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White Spruce: Botany, Physiology/Nutrition

A Historical Review by Dr. Roy F. Sutton

Canadian Forest Service
Great Lakes Forestry Centre
Information Report
GLC-X-33

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In 2022, the GLFC Knowledge Exchange Coordinator, Stan Phippen, received requests for the unpublished manuscript of Dr.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. Latin 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 planted trees.[4] Much of that planting effort aimed to establish white spruce dominated

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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.

[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.

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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3. BOTANY

Distinguishing morphology, white spruce

Determining that a tree is a member of a spruce species is not difficult; evergreen needles that are more or less four-angled, and especially the pulvinus, give it away (*See 1.4 Picea* (GLC-X-32)). But beyond that, determination can become more difficult. Intensive sampling in the Smithers/Hazelton/Houston area of British Columbia showed Douglas (1975), according to Coates et al. (1994), that cone scale morphology was the feature most useful in differentiating species of spruce; the length, width, length: width ratio, the 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 as a percentage of the total length of the scale) were most useful in this regard. Daubenmire (1974), after range-wide sampling, had already recognized the importance of the two latter characters. Taylor (1959) had noted that the most obvious morphological difference between typical white spruce (*Picea glauca* (Moench) Voss) and typical Engelmann spruce (*Picea engelmannii* Engelmann) was the cone scale, and Horton (1956a, 1959) found that the most useful diagnostic features of the two spruces are in the cone; differences occur in the flower, shoot and needle, “but those in the cone are most easily assessed” (Horton 1959). Coupé et al. (1982) recommended that cone scale characters be based on samples taken from the mid-section of each of 10 cones from each of five trees in the population of interest.

Without cones, morphological differentiation among spruce species and their hybrids is more difficult. Species classification for seeds collected from spruce stands in which introgressive hybridization between white and Sitka spruces (*Picea sitchensis* (Bong.) Carrière) may have occurred is important for determining appropriate cultural regimes in the nursery. If, for instance, white spruce grown at container nurseries in southwestern British Columbia are not given an extended photoperiod, leader growth ceases early in the first growing season, and seedlings do not reach the minimum height specifications (Arnott 1974b, 1979). But, if an extended photoperiod is provided for Sitka spruce, seedlings become unacceptably tall by the end of the first growing season (Arnott, unpublished data, cited by Yeh and Arnott 1986). Species classification of seedlots collected in areas where hybridization of white and Sitka spruces has been reported has depended on (i) easily measured cone scale characters of seed trees, especially free scale length, (ii) visual judgements of morphological characters, e.g., growth rhythm, shoot and root weight, and needle serration, or (iii) some combination of (i) and (ii) (Yeh and Arnott 1986). Useful to a degree, these classification procedures have important limitations; genetic composition of the seeds produced by a stand is determined by both the seed trees and the pollen parents, and species classification of hybrid seedlots and estimates of their level of introgression on the basis of seed-tree characteristics can be unreliable when hybrid seedlots vary in their introgressiveness in consequence of spatial and temporal variations in contributions from the pollen parent (Yeh and Arnott 1986). Secondly, morphological characters are markedly influenced by ontogenetic and environmental influences, so that to discern spruce hybrid seedlot composition with accuracy, hybrid seedlots must differ substantially in morphology from both parent species. Yeh and Arnott (1986) pointed out the difficulties of estimating accurately the degree of introgression between white and Sitka spruces; introgression may have occurred at low levels, and/or hybrid seed lots may

vary in their degree of introgression in consequence of repeated backcrossing with parental species.

After examining seedling morphology in nine seedlots that included two white spruce, three Sitka spruce, and four putative hybrid spruces from the coast-interior zone of reported introgression in northwestern British Columbia, Yeh and Arnott (1986) found that the degree of needle serration and the pattern of terminal budset when photoperiod was reduced were the two most reliable of 10 morphological characters for seedlot identification.

Coates et al. (1994) summarized the characters most useful in distinguishing among white, Engelmann, and Sitka spruces (Table 3.1). The mean free scale length and the percentage free scale of white spruce are typically smaller than those of Engelmann and Sitka spruces; Sitka spruce cone scales are narrower and have a greater length:width ratio than Engelmann spruce. Hybrids exhibit intermediate characteristics, and most commonly have narrow cone scales and a high ratio of scale length to width (characteristic of *P. glauca × sitchensis*) combined with the relatively short free scale and low free scale percentage (characteristic of *P. glauca × engelmannii*).

Table 3.1. Summary of characters most useful in differentiating among *Picea glauca*, *P. engelmannii*, and *P. sitchensis*. (after Coates et al. 1994)[a].

