. In White Spruce–Fir ecosystems, black spruce presence was > 61%; in Black Spruce ecosystems, white spruce presence was 41%

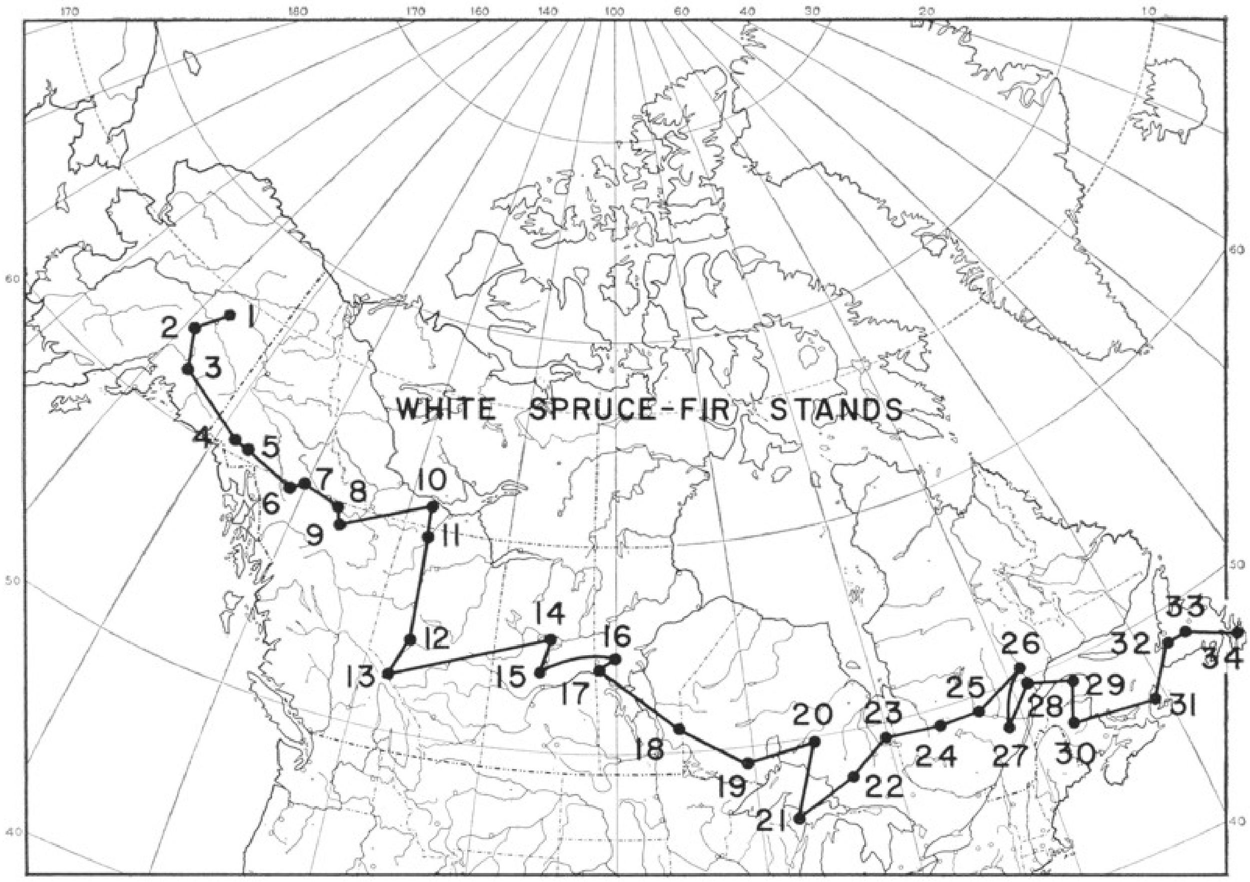

Figure 2. 3. Locations of sampled stands (La Roi 1967).

to 60%; black spruce, ranking second after white birch as an associate of white spruce and fir, was almost always present in stands of the central region, but absent from four of five stands at both eastern and western ends of the series. Jack pine occurred in four stands between central Saskatchewan and central Ontario. Subalpine fir and lodgepole pine occurred with white spruce in the boreal–subalpine taiga transition of the Canadian Rockies. Red spruce and yellow birch occurred with balsam fir–white spruce in the extreme southeast (La Roi 1967).

La Roi's (1967) findings about the Low Tree–Tall Shrub layer are also of interest. American green alder (*Alnus alnobetula* ssp. *crispa* (Aiton) Raus) was the sole member of the stratum that was common through most of the range of sampled white spruce–fir stands, though it was absent from eight stands at the eastern end of the series. Other species were confined to either the eastern or western end (excepting beaked hazlenut (*Corylus cornuta* Marsh.), with a predominantly central occurrence. These distributions enable white spruce–fir stands to be separated into three fairly distinctive geographic segments: Northwestern (willow spp.); Central (American green alder, chokecherry (*Prunus virginiana* L.), and pin cherry (*Prunus pensylvanica* L. f.), usually the only shrubs); and East of Lake Winnipeg (mountain maple (*Acer spicatum* Lamark), showy mountain-ash (*Sorbus decora* (Sarg.) C.K. Schneid.), and beaked hazelnut commonly present).

There were no pronounced regional discontinuities in the floristic composition of La Roi's (1967) Medium and Low Shrub Stratum. Four widely distributed species had very high presence values: squashberry (*Viburnum edule* (Michaux) Rafinesque) (68%), swamp red currant (*Ribes* *triste* Pallas) and prickly rose (*Rosa acicularis* Lindley) (62%), and red raspberry (*Rubus idaeus* L.) (59%). However, there were progressive and cumulative changes in the flora of this stratum from northwest to southeast, e.g., soapberry (*Shepherdia canadensis* (L.) Nuttall) occurred in 11 of 13 stands from Alaska to central Alberta, but only once elsewhere; common juniper (*Juniperus communis* L.), present in six of 11 stands from northern British Columbia to Lake Winnipeg and nowhere else; saskatoon (*Amelanchier alnifolia* (Nuttall) Nuttall ex M. Roemer), present in six of the eight stands between the Mackenzie District, N.W.T., and northwestern Ontario, but nowhere else; limber honeysuckle (*Lonicera dioica* L.), present only in eight of the 12 stands between Great Slave Lake and Lake Michigan; and northern bush-honeysuckle (*Diervilla lonicera* Miller), present in only seven of the eight stands between Lake Winnipeg and western Quebec.

The distribution of herb and dwarf shrub species in the 34 white spruce–fir stands sampled by La Roi (1967) is given in Table 2.5.

The latitudinal width of the boreal forest narrows in the central-eastern section south of James Bay owing to climatic compression between the cold, year-round influence of Hudson Bay to the north and the warmer, ameliorative effects of the Great Lakes to the south (Carleton and Maycock 1978). White and black spruces are characteristic species, and other conifers are tamarack (absent only in the far northwest), balsam fir and jack pine (prominent in the central and eastern portions), and alpine fir and lodgepole pine (in the extreme western and northwestern parts) (Rowe 1972). The forests are generally coniferous, but there is a general admixture of white birch and its varieties, trembling aspen, and balsam poplar. The poplars are prominent in the zone of transition to prairie. The proportion of black spruce and tamarack increases northward (Rowe 1972), but along river valleys of the James Bay lowlands in the north-central part of the region, there occurs pure closed boreal woodland, predominantly white spruce and balsam poplar, mostly in monoculture but often in mixed stands (Carleton and Maycock 1978).

Foster (1984) carried out a floristic analysis of the forest vegetation of southeastern Labrador using the phytosociological methods of Braun-Blanquet. A phytosociological table was constructed with the FORTRAN program TWINSPAN, which produces hierarchical classifications by two-way indicator species analysis; 88 relevés incorporating 77 species are grouped into five major assemblages: birch; fir–spruce–feather moss; spruce–fir; spruce–*Pleurozium*; and spruce–*Sphagnum fuscum* (Schimp.) Klinggr communities. The five communities, as arranged from birch to spruce–*S. fuscum*, display decreasing trends in productivity, site quality and richness of vascular flora, as well as increasing prominence of oligotrophic species, primarily cryptogams and ericaceous shrubs. Black spruce and balsam fir comprise more than 95% of the forest canopy in this region, whereas paper birch is restricted to moist and well-drained slopes, and white spruce, aspen and balsam poplar are rare.

Table 2. 5. Geographic distribution of herb and dwarf shrub species in white spruce – fir stands. Population size notation is areal coverage as a percentage[a].

	Presence	**White spruce – fir stand number**																																	
Species	**%**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Vaccinium uliginosum	12	1	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solidago multiradiata	18	1	-	1	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gentiana propinqua	12	-	-	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Empetrum nigrum	21	1	4	3	-	-	3	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lupinus arclicus	15	-	-	5	1	-	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arctostaphylos rubra	15	-	-	1	3	1	6	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix myrtilli folia	15	-	-	1	1	-	6	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Achillea millefolium	15	-	-	-	1	1	1	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corallorhiza trifida	21	-	1	1	-	-	1	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hedysarumalpinum	18	-	-	1	1	2	-	-	-	1	-	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vacciniumvitis – idaea	35	2	6	6	-	-	3	1	5	5	5	1	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geocaulon lividum	35	1	-	-	1	-	1	1	5	2	3	1	-	6	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arctostaphylos uva – rusi	21	-	-	-	1	1	-	1	-	-	1	-	-	4	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pyrola asarifolia	44	3	3	2	1	-	-	2	2	1	1	1	5	-	1	2	-	1	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Carex concinna	15	-	-		1	1	-	-	-	-	-	-	-	-	4	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Equisetum scirpoides	38	-	1	1	1	-	1	-	1	2	1	1	-	-	1	-	-	1	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Mertensia paniculata	50	1	5	-	1	2	1	2	1	1	-	5	6	-	4	6	1	1		2	3		-	1	-	-	-	-	-	-	-	-	-	-	-
Equisedum arvense	38	1	2	1	-	-		1	1	2	-	3	1		1		-	1	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Galiumboreale	29	3	-	-	-	1	-	1	-	-	1	1	-	3	-	2	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elymus innovatus	21	-	-	-	-	-	-	-	1	2	1	1	-	6	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	-	-
Epilobium angustifolium	53	1	1	2	2	2	1	3	2	1	1	1	-	1	1	1	1	-	-	-	-	-	-	-	-	1	-	-	-	1	-		-	1	-
Fragaria sirginiana	38	-	-	-	1	1	1	-	-	-	1	2	1	5	2	2	1	1	2	1	-	-	-	-	-	-	-	-		-	-	-	-	-	-
Lathyrus ochroleucus	18	-	-	-	-	-		-	-	-	1	1	1	1	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fragaria vesca	12	-	-	-	-	-	-	-	-	-	-	2	3	-	1	1	-	-	-	-	-	-	-	-	-		-	-		-	-		-	-	-
Pyrola virens	35	-	-	-	-	-	-	-	1	-	1	1	1	1	1	2	1	1	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Habenaria obtusata	35	1	1	1	1		1	1		-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	1	1
Equisetum sylvaticum	29	1	2	-	-	-	-	-	-	-	-	-	1	-	3	1	-	-	-	1	1	1	-	1	-	-	-	1	-	-	-	-	-	-	-
Pyrola secunda	85	1	2	2	1	1	1	4	3	2	1	1	1	4	2	2	1	1	1	-	-	1	1	1	1	1	1	-	1	1	1	1	-	1	-
Viola renifolia	47	-	-	-	-	-	-	1	1	-	1	1	2	-	1	1	1	1	2	1	1	-	1	2	1	1	-	-	-	-	-	-	-	-	-
Petasites palmatus	35	-	-	-	-	-	1	-	1	-	-		1		2	2	-	1	1	2	3	1	-	1	-	-	1	-	-	-	-	-	-	-	-
Monesesuniflora	68	1	1	1	1	-	1	1	1	1	1	-	1	-	1	2	-	-	-	-	-	1	1	1	1	1	-	1	1	1	1	-	1	1	-
Linnaea borealis	97	6	5	5	3	4	3	4	3	3	3	5	5	6	4	6	2	3	3	-	1	2	3	4	2	2	2	1	2	2	2	1	1	3	4
Mitella nuda	68	-	-	-	-	-	1	1	2	1	1	4	6	-	4	5	1	1	4	5	6	3	1	4	1	1	-	-	1	1	1	-	-	1	-
Apocynum androsaemi folium	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Cornus canadensis	88	6	3	-	-	-	1	6	2	5	2	6	6	-	5	6	1	2	3	1	4	3	6	4	3	3	3	5	3	5	4	3	4	4	5
Goodyera repens	59	1	-	-	-	-	-	-	1	1	-	1	1	2	1	-	1	-	1	1	1	1	-	1	1	1	-	-	1	1	-	1	-	2	1
Lycopodiumannotinum	56	1	2	-	-	-	-	1	-	-	-	-	1	-	1	1	-	-	1	1	1	2	1	2	3	1	1	1	-	1	-	-	1	1	-
Circaea alpina	24	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	1	1	-	1	-	1	-	-	-	-	-	-	-	-	1	-
Anemon aquinquefolia	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	4	1	1	1	-	-	-	-	-	-	-	-	-	-	-
Actaea rubra	38	-	-	-	-	-	-	-	-	-	-	2	1	-	1	1	-	-	1	1	1	1	1	1	-	1	-	-	1	-	-	-	-	1	-

Table 2.5. Geographic distribution of herb and dwarf shrub species in white spruce – fir stands. Population size notation is areal coverage as a percentage[a] (continued).

	Presence	White spruce – fir stand number																																	
Species	**%**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Galium triflorum	35	-	-	-	-	-	-	-	-		-	-	2	-	1	1	-	-	1	2	2	1	1	1	1	1	-	-	-	-	-	-	-	1	-
Aralia nudicaulis	53	-			-	-	-	-	-	-	-	1	6	-	6	3	1	3	6	6	5	2	6	5	4	5	-	-	4	1	1	1	-	-	-
Rubus pubescens	62	-	-	-	-	-	-	-	-	-	1	6	6		6	5	1	1	5	1	6	1	1	3	2	1		1	2	1	1	1		1	-
Aster macrophyllus	18	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	5	6	1	4	2	1	-	-	-	-	-	-	-	-	-	-
Habenaria orbiculata	12	-	-	-	-	-	-	-	1	-	-	-	-	-		-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Gymnocorpium dryopteris	44	-	-	-	-	-	-	-	-	-	-	-	6	-	1	1	-	-	-	1	1	2	1	2	2	2	1	1	1	1	-	-	-	2	-
Vacciniurn myrtilloides	32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	2	1	1	1	-	1	-	-	1	1	-	-	-
Schizachne purpurascens	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	-	-				-	1	-	-	-
Athyrium filix-femina	12	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Cinna latifolia	32	-	-	-	-	-	-	-	-	-	-	-	2	-	-		-	-	-	1	1	1	1	1	1	1	-	1	-	-	1	-	-	1	-
Vaccinium anqustifolium	15	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	1	-	-	-	-	-		-	-
Maianthemum canadense	65	-	-	-	-	-	-	-	-	-	-	-	2	-	3	2	1	1	3	4	1	2	4	3	4	5	2	2	5	1	2	1	4	5	1
Pteridium aquilinum	12	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-	-	3	-	-	-	-
Trientalis borealis	59	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-	1	3	2	1	1	2	2	2	1	3	2	2	2	1	1	2	2	5
Streptopus roseus	41	-	-	-	-		-	-	-	-	-	-	-	-	-		-	-	1	1	1	1	2	1	1	1	2	-	2	1	1	1	1	-	-
Sreptopus amplexifolius	18	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2-	1	-	-	-	-	1	-
Osmunda claytoniana	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1	-	3	-	-	-	-
Lycopodium obscurum	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	1	1	1	1	1	1	1	-	1	-	1	1	-
Clintonia borealis	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	1	1	6	2	3	3	6	1	4	3	2	1	5	1	1
Ozalis montana	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	6	6	6	6	6	6	6	5	2	-	-	-
Coptis groenlandica	47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	2	4	2	3	2	1	3	1	2	3	1	1	1
Dryopteris austriaca	47	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	1	2	2	4	2	3	5	2	1	6	6	6
Viola incognita	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	1	-	1	1	-	-	1		1	1	1	1	-
Gaultheria hispidula	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	2	2	1	1	1	1	1	-	-	1
Monotropa uniflora	24		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1	-	-	-	-	-	1	1	1	1	1	-
Solidago macrophylla	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	1	1	1	-	-	-	-
Thelypteris phegopteris	24	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	1	-	-	2	1	1	1	1	-	-
Lycopodium lucidulum	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	1	1	1	1	-
Listera cordata	15	-	-		-	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	-	-	1	1

[a] (1 = 0 – 0.33%, 2 = 0.34 – 1.0, 3 = 1.1 – 2.0, 4 = 2.1 – 3.3, 5 = 3.4 – 5.0, 6 = >5, dash = absent)

Data sets presented by Gordon (1981) are part of a matrix of contributions of 116 international forest research sites from around the world that are associated with designated projects of the International Biological Program. They were collected into the Woodlands Data Set to facilitate comparisons involving a large number of diverse woodland ecosystems and specifically to address productivity. The data relate to four spruce forest ecosystems, representing a soil moisture catena of dry, fresh, moist and wet sites in Ontario Site Region 5E. Principal species are red, black and white spruces, balsam fir, eastern hemlock, red maple and yellow birch. The data include many variables, such as growing season, mean annual and growing season temperature and precipitation etc., standard stand mensurational data, compartment biomass and increment for all components (e.g., overstorey leaves, flowers, fruits, branches, bark etc.) understorey of the same, living and dead roots, standing crop above and below ground, leaf area indices, productivity above and below ground etc. and major fluxes such as litterfall.

2.5.1 Forest cover types

Cover types are categories of forest defined by species composition of their vegetation. The Society of American Foresters (SAF 1954) recognized six forest types in which white spruce occurs as an integral component: pure white spruce (east); white spruce and balsam fir; white spruce, balsam fir, and aspen; white spruce, balsam fir, and paper birch; pure white spruce (west); and white spruce and birch. In 13 other forest types, white spruce occurs as an incidental, minor component.

Especially in central and eastern Canada, white spruce occurs as a rather minor component in a variety of forest stands loosely termed “mixedwoods”, a tentative definition of which was included in the problem program analysis for Problem Program 07 Spruce–Fir Management undertaken by the Ontario Region, Canadian Forest Service in 1970: “essentially a mixedwood forest type averaging by volume approximately 60% conifer (essentially white spruce and balsam fir) and 40% hardwood (essentially white birch and poplar in a 50:50 ratio)”.

2.5.1.1 Pure white spruce

White spruce forms pure stands, e.g., on wet (“swamp spruce”), dry (“prairie spruce”), and upland fire sites in the prairie provinces (Rowe 1972), in the coastal fog belt of northern Quebec and Labrador (Payette 1980), and in old fields in eastern North America (Drinkwater 1957, Jablanczy 1969). In many parts of the maritime provinces of Canada, abandoned fields quickly become stocked to even-aged stands of white spruce (cf. Fig. 4 of Loucks 1962 [Figure 2.4]). Pure stands are also widespread in all the western provinces of Canada, in the Northwest Territories, and in Alaska, and are especially common in the interior of northern British Columbia. In Alaska and northwest Canada, white spruce grows particularly well on fluvial deposits along the Peace and other rivers in northern Alberta (Jeffrey 1961) and Alaska (Youngblood and Max 1992). The most widespread development of pure or virtually pure stands of white spruce is in interior Alaska, the Northwest Territories, interior British Columbia,

Figure 2. 4 In many parts of the maritime provinces the abandoned fields are quickly stocked to even-aged stands of white spruce. Behind a young stand on recently abandoned land is an older stand (from Loucks 1962).

and Alberta on a wide range of sites, including river bottom alluvium, river floodplains and terraces, and south-facing upland slopes (Eyre 1980, Nienstaedt and Zasada 1990). The main associated tree species in the White Spruce Cover Type in Alaska include paper birch, trembling aspen, balsam poplar, and black spruce. In western Canada, additional associates include subalpine fir, balsam fir, Douglas-fir, jack pine, and lodgepole pine. White spruce is considered the climax species, excepting “certain river bottom sites” where black spruce might replace white spruce (Viereck 1970a). Seral species replaced by white spruce include all its main associates.

The White Spruce Cover Type may include other species in small numbers. In Alaska, associates include paper birch, trembling aspen, balsam poplar, and black spruce; in western Canada, additional associates are subalpine fir, balsam fir, Douglas-fir, jack pine, and lodgepole pine (Dyrness 1980). Seral species giving way to white spruce include paper birch, aspen, balsam poplar, jack pine, and lodgepole pine. On certain river bottom sites, however, black spruce may replace white spruce (Viereck 1970a). Earlier successional stages leading to the white spruce climax are the white spruce–paper birch, white spruce–aspen, balsam poplar, jack pine, and lodgepole pine types. The type shows little variation. The forest is generally closed and the trees well formed, other than those close to the timberline. Lesser vegetation in mature stands is dominated by mosses. Vascular plants are typically few, but shrubs and herbs that occur “with a degree of regularity” include: alder, willows, mountain cranberry, red bearberry (*Arctous rubra* (Rehder & E.H. Wilson) Nakai), black crowberry, prickly rose, currant species (*Ribes* L. spp.), soapberry, blueberry (*Vaccinium* L. spp.), bunchberry (*Cornus canadensis* L.), twinflower (*Linnaea borealis* L.), tall bluebells (*Mertensia paniculata* (Aiton) G. Don), northern comandra (*Geocaulon lividum* (Richardson) Fernald), horsetail (*Equisetum* L. spp.), bluejoint reedgrass (*Calamagrostis canadensis* (Michaux) Palisot de Beauvois), sedge (*Carex* L. spp.), as well as ground-dwelling mosses and lichens. Several white spruce communities have been identified in interior Alaska: white spruce/feathermoss; white spruce/dwarf birch/feathermoss; white spruce/dwarf birch/sphagnum; white spruce/avens/moss; and white spruce/alder/bluejoint (Viereck 1975, Dyrness 1980).

Of the Eastern Forest Cover Types recognized by the Society of American Foresters (Eyre 1980), only one, White Spruce, names that species in its title. The eastern White Spruce Cover Type, as defined, encompasses white spruce both in pure stands, and in mixed stands “in which white spruce is the major [undefined] component” (Payette 1980).

In most of its range, white spruce occurs more typically in association with trees of other species than in pure stands.

2.5.1.2 White spruce mixtures

Mixedwoods

In many respects, the most characteristic occurrence of white spruce is as an important but not always common component of boreal mixedwoods. For instance, in the Lake Edward, Laviolette County area of Quebec, near the southeastern edge of the Laurentian Plateau, the mixedwood is forest of yellow birch, sugar maple (*Acer saccharum* Marsh.), beech, balsam fir, red spruce, with less common red maple (*Acer rubrum* L.), white birch, and, scattered on the ridges and lake margins, white pine, with black spruce and Atlantic white-cedar (*Chamaecyparis thyoides* (L.) B.S.P.) in swamps and on rocky moss-covered lake shores, larch in some of the more open swamps, hemlock widely scattered in association with hardwoods, and black ash (in small swamps, and on stream banks in the upland types, scattered white spruce are found, chiefly on alluvial soil (Ray 1956).

In New Hampshire, scattered white spruce occurred in an old-field stand of red spruce and 5% balsam fir (Baldwin 1933).

Nienstaedt and Zasada (1990) present an excellent summary of the Society of American Foresters (Eyre 1980) account of forest cover associated with white spruce. The separation into Eastern Forest and Western Forest delineates real ecological differences.

The Eastern Forest includes the forest cover type White Spruce (Type 107) in which white spruce occurs in either pure stands, or mixed stands in which white spruce is the major component. Associated tree species include black spruce, paper birch, trembling aspen, red spruce, balsam fir, and, less commonly, yellow birch, and sugar maple. In New England, the maritime provinces of Canada, and within the fog belt in Quebec and Labrador, the white spruce cover type is minor and confined to abandoned fields. It is more widespread elsewhere in eastern Canada and as far north as the tree line in Ungava and along Hudson Bay. In northern Quebec, the lichen (*Cladonia*) woodland, the feathermoss forest, and the shrub forest with dwarf birch and heath species are common white spruce communities.

White spruce is an associated species in the following Eastern Forest cover types, by the Society of American Foresters: In the Boreal Forest Region: (1) Jack pine, (5) Balsam fir, (12) Black spruce, (16) Aspen, (18) Paper birch, and (38) Tamarack. In the Northern Forest Region: (15) Red pine, (21) Eastern white pine, (24) Hemlock-Yellow birch, (25) Sugar maple-Beech-Yellow birch, (27) Sugar maple, (30) Red spruce-yellow birch, (32) Red spruce, (33) Red spruce-Balsam fir, (37) Northern [Eastern] White-cedar, and (39) Black ash-American elm-Red maple.

In Types 15, 16, and 18, white spruce attains increasing importance in the stand composition as the progression progresses and more tolerant species take over.

In Alaska and the Northwest Territories, the Western Forest White Spruce cover type (Type 201) is largely confined to stream bottoms, river floodplains, terraces, and warm south-facing upland sites. Further south in British Columbia and Alberta, it is distributed more broadly at elevations between 760 m and 1,520 m. Associated tree species in Alaska include paper birch, trembling aspen, black spruce, and balsam poplar. In western Canada, subalpine fir, balsam fir, Douglas-fir, jack pine, and lodgepole pine are important associates.

The type varies little and generally occurs as closed stands. White spruce plant communities In interior Alaska include white spruce/feathermoss, white spruce/dwarf birch/feathermoss, white spruce/mountain avens (*Dryas* L.)/moss, and white spruce/alder/bluejoint grass. Two communities are common in northwestern Canada and in Alaska: white spruce/willow/buffaloberry (*Shepherdia* spp.)/northern goldenrod (*Solidago multiradiat*a Aiton)/crowberry (*Empetrum* L. spp.); and white spruce/willow/buffaloberry/huckleberry (*Gaylussacia* Kunth spp.)/raspberry (*Rubus* L. spp.)/vetchling (*Lathyrus* L. spp.).

Cayford (1957) described a mixedwood type consisting mainly of white spruce and trembling aspen that is widely distributed in western Canada, east of the Rockies. In interior British Columbia, the most common boreal mixedwood type found on upland sites is aspen/white spruce (DeLong 1991). Two situations dominate in this type: either the white spruce regenerates within a few years of the aspen, or there is a delay of 20 or more years. The first situation requires a severe disturbance, usually a hot burn, to expose mineral soil, as well as a good crop of viable seed from a nearby live seed source so that regeneration occurs before aspen suckers dominate the site. In the absence of sufficient white spruce seed at this stage, aspen and other aggressive pioneer vegetation, such as bluejoint grass, are quickly established. Aspen density often reaches 80,000 stems/ha in young stands in the first 5 years.

By the age of 30 to 40 years, most such stands have reduced density to 2,000 stems/ha or fewer, and this reduction provides another opportunity for white spruce to seed in. Apart from the reduction in aspen density, by this time the understorey vegetation has diversified and includes relatively uncompetitive, low-growing herbs, such as bunchberry, dwarf raspberry (*Rubus pubescens* Rafinesque), and creamy-coloured vetchling (*Lathyrus ochroleucus* Hooker). Given a good seed year and a relatively moist summer, spruce is able to regenerate on any vacant microsite. Favoured microsites are rotten wood and exposed mineral soil, but some seedlings may be able to establish themselves on leaf mould, and even on moss (DeLong 1991).

In interior British Columbia, the most common mixedwood type found on lowland alluvial deposits is balsam poplar/white spruce, an ecosystem that generally originates from periodic flooding, which does not kill balsam poplar and leaves a mineral soil seedbed. White spruce grows well on these rich, wet sites in the absence of major flooding and will eventually dominate the site (DeLong 1991).

Other mixedwood forest types are uncommon in the West and are generally of small extent. Willow /white spruce and white birch are the most notable of these. Willow/spruce mixedwood generally occurs on very wet sites with fairly thick organic layers, which Rowe (1955) in Manitoba called the Swamp Spruce Cover Type, featuring white spruce in an advanced stage in succession on wet sites, e.g., in a zone interposed between tamarack and upland spruce – poplar surrounding sloughs, much after the manner of black spruce elsewhere. These sites are too wet for aspen, but balsam poplar is sporadically present, and balsam fir may invade older stands.

The aspen/white spruce mixedwood type is the main component type of the broad Mixedwood Section (B.18) of Halliday’s (1937) Western Boreal Forest Region, extending from southwestern Manitoba northwestward across central Saskatchewan and central and northern Alberta. Minor associates of the two main species are black spruce, jack pine, balsam fir, balsam poplar, and white birch. Aspen usually forms an overstorey in young and intermediate-aged stands, but in older stands the tallest spruce exceed the height of the aspen. Beyond about 70 years of age, the percentage of spruce increases as a consequence of aspen deterioration (Riley 1952), but the proportion of aspen in some stands older than 100 years may still be high.

A study in five mixed stands of aspen and white spruce in Saskatchewan not surprisingly found that large differences in growth between free and suppressed spruce may occur (Cayford 1957).

In mixed stands up to 100 years old, an aspen overstorey may reduce white spruce volume by as much as 50% compared with nearby free-growing spruce of the same age. The quality of white spruce suppressed under an aspen overstorey will be diminished, with leaders damaged by whipping and common defects such as forked top, crook and sweep.

In the White Spruce – Aspen cover type (Type 251), either species may be dominant, but each species must make up at least 20 percent of the total basal area. Paper birch and black spruce may also be represented in Alaskan stands along with balsam fir and lodgepole pine in Canadian stands. The type is common throughout western Canada at lower elevations, and in all of interior Alaska. Associated shrubs in Alaska are American green alder, willows, common bearberry (*Arctostaphylos uva-ursi* (L.) Sprengel), soapberry, squashberry, and mountain cranberry. Associated shrubs in the prairie provinces are thin-leaved snowberry (*Symphoricarpos albus* (L.) S.F. Blake), red-osier dogwood (*Cornus sericea* L.), saskatoon, and western chokecherry (*Prunus virginiana* var. *demissa* (Nuttall) Torrey).

A generalized logistic model of individual tree mortality for aspen, white spruce, and lodgepole pine in Alberta mixedwood forests was developed by Yao et al. (2001) for trembling aspen, white spruce, and lodgepole pine in boreal mixedwood forests in Alberta, based on an empirical database of permanent sample plots.

Accurate prediction of tree mortality is an essential feature in any stand growth system (Monserud 1976, Yao et al. 2001). Early mortality models predicted the future number of trees per unit area, i.e., at stand level. Individual tree mortality models differ from stand level mortality models in that each individual tree involved in the growth prediction receives an estimate of the probability of survival (Clutter et al. 1983). Mortality in mixedwood stands is more difficult to predict than in pure stands. The survival probability was modelled for the three major commercial species, and the model is suitable for observations from unequal remeasurement intervals. The maximum likelihood estimation was used to fit the model, the likelihood ratio test was combined with the authors' understanding of mortality process to select the important variables, and fit was evaluated using the Hosmer-Lemeshow goodness-of-fit test. The fitted model predicts the survival probability of an individual tree based on the tree diameter at breast height, annual diameter increment, stand basal area, species composition and site productivity. Three generalized logistic models of individual tree mortality for white spruce, aspen, and lodgepole pine confirmed some commonly held beliefs related to Alberta mixedwood stands that are older than 30 years. Aspen is the shortest-lived species, with the lowest survival probability, while white spruce is the longest-lived and has the highest overall survival probability. Even with a high stand basal area and aspen component, the shade-tolerant spruce maintained high survival. As might be expected, small trees showed higher mortality, regardless of basal area. The models show that survival probability decreases with very large dbh. Mechanisms that were suggested to explain this phenomenon included the increased proportional allocation of carbon to support respiration, increased allocation to fine roots, decreased photosynthetic efficiency caused by increasing nutrient limitations in older stands, genetically programmed slowing of growth, and decreased photosynthesis caused by increased hydraulic resistance in larger trees. In mixedwood stands of aspen and spruce, the shade-intolerant aspen has faster early growth and rapidly occupies the upper canopy (Peterson and Peterson 1992). For about 50 years, aspen continues to dominate the site, but white spruce becomes progressively more conspicuous in the understorey. The model for aspen suggests that aspen survival decreases with increasing spruce composition, whereas the model for spruce indicates that aspen competition did not significantly influence spruce mortality.

In the White Spruce – Paper Birch cover type (Nienstaedt and Zasada 1990), either spruce or birch may be dominant and both must make up at least 20% of the total basal area (Type 202). Associated species are aspen, lodgepole pine, subalpine fir, and black spruce. The type is common in western Canada and in Alaska from the Arctic Circle to the Kenai Peninsula. Understorey species include: willow, American green alder, highbush cranberry (*Viburnum opulus* var. a*mericanum* Aiton), mountain cranberry, bunchberry, prickly rose, and common Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd).

Both the White Spruce – Aspen and White Spruce – Paper Birch cover types are commonly considered to be successional stages leading to a climax of pure white spruce. The Black Spruce – White Spruce cover type (Type 253) may be the climax on some sites near the altitudinal and northern tree lines, or it may be successional to black spruce on some intermediate sites on old river terraces. Black Spruce – White Spruce is the lichen – woodland type from Hudson Bay to northwestern Alaska along the treeline, as well as in open stands at the alpine treeline in interior Alaska and northwestern Canada. The type also occurs on sites intermediate to the two species, e.g., old terraces above the floodplain. Associate species may include white birch, tamarack, balsam poplar, aspen, and balsam fir. A continuous shrub layer of glandular birch, alder, and willows, in open stands near the treeline may give way on dry sites to feathermosses and *Cladonia* lichens. Other shrubs common within the cover type are Labrador tea, bog bilberry (*Vaccinium uliginosum* L.), mountain cranberry, and black crowberry.

White spruce also occurs as a minor component in eight Western Forest cover types: (203) Balsam poplar, (204) Black spruce, (206) Engelmann spruce-Subalpine fir, (217) Aspen, (218) Lodgepole pine, (237) Interior ponderosa pine, (252) Paper birch, and (254) Black spruce-Paper birch. Several of these cover types are successionally intermediate. For example, Type 252 paper birch may advance through White spruce – Paper birch to pure White spruce. Type 203 Balsam poplar is eventually overtopped and replaced by white spruce.

In the Canadian boreal spruce – fir forest, American green alder is the most widespread tall shrub, with little tree willow (*Salix arbusculoides* Andersson), grey-leaved willow (*Salix glauca* L.), and Bebb's willow (*Salix bebbiana* Sarg.) important in the western range. In the east, mountain maple, showy mountain-ash, and American mountain-ash (*Sorbus americana* Marsh.) are important. Highbush cranberry, swamp red currant, prickly rose, and red raspberry are the most common shrubs of the medium and lower layers. In the herb – dwarf shrub layer, fireweed (*Chamaenerion angustifolium* (L.) Scopoli), one-sided wintergreen (*Orthilia secunda* (L.) House), one-flowered wintergreen (*Moneses uniflora* (L.) A. Gray), twinflower, naked mitrewort (*Mitella nuda* L.), bunchberry, dwarf rattlesnake-plantain (*Goodyera repens* (L.) R. Brown), stiff clubmoss (*Spinulum annotinum* (L.) A. Haines), and horsetail are common (La Roi 1967).

The most common mosses in Canadian boreal spruce – fir stands are red-stemmed feathermoss, stairstep moss, knight's plume moss, curly heron's-bill moss (*Dicranum fuscescens* Turn.), and sickle moss (*Sanionia uncinata* (Hedw.) Loeske). The most common liverworts are tree fringewort (*Ptilidium pulcherrimum* (G. Web.) Hampe), ciliate fringewort (*Ptilidium ciliare* (L.) Hampe), notchwort (*Lophozia* (Dum.) Dum. spp.), and hairy threadwort (*Blepharostoma trichophyllum* (L.) Dum.). Common lichens include common freckle pelt lichen (*Peltigera apthosa* (L.) Willd.), dog pelt lichen (*Pelitigera canina* (L.) Willd.), grey reindeer lichen (*Cladonia rangiferina* (L.) F.H. Wigg.), *Cladina arbuscula* ssp. arbuscula (Wallr.) Hale & W.L. Culb., star-tipped reindeer lichen (*Cladonia stellaris* (Opiz) Pouzar & Vezda), smooth soldiers lichen (*Cladonia gracilis* (L.) Willd.), and true Iceland lichen (*Cetraria islandica* (L.) Ach.) (La Roi and Stringer 1976).

White spruce associates with balsam fir and sometimes with black spruce and tamarack in coastal areas of Atlantic Canada; in Maine, a seacoast associate is red spruce (Payette 1980). In eastern Canada and northern New England, white spruce associates with paper birch, aspen, balsam fir, red spruce, yellow birch, and sugar maple. Cover types that were no longer recognized in the Eyre (1980) revision include White Spruce/Balsam Fir and White Spruce/Balsam Fir/Paper Birch, both of which are "now considered a variant of white spruce".

In an area of boreal forest between James Bay and the Great Lakes, between longitudes 75° – 85° W north of latitude 47° N, white spruce was found in 22% of 152 stands sampled (Carleton and Maycock 1978). Black spruce (63%), balsam fir (55%), jack pine (31%), trembling aspen (31%), and white birch (26%) showed a higher presence, and balsam poplar occurred in 13% of the stands. No other species reached a presence of 10%. Scatter diagrams of the tree importance vs. sapling importance for several species, including white spruce, suggest that they are adapted to the colonization of open, non-forested sites:

> "*Populus balsamifera* and *Picea glauca* invade newly exposed fluvial silts and some upland sites. Unlike black spruce, white spruce sheds most of its annual seed crop shortly after cone maturity in early fall (Stiell 1976) and this corresponds with a time when river levels are at their lowest. In addition, saplings of white spruce do appear in some upland stands often overlying a coarse, moist sandy substrate. However, these are always associated with one or two old white spruce in close proximity. This feature is most marked in jack pine stands close to Lake Superior where a 'blanket effect' from white spruce in the prevalent formation, an upland white spruce – paper birch – balsam fir mixture, occurs. Thus, white spruce seedlings and saplings are found in all forests of the area." (Carleton and Maycock 1978).

The forests of the Labrador Peninsula include widespread black spruce and balsam fir with some white spruce and eastern larch. White spruce constitutes less than 5% of the forest, and its range coincides closely with that of black spruce, but extends slightly further north (Wilton 1964). In the Melville – Grand Lake area, mixed stands of balsam fir, black spruce and scattered white spruce are typical of deep soils in the river valleys and lowland plains (Wilton 1959). In the Fir/Spruce/Birch/Rich Herb, Undisturbed type, white spruce in association with balsam fir (78%) and black spruce (17%) contributes only 2% to 3% to the tree cover, but scattered specimens 94 cm dbh and 32 m tall have been measured (Wilton 1959). Elsewhere in the Peninsula, black spruce is ubiquitous and white spruce rare.