Character	***P. glauca***	***P. engelmannii***	***P. sitchensis***
Young twigs	smooth, shiny, not usually hairy	hairy, occasionally smooth	smooth, shiny
Needles	4-angled	4-angled	somewhat flattened
Cones	2.5–3.5 cm, < 6 cm long	4–5 cm long	6–9 cm long
Cone scales: – morphology	elliptical, rounded to blunt, margin smooth, broader than long, stiffer than *P. engelmannii*	blunt to sharp-pointed, finely irregular, wavy margin (ragged), longer than broad	rounded, finely irregularly toothed, somewhat stiff, longer than broad, narrower than *P. engelmannii*
– mean free scale length	short (1.0–2.0 mm)	longer than *P. glauca*, slightly longer than *P. sitchensis* (<6.3 mm)	longer than *P. glauca*, narrower than *P. engelmanii* (4.0–5.0 mm)
– free scale percentage	small (8–16%)	greatest (30–40%)	greater than *P. glauca* (24–34%)

[a] Hybrids show intermediate characteristics. Sources: Douglas (1975), van Barneveld et al. (1980), and Coupé et al. (1982).

Biochemical differentiation among species is also useful, especially with regard to hybridization. Populations of Lutz spruce (*Picea × lutzii* Little) in which low levels of introgression have occurred are difficult to identify by morphological traits, most of which are very similar in white and Sitka spruces (Copes and Beckwith 1977), reflecting recent separation of the two species (Wright 1955). Although enzymes had been used for analysis since at least 1845 (Bergmeyer 1963), Hanover and Wilkinson (1970) were among the first to apply biochemical techniques to taxonomic problems in conifers. Using paper chromatography, they examined phenols in

needles and found that white, Sitka, and suspected hybrid spruces from the Skeena River area could be separated by three compounds.

Electrophoresis has subsequently become the standard biochemical method for evaluating enzymes in plants. Enzymes having the same catalytic function, but originating from different organs or even different cell compartments of the same organ can be separated into different enzyme proteins, which have the same specificity (Schmidt et al. 1963). Such heterogenous enzyme proteins, named *isoenzymes* by Markert and Möller (1959), are now generally known as *isozymes* (cf. Tigerstedt 1973) or *allozymes* (Cheliak and Pitel 1984).

3.0 BOTANICAL CHARACTERISTICS, TYPIC WHITE SPRUCE

A snapshot of white spruce in Ontario is given by Payandeh's (1984) description of dimensional relationships based on measurements of 220 white spruce on semi-permanent growth plots at three locations: Black Sturgeon Lake northeast of Thunder Bay, Beardmore north of Nipigon, and Searchmont north of Sault Ste. Marie, Ontario. All trees were dominants or co-dominants located within closed-canopy stands of 2 ha or more (Table 3.2). Regressions for dimensional relationships were computed (Table 3.3).

Table 3.2. Statistical summary of white spruce data used for establishing dimensional relationships in the spruce-fir type of northwestern Ontario (after Payandeh 1984).

Variable	Minimum	Maximum	Mean	S.D.	CV (%)
DBH (cm)	8.9	54.0	24.61	7.90	32.1
Age (years)	24.0	138.0	55.43	17.80	32.1
Height (m)	7.0	26.8	16.17	3.55	22.0
Crown diameter (m)	1.5	8.5	3.55	1.27	35.7
Crown length (m)	3.4	17.1	9.23	2.83	30.7
Volume (m^3)	0.042	2.277	0.423	0.353	83.5
Merchantable volume (m^3)	0.029	2.178	0.398	0.340	85.4

Table 3.3. Estimated regression coefficients for dimensional relationships for white spruce in the spruce–fir type of northwestern Ontario (after Payandeh 1984).

Relationship	B_0	B_1	B_2	B_3	B_4	R^2	SE	Bias
DBH-age		2.984	0.996	-0.020	1.543	0.624	4.647	-0.010
Height-age		1.868	0.917	-0.028	1.502	0.770	1.689	-0.021
Crown diameter–height		0.647	-0.287	0.884	0.410	0.729	0.028	
Crown length–height		0.721	-0.318	1.239	0.580	2.028	0.101	
DBH–height		1.225	-0.259	1.339	0.750	4.040	0.048	
Crown diameter–DBH	12.644	-14.504	0.084	-0.211		0.524	0.667	-0.851
Crown length–DBH	1.372	0.349	0.013	0.962		0.723	1.497	0.045
Height–DBH	1.372	0.701	0.419	0.590		0.857	1.294	-0.015
Total volume–DBH		0.000094	0.073	2.490		0.986	0.042	-0.402
Merchantable volume–DBH		0.000079	0.118	2.485		0.987	0.039	0.679

The botanical components of typical white spruce are now described individually.

3.1 Crown form

The crown form of mature trees over much of the range is commonly dense, obtusely rounded and more or less symmetrical (Figure 3.1), but more than one distinct form may be found in a single stand (Rudolf 1956), and regional variation is pronounced.