In the east, there is considerable intermixture with species from the Great Lakes–St. Lawrence Forest Region, e.g., eastern white pine, red pine, yellow birch, sugar maple, black ash, and eastern white cedar (Rowe 1972).

The species is more strongly represented in the northwestern than in the northeastern parts of the range. For instance, white spruce occurs “almost universally throughout” southern Yukon, while black spruce is “scarce or absent” (Hare 1950), and white spruce is the only conifer in the extensive woodlands of the Mackenzie Delta (Ritchie 1987). White spruce extends to the Arctic Ocean along north-flowing rivers, such as the Anderson, Horton, and Coppermine. In contrast, white spruce is relatively uncommon in much of interior Labrador (Wilton 1964, Ritchie 1987). The Labrador – Ungava area, east of Lake St. John “is largely covered by close-forest associations of black spruce and balsam fir” (Hare 1950), though white spruce is the main species in the humid climate of a narrow (2 km to 10 km) strip along the east coast of Hudson Bay (Ritchie 1987). In the central boreal zone of Quebec, where snowfall is heaviest, the forest is dominated by balsam fir and black spruce, whereas white spruce occurs only locally (Ritchie 1987). White spruce is more common west of Lake St. John in the Labrador – Ungava peninsula. Along the Atlantic coast, white spruce forms the treeline in association with tamarack and black spruce (Payette 1983).

In the Cordilleran (main continental mountain axis) region, white spruce is locally common in submontane and lowland habitats associated with trembling aspen, but it is rare in, or absent from, the subalpine Engelmann spruce – subalpine fir communities (Ritchie 1987). White spruce occurs in all five sections of Rowe’s (1972) Forest Regions of Canada. In the Ponderosa Pine and Douglas-fir section, white spruce occupies river flats and creek sides, and, although it tends to maintain an altitudinal position below that of Engelmann spruce, the latter species is often found on lowland alluvium. At higher elevations in the Central Douglas-fir section, the intergrading Engelmann – white spruce complex and alpine fir enter from the subalpine forest. In the Northern Aspen section, white spruce and some Engelmann spruce, together with lodgepole pine and scattered interior Douglas-fir, are mixed with the predominant aspen. The characteristic forest type of the Montane Transition section consists of white spruce in the north, Engelmann spruce and the white × Engelmann hybrids elsewhere, and alpine fir. On the eastern side of the section, Engelmann spruce forms mixed stands with western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock, as well as with Douglas-fir. Even in the localized Douglas-fir and lodgepole pine section, white spruce, with some black spruce, commonly dominate sites with northerly aspects, seepage sites, and ravine bottoms.

In the northern Cordillera, white spruce is abundant especially on alluvial and well-drained upland soils, where it forms the treeline (Ritchie 1987).

In general, white spruce tends to occupy fertile sites that are moderately to well drained, whereas black spruce occupies sites that are less fertile and more poorly drained. However, white spruce also occurs, albeit less typically, on poor and imperfectly drained sites, as in the *Picea glauca – Equisetum* and *Picea glauca*/*Populus – Cornus*/*Rubus* ecosystems (Kabzems et al.

1986) and the “swamp spruce” type in the Prairie Provinces (Rowe 1972). White spruce is as fully able as black spruce to withstand climatic rigors other than spring frosts, but is less well adapted to regenerate after fire.

White spruce also occurs in forests of Rowe’s (1972) Great Lakes–St. Lawrence and Acadian Forest Regions in Canada, and as a less prominent component of the spruce–fir–hardwood type groups in the Lake States (Hansen 1980) and Northeastern (Hansen 1980) Regions of the United States. The interactions among the diverse components of the spruce–fir–hardwoods provide further useful ecological and physiological information.

The Huron–Ontario section includes Manitoulin Island, on which sugar maple forms the dominant association with a varying admixture of red maple, white elm (*Ulmus americana* L.), basswood (*Tilia americana* L.), yellow birch, red oak, bur oak (*Quercus macrocarpa* Michx.), eastern hop-hornbeam (*Ostrya virginiana* (Mill. K. Koch), beech, largetooth aspen, white birch, white ash (*Fraxinus americana* L.), black ash, red ash (*Fraxinus pennsylvanica* Marsh.), and small numbers of white spruce, red pine, eastern white pine, balsam fir, eastern hemlock, and, according to Rowe (1972), eastern red cedar, though Hosie (1969) excluded Manitoulin from the distribution. Eastern white cedar is more likely.

Eastern hemlock, eastern white pine, white spruce, and balsam fir usually occur on shallow, acidic, or eroding materials in the Upper St. Lawrence Section; and after fires, largetooth aspen and white birch, together with white spruce and balsam fir, play a prominent role in the pioneer forest stands (Rowe 1972).

In the Middle St. Lawrence section, the prevailing mixed forest reflects both boreal and disturbance influences. Important forest types are formed by white spruce and balsam fir, as well as by sugar maple, yellow birch, eastern hemlock, eastern white pine, red maple, and grey birch (*Betula populifolia* Marsh.). Local associates are red oak, beech, white ash, white elm, and red pine.

The forest cover of the Laurentian Section is largely upland tolerant hardwood stands with mixedwoods and softwoods in the valleys. The chief species on hill slopes are yellow birch, sugar maple, red spruce, balsam fir, red maple, and white birch, but eastern hemlock (*Tsuga canadensis* (L.) Carrière), beech, white pine, and white spruce are distributed throughout.

The characteristic species of the Algonquin – Pontiac Section are sugar maple, red maple, yellow birch, eastern hemlock, and eastern white pine, are prominent, often in mixture with boreal conifers, notably red spruce and balsam fir, but also some white spruce (Rowe 1972).

Various amounts of white spruce, balsam fir, trembling aspen, white birch, red oak, and basswood are present throughout forests of the Middle Ottawa Section, the usual constituents of which are sugar maple, beech, yellow birch, red maple, and eastern hemlock, almost always accompanied by eastern white pine and red pine. Other species with minor representation include butternut, bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch), bur oak, white ash, and black cherry (*Prunus serotina* Ehrh.) (Rowe 1972).

In the Georgian Bay Section of the Great Lakes–St. Lawrence Forest Region, white spruce is common on sand flats and other coarse textured soils. Scrubby stands of jack pine, trembling aspen, red oak, white birch, white spruce, and black spruce occur along the thin-soiled rocky shores of Georgian Bay.

Sugar maple, yellow birch, white spruce, balsam fir, eastern white pine, and eastern hemlock are the species associated with the richer, well-drained slopes in the Eastern Townships Section. On ridges, exposed sites, and shallow soils, the prevailing dominants are white spruce, balsam fir, and white birch. Grey birch, accompanied by white spruce, trembling aspen, and largetooth aspen, are particularly prominent on old fields (Rowe 1972).

Immediately adjacent to the south shore of the St. Lawrence River in the Temiscouta – Restigouche Section lies a narrow zone of coniferous forest dominated by white spruce with some white birch, eastern white cedar, tamarack, and trembling aspen. Inland, the forest as a whole is characterized by sugar maple, beech, and yellow birch on the hill tops, with balsam fir and white spruce in the valleys. Alluvial flats support balsam poplar, black ash, white elm, and white spruce (Rowe 1972).

The Saguenay Section has forest that is essentially boreal in appearance, with communities of jack pine predominating on sandy areas, and trembling aspen, white birch, white spruce, black spruce, and balsam fir common on other sites (Rowe 1972).

In the Haileybury Clay Section, white spruce is not abundant and is distributed mainly along rivers and lake shores and on well-drained slopes (Rowe 1972).

The typical association of the Temagami Section consists of eastern white pine with scattered white birch and white spruce, the latter often equalling the pine in abundance. Another common but variable type is a mixture of those species with balsam fir, trembling aspen, and largetooth aspen (Rowe 1972).

In the Algoma section, the characteristic mixture consists of yellow birch, white spruce, balsam fir, sugar maple, hop-hornbeam, and eastern white cedar. Eastern white pine and occasional red pine dominate on the upper, steep south-facing slopes; white spruce, eastern white cedar, and balsam fir occupy the middle and lower slopes. A white spruce – balsam fir association, which usually includes white birch and black spruce, is prominent on the river terraces and adjoining flats in the northern part of the Section (Rowe 1972).

The Quetico section commonly has pure and mixed stands of jack pine, trembling aspen, largetooth aspen, white birch, balsam fir, white spruce and black spruce, associated with varying amounts of eastern white pine and red pine. The fir – white spruce – white birch type is particularly common, and in low-lying areas a spruce – fir forest type is often present (Rowe 1972).

Large areas of balsam poplar, trembling aspen, white spruce, balsam fir, and scattered tamarack are found inland from rivers in the Rainy River Section (Rowe 1972).

The Acadian Forest Region also has a wide representation of white spruce, being absent from but two of 14 Sections and Subsections.

The forest of the New Brunswick Uplands section is composed mainly of balsam fir, black spruce, white spruce, and white birch, with eastern white pine commonly occurring in mixture with those species. Black spruce is more common than white spruce (Rowe 1972).

The Upper Miramichi – Tobique section carries sugar maple, yellow birch, and beech on upper well-drained slopes and low hilltops, and mixed stands of those species together with red spruce, white spruce, eastern hemlock, and balsam fir. Forests of the river valleys are composed mainly of the spruces, fir, eastern white cedar, and tamarack. As well, in the northern and northwestern parts of the Section, balsam fir, white birch, white spruce, and black spruce are conspicuous on upland sites (Rowe 1972).

In the Carleton section, mixed stands on long steep slopes have balsam fir, white spruce, and eastern hemlock as their most common constituents (Rowe 1972).

The South Atlantic Shore section of Nova Scotia is characterized by a narrow strip of coniferous forest consisting of white spruce, balsam fir, and black spruce, with white birch and red maple associates. Most of the forest has originated after fire, clearance, or other major disturbance (Rowe 1972).

In the East Atlantic Shore section, dense low stands of balsam fir, black spruce, and white spruce are found along the coastal strip. White spruce is less abundant than either black spruce or balsam fir except along the immediate coastline, where the high tolerance of white spruce to salt spray (Payette 1980, Ecoregions Working Group 1989) fits the species to occupy exposed coastal areas, often to the exclusion of other species. White spruce also forms nearly pure stands in old clearings and disturbed areas. Red spruce is virtually absent (Rowe 1972).

The Cape Breton Plateau section carries balsam fir, white spruce, black spruce, and white birch as the main species, with the fir dominating most forest types. Tamarack and showy mountain-ash are associates (Rowe 1972).

White spruce and balsam fir are the primary constituents of stands on the heavy soils of the Cape Breton – Antigonish lowlands, with the great abundance of white spruce being attributable largely to its invasion of abandoned farmland. Alluvium is colonized by white spruce, balsam poplar, white ash, and occasionally white elm. Hilly land tends to support mixed stands of red maple, white birch, yellow birch, balsam fir, and white spruce. Occasional associates of sugar maple, beech, yellow birch, and red maple on the highland slopes are eastern white pine, white spruce, eastern hemlock, and balsam fir. Red spruce is uncommon (Rowe 1972).

Forest stands of white spruce, black spruce, balsam fir, and tamarack are usual on upland flats and in broad valley bottoms in the west and along the north shore of the Prince Edward Island Section. On the somewhat higher land of the central and eastern parts, tolerant hardwoods prevail and the conifers occur mainly in narrow belts along streams, red spruce and eastern hemlock on lower slopes, white spruce and balsam fir on valley flats, black spruce and tamarack in peaty depressions (Rowe 1972).

Widespread disturbance has resulted in an abundance of white spruce in the Fundy Coast Section. Immediately adjacent to the northern shore of the Bay is a patchy forest of poor quality composed of white spruce and black spruce, balsam fir, and tamarack. Inland, balsam fir and red spruce make up most of the forest stands, though white spruce and black spruce continue to be plentiful. White spruce rather than red spruce has invaded old fields on the south side of the Bay (Rowe 1972).

In the Southern Uplands section, white spruce occurs on soils somewhat heavier than sands in the lowlands, in intermixture with red pine, eastern white pine, red maple, balsam fir, and red spruce. White spruce has invaded abandoned fields here as well (Rowe 1972).

Forests of the well-drained sites are predominantly coniferous, and include white spruce, red spruce, black spruce, balsam fir, eastern hemlock, and eastern white pine. Intermixed with these are white birch, red maple, sugar maple, yellow birch, and beech. Abandoned farmland is invaded by white spruce, red spruce, and balsam fir (Rowe 1972).

The Cobequid section is the chief hardwood region of the Nova Scotia mainland. Low ridges and hills generally support beech, yellow birch, sugar maple, and red maple, with scattered red spruce, white spruce, and balsam fir. Towards the bottoms of hills, and in ravines and valleys, where sites are cool and moist, mixtures of eastern hemlock, red spruce, yellow birch, red maple, balsam fir, and white spruce are usual. There has been a marked conversion to white spruce on abandoned farmland in the Pictou Basin (Rowe 1972).

In the Lake States, balsam fir is usually considered the key species characterizing the spruce – fir – hardwood type, where “The spruces, especially white spruce, are commonly associated, but in fewer numbers” (Hansen 1980). The longer lifespan and larger size of white spruce compared with balsam fir compensate to some extent for white spruce’s lesser tolerance, and enables the spruce to persist in this type (Hansen 1980). Red spruce, which does not extend into the Lake States (Barrett 1980), is the major partner of associations with white spruce in the Northeastern Region, e.g., red spruce – yellow birch and red spruce – balsam fir (Fowells 1965). However, the spruce component of stands of spruce – fir can be solely white spruce (Frank 1973).

The species with which white spruce is most commonly associated in the central part of its boreal range are black spruce, balsam fir, white birch, trembling aspen, and balsam poplar. If the full range is considered, the number of associated species increases greatly to include: tamarack, lodgepole pine, jack pine, white pine, Engelmann spruce, red spruce, eastern white cedar, sugar maple, red maple, yellow birch, cherry birch (*Betula lenta* L.), beech, basswood, eastern hemlock, northern red oak, swamp pin oak(*Quercus palustris* Münchh.), white ash, green ash, black cherry, pin cherry, white elm, rock elm (*Ulmus thomasii* Sarg.), eastern hop-hornbeam, blue-beech (*Carpinus caroliniana* Walt.), and downy serviceberry (*Amelanchier arborea* (F. Michaux) Fernald) (Westveld 1949, Forbes and Meyer 1955, Nienstaedt 1957, Rowe 1972, Fowells 1965). In general, the proportion of white spruce in the boreal forest increases from east to west.

In interior Alaska, white spruce, as well as occurring in a virtually pure white spruce cover type, is a major component of two other cover types, White Spruce/Aspen (Dyrness 1980) and White Spruce/Paper Birch (Zasada 1980), in which either white spruce or its named associate contributes more than 20% to the total basal area.

Minor associates in the White Spruce/Aspen cover type include paper birch, black spruce, and, particularly in western Canada, balsam fir and lodgepole pine (Dyrness 1980, Eyre 1980). The cover type commonly develops after fire, and is a successional stage, lasting perhaps 100 years, leading to a climax dominated by white spruce. The type occurs most frequently on warm and well-drained upland sites. Shallow stony sandy loams are tolerated, but best development occurs on well-drained silt loams and clay loams (Dyrness 1980). Shrubs conspicuous in the cover type in Alaska include: American green alder, willow spp., common bearberry, soapberry, highbush cranberry, and mountain cranberry. In the Prairie Provinces, characteristic shrubs include: thin-leaved snowberry, red-osier dogwood, saskatoon, and western chokecherry. Typical herbs include northern comandra, horsetail, bluejoint reedgrass, bunchberry, and sedge. Ground-dwelling mosses and lichens are locally important (Eyre 1980).

The Alaskan White Spruce/Aspen Cover Type grades into the White Spruce/Paper Birch Cover Type on sites that are somewhat cooler and moister. The type is widely distributed, in Alaska from above the Arctic Circle to the Kenai Peninsula, and in western Canada. Aspen, lodgepole pine, subalpine fir, and black spruce are minor associates (Eyre 1980, Zasada 1980). The White Spruce/Paper Birch cover type usually occurs on well-drained to moderately well-drained upland sites and often represents a successional stage between the Paper Birch Cover Type and the White Spruce Cover Type. The lesser vegetation includes: willow species, American green alder, highbush cranberry, prickly rose, mountain cranberry, bunchberry, common Labrador tea, bluejoint reedgrass, fireweed, northern comandra, and horsetail. Feathermosses and lichens increase in prominence with increasing proportions of white spruce.

Effects of hardwood admixture

Rothe et al. (2003) investigated three Douglas-fir – red alder stands in Oregon, USA, and five Norway spruce – European beech (*Fagus sylvatica* L.) stands in Bavaria, Germany, to test the hypothesis that admixtures of broadleaved trees improve the nutritional status of associated conifers. At each site needle samples from 20 to 30 conifer trees with varying proportions of broadleaves adjacent to the sample trees were taken and analysed for needle mass and the macronutrients N, P, K, Ca and Mg. The neighbourhood of each tree was described by the proportion of deciduous basal area within an 8 m circle. Ordination methods (principal component analysis; redundancy analysis) were used to test the dependency of the multivariate nutritional pattern in conifers on deciduous neighbours and rank correlation and regression were used to analyse bivariate relationships between tree species composition and descriptors of needle status. The statistical analyses yielded no evidence that deciduous admixtures improve foliar nutrition of conifers. Rothe et al. (2003) concluded that, together with other empirical studies, their results show that beneficial effects of broadleaf admixtures on conifer nutrition are less than commonly postulated.

Autecology

Information on the autecology of 12 commercial tree species occurring in the North Central (NC) Region of Ontario was compiled and reported by Sims et al. (1990). This provides forest and resource managers working in the NC Region with summarized ecological information for white spruce, balsam fir, black spruce, tamarack/eastern larch, jack pine, red pine, white pine, eastern white cedar, balsam poplar, trembling aspen, white birch/paper birch, and black ash. Based on the Northwestern Ontario Forest Ecosystem Classification's extensive databases, vegetation, soil, and site conditions associated with each species are summarized for the NC Region.

Associates – White birch

"Fir is generally inferior in quality to spruce and it is more susceptible to insects and disease... It is suggested that poor quality of fir arises in part from diseases introduced through wounds caused by browsing. Damage of this kind is least when fir reproduction is not suppressed...The nature of the surface soil appears to be of primary importance to spruce and fir, whereas aspen may be influenced mostly by the subsoil" (MacLean 1960).

Quantitative data in Maycock and Curtis' (1960) study "fail to indicate that *P. glauca* and *A. balsamea* reach their optimum development in the most mesic sites available. To the contrary, these species indicate completely different relationships, with *Picea* attaining optimum development on the dry sites and *Abies* in the wet situations [of the white spruce-restricted range of sites chosen]... Neither species reproduces successfully in the dense shade of any forest cover... In stands where reproduction appeared to be successful, disturbance was or had been active, often caused by the death of older members of the canopy, by wind thinning and in a few locations by light infestations of budworm. Both *Picea* and *Abies* reproduce profusely in open situations on exposed mineral soil. Fallen logs also provide suitable seedbeds, although saplings that had established themselves on rotting logs often succumbed, apparently from suppression... [L]arge specimens of *Picea* and *Abies*...[v]ery often...were younger than the hardwoods; and the rotting log at the base indicated [that] establishment [had been] on logs in openings as in gap-phase replacement...".

In Itasca County, Minnesota, Grant (1934) noted that white spruce "is here largely confined to the subclimax fir – paper birch association Natural regeneration". Factors affecting natural regeneration of white spruce on prepared seedbeds in stands of mature white spruce – trembling aspen on the Riding Mountain in Manitoba were discussed by Waldron (1966). Weather, seedbed, litter, crown cover, site, lesser vegetation, and animals were important in influencing germination, early survival, and growth of white spruce. "It was apparent from [the results obtained] that shelterwood cutting in accompaniment with the preparation of mineral soil seedbeds on the fresh to moist sites using a bulldozer and straight blade can be used to create conditions suitable for the establishment of natural white spruce regeneration" (Waldron 1966).

Frank and Bjorkbom (1973), too, considered the shelterwood system in northern New England and New York a desirable procedure for obtaining natural regeneration of spruce – fir. "In this method, at least two harvests are made. The first harvest, made to establish reproduction, should be made in a good seed year. About one-third to one-half of the basal area of the stand should be removed at this time, and the cut should be uniformly distributed. Harvests greater than this might leave the stand susceptible to wind damage. This harvest should remove the least desirable trees, leaving the larger and more vigorous trees of desirable species to provide seed. Factors to consider in tree selection are: susceptibility to wind damage; reduction of seed sources of less desirable species; and the spacing, vigor, and quality of the reserve stand. When the regeneration is well established, the remainder of the original stand can be harvested in one or more operations" (Frank and Bjorkbom 1973).

Strip- or patch-cutting are other methods described by Frank and Bjorkbom (1973): "For balsam fir and black spruce, openings should be no more than 2.5 to 3.0 chains [50 to 60 m] wide; and for red spruce and white spruce, they should be no more than 6.0 chains [120 m] wide".

As well, Steneker (1967) has noted that "Experimental improvement cuttings, to favour the white spruce component of mixedwood stands in Manitoba, were first carried out by the Department of Forestry and Rural Development [sic] in 1936... Later, between 1951 and 1954, a series of eight experimental release cuttings were made in 15- to 60-year-old stands in Manitoba and Saskatchewan, to determine the effects of partial and complete removal of the aspen upon the development of the white spruce understorey…Ten-year growth results...have shown that: (a) Diameter increment of spruce can be doubled by removing the aspen canopy, (b) Height increment of spruce under immediate overhead suppression and in physical contact with the aspen crowns can be doubled by release, (c) The combined stimulus to height and diameter increment from release can increase merchantable volume production of spruce by about 60 per cent" (Steneker 1967).

Carmean and Hahn (1981) presented revised site index curves for balsam fir and white spruce in the Lake States (Figure 2.5).

White spruce has been planted with success in corridored boreal mixedwood stands in northern Ontario, e.g., in the Timmins Forest Management Agreement (FMA) of Waferboard Corporation (Smith 1987), and in George Marek's plantings near Beardmore, Ontario.

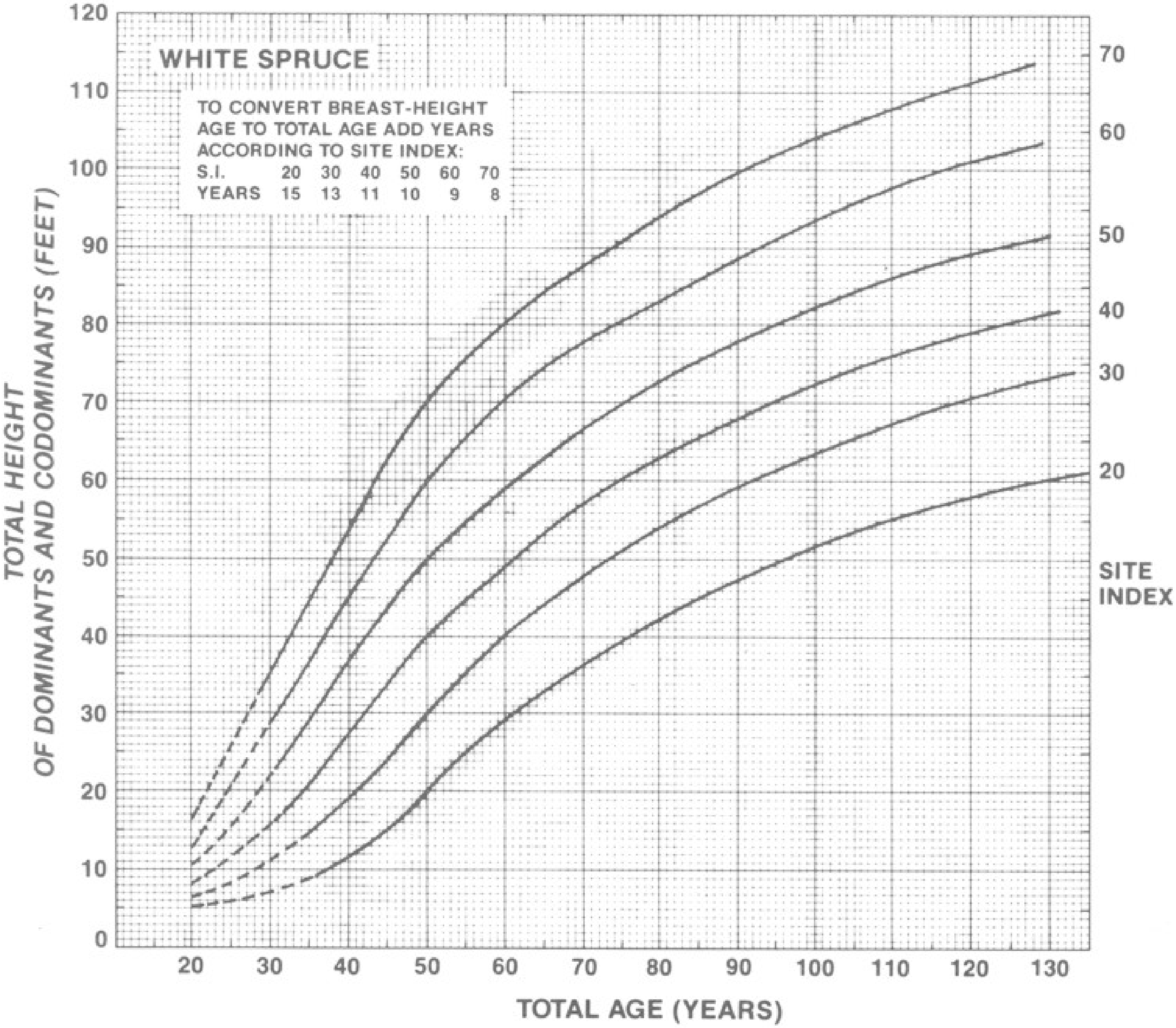

Figure 2. 5. Site index curves for white spruce in the Lake States. These are revised (Carmean and Hahn 1981) from the original curves published by Gevorkiantz (1957).

Associates – Balsam fir

The most complete review of balsam fir is that by Bakuzis and Hansen (1965). Johnston (1986) has prepared a useful handbook for managers of balsam fir in the North Central states. Balsam fir occurs in pure stands in the Lake States, but it more commonly occurs in mixture: on dry-to-mesic uplands, balsam fir "is commonly mixed with...white spruce, paper birch, and quaking aspen" (Johnston 1986).

Associates – Alpine fir

Interior spruce and balsam fir[14] (*Abies lasiocarpa*,) in uniform mixture in the proportion by net volume of about 80% spruce and 20% balsam fir, constitute what Barnes (1937) described as the natural stand in the spruce – balsam forest types of the central interior of British Columbia,

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[14] Barnes 1937 used "balsam fir" as a colloquial term for "alpine fir", now called subalpine fir (ed. note: Phippen 2022).

wherein spruce ("characteristically sound and of fine quality") ranges in age up to about 350 years and fir ("characteristically decayed") up to 250 years. Natural regeneration under the mature overstorey left as a residual stand after logging, while "fairly satisfactory" in respect of stocking, had a spruce component of only 20%.

Paterson (1958) observed that "true" spruce – balsam [15](interior spruce – alpine fir) forests in British Columbia occur on podzolic forest soil, and referred to the commonly held opinion that any soil where precipitation is enough to support the growth of spruce will, in time, naturally develop a podzol under spruce.

Associates – Lesser vegetation

"The lesser vegetation associated with aspen – birch – spruce – fir is nearly always a herb or tall shrub – herb type. Mosses are a minor component of most vegetative types although they seem to be more prevalent in Forest Section B.8 than in either B.4 or B.9" (MacLean 1960).

MacLean (1960) described nine plant communities found with aspen – birch – spruce – fir, noting typical soils and the dominant, abundant, and frequent species (dominant = an outstanding feature of the community, abundant = one or more specimens almost always visible from any given point, and frequent = not so evident but constantly being encountered).

"The ground cover is characterized by (wild sarsaparilla) *Aralia nudicaulis*, (rose twisted-stalk) *Streptopus roseus,* (wild-lily-of-the-valley) *Maianthemum canadense*, (yellow clintonia) *Clintonia borealis*, (northern starflower) *Trientalis americana*, (bedstraw) *Galium* spp., (downy yellow violet) *Viola pubescens*, (large-leaved aster) *Aster macrophyllum*, (Virginia strawberry) *Fragaria virginiana*, and (northern dewberry) *Rubus villosus*" (Wilde et al. 1954).[16]

Maycock and Curtis (1960) found that not all herbaceous and shrub species were distributed along the moisture gradient in a normal distribution. Many species showed relationships similar to those described for jack pine and black spruce, indicating a preference for both dry and wet situations. Trailing arbutus (*Epigaea repens* L.)*, tamarack*, creeping snowberry (*Gaultheria hispidula* (L.) Muhlenberg ex Bigelow), willow spp., and early lowbush blueberry (*Vaccinium angustifolia* Aiton) are such species. Twinflower, velvet-leaved blueberry (*Vaccinium myrtilloides* Michaux), and common Labrador tea are others.

"It was early recognized that the trees apparently do not influence ground cover in mixed boreal conifer – hardwood vegetation in this region to the extent that they might in vegetation farther south. Often the same type and composition of tree cover is accompanied by markedly

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[15] Patterson 1958 used "balsam fir", now called subalpine fir (ed. note: Phippen 2022).

[16] *Aralia nudicaulis = Aralia nudicaulis* L., *Streptopus roseus = Streptopus lanceolatus* (Aiton) Reveal, *Maianthemum canadense = Maianthemum canadense* Desfontaines, *Clintonia borealis = Clintonia borealis* (Aiton) Rafinesque, *Trientalis americana = Lysimachia borealis* (Rafinesque) U. Manns & Anderberg, *Galium* spp. = *Galium* L. spp., *Viola pubescens = Viola pubescens* Aiton, *Aster macrophyllum = Eurybia macrophylla* (L.) Cassini, *Fragaria virginiana = Fragaria virginiana* Miller, *Rubus villosus = Rubus flagellaris* Willdenow, *Eurybia macrophylla* (L.) Cassini, *Fragaria virginiana = Fragaria virginiana* Miller, *Rubus villosus* = *Rubus flagellaris* Willdenow

different combinations of herbs and shrubs in the understory. This situation might perhaps indicate that the community is primarily composed of the herb, shrub, moss and lichen layers, and that the trees, apart from their effect on overall environment, are incidental members" (Maycock and Curtis 1960).

Wilde et al. (1954) referred to the comparative scarcity of competing shrubs in forest stands on calcareous podzols; in melanized loams and clays (boreal rendzinas) stands, shrubs are more prominent. Wilde et al. (1954) described one virgin stand as having a "nearly impenetrable' understorey 3 to 7 feet [1 to 2 m] in height, "consisting of *Viburnum opulus*, *Rhamnus alnifolia*, *Acer spicatum*, *Corylus rostrata*, and *Lonicera canadensis*, with some white spruce and balsam fir saplings and seedlings".

White spruce occurs in 79 of the 90 sections and subsections of Canada's forest recognized by Rowe (1972): 43 of 45 divisions and subdivisions of the Boreal Forest Region; two of three divisions of the Sub-Alpine Forest Region; all five of the Montane Forest Sections; both of the Columbia Forest Sections; 15 of the 16 divisions of the Great Lakes–St. Lawrence Forest Region; and all but two of the 14 divisions of the Acadian Forest Region. The species is absent only from the Pacific Coast and Deciduous Forest Regions.

Data collected by Jeffrey (1964) along the lower Liard River (60° – 61° N, 123°30′ W) illustrate the diversity of white spruce forest site types and the related differences in white spruce performance (Table 2.6).

Table 2. 6. Age-height relationships for white spruce in various forest site types in the Northwest Territories. (after Jeffrey 1964).

Forest site type	Height (m)	Age (years)
Mixed conifer, high elevation, Mackenzie Mountains	8 – 11	60 – 70
Mixed conifer, low elevation	12	60 – 70
Mixedwood (white spruce – white birch), steep terrace	24 – 27	110 – 130
Mixedwood, Mackenzie lowland	26 – 32	100
White spruce – white birch, terrace, neutral loam	21 – 24	80 – 90
White spruce – white birch, terrace, neutral loam	<31	<170
Mixedwood, terrace, strongly acid sand	21 – 24	80 – 90
Mixedwood, terrace, strongly acid sand	<31	<172
Mixedwood, upper terrace	29 – 34	110 – 175
Mixedwood, upper terrace	-	<233
Mixedwood, ancient floodplain, mod-slightly acid loam	27	180 – 190
Mixedwood, ancient floodplain, very acid podzolic	30 – 33	120 – 130
White spruce – white birch, intermediate floodplain, neutral loam	18 – 21	100
White spruce – white birch, intermediate floodplain, neutral loam	27 – 30	140 – 150
White spruce – balsam poplar, recent floodplain	30	170 – 190
White spruce – white birch, recent floodplain	24	120

2.6 Regional variation

2.6.1 Eastern North America

Stand composition in relation to site in spruce – fir – northern hardwood forest in Maine was studied by Thorpe (1986) by means of transects across the topography of a 2,136 ha study area, at elevations from 400 m to 500 m. Data were collected on stand composition, topography, soil, ground vegetation, and site index. The ratio of balsam fir to red and black spruces increased with nutrient scale values. The spruce component shifted from black spruce to red/black hybrids, to red spruce with better drainage and more fertile conditions. White spruce and northern white cedar were restricted to nutrient-rich sites.

2.6.1.1 NW New Brunswick

Loucks (1960) studied a cool, humid region in NW New Brunswick supporting forests of sugar maple, beech, and yellow birch on the hills, and balsam fir, white spruce, cedar, and black spruce on the slopes and valley bottoms. The vegetation record was used to calculate a matrix of indices expressing the similarity of each stand to all the others. These values were used to construct a spatial arrangement or ordination of the samples based on phytosociological features. An ordination technique based on the environmental data for each sample was developed. The stable features of the environment were considered in three groups, relating to moisture, nutrient supply, and local climate. Scalars synthesised diverse types of measurement into single expressions. There were three major factors that were considered in the synthetic moisture-regime scalar, six in the nutrient regime scalar, and four in the local climate regime scalar. Loucks found distinct gradients in tree species composition corresponded with the scalars. The relation of forest growth and species complexity to the nutrient regime scalar followed the sigmoid growth curve, and comparison of species distributions in the two ordinations demonstrated a marked degree of correspondence. The axes of the phytosociological ordination tended to form the diagonals of the environmental ordination. The primary factors influencing various portions of the phytosociological axes were determined by plotting them against the environmental scalars. Loucks found that probability tests showed that the scalar methods could reliably predict the structure and composition of the forest communities on the undisturbed sites studied, and concluded that the co-ordinate method provided an objective way for rational qualification and subsequent classification of terrestrial ecosystems.

Loucks (1962) went on to develop a forest classification for the Maritime Provinces of Canada in which he recognised ecoregions each with its own distinctive tree associations and climates. An abbreviated version of Loucks' Table 1 that includes only white spruce, shows that species present in six of seven Zones and 11 of 18 Ecoregions (Table 2.7).

Table 2. 7. Zones and Ecoregions (Loucks 1962) in the Maritime Provinces having white spruce among their characteristic tree species.

Zone	Ecoregion	Associated Species[a]	Associated Climate
Sugar maple – Hemlock – Pine	Restigouche – Bras d'Or	sM Be bF yB wP	Moderately cool, moderately dry
Sugar maple – Yellow birch – Fir	Maritime Uplands	sM Be bF yB wP rS rM	Cool, moist
Red spruce – Hemlock – Pine	Maritime Lowlands	bF rS bS eH wP rM jP Be	Moderately cool, moderately dry
Spruce – Fir Coast	Fundy Bay	A) bF wB	Cool, wet
		B) rS bF wB bS yB Mo	Cool, wet
	Atlantic Shore	bF bS wB	Cool, wet
Fir – Pine – Birch	New Brunswick Highlands	(a) bF wB wP	Cold, moist
		(b) bF wB wP tA bS jP rS	Cold, mod dry
	Gaspé – Cape Breton	bF wB bS	Cold, wet
Spruce Taiga	Cape Breton Plateau	(a) bS bF	Cold, wet
		(b) bS bF wB Mo	Cold, wet

[a] Abbreviations of tree names cited in Day 1967.

2.6.2 Great Lakes

The various members of an upland conifer community in the Algonquin region of Ontario were very similar physiognomically, with the same groups of tree species (white spruce, white pine, and balsam fir) constituting the main dominants, though in various proportions (Maycock 1956).

Maycock and Curtis (1960) determined environmental relationships of species in the Great Lakes region by two objective procedures, and found not even partial groupings of species, but rather "a continuous series of intergrading and overlapping amplitudes of tolerance":

Thus, if one persists in attempting to categorize vegetational types only two treatments are possible, either the indiscriminate lumping of diverse types or the establishment of a large number of unruly associations. Either treatment will defeat the intended advantages of classifying. The most reasonable alternative would be to treat continuous phenomena in a fashion that recognizes the continuity and yet permits a segregation for theoretical and practical purposes. Both the moisture gradient and multi-dimensional treatments attempted permit this desired result.

Thus, the forests of the Great Lakes region are not a distinct associational unit. They do not collectively comprise an ecotone between two completely separate community types. They can best be considered as a portion of a vegetational gradient representing a part of a vegetational complex, which in the southern areas of the Great Lakes region is composed entirely of broadleaf tree species and in the areas northward becomes predominantly needle-leaved in character. Similarly, a gradual replacement of understory associates takes place with greater proportions of boreal representatives northward (Maycock and Curtis 1960).

Conversion of aspen to conifers

According to Kittredge and Gevorkiantz (1929), fires "are chiefly responsible for the scarcity of conifers and for their absence over large areas of the aspen lands", as they destroy advance growth, seedlings, and seed trees.

In Stiell's (1976) publication, stand conversion to white spruce is accorded just one page, and only three literature citations are given. In relation to bringing the mixedwoods under management, this is a major deficiency. A considerable amount of corridoring and other experience has accumulated in Ontario in recent years, and this could usefully be reported and presented in a unified account.

2.6.3 Prairie Provinces

In the area between the SW shore of Hudson Bay and NW regions of Saskatchewan, white spruce is confined to very local physiographic features: south-facing slopes with well drained, light-textured mineral soils; and river alluvium (Ritchie 1956), equivalent to Raup's upland mesophytic and floodplain forest types. The predominant and stable forest of mesic sites is dominated by black spruce, with a ground flora of wet-form mosses. White spruce is rare and occurs only on sites exceptionally favourable to it.

2.6.4 Yukon, Territories, Alaska

Regional vegetation changes in the western boreal forest of southwestern Yukon during the Late Pleistocene and Holocene were revealed by pollen analyses (Cwynar 1988). A *Populus* woodland with an understorey of soapberry and extensive open areas dominated by Artemisia occurred from 11,030 BP to 9,250 BP. Juniper populations expanded at 9,700 BP and then more mesic forest communities developed when white spruce populations increased and *Populus* declined at 9,250 BP. At 6,100 BP a remarkable shift occurred from white spruce with juniper to a mixed spruce forest dominated by black spruce. At 4,100 BP white spruce increased at the expense of black spruce, and juniper again became important. By 1,900 BP, lodgepole pine had become dominant as black spruce declined and disappeared. The vegetation sequence implies an initial period of aridity from 11,030 BP to 9,250 BP, a moister period from 9,250 BP to 6,100 BP when white spruce was abundant, and then a very moist period from 6,100 to 4,100 BP during the dominance of black spruce. A prolonged period of increasing aridity led to the modern semi-arid climate.

In northern Yukon, Lichti-Federovich (1973) obtained pollen diagrams from exposures of Late Quaternary sediments in the Old Crow River plain, where the vegetation consists largely of tundra and shrub tundra, with scattered groves of white spruce and black spruce. Reconstructions of the Late Quaternary vegetation were consonant with a climate, between early and late Wisconsin glaciations, marked by three stages: severe tundra climate, milder forest or tundra-and-forest climate, and severe tundra climate. The pollen stratigraphy for the post-glacial silts and peats was incomplete, but the available data suggested that vegetation similar to that of the present day had become established in the area by the middle of the post-glacial period.

The US Bureau of Land Management (BLM 1958) estimated the area of interior forest in Alaska at 50 million ha, with white spruce – birch the most widely distributed forest type.

Pollen analyses of lake bottom sediments up to 4,600 radio-carbon years old in the Healy Lake area of Alaska showed some indication that lodgepole pine had migrated towards the area from the south-east during the Holocene, but otherwise there was no difference in vegetation from the present: white spruce, black spruce, white birch, dwarf birch, trembling aspen, balsam poplar, and willows (Anderson 1975).

Raup (1945a) hypothesised that the stands of aspen and lodgepole pine along the Alaska Highway, between Dawson Creek and Whitehorse, owe their abundance to fire, and concluded that they do not reproduce themselves once they reach maturity, unlike the white and black spruces and alpine fir, the most mesophytic species in the region. In the absence of fire, the spruces and fir occupy the same site generation after generation (Raup 1945a).

Forests of white spruce, white birch, aspen, and lodgepole pine occupy interior Alaska (Raup 1945b). In places, "the forest consists only of *Picea glauca*, sometimes interspersed with grassy meadows". Widespread fires have occurred in both the distant and recent past. Raup stated that "the only timber of much commercial value along the Alaska Highway is on the river flood plains and some of the foothill slopes. White spruce grows to a height of 100 ft. [30.5 m] or more with 18 in. to 24 in. [45 cm to 70 cm] dbh at the flood plains, and the alpine fir and spruces attain similar dimensions on the foothills" (Raup 1945b).

Environmental and successional relationships of the forest communities of the Porcupine River drainage in interior Alaska were investigated by Yarie (1983). The structure and function of taiga ecosystems over a 3,600,000 ha area in northeastern interior Alaska was shown to be consistent with a hypothesis relating vegetative structure and dynamics to site nutrient status and soil temperature. Ordination of model community descriptions and correlation of the ordination values with environmental parameters indicated that controls of vegetative structure and function found for the Fairbanks area, where the hypothesis was developed, can be applied to interior Alaska taiga. High productivity sites were associated with warmer soil temperatures, smaller accumulation of soil organic matter, and lower C:N ratios. Lower productivity sites, generally dominated by black spruce, were associated with the opposite trends. White spruce and broad-leaved species occupied the more productive sites.

2.7 Ecological succession

Forest succession in its traditional sense implies two important features that resist direct examination (Solomon et al. 1981). First, classical definitions generally connote directional changes in species composition and community structure through time, yet the time frame needed for documentation of change far exceeds an average lifespan: “There is hardly the opportunity to observe the direction, let alone the species succession, that occurs within our lifetime” (Solomon et al. 1981). The second feature that defies quantitative description is the end point or climax.

Cottam (1981), for instance, argued that the biggest problem with the concept of succession in the boreal forest, in interior Alaska at least, is that there are practically no stands more than 200 years old. Fire is universal, and so frequent that speculation about what the forest would be in the absence of fire seems unproductive, though Van Cleve and Viereck (1981) noted suggestions by others that some upland white spruce stands on well-drained upland sites in Alaska might be replaced by black spruce, and cited Wilde and Krause’s (1960) comment on upland spruce stands near Fairbanks: “The poor regeneration of white spruce on these moss-covered soils casts doubt on the climax nature of these species in the subarctic environment. A wide opening in the canopy is likely to cause invasion by sphagnum and black spruce, an association which would preclude the regeneration of white spruce”. Climax becomes a hypothetical concept in the face of recurring fire.

Soils, climates, and species availability all influence the direction and outcome of ecological succession. In the simplest case, newly deposited mineral soil becomes vegetated with the development of seedlings from seed fortuitously falling onto it. Van Cleve and Viereck (1981) described the primary succession on the floodplain of the Tanana River developing from willow and alder through mature white spruce stands. Until sufficient alluvium has accumulated to raise the soil surface above the zone of frequent intra-year flooding, physical and chemical controls dominate ecosystem structure and function. These mineral soil surfaces may appear to be ideal for seed germination and establishment, but frequent inundation, sediment deposition, and erosion make them highly unstable for plant establishment. The first plants to persist are usually herbs such as alpine hedysarum (*Hedysarum Americanum* (Michaux ex Pursh) Britton), meadow horsetail (*Equisetum pratense* Ehrhart), and bluejoint reed grass, and the shrubs Alaska willow (*Salix alaxensis* (Andersson) Coville), sandbar willow (*Salix interior* Rowlee), and mountain alder (*Alnus incana* ssp. *tenuifolia* (Nutt.) Breitung). In the Alaskan situation, a salt crust several millimetres thick and composed of gypsum crystals mixed with soil particles develops on the bare surface, and may prevent the germination and establishment of trembling aspen, which is absent from the primary successional sequence on the floodplain, notwithstanding an abundant seed source from adjacent uplands. Mid-successional stages lasting 75 to 90 years then extend the closed shrub stage through to mature balsam poplar. However, only after terrace elevation has reached the point where sediment deposition has become relatively infrequent, or the course of the river has markedly shifted to result in a quiescent period with regard to sedimentation, can white spruce become established. White spruce does not appear to be able to survive repeated flooding within a single year, or even an annual coating of sediment on needles. The shift from a poplar to a spruce stand is gradual, and may take the best part of a century (Van Cleve and Viereck 1981). White spruce growth is rapid but less so than that of the balsam poplar. However, the white spruce slowly become dominant as they grow larger and the balsam poplar begin to topple.

The accumulation with time of a thick organic layer is perhaps the most important feature of succession in taiga. Whereas the thickness of the organic layer in the floodplain succession seldom exceeds 4 cm to 5 cm before, periodically, it is buried by flood-deposited silt, the deposition of organic material in the mature spruce stand exceeds the rate of decomposition, and the thickness of the layer gradually increases to 8 cm to 10 cm or more.

Floodplain deposits in the Northwest Territory, Canada, are important in relation to the development of productive forest types with a component of white spruce (Jeffrey 1964). The most recently exposed surfaces are occupied by sandbar vegetation or riparian shrub willows and grey alder (*Alnus incana* (L.) Moench); with increasing elevation, the shrubs give way successively to balsam poplar and white spruce forest. In contrast, older floodplains, with predominantly Brown Wooded soils, typically carry white spruce – trembling aspen mixedwood forest.

Balsam poplar – *hyemale*[17]and balsam poplar – *Equisetum pratense* occur on point-bar deposits close to the river, with the former somewhat more favourable to the establishment of white spruce seedlings than the latter. Balsam poplar –*Equisetum pratense* and balsam poplar – white spruce – *Equisetum pratense* forest are vulnerable to stand deterioration in consequence of their unreceptive conditions for white spruce establishment. Open, decadent stands are common. Jeffrey (1964) suggested possible pathways of physiographic-vegetational change on point-bar deposits of recent Liard River floodplains in the Northwest Territories (Figure 2.6).

The terraces, ancient and modern, along the Liard River, have their origin as floodplain deposits, subsequently dissected by erosion, and occur at various elevations up to 300 m above river level. The most common forests on the terraces are mixedwood and mixed broadleaf, and generally lack white spruce except on steep slopes that connect one terrace level to another. White spruce – balsam poplar forest occurs on small localized floodplains of secondary streams (Jeffrey 1964).

Interrelationships among nutrient cycling, regeneration, and subsequent forest development on floodplains in interior Alaska were addressed by Van Cleve et al. (1980), who pointed out that the various stages in primary succession reflect physical, chemical, and biological controls of ecosystem structure and function. Thus, each successional stage has a species combination in harmony with site quality. Short-circuiting succession by planting a late successional species such as white spruce on an early successional surface may result in markedly reduced growth rates because of nitrogen insufficiency. Without application of substantial amounts of fertilizer,

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[17] *Equisetum hiemale* = *Equisetum hyemale* L.

use would have to be made of early successional alder and its site-ameliorating additions of nitrogen.

Neiland and Viereck noted that "The slow establishment and growth of spruce under birch stands [in Alaska] may be partially due to effects of shading and general competition for water and nutrients, but may also be more directly related to the birch itself. Heikinheimo (1915, cited by Lutz 1956) found that birch ash inhibited white spruce seedlings, and Gregory (1966) found that birch litter has a smothering effect on spruce seedlings" (Neiland and Viereck 1977).

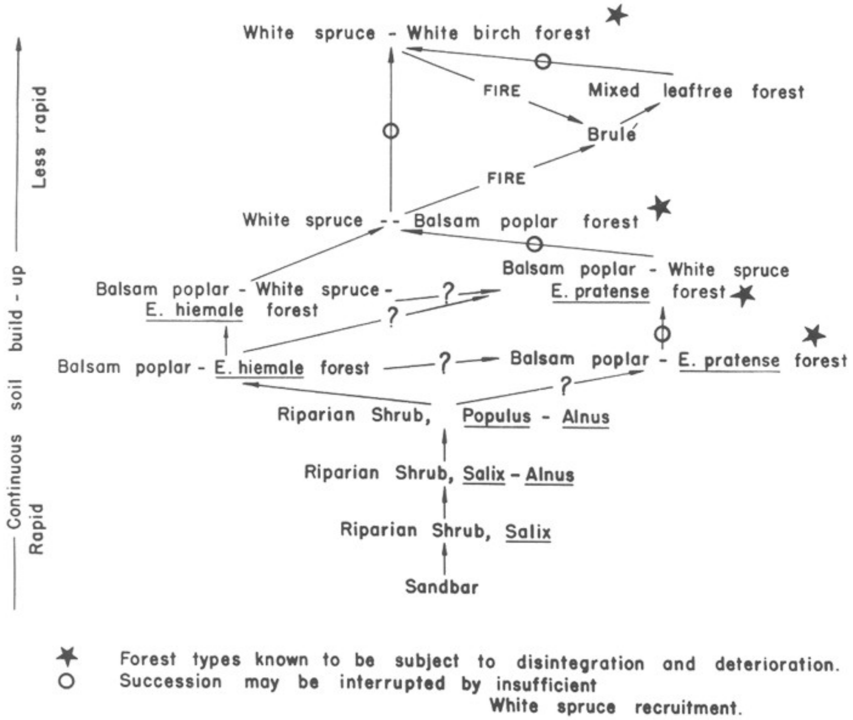

Figure 2. 6 "Diagram showing possible trends of physiographic-vegetational change on point-bar deposits of the recent floodplain. Directions of development for which very little supporting evidence can be presented are interrupted by question marks. Stages where further development may be interrupted by lack of white spruce recruitment are shown. Also marked are forest types shown to be subject to deterioration and disintegration to such a condition that further development as postulated cannot be assumed" (Jeffrey1964).

On dry upland sites, especially south-facing slopes, the mature vegetation is white spruce, white birch, trembling aspen, or a combination of these species. Succession follows in one of two general patterns. In most cases, aspen and birch develop as a successional stage after fire before reaching the spruce stage. But, occasionally, with optimal site conditions and a source of seed, white spruce will invade with the hardwoods or within a few years thereafter, thereby producing even-aged white spruce stands without an intervening hardwood stage.

2.7.1 Fire

In fire stands less than 60 years old in the aspen – birch – spruce – fir type in Ontario, spruce comprised 90% of the total number of spruce and balsam fir stems (MacLean 1960). On cut-over land, spruce made up only 16% of the spruce/fir reproduction.

Recolonization by white spruce and balsam fir of a forest destroyed by an intense fire in 1923 was studied 68 years thereafter by Galipeau et al. (1997) who found a bimodal age-class structure, the first regeneration mode beginning in the 5-year period following and fire and continuing for more than 20 years, and the second wave of recruitment beginning in the 1960s , peaking in the 1970s, and ending in the mid-1980s. The average density of the initial white spruce cohort decreases from 693 to 51 spruce/ha with distance from the seed source, but the second cohort shows much less variation with distance, with 17% of the variation rather than 37% in the first cohort. Soil parent material determined the greatest portion of the variability (30%) in white spruce seedling densities. Spruce densities on sandy to loamy till deposits were four to five times greater than those on clays. Distance from seed source was of secondary importance influencing regeneration densities. Together, soil parent material and distance to seed source predict 53% of the white spruce regeneration following fire.

In Alaska, Van Cleve and Viereck (1981) recognized the typical upland white spruce succession sequence following fire: newly burned stage; herb – tree seedling stage; shrub – tree seedling stage; dense hardwood stage (birch and aspen); mature hardwood stage; mixed white spruce – hardwood stage; and mature white spruce/moss stage. Invasion usually begins with light-seeded species, e.g., fireweed and willow shrubs, especially Bebb's willow and Scouler's willow (*Salix scouleriana* Barratt ex Hook.). Viable seeds already in the soil are stimulated to germinate, which may account for the rapid post-fire appearance of Bicknell's geranium (*Geranium bicknellii* Britton) and pink corydalis (*Capnoides sempervirens* (L.) Borkhausen). Mosses and liverworts, especially green-tongue liverwort (*Marchantia polymorpha* L.) and fire moss (*Ceratodon purpureus* (Hedw.) Brid), quickly invade mineral soil exposed by fire. Shrubs such as squashberry, prickly rose, willows, aspen and birch may resprout from stumps and roots. A heavy shrub and sapling canopy slowly develops, and reduces the herbaceous layer and shades out most of the pioneer mosses. Birch and aspen might reach a density of 30,000 stems/ha, but spruce seedlings may be abundant albeit inconspicuous because of slow growth. In the dense hardwood stage, perhaps 25 to 50 years after the fire, aspen and birch shade out much of the understorey, with shade-tolerant highbush cranberry and prickly rose usurping willows. For the next 50 years, hardwoods dominate the site, but white spruce may become conspicuous in the understorey. Rose, highbush cranberry, and American green alder form an open shrub layer with just a few remaining clumps of Bebb's willow. The low subshrubs twinflower, mountain cranberry, and common Labrador tea form a scattered layer. Field horsetail (*Equisetum arvense* L.) and bunchberry replace bluejoint reedgrass and fireweed in the herb layer. Stairstep moss, red-stemmed feathermoss, haircap moss (*Polytrichum* Hedw. spp.), and broom mosses cover only 5%. White spruce becomes dominant about 100 years after the fire, often with a component of birch. The mature spruce stage, with only scattered remnant birch and a thick continuous layer of feathermosses, is reached by about 200 years after the fire. Evidence to determine subsequent development is hard to come by.

Opinions on this topic are varied. Lutz (1956) and Foote (1976), considered the white spruce stands to be the climax vegetation on these sites, i.e., the end point in succession following fire on well-drained upland sites. Wilde and Krause (1960) doubted the climax nature of white spruce in upland spruce stands having a thick moss layer because of the poor regeneration of white spruce, as well as the probability that a wide opening in the canopy is likely to cause invasion by sphagnum and black spruce, an association that would preclude regeneration by white spruce. That possibility was conceded by Van Cleve and Viereck (1981), who, however, noted that they had not observed black spruce replacing white spruce on south-facing slopes in interior Alaska, "although this does occur in the successional sequence on the floodplain".

Peters et al. (2005) showed the importance to white spruce regeneration of the interaction between mast year and fire. Over a 59-year period, there was significantly more regeneration after fires that occurred in mast years than after fires that occurred in years of low cone production. A key factor in the fire × mast year interaction was the rapidity of the deterioration of seedbed receptivity after fire. Their investigations were carried out in Alberta, and, although greater prolongation of seedbed receptivity has been reported in other studies (e.g. Zasada and Gregory 1969, Purdy et al. 2002), the relationship may apply to a much wider area.

Notwithstanding the importance of fire × mast year interaction (Peters et al. 2005), subsequent regeneration will be more important in stands lacking a white spruce seed source at the time of a fire (Lieffers et al. 1996). Regeneration on decayed logs may support later ingress if seed becomes available, but the trees may not reach reproductive maturity before the next stand-replacing fire (Peters 2003). Sites with little white spruce regeneration immediately after fire may have too few seed trees in the long term to maintain the white spruce component, which, therefore, may depend critically on the coincidence of fire and mast years.

2.7.2 Wind

The uprooting of trees in boreal spruce forests exposes a variety of colonizable substrates and may mediate coexistence of plant species. A study in northern Sweden that examined the temporal forest floor disturbance pattern caused by uprooted trees over a period of 120 years at four boreal Norway spruce sites found a significant correlation between the frequency of high winds and number of uprooted trees, and the fall direction was closely related to the main direction of high winds (Jonsson and Dynesius 1993). The temporal distribution was strongly aggregated, resulting in large variations in disturbance rates between different decades.

2.7.3 Climax

Maycock and Curtis haven noted that “In northern regions the question of terminal climax becomes highly doubtful, since large scale catastrophe is prevalent and prevents the termination of succession. The hypothetical climax has little meaning in areas continually subjected to fire, windthrow and budworm infestation. These and other disturbances cause a reversion of successional development and permit the continuous entrance of species suited to such conditions. Throughout the Great Lakes area and northward, *Picea* and *Abies* certainly represent such species. It must be recognized that this question of climax is a separate and distinct consideration. It should not and cannot prevent the investigation of community structure and species relationships and it certainly should not be permitted to replace them” (Maycock and Curtis 1960).

2.7.4 Forest floor

The accumulation of nitrogen-poor litter on the forest floor of spruce forest, and the meagre availability of soil nitrogen, have been hypothesized by Pastor et al. (1987) to contribute to spruce “decline”. Their model, LINKAGES, showed the importance of this factor.

In addition, as the litter layer becomes thicker, its insulating effect will reduce soil temperatures, slowing nutrient release and root growth. In the boreal forest of Alaska, the thickness of the organic layer in white spruce stands on south-facing slopes reaches a maximum of 12 cm, but, although soil temperatures become somewhat cooler, the degree-day summation remains above 1,000, and there is no permafrost in the successional sequence on south-facing slopes (Van Cleve and Viereck 1981). A newly burned stand with a layer of dark ash replacing most of the organic layer may have soil degree-day sums exceeding 2,000 degrees.

Clearcutting in boreal mixedwood forest stands dominated by trembling aspen and white spruce alters the chemical properties of the forest floor (Hannam et al. 2005). This may affect the productivity of such sites. Hannam et al. (2005) used proximate analysis, carbon-13 (13C) isotopic determination, and cross-polarization, magic-angle spinning (CPMAS)13C nuclear magnetic resonance (NMR) spectroscopy to examine differences in the characteristics of the forest floors from uncut stands and clearcut stands dominated by white spruce and trembling aspen in northern Alberta. Clearcutting had been carried out 3.5 to 4.5 years earlier. Proximate analysis revealed no difference in the chemical properties of forest floors from clearcut and uncut stands in either stand type, but the acid-insoluble residue of forest floors from clearcut aspen stands was enriched in 13C compared with those from uncut aspen stands. CPMAS 13C NMR spectroscopy revealed that forest floors from clearcuts were enriched in total aromatic C, particularly in aspen stands, and depleted in phenolic C, particularly in spruce stands. These results were interpreted by Hannam et al. (2005) as indicating a greater humification of forest floors in the clearcuts, possibly reflecting stand-type differences in the amount of labile C available to the microbial community in the forest floor, and reductions in above- and below-ground inputs to the forest floor following clearcutting in both stand types. Such changes in the chemical properties of forest floors could exacerbate C limitations in those soils and affect nutrient cycling.

2.8 Ecological classification(s)

Various systems of ecological land classification have been developed in support of forest management in Canada and elsewhere (Wiken 1973, Bajzak and Roberts 1996, Mah et al. 1996). The Canadian Committee on Ecological Land Classification (CCELC) system was based on seven hierarchical levels (Table 2.8). Ecological land classification seeks to delineate and classify ecologically distinctive areas of the earth’s surface, each area viewed as a discrete system resulting from the interplay among geologic, geomorphologic, edaphic, vegetative, climatic, faunal, and human factors, the influence of any one or group of those factors varying with the given ecological land unit (Wiken 1986).

The spatial units proposed by CCELC were revised by the Ecological Stratification Working Group (1995) to incorporate further developments in regional ecological classification and mapping; provide links to other biophysical and socioeconomic databases; and to facilitate retrieval of descriptions of ecozones and ecoregions. The revision by the Ecological Stratification Working Group (1995) omitted levels in the CCELC hierarchy that were described as less suited to meeting the needs of environmental reporting and monitoring. Ecozone, Ecoregion, and Ecodistrict were retained.

Table 2. 8. Hierarchical levels of the Canadian Committee on Ecological Land Classification (CCELC) system. (After Wiken 1973).

Level	Description	Common map scale
Ecozone	Areas of large land masses representing very generalized ecological units, based on the idea that the earth's surface is interactive and continuously adjusting to the mix of biotic and abiotic factors present at any given time (e.g., Boreal Shield)	1:50 000 000 to 1:10 000 000
Ecoprovince	Areas of the earth's surface characterized by major structural or surface forms, faunal realms, vegetation, hydrology, soil, and climatic zones (e.g., Island of Newfoundland)	1:10 000 000 to 1:5 000 000
Ecoregion	A part of an ecoprovince characterized by distinctive ecological responses to climate as expressed by vegetation, soil, water, and fauna (e.g., Northern Peninsula Lowland)	1:3 000 000 to 1:1 000 000
Ecodistrict	A part of an ecoregion characterized by a distinctive pattern of relief, geology, geomorphology, vegetation, water and fauna	1:500 000 to 1:125 000
Ecosection	A part of an ecodistrict throughout which there is a recurring pattern of terrain, soil, vegetation, water bodies and fauna	1:250 000 to 1:50 000
Ecosite	A part of an ecosection having a relatively uniform parent material, soil, hydrology, and chronosequence of vegetation	1:50 000 to 1:10 000
Ecoelement	A part of an ecosite displaying uniform soil, topographical, vegetative and hydrological characteristics	1:10 000 to 1:2 500

2.8.1 British Columbia ecological classification

The ecology of white and/or Engelmann spruce ecosystems in British Columbia have been intensively characterized (Coates et al. 1994). Spruce ecosystems have been described and classified within the framework of the biogeoclimatic ecosystem classification developed by Krajina (1965, 1969) and his co-workers, and adapted by the British Columbia Ministry of Forests (Pojar et al. 1987).

White spruce or Engelmann spruce and their hybrids occur in 12 of the 14 biogeoclimatic zones of British Columbia (Coates et al. 1994):

> White spruce and hybrids with mostly white spruce characteristics dominate the Boreal White and Black Spruce (BWBS), Sub-Boreal Spruce (SBS) and Spruce – Willow – Birch (SWB) zones of the central and northern interior. Engelmann spruce and its hybrids are widespread in the cool Montane Spruce (MS) and Engelmann Spruce – Subalpine Fir (ESSF) zones of the southern interior. Other zones in which interior spruce is common, but not dominant, include the Interior Cedar – Hemlock (ICH), Interior Douglas-fir (IDF), and Sub-Boreal Pine – Spruce (SBPS) zones. Interior spruce also occurs sporadically in the Ponderosa Pine (PP), Mountain Hemlock (MH) and Coastal Western Hemlock (CWH) zones and in krummholz form at the lower elevations of interior portions of the Alpine Tundra (AT) zone (Coates et al. 1994).

The following sections include descriptions of spruce and associates, abstracted from Coates et al. (1994), and provide an excellent account of the variety of communities in which white, interior, and Engelmann spruces occur in British Columbia:

Alpine Tundra Zone (AT)

Throughout British Columbia, east of the Coast Mountains, interior spruce is one of the most common krummholz species, but in most areas it is outnumbered by subalpine fir (*A. lasiocarpa*), which appears to be better adapted to the harsh conditions (Kearney 1982).

Subalpine fir is the most common associate of spruce in krummholz vegetation. Other associated coniferous species include subalpine larch (*Larix lyalli* Parl.), whitebark pine (*Pinus albicaulis* Engelmann), limber pine (*Pinus flexilis* James), and western white pine (*Pinus monticola* Dougl. Ex D. Don) in southern British Columbia, and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) on the eastern slopes of the Coast Range and in the Revelstoke area. Lodgepole pine is a minor associate in most of the British Columbia interior, except in dry alpine areas of southwest Cariboo/Chilcotin district where it is abundant (Pojar 1985). Ericaceous species (grouseberry (*Vaccinium scoparium* Leiberg ex Coville), mountain huckleberry (*Vaccinium membranaceum* Douglas ex Torrey), dwarf bilberry (*Vaccinium cespitosum* Michaux), white mountain heather (*Cassiope mertensiana* (Bong.) G. Don), pink mountain heather (*Phyllodoce empetriformis* (Smith) D. Don) are common in the snow accumulation zone around the base of krummholz colonies.

Spruce – Willow – Birch Zone (SWB)

White spruce is the most abundant conifer in the zone, except at the upper (parkland) elevations, where subalpine fir dominates. Engelmann spruce and hybrid white × Engelmann spruce is a primary feature distinguishing the SWB from the more southerly ESSF zone.

Subalpine fir is the most common associate of white spruce in the SWB zone. Black spruce, lodgepole pine and trembling aspen are relatively minor associates. Many spruce stands are quite open, with a well-developed shrub layer dominated by a variety of willows (grey-leaved willow, tea-leaved willow (*Salix planifolia* Pursh), Scouler's willow, Bebb's willow) and resin birch. Other common shrubs include shrubby cinquefoil (*Dasiphora fruticosa* (L.) Rydberg), soapberry, black crowberry, mountain cranberry, dwarf bilberry and common Labrador tea. Common herbs are twinflowe*r*, northern rough fescue (*Festuca altaica* Trinius), fireweed, arctic lupin (*Lupinus arcticus* S. Watson) and tall bluebells. In addition to the feather mosses red-stemmed feathermoss and stairstep moss, the forest floor contains a diversity of lichens.

Boreal White and Black Spruce (BWBS)

White spruce is the predominant tree species in the BWBS, except in the Fort Nelson area where the poorly drained lowlands are dominated by black spruce. Engelmann spruce is absent, though some white × Engelmann hybrids may occur at southern margins of the zone bordering the SBS zone.

Mixed stands of white spruce and trembling aspen (often with a minor component of balsam poplar, birch (paper birch, Alaska paper birch (*Betula neoalaskana* Sarg.) or lodgepole pine) are the most common components of forest cover on warm mesic sites in the BWBS. On colder sites, e.g., on north-facing slopes, pure white spruce or mixtures of white and black spruces dominate. Lodgepole pine is the typical associate of white spruce on coarse-textured parent materials, while balsam poplar – spruce mixtures are frequent on floodplains. Subalpine fir is common in western parts of the zone, but is rare east of the Rockies. Wetland black spruce stands often have a minor component of slow-growing white spruce. Typical vegetation in boreal white spruce stands includes the common shrubs prickly rose, squashberry, soap berry, Bebb's willow, and American green alder, with swamp red currant and bracted honeysuckle (*Lonicera involucrata* (Richardson) Banks ex Sprengel) on wet sites, and common Labrador tea and mountain cranberry on cold sites. Characteristic herbs are twinflower, dwarf raspberry, tall bluebells, arctic sweet coltsfoot (*Petasites frigidus* (L.) Fries), pink pyrola (*Pyrola asarifolia* Michaux), bunchberry and bluejoint reedgrass, with horsetail on wet sites. The thick carpet of moss is of stairstep moss, red-stemmed feathermoss and knight's plume moss, and common freckle pelt lichen.

Sub-Boreal Pine – Spruce Zone (SBPS)

White spruce is a distant second in importance to lodgepole pine in the SBPS. It occurs most commonly in the understorey to pine, but scattered stands dominated by white spruce can be found on moist sites. Pure Engelmann is absent, and any hybrids appear to have mainly white spruce characteristics.

Lodgepole pine is the most common associate of white spruce in the SBPS. White spruce also occurs with trembling aspen in seral stands, and mixtures of black and white spruces occupy cold low-lying sites. Floodplain stands of black cottonwood (*Populus trichocarpa* Torr. & A. Gray) and white spruce occur uncommonly.

Typical understorey vegetation of moist spruce ecosystems includes the shrubs bracted honeysuckle, prickly rose, soapberry, common juniper, grey-leaved willow, glandular birch, bristly black currant (*Ribes lacustre* (Persoon) Poiret), northern black currant (*Ribes hudsonianum* Richardson) and squashberry, and the herbs bunchberry, twinflower, fireweed, arctic sweet coltsfoot, wild strawberry, field horsetail, bluejoint reedgrass and naked mitrewort. In addition to the usual feather mosses (red-stemmed feathermoss, stairstep moss and knight's plume moss) the moss layer characteristically includes ribbed bog moss (*Aulacomnium palustre* (Hedw.) Schwaegr.) and *Peltigera*, *Cladina* and *Cladonia* lichens.

Sub-Boreal Spruce Zone (SBS)

Interior spruce (mostly hybrid white × Engelmann, with some pure white spruce) is dominant throughout.

Lodgepole pine is the most common associate of interior spruce in the SBS. Subalpine fir is abundant in cooler, moister subzones. Trembling aspen and Douglas-fir are often found with spruce on warmer, drier, more southerly subzones. Black cottonwood is the main associate of interior spruce on active floodplain sites, and mixtures of white and black spruces are common on wetlands.

Understorey vegetation in mesic spruce stands typically includes a moderately well-developed shrub layer dominated by mountain huckleberry, western thimbleberry (*Rubus* parviflorus Nuttall), squashberry, prickly rose, American green alder, a variety of herbs (bunchberry, single-flowered clintonia (*Clintonia uniflora* (Menzies ex Schultes) Kunth), dwarf raspberry, five-leaved dwarf bramble (*Rubus pedatus* Smith), heart-leaved arnica (*Arnica cordifolia* Hooker), large false Solomon's seal (*Maianthemum racemosum* (L.) Link), one-sided wintergreen, wild sarsaparilla) and a well-developed carpet of feathermosses (red-stemmed feathermoss, knight's plume moss, stairstep moss, electrified cat's-tail moss (*Rhytidiadelphus triquetrus* (Hedw.) Warnst.). Wetter spruce sites have bracted honeysuckle, red-osier dogwood, common oak fern (*Gymnocarpium dryopteris* (L.) Newman), three-leaved foamflower (*Tiarella trifoliata* L.), field horsetail and *Mnium* mosses. Characteristic species of spruce bog, fen, or swamp ecosystems are willow spp., glandular birch, common Labrador tea, sedge and Sphagnum moss.

Engelmann Spruce – Subalpine Fir Zone (ESSF)

Over most of southern British Columbia, spruce dominates the canopy of mature stands in the ESSF, while subalpine fir is most abundant in the understorey. At higher elevations, particularly in the north and in wet, heavy snowfall areas, subalpine fir dominates and spruce is a minor component. In southern British Columbia, the spruce is pure Engelmann, but white spruce characteristics become increasingly evident northward, first only at lower elevations, then at all elevations. At the northern limits of the ESSF, Engelmann spruce characteristics are rare.

Subalpine fir is ubiquitous in the ESSF and is the most common associate of spruce throughout. Lodgepole pine is the most common seral species. Deciduous species, such as trembling aspen, paper birch, and black cottonwood, are present but uncommon. Whitebark pine and, in southeastern British Columbia only, limber pine and alpine larch occur in association with spruce, especially in the driest ecosystems, usually at high elevations, where spruce is not abundant. At low elevations in the ESSF, associates of spruce are Douglas-fir, western redcedar, western hemlock and western white pine. Mountain hemlock and Pacific silver fir are also found with spruce in the ESSF, principally adjacent to the Mountain Hemlock Zone. The dominant plant community in the ESSF has an understorey of ericaceous shrubs, mainly white-flowered rhododendron (*Rhododendron albiflorum* Hooker), mountain huckleberry, and false azalea (*Menziesia ferruginea* J.E. Smith), with oval-leaved blueberry (*Vaccinium ovalifolium* Smith) in high-precipitation areas and grouseberry in dry areas. Bristly black currant, devil's club (*Oplopanax horridus* (Smith) Miquel) and bracted honeysuckle are common shrubs on moist to wet sites. Herbs characteristic of the ESSF forest include Sitka valerian (*Valeriana sitchensis* Bongard), common oak fern, five-leaved dwarf bramble, rose twisted-stalk, green false hellebore (*Veratrum viride* Aiton), common lady fern (*Athyrium filix-femina* (L.) Roth ex Mertens), bunchberry, stiff clubmoss, foamflower (*Tiarella* L. spp). and heart-leaved arnica. Dominant bryophytes are red-stemmed feathermoss, broom mosses, and pawwort (*Barbilophozia* Loeske spp.). Lichens are abundant on the forest floor and include *Peltigera* spp., arctic kidney lichen (*Nephroma arcticum* L. Torss.), and *Cladonia* spp. At the upper parkland elevations of the ESSF, closed forest and tree islands of spruce and subalpine fir are interspersed with moist herb meadows and drier ericaceous heath. The meadows typically include the herbs: Sitka valerian, green false hellebore, arrow-leaved ragwort (*Senecio triangularis* Hooker), arctic lupin, western meadow-rue (*Thalictrum occidentale* A. Gray), fireweed, bracted lousewort (*Pedicularis bracteosa* Bentham), great red paintbrush (*Castilleja* miniata Dougl. Ex Hooker var. *miniata*), wandering fleabane (*Erigeron peregrinus* (Banks ex Pursh) Greene), sedge and woodrush (*Luzula* de Candolle spp.) Subalpine heath includes black crowberry, white mountain heather, four-angled mountain heather (*Cassiope tetragona* (L.) D.

Don), pink mountain heather, yellow mountain heather (*Phyllodoce glanduliflora* (Hooker) Coville*),* and dwarf bilberry.

Montane Spruce Zone (MS)

Spruce is second in abundance to lodgepole pine in the MS zone. Engelmann x white hybrids predominate, but pure Engelmann spruce occurs at higher elevations. White spruce occurs in some northern parts of the zone.

A distinctive feature of the MS zone is the prevalence of young and maturing stands of lodgepole pine of fire origin. Spruce, together with some subalpine fir, dominates later successional stands, especially on moister sites. Douglas-fir, trembling aspen, and, in the Rocky Mountain Trench only, western larch (*Larix occidentalis* Nutt) are common seral species. Characteristic understorey species in spruce stands are Utah honeysuckle (*Lonicera utahensis* S. Watson), falsebox (*Paxistima myrsinites* (Pursh) Rafinesque)*,* mountain huckleberry, grouseberry, American green alder, pine reedgrass (*Calamagrostis rubescens* Buckley), heart-leaved arnica, twinflower, and red-stemmed feathermoss. Western Labrador tea (*Rhododendron neoglandulosum Harmaja*), bristly black currant, and field horsetail typically occur in wetter ecosystems; common juniper and common bearberry are found on dry sites.

Ponderosa Pine Zone (PP)

White spruce or white × Engelmann hybrids are found only rarely within the PP zone, and occur in cool, moist, sheltered situations, e.g., steep, north-facing canyon headwalls.

Interior Douglas-fir Zone (IDF)

Hybrid Engelmann × white spruce is secondary to Douglas-fir, and occurs mainly in wetter subzones and at higher elevations transitional to the Montane Spruce, Sub-Boreal Spruce, and Engelmann Spruce – Subalpine Fir Zones.

The most common associate of spruce is Douglas-fir, which dominates the zone. Lodgepole pine is abundant in the IDF but tends to be present only in small amounts on the wetter spruce sites. Western redcedar, western larch, and grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) occur together with spruce, particularly in the southeastern part of the zone. Trembling aspen, paper birch, and black cottonwood are common seral species. Mixed shrub or horsetail-dominated plant communities are typical of moist, rich ecosystems that include spruce. Common shrub associates include: bristly black currant, bracted honeysuckle, red-osier dogwood, prickly rose, thin-leaved snowberry and Douglas maple. The well-developed herb layer contains twinflower, bunchberry, wild sarsaparilla, red baneberry (*Actaea rubra* (Aiton) Willdenow), and mountain sweet cicely (*Osmorhiza berteroi* de Candolle), together with horsetail and sedge on wetter sites. Bog forests with Sphagnum spp., common Labrador tea, and creeping snowberry are infrequent but usually have a tree canopy of pure spruce.

Interior Cedar – Hemlock Zone (ICH)

Interior spruce is a common secondary component of ICH forests. It is most abundant in the northern and eastern parts of the zone, close to the Sub-Boreal Spruce Zone, or at high elevations bordering the Engelmann Spruce – Subalpine Fir Zone. It is least abundant in drier parts of the ICH. White spruce, Engelmann spruce, and their hybrids are all present, Engelmann spruce dominating in southeastern British Columbia, particularly at high elevations, and white spruce dominating in the north. In the coast – interior transition of northwestern British Columbia, interior spruce hybridizes with Sitka spruce.

The ICH has a greater diversity of tree species than any other interior zone. Western hemlock and western redcedar are the climax dominants, and interior spruce often accompanies them as a secondary component. Subalpine fir is a major associate to the north. Black cottonwood, lodgepole pine, trembling aspen, and paper birch are found with spruce in seral communities throughout most of the zone. In the central and southern ICH, spruce may also occur in association with Douglas-fir, western larch, western white pine, and grand fir. A typical spruce or redcedar – spruce stand on a seepage ecosystem has a diverse shrub layer dominated by devil's club, bristly black currant, red-osier dogwood, Douglas maple, western thimbleberry, squashberry, and bracted honeysuckle. Characteristic herbs include common oak fern, common lady fern, three-leaved foamflower, stream violet (*Viola glabella* Nuttall), small enchanter's nightshade (*Circaea alpina* L.), twistedstalk (*Streptopus* Michaux spp.), mountain sweet cicely, spreading wood fern (*Dryopteris expansa* (C. Presl.) Fraser-Jenkins & Jermy), and red baneberry. On swampier sites, yellow skunk cabbage (*Lysichiton americanus* Hultén & H. St.John), horsetail, and electrified cat's-tail moss and stairstep moss are found. Seral communities on mesic sites in the north of the ICH have a mixed overstorey of spruce, subalpine fir, lodgepole pine, paper birch, and trembling aspen. Typical shrubs are: western thimbleberry, squashberry, prickly rose, falsebox, saskatoon, soapberry, American green alder, and mountain huckleberry. Major herbs include: bunchberry, single-flowered clintonia, wild sarsaparilla, Sierra Nevada vetchling (*Lathyrus nevadensis* S. Watson), dwarf raspberry, Solomon's seal (*Maianthemum* F.H. Wiggers spp.), one-sided wintergreen, mountain sweet cicely, and arctic sweet coltsfoot. The moss carpet is dominated by electrified cat's-tail moss, knight's plume moss, red-stemmed feathermoss, and stairstep moss.

Coastal Western Hemlock Zone (CWH)

White spruce is absent from the CWH, but Engelmann spruce occurs in eastern portions of the coast – interior transition subzone in southwestern British Columbia. Some hybridization may occur between Engelmann spruce and Sitka spruce, but there is little indication of introgression (Klinka et al. 1982). A Sitka × white × Engelmann hybrid swarm occurs at the eastern margins of the subzone covering the Skeena and Nass River drainages (Haeussler et al. 1984). In the CWHms subzone, Klinka et al. (1982) found Engelmann spruce with site indices of 35 – 47 m at 100 years. Floristically, the ecosystems were classified as belonging to the common lady fern – devil's club – western redcedar – Pacific silver fir association.

2.8.2 Alaskan Forest Ecology

A classification system based on a temperature/moisture gradient for the common Alaska taiga vegetation types was proposed by Viereck (1975) to help resource management. The distribution of white spruce is commonly used to indicate the taiga zone in Alaska. Other tree species of more limited extent within the zone are black spruce, tamarack, balsam poplar and trembling aspen.

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APPENDIX

Scientific name[1]	**English Common Name[1]**	**French Common Name[1]**	**Original Scientific Name[2]**	**Original Common Name[2]**
Abies alba Mill.	European silver fir	sapin blanc	*A. alba*	silver firs
Abies amabilis Dougl. ex J. Forbes	Pacific silver fir	sapin gracieux	*Abies amabilis*	silver firs
Abies balsamea (L.) Mill.	balsam fir	sapin baumier	*Abies balsamea* [L.]	balsam fir
Abies excelsa Lam.	-	-	*Abies excelsa*	-
Abies grandis (Douglas ex D. Don) Lindley	grand fir	sapin grandissime	*Abies grandis*	grand fir
Abies lasiocarpa (Hook.) Nutt.	subalpine fir	sapin subalpin	*Abies lasiocarpa* (Hook.) Nutt.	alpine fir
Abies Mill.	fir	sapin	*Abies*	-
Acer glabrum var. *douglasii* (Hook.) Dippel	Douglas maple	érable nain	*Acer glabrum* Torr. var. *douglasii*	Douglas maple
Acer L.	maple	érable	*Acer*	-
Acer rubrum L.	red maple	érable rouge	*Acer rubrum* L.	red maple
Acer saccharum Marsh.	sugar maple	érable à sucre	*Acer saccharum* Marsh.	sugar maple
Acer spicatum Lamarck	mountain maple	érable à épis	*Acer spicatum*	-
Actaea rubra (Aiton) Willdenow	red baneberry	actée rouge	*Actaea rubra*	-
Alnus alnobetula ssp. *crispa* (Aiton) Raus	American green alder	aulne crispé	*Alnus crispa*	green alder
Alnus incana (L.) Moench	grey alder	aulne blanc	*Alnus incana*	-
Alnus incana ssp. *tenuifolia* (Nutt.) Breitung	mountain alder	aulne à feuilles minces	*Alnus tenuifolia*	-
Alnus Mill.	alder	aulne	*Alnus*	-
Amelanchier alnifolia (Nuttall) Nuttall ex M. Roemer	saskatoon	amélanchier à feuilles d’aulne	*Amelanchier alnifolia*	-
Amelanchier arborea (F. Michaux) Fernald	downy serviceberry	amélanchier arborescent	-	downy serviceberry
Aralia nudicaulis L.	wild sarsaparilla	aralie à tige nue	*Aralia nudicaulis*	-
Arctostaphylos uva-ursi (L.) Sprengel	common bearberry	raisin d’ours	*Arctostaphylos uva-ursi*	common bearberry
Arctous rubra (Rehder & E.H. Wilson) Nakai	red bearberry	busserole rouge	-	red-fruit bearberry
Arnica cordifolia Hooker	heart-leaved arnica	arnica à feuilles cordées	*Arnica cordifolia*	-

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Athyrium filix-femina (L.) Roth ex Mertens	common lady fern	athyrie fougère-femelle	*Athyrium filix-femina*	-
Aulacomnium palustre (Hedw.) Schwaegr.	ribbed bog moss	aulacomnie des marais	*Aulacomnium palustre*	-
Barbilophozia Loeske spp.	pawwort	barbille	*Barbilophozia* spp.	-
Betula alleghaniensis (Britt.)	yellow birch	bouleau jaune	*Betula alleghaniensis*	yellow birch
Betula glandulosa Michaux	glandular birch	bouleau glanduleux	*Betula glandulosa*	Resin birch
Betula lenta L.	cherry birch	bouleau flexible	-	sweet birch
Betula nana L.	dwarf birch	bouleau nain	*Betula nana*	dwarf birch
Betula neoalaskana Sarg.	Alaska paper birch	bouleau d'Alaska	*B. neoalaskana*	-
Betula papyrifera Marsh.	paper birch	bouleau à papier	*Betula papyrifera* Marsh.	paper birch
Betula populifolia Marsh.	grey birch	bouleau gris	*Betula populifolia*	gray birch
Blepharostoma trichophyllum (L.) Dum.	hairy threadwort	ciliaire doigts-de-fée	*Blepharostoma trichophyllum*	-
Calamagrostis canadensis (Michaux) Palisot de Beauvois	bluejoint reedgrass	calamagrostide du Canada	*Calamagrostis canadensis*	bluejoint grass
Calamagrostis rubescens Buckley	pine reedgrass	calamagrostide rouge	*Calamagrostis rubescens*	-
Capnoides sempervirens (L.) Borkhausen	pink corydalis	corydale toujours verte	*Corydalis sempervirens*	-
Carex L. spp.	sedge	carex	*Carex* spp.	sedge species
Carpinus caroliniana Walt.	blue-beech	charme de Caroline	-	blue-beech
Carya Nuttall			*Carya*	
Carya cordiformis (Wangenh.) K. Koch	bitternut hickory	caryer cordiforme	*Carya cordiformis*	bitternut hickory
Cassiope mertensiana (Bong.) G. Don	white mountain heather	cassiope de Mertens	*Cassiope mertensiana*	-
Cassiope tetragona (L.) D. Don	four-angled mountain heather	cassiope tétragone	*Cassiope tetragona*	-
Castilleja miniata Dougl. Ex Hooker var. *miniata*	great red paintbrush	castilléjie rougeâtre	*Castelleja miniata*	-
Cathaya Chun & Kuang	-	-	*Cathaya*	-
Cedrus Trew	cedar	cèdre	*Cedrus*	-
Ceratodon purpureus (Hedw.) Brid.	fire moss	cératodon pourpre	*Cedrus*	*Ceratodon purpureus* (Hedw.) Brid.
Cetraria islandica (L.) Ach.	true Iceland lichen	cétraire d'Islande	*Cetraria islandica*	-

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Chamaecyparis thyoides (L.) B.S.P.	Atlantic white-cedar	cèdre blanc de l'Atlantique	*Chamaecyparis thyoides*	white-cedar
Chamaenerion angustifolium (L.) Scopoli	fireweed	épilobe à feuilles étroites	*Epilobium angustifolium*	fireweed
Circaea alpina L.	small enchanter's nightshade	circée alpine	*Circaea alpina*	-
Cladina arbuscula ssp. *arbuscula* (Wallr.) Hale & W.L. Culb.	-	-	*C. sylvatica*	-
Cladonia gracilis (L.) Willd.	smooth soldiers lichen	cladonie grêle	*C. gracilis*	-
Cladonia rangiferina (L.) F.H. Wigg.	grey reindeer lichen	cladine rangifère	*Cladonia rangiferina*	-
Cladonia spp.	-	-	*Cladonia* spp.	-
Cladonia stellaris (Opiz) Pouzar & Vezda	star-tipped reindeer lichen	cladonie étoilée	*Cladonia stellaris* (Opiz) Pouzar & Vezda	-
-	-	-	*C. alpestris*	-
Clintonia borealis (Aiton) Rafinesque	yellow clintonia	clintonie boréale	*Clintonia borealis*	-
Clintonia uniflora (Menzies ex Schultes) Kunth	single-flowered clintonia	clintonie uniflore	*Clintonia uniflora*	-
Cornus canadensis L.	bunchberry	quatre-temps	-	bunchberry
Cornus sericea L.	red-osier dogwood	cornouiller hart-rouge	*Cornus stolonifera*	red-osier dogwood
Corylus cornuta Marsh.	beaked hazlenut	noisetier à long bec	*Corylus cornuta*	-
Dasiphora fruticosa (L.) Rydberg	shrubby cinquefoil	potentille frutescente	*Potentilla fruticosa*	-
Dicranum fuscescens Turn.	curly heron's-bill moss	dicrane commun	*Dicranum fuscescens*	-
Dicranum Hedw. spp.	broom mosses	espèces de dicranes	*Dicranum* Hedw. spp.	-
Diervilla lonicera Miller	northern bush-honeysuckle	dièreville chèvrefeuille	*Diervilla lonicera*	-
Dryas L.	mountain avens	dryade	*Dryas*	avens
Dryopteris expansa (C. Presl.) Fraser-Jenkins & Jermy	spreading wood fern	dryoptère dressée	*Dryopteris assimilis*	-
Empetrum L. spp.	crowberry	camarine	*Empetrum* spp.	crowberry
Empetrum nigrum L.	black crowberry	camarine noire	*Empetrum nigrum*	black crowberry
Epigaea repens L.	trailing arbutus	épigée rampante	*Epigaea repens*	-
Equisetum arvense L.	field horsetail	prêle des champs	*Equisetum arvense*	-
Equisetum hyemale L.	common scouring-rush	prêle d'hiver	*Equisetum hiemale*	-
Equisetum L. spp.	horsetail	prêle	-	horsetail

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Equisetum pratense Ehrhart	meadow horsetail	prêle des prés	*Equisetum pratense*	-
Erigeron peregrinus (Banks ex Pursh) Greene	wandering fleabane	vergerette voyageuse	*Erigeron peregrinus*	-
Eurybia macrophylla (L.) Cassini	large-leaved aster	aster à grandes feuilles	*Aster macrophyllum*	-
Fagus L.	beech	hêtre	*Fagus*	-
Fagus sylvatica L	European beech	hêtre commun	-	European beech
Festuca altaica Trinius	northern rough fescue	fétuque de l'Altaï	*Festuca altaica*	-
Fragaria virginiana Miller	Virginia strawberry	fraisier des champs	*Fragaria virginiana*	-
Fraxinus L.	ash	frêne		ash
Fraxinus americana L.	white ash	frêne blanc	*Fraxinus americana* L.	white ash
Fraxinus nigra Marsh.	black ash	frêne noir	*Fraxinus nigra*	black ash
Fraxinus pennsylvanica Marsh.	red ash	frêne rouge	*Fraxinus pennsylvanica*	red ash
Galium L. spp.	bedstraw	gaillet	*Galium* spp.	-
Gaultheria hispidula (L.) Muhlenberg ex Bigelow	creeping snowberry	petit thé	*Gaultheria hispidula*	-
Gaylussacia Kunth spp.	huckleberry	gaylussaquier	*Gaylussacia* spp.	huckleberry
Geocaulon lividum (Richardson) Fernald	northern comandra	comandre livide	-	northern comandra
Geranium bicknellii Britton	Bicknell's geranium	géranium de Bicknell	*Geranium bicknellii*	-
Goodyera repens (L.) R. Brown	dwarf rattlesnake-plantain	goodyérie rampante	*Goodyera repens*	dwarf rattlesnake-plantain
Gymnocarpium dryopteris (L.) Newman	common oak fern	gymnocarpe fougère-du-chêne	*Gymnocarpium dryopteris*	-
Hedysarum americanum (Michaux ex Pursh) Britton	alpine hedysarum	sainfoin alpin	*Hedysarum alpinum*	-
Hylocomium splendens (Hedw.) B.S.G.	stairstep moss	hylocomie brillante	*Hylocomium splendens* (Hedw.) B.S.G.	-
Juglans cinerea L.	butternut	noyer cendré	*Juglans cinerea* L.	butternut
Juniperus communis L.	common juniper	genévrier commun	*Juniperus communis*	-
Keteleeria Carrière			*Keteleeria*	
Larix laricina (Du Roi) K. Koch	tamarack	mélèze laricin	*Larix laricina* (Du Roi) K. Koch	tamarack
Larix lyalli Parl.	subalpine larch	mélèze subalpin	*Larix lyalli*	alpine larch
Larix Mill.	larch	mélèze	*Larix*	-
Larix occidentalis Nutt.	western larch	mélèze de l'Ouest	*Larix occidentalis*	western larch

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Lathyrus L. spp.	vetchling	gesses	*Lathyrus* spp.	peavine
Lathyrus nevadensis S. Watson	Sierra Nevada vetchling	gesse de la Sierra Nevada	*Lathyrus nevadensis*	-
Lathyrus ochroleucus Hooker	creamy-coloured vetchling	gesse jaunâtre	*Lathyrus ochroleucus*	creamy peavine
Linnaea borealis L.	twinflower	linnée boréale	-	twinflower
Lonicera dioica L.	limber honeysuckle	chèvrefeuille glauque	*Lonicera dioica*	-
Lonicera involucrata (Richardson) Banks ex Sprengel	bracted honeysuckle	chèvrefeuille involucré	*Lonicera involucrata*	-
Lonicera utahensis S. Watson	Utah honeysuckle	chèvrefeuille d'Utah	*Lonicera utahensis*	-
Lophozia (Dum.) Dum. spp.	notchwort	lophozie	*Lophozia* spp.	-
Lupinus arcticus S. Watson	arctic lupin	lupin arctique	*Lupinus arcticus*	-
Luzula de Candolle spp.	woodrush	luzule	*Luzula* spp.	-
Lysichiton americanus Hultén & H. St.John	yellow skunk cabbage	lysichiton d'Amérique	*Lysichiton americanum*	-
Lysimachia borealis (Rafinesque) U. Manns & Anderberg	northern starflower	trientale boréale	*Trientalis americana*	-
Maianthemum canadense Desfontaines	wild-lily-of-the-valley	maïanthème du Canada	*Maianthemum canadense*	-
Maianthemum F.H. Wiggers spp.	Solomon's seal	smilacine	*Maianthemum* spp.	-
Maianthemum racemosum (L.) Link	large false Solomon's seal	smilacine à grappes	*Maianthemum racemosa*	-
Marchantia polymorpha L.	green-tongue liverwort	marchantie polymorphe	*Marchantia polymorpha*	-
Menziesia ferruginea J.E. Smith	false azalea	menziésie ferrugineuse	*Menziesia ferruginea*	-
Mertensia paniculata (Aiton) G. Don	tall bluebells	mertensie paniculée	-	tall lungwort
Mitella nuda L.	naked mitrewort	mitrelle nue	*Mitella nuda*	naked bishops-cap
Moneses uniflora (L.) A. Gray	one-flowered wintergreen	monésès uniflore	*Moneses uniflora*	one-flowered wintergreen
Nephroma arcticum L. Torss.	arctic kidney lichen	néphrome arctique	*Nephroma arcticum*	-
Oplopanax horridus (Smith) Miquel	devil's club	bois piquant	*Oplopanax horridus*	-
Orthilia secunda (L.) House	one-sided wintergreen	pyrole unilatérale	*Pyrola secunda*	one-sided wintergreen
Osmorhiza berteroi de Candolle	mountain sweet cicely	osmorhize de Bertero	*Osmorhiza chilensis*	-
Ostrya virginiana (Mill.) K. Koch	eastern hop-hornbeam	ostryer de Virginie	*Ostrya virginiana* (Mill.)	hop-hornbeam
Paxistima myrsinites (Pursh) Rafinesque	falsebox	pachistima myrte	*Paxistima myrsinites*	-

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Pedicularis bracteosa Bentham	bracted lousewort	pédiculaire à fleurs bractéolées	*Pedicularis bracteosum*	-
Pelitigera canina (L.) Willd.	dog pelt lichen	peltigère canine	*P. canina*	-
Peltigera apthosa (L.) Willd.	common freckle pelt lichen	peltigère aphteuse	*Peltigera apthosa*	-
Petasites frigidus (L.) Fries	arctic sweet coltsfoot	pétasite des régions froides	*Petasites palmatus*	-
Phyllodoce empetriformis (Smith) D. Don	pink mountain heather	phyllodoce à feuilles de camarine	*Phyllodoce empetriformis*	-
Phyllodoce glanduliflora (Hooker) Coville	yellow mountain heather	phyllodoce glanduleuse	*Phyllodoce glandulifera*	-
Picea A. Dietrich	spruces	épinettes	*Picea*	spruces
Picea abies (L.) Karst	Norway spruce	épinette de Norvège	*Picea abies* (L.) Karst	Norway spruce
Picea asperata Masters	dragon spruce	épicéa de Chine	*Picea asperata* Masters	-
Picea banksii n. sp.	-	-	*Picea banksii* n. sp.	-
Picea canadensis (Mill.) B.S.P. [=*P. glauca*]	-	-	*P. canadensis* Mill.) B.S.P. [=*P. glauca*]	-
Picea engelmannii Engelmann	Engelmann spruce	épinette d'Engelmann	*P. engelmannii* Parry	Engelmann spruce
Picea glauca (Moench) Voss	white spruce	épinette blanche	*Picea glauca* [Moench] Voss	white spruce
Picea glauca × *P. sitchensis*	Lutz spruce	épinette de Lutz	*P. glauca* × *sitchensis*	Roche spruce
Picea glauca × *P. mariana*	Rosendahl spruce	épinette Rosendahl	*P. glauca* × *P. mariana*	Rosendahl spruce
Picea glauca var. *densata* Bailey	Black Hills spruce	épinette Black Hills	*P. glauca* var. *densata* Bailey	Black Hills spruce
Picea glauca var. *porsildii* Raup	Porsild spruce	épinette Porsild	*P. glauca* var. *porsildii* Raup	Porsild spruce
Picea glehnii (F. Schmidt) Mast*.*	Sakhalin spruce	épicéa de Glehn	*Picea glehnii*	-
Picea jezoensis(Siebold. & Zucc.) Carr.	Yezo spruce	épinette Yezo	*Picea jezoensis*	-
Picea koyamai Shirasawa	Koyama's spruce	épinette Koyama's	*Picea koyamai* Shirasawa	-
Picea likiangensis (Franch.) Pritz.	Lijiang spruce	épicéa de Likiang	*Picea likiangensis*	-
Picea mariana (Mill.) B.S.P	black spruce	épinette noire	*P. mariana* [Mill.] BSP	black spruce
Picea omorika (Pančić) Purk	Serbian spruce	épicéa de Serbie	*Picea omorika* (Pančić) Purk	-
Picea pectinata Lam.	-	-	*Picea pectinata*	-
Picea pungens Engelm.	blue spruce	épinette du Colorado	*Picea pungens* Engelm.	-
Picea rubens Sarg.	red spruce	épinette rouge	*P. rubens* Sarg.	red spruce
Picea schrenkiana Fisch. & C. A. Mey.	Schrenk's spruce	épinette Schrenk's	*Picea schrenkiana*	-

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Picea sitchensis (Bong.) Carrière	Sitka spruce	épinette de Sitka	*Picea sitchensis* [Bong.]	Sitka spruce
Picea x albertiana S. Brown	interior spruce	-	*Picea albertiana* sp. nov. S. Brown	-
Picea x lutzii Little	Lutz spruce	épinette de Lutz	*Picea × lutzii*	Roche spruce
Pinus albicaulis Englemann	whitebark pine	pin à écorce blanche	*Pinus albicaulis*	whitebark pine
Pinus banksiana (Lamb.)	jack pine	pin gris	*Pinus banksiana* Lamb.	jack pine
Pinus contorta Dougl. ex Loud.	lodgepole pine	pin tordu	*Pinus contorta* Dougl. ex Loud	lodgepole pine
Pinus flexilis E. James	limber pine	pin flexible	*Pinus flexilis*	limber pine
Pinus L.	pine	pin	*Pinus*	-
Pinus monticola Dougl. Ex D. Don	western white pine	pin argenté	*Pinus monticola*	western white pine
Pinus mugo (Turra)	mugo pine	pin mugo	*Pinus montana* Mil.	-
Pinus pinaster Aiton	maritime pine	pin maritim	*Pinus pinaster* Aiton.	-
Pinus ponderosa Dougl. ex Laws. & C. Laws.	ponderosa pine	pin ponderosa	-	ponderosa pine
Pinus resinosa (Ait.)	red pine	pin rouge	*Pinus resinosa*	red pine
Pinus strobus (L.)	white pine	pin blanc	*Pinus strobus*	white pine
Pleurozium schreberi (Brid.) Mitt.	red-stemmed feathermoss	pleurozie dorée	*Pleurozium schreberi* (Brid.) Mitt.	-
Polytrichum Hedw. spp.	haircap moss	polytric	*Polytrichum* spp.	-
Populus balsamifera L.	balsam poplar	peuplier à grandes dents	*Populus balsamifera* L.	balsam poplar
Populus grandidentata Michx.	large-toothed aspen	-	*Populus grandidentata*	bigtooth aspen
Populus L.	poplar	-	*Populus*	-
Populus tremuloides Michx.	trembling aspen	peuplier faux-tremble	*Populus tremuloides* Michx.	trembling aspen
Populus trichocarpa Torr. & A. Gray	black cottonwood	peuplier de l'Ouest	*P. balsamifera* ssp. *trichocarpa*	black cottonwood
Prunus pensylvanica L. f.	pin cherry	cerisier de Pennsylvanie	*Prunus pensylvanica*	-
Prunus serotina Ehrh.	black cherry	cerisier tardif	*Prunus serotina* Ehrh.	black cherry
Prunus virginiana L.	chokecherry	cerisier de Virginie	*Prunus virginiana*	-
Prunus virginiana var. *demissa* (Nuttall) Torrey	western chokecherry	cerisier du Pacifique	*Prunus virginiana var. Demissa*	western chokecherry
Pseudolarix Gordon & Glend.	larch	mélèze	*Pseudolarix*	-
Pseudotsgua menziesii (Mirb.) Franco	Douglas-fir	douglas de Menzies	*Pseudotsgua menziesii* (Mirb.)	Douglas-fir
Pseudotsuga Carrière	douglas-fir	douglas de Menzies	*Pseudotsuga*	-
Ptilidium ciliare (L.) Hampe	ciliate fringewort	ptilidie des rochers	*P. ciliare*	-

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Ptilidium pulcherrimum (G. Web.) Hampe	tree fringewort	ptilidie des forêts	*Ptilidium pulcherrimum*	-
Ptlium crista-castrensis (Hedw.) De Not.	knight's plume moss	hypne plumeuse	*Ptlium crista-castrensis* (Hedw.) De Not.	-
Pyrola asarifolia Michaux	pink pyrola	pyrole à feuilles d'asaret	*Pyrola asarifolia*	-
Quercus L.	oak	chêne	*Quercus*	oak
Quercus macrocarpa Michx.	bur oak	chêne à gros fruits	*Quercus macrocarpa* Michx.	bur oak
Quercus palustris Münchh.	swamp pin oak	chêne des marais	-	Northern pink oak
Rhododendron albiflorum Hooker	white-flowered rhododendron	rhododendron à fleurs blanches	*Rhododendron albiflorum*	-
Rhododendron groenlandicum (Oeder) Kron & Judd	common Labrador tea	thé du Labrador	*Ledum groenlandicum*	Labrador tea
Rhododendron neoglandulosum Harmaja	western Labrador tea	rhododendron glanduleux	*Ledum glandulosum*	-
Rhododendron tomentosum Harmaja	northern Labrador tea	petit thé du Labrador	*Rhododendron tomentosum*	northern Labrador tea
Rhytidiadelphus triquetrus (Hedw.) Warnst.	electrified cat's-tail moss	ébouriffe triangulaire	*Rhytidiadelphus triquetrus*	-
Ribes hudsonianum Richardson	northern black currant	gadellier de la baie d'Hudson	*R. hudsonianum*	-
Ribes L. spp.	currant	groseillier	-	currant
Ribes lacustre (Persoon) Poiret	bristly black currant	gadellier lacustre	*Ribes lacustre*	-
Ribes triste Pallas	swamp red currant	gadellier amer	*Ribes triste*	-
Rosa acicularis Lindley	prickly rose	rosier aciculaire	*Rosa acicularis*	-
Rubus flagellaris Willdenow	northern dewberry	ronce à flagelles	*Rubus villosus*	-
Rubus idaeus L.	red raspberry	framboisier rouge	*Rubus idaeus*	-
Rubus L. spp.	raspberry	mûre sauvage	*Rubus* spp.	dewberry
Rubus parviflorus Nuttall	western thimbleberry	ronce à petites fleurs	*Rubus parviflorus*	-
Rubus pedatus Smith	five-leaved dwarf bramble	ronce à feuilles pédatifides	*Rubus pedatus*	-
Rubus pubescens Rafinesque	dwarf raspberry	ronce pubescente	*Rubus pubescens*	trailing raspberry
Salix alaxensis (Andersson) Coville	Alaska willow	saule feutré	*Salix alaxensis*	-
Salix arbusculoides Andersson	little-tree willow	saule arbustif	*Salix arbusculoides*	littletree willow
Salix bebbiana Sarg.	Bebb's willow	saule de Bebb	*S. bebbiana*	Bebb willow
Salix glauca L.	grey-leaved willow	saule glauque	*S. glauca*	gray willow

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Salix interior Rowlee	sandbar willow	saule de l'intérieur	*S. interior*	-
Salix L.	willow	saule	-	willow
Salix planifolia Pursh	tea-leaved willow	saule à feuilles planes	*S. planifolia*	-
Salix scouleriana Barratt ex Hook.	Scouler's willow	saule de Scouler	*S. scouleriana*	-
Sanionia uncinata (Hedw.) Loeske	sickle moss	faucillette à feuilles plissées	*Drepanocladus uncinatus*	-
Senecio triangularis Hooker	arrow-leaved ragwort	séneçon triangulaire	*Senecio triangularis*	-
Shepherdia canadensis (L.) Nuttall	soapberry	shépherdie du Canada	*Shepherdia canadensis*	-
Solidago multiradiata Aiton	northern goldenrod	verge d'or à rayons nombreux	*Solidago multiradiata*	northern goldenrod
Sorbus americana Marsh.	American mountain-ash	sorbier d'Amérique	*S. americana*	American mountain-ash
Sorbus decora (Sarg.) C.K. Schneid.	showy mountain-ash	sorbier plaisant	*Pyrus decora*	-
Sorbus L.	mountain-ash	sorbier	*Sorbus*	-
Sphagnum Dill. spp.	peat mosses	sphaignes	*Sphagnum* Dill. spp.	-
Sphagnum fuscum (Schimp.) Klinggr.	brown peat moss	sphaigne brune	*Sphagnum fuscum*	-
Spinulum annotinum (L.) A. Haines	stiff clubmoss	lycopode innovant	*Lycopodium annotinum*	stiff clubmoss
Streptopus lanceolatus (Aiton) Reveal	rose twisted-stalk	streptope rose	*Streptopus roseus*	-
Streptopus Michaux spp.	twistedstalk	streptope	*Streptopus* spp.	-
Symphoricarpos albus (L.) S.F. Blake	thin-leaved snowberry	symphorine blanche	*Symphoricarpos albus*	common snowberry
Thalictrum occidentale A. Gray	western meadow-rue	pigamon de l'Ouest	*Thalictrum occidentale*	-
Thuja occidentalis (L.)	eastern white cedar	thuya occidental	*Thuja occidentalis*	cedar
Thuja plicata Donn ex D. Don	western red cedar	thuya géant	*Thuja plicata*	western red cedar
Tiarella L. spp.	foamflower	tiarelle	*Tiarella* spp.	-
Tiarella trifoliata L.	three-leaved foamflower	tiarelle trifoliée	*Tiarella trifoliata*	-
Tilia americana L.	basswood	tilleul d'Amérique	*Tilia americana* L.	basswood
Tsuga (Endler) Carrière	hemlock	pruche	*Tsuga*	-
Tsuga canadensis (L.) Carrière	eastern hemlock	pruche du Canada	-	eastern hemlock
Tsuga heterophylla (Raf.) Sarg.	western hemlock	pruche de l'Ouest	*Tsuga heterophylla* (Raf.) Sarg.	-
Tsuga mertensiana (Bong.) Carrière	mountain hemlock	pruche subalpine	*Tsuga mertensiana*	mountain hemlock
Ulmus americana L.	white elm	orme d'Amérique	*Ulmus americana* L.	white elm
Ulmus thomasii Sarg.	rock elm	orme liège	-	rock elm
Vaccinium angustifolium Aiton	early lowbush blueberry	bleuet à feuilles étroites	*Vaccinium angustifolia*	-
Vaccinium cespitosum Michaux	dwarf bilberry	airelle gazonnante	*Vaccinium caespitosum*	-

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Vaccinium L. spp.	blueberry	bleuet	-	blueberry species
Vaccinium membranaceum Douglas ex Torrey	mountain huckleberry	airelle à feuilles membraneuses	*V. membranaceum*	-
Vaccinium myrtilloides Michaux	velvet-leaved blueberry	bleuet fausse-myrtille	*Vaccinium myrtilloides*	-
Vaccinium ovalifolium Smith	oval-leaved blueberry	airelle à feuilles ovées	*Vaccinium ovalifolium*	-
Vaccinium scoparium Leiberg ex Coville	grouseberry	airelle à fruits roses	*Vaccinium scoparium*	-
Vaccinium uliginosum L.	bog bilberry	airelle des marécage	*Vaccinium uliginosum*	bog blueberry
Vaccinium vitis-idaea L.	mountain cranberry	airelle rouge	*Vaccinium vitis-idaea*	mountain cranberry
Valeriana sitchensis Bongard	Sitka valerian	valériane de Sitka	*Valeriana sitchensis*	-
Veratrum viride Aiton	green false hellebore	vérâtre vert	*Veratrum viride*	-
Viburnum edule (Michaux) Rafinesque	squashberry	viorne comestible	*Viburnum edule*	-
Viburnum opulus var. *americanum* Aiton	highbush cranberry	viorne trilobée	*Viburnum trilobum*	highbush cranberry
Viola glabella Nuttall	stream violet	violette glabre	*Viola glabella*	-
Viola pubescens Aiton	downy yellow violet	violette pubescente	*Viola pubescens*	-

[1] Updated Scientific and Common names.

[2] Original Scientific and English names from the submitted manuscript

Sources of information:

Baldwin, K. et al. 2020. Vegetation Zones of Canada: a Biogeoclimatic Perspective (Information Report GLC-X-25). Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre 172 p. (https://cfs.nrcan.gc.ca/publications?id=40507)

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Natural Resources Canada- Trees: https://tidcf.nrcan.gc.ca/en/trees

Nature Serve: https://explorer.natureserve.org/

ABOUT THE AUTHOR

On June 2nd, 2008, in his 82nd year, Roy Sutton passed away at his home in Sault Ste. Marie, Ontario after a lengthy illness. Roy was born in 1926 in Stourbridge, Worcestershire, England. He grew up in Birmingham, England and attended grammar (high school) until he was almost 16. Roy's exposure to forestry began early, at summer school work camps associated with the UK Forestry Commission, where he worked at tasks such as peeling pit props and cutting oak tops into cordwood for charcoal making.

He was called up for military service at age 18 and was assigned to the Royal Signal Communications Unit in August 1944. In August 1945, Roy was posted overseas and saw service in India, Ceylon, Singapore and Hong Kong.

Roy returned to Britain in 1947, and signed on as a forest worker with the Forestry Commission in 1948. He was soon selected for two years of training at Parkend, Gloucestershire, one of four Forestry Commission Forester Training schools. After graduation, Roy worked for a year in forestry operations as a field forester with the Forestry Commission. He was encouraged to enroll in the B.Sc.F. program at Edinburgh University, graduating in 1955 with the highest academic standing in his class. Roy was then awarded a Beaverbrook Post-Graduate Fellowship to study forestry in Canada, which brought about the first stage of a distinguished career in Canadian forest science. He graduated from the University of New Brunswick in 1957 with an M.Sc.F., having completed a thesis on forest humus morphology.

Roy joined the federal government in 1956 and began what he later described as a "50-year labour of love with the succession of federal forestry departments that followed Northern Affairs and Natural Resources," working first in Ottawa (1956 – 60), and then Richmond Hill (1960 – 66), before finally moving to Sault Ste. Marie in 1966.

An article in the June 1992 Forestry Chronicle quoted Roy's reflection that "White spruce is my love." That passion began with his Ph.D. studies at Cornell University in New York. He graduated in 1968, completing a 500-page thesis entitled *Ecology of young white spruce* (*Picea glauca* [Moench] Voss).

The silviculture of white spruce was the focus of much of Roy's highly productive research career with the Canadian Forest Service. He authored over 100 publications, and was highly regarded as a dedicated and thorough researcher, whose investigations advanced both the science and practice of forestry. Roy's official retirement in 1993 resulted in little change in the pace of his research activity. He was made a Scientist Emeritus and continued to work and publish until 2007. As a matching bookend to his Ph.D. thesis, Roy set himself the retirement project of integrating the large body of published research on white spruce into a major monograph. This monograph is now making its way through the publication process, and it will endure as a fitting legacy of Roy's life-long dedication to furthering knowledge about this species. Roy contributed significantly to the Canadian Institute of Forestry/Institut forestier du Canada, serving as Book Review Editor for The Forestry Chronicle from June 1973 to December

1991. During this period he arranged the book reviews for each issue, and wrote a large number of the reviews himself. Roy’s outstanding service to the CIF/IFC was recognized in 1985 through a special institute award. His longstanding contribution to the CIF/IFC and to forest science was further acknowledged in 1999 when he was recognized as a Fellow of the Institute.

Roy’s interest was not confined to the scientific aspects of forestry. He was a member of the Ontario Woodlot Association, and he owned and actively managed a woodlot near Bruce Mines. Here he was able to put into practice some of the results of his research.

Although Roy’s professional life focused on forest science, he also played a leading role in the Sault Ste. Marie arts community. He served as President of the Arts Council of Sault Ste. Marie and as secretary and board member of the Community Theatre Board. In 2005, he was awarded the city’s Cultural Advisory Board Community Recognition Award “for his significant contribution and commitment to the cultural well- being of the community.”

Roy was a devoted husband and father, and is survived by his wife Maria, and daughters Penelope and Patience.[18]

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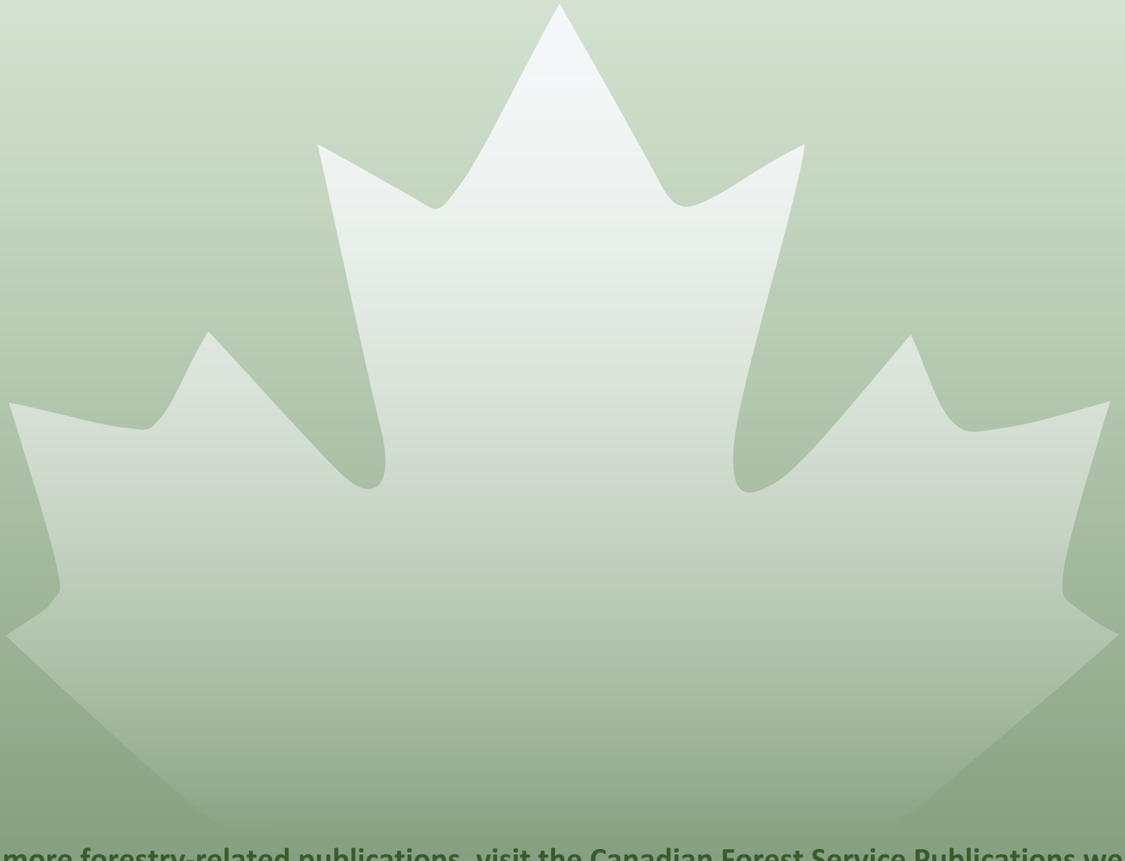
[18] September/October 2008, Vol. 84, No. 5 — The Forestry Chronicle.



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