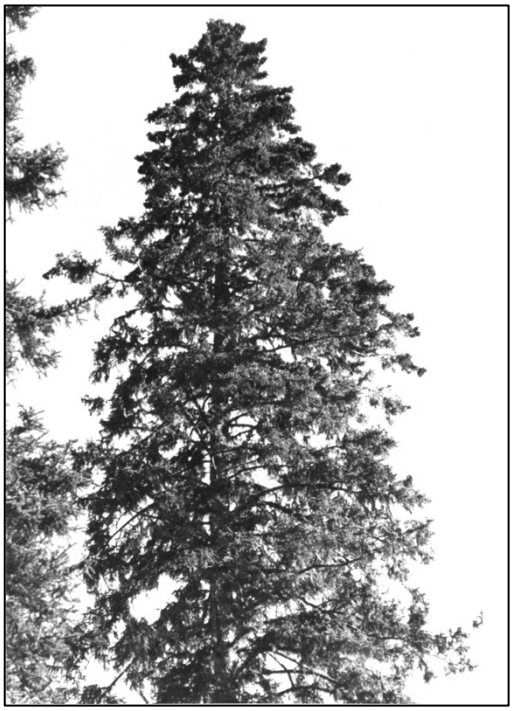

Figure 3.1 Crown of mature white spruce.

In Newfoundland, white spruce is short with wide-spreading limbs, whereas in southern Yukon and Watson Lake a tree 100 feet (30 m) high can have a crown spread of only 8 feet (2.4 m). At the mouth of the MacKenzie River, where the climate is again cloudy, white spruce has a spreading crown very much like that in Ontario (Robinson 1969[5] , personal communication). Robinson, a fine observer, suggested that this reflected the hybridization of white with Engelmann spruce in northern Alberta and southern Yukon, or that different crown forms are produced under different climatic conditions during the growing season, i.e., long clear days versus cloudy, moist weather.

A particularly narrow and short-branched crown form, described by Sayn-Wittgenstein (1960) as “needlelike”, occurs typically in the far north, possibly a response to climatic rigors. In the treeline zone near Churchill, Manitoba, five crown forms of white spruce (Figure 3.2) were identified by Scott et al. (1987). The shrub-like form I crowns result from the destruction of “exposed annual stem growth” by abrasion from particles of wind-driven snow; the stems are contorted as lateral branches successively take over from fatally damaged stem terminal buds. A basal rosette of branches develops, mostly on the leeward side, below the level of winter snow cover. Crown-form I trees, “mature if at least 100 years old”, occurred in the tundra. Crown forms II, III, and IV, identified by Scott et al. (1987), also exhibit basal rosettes, but penetrate the abrasion zone (Figure 3.2). Form II crowns are characterized by stems devoid of branches on all sides through the abrasion zone of about 1 m above the level of winter snow, with some live foliage above that level on the lee side only. Form III crowns have more foliage, including some on all sides, though “flagged” on the lee side. Form IV crowns show a zone of abrasion on the windward side but have some live foliage at all levels. Crown forms II to IV, occurring in the forest–tundra, were considered by Scott et al. (1987) to be mature in trees 4 m or more in height. Morphology of white spruce is highly variable in Alaska (Alden and Loopstra 1987).

[5] Canadian Forest Service, Ottawa, Ontario

Crown form might also be influenced by soil fertility. In radiata pine (*Pinus radiata* D. Don), at least, Stone and Will (1965) in New Zealand found narrow crowns and fine branching were associated with low levels of foliar nitrogen.

Lower branches are self-pruned only in dense stands, and then with reluctance.

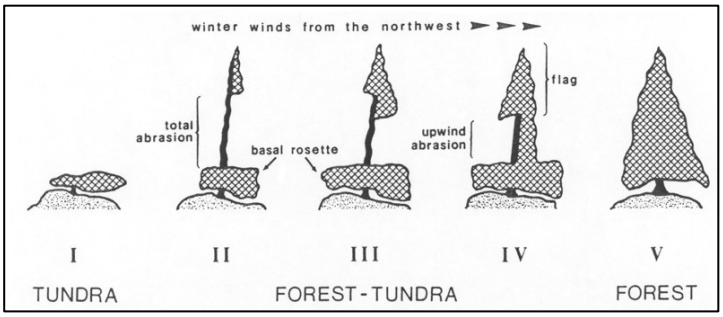

Figure 3.2 Diagrams of the five white spruce crown forms in the Churchill area. Crown forms I, III, and V are representative of trees from the tundra, forest-tundra, and forest, respectively.

3.1.1 Shoots

Shoots develop from vegetative buds, which normally flush in spring in concert with rising temperatures. After germination, seedlings produce and expand new needles continuously, a process termed by Pollard and Ying (1979) *indeterminate* or *free growth*. Free growth continues until constrained by an environmental limitation, often declining day length. The resting buds that then develop will flush the following spring, often resuming free growth. The percentage of seedlings exhibiting free growth decreases rapidly after the second growing season and essentially reaches zero within 5 years (Nienstaedt and Zasada 1990). Thereafter, growth becomes *determinate* or *fixed*, the amount of new foliage produced being determined by the number of needle primordia laid down during the previous growing season (Pollard 1974b, Pollard and Logan 1977). The height growth potential of spruce seedlings is thus affected by the weather and environmental conditions during the previous year, as well as during the period of shoot elongation.

The initial growth period might be followed by a lull of 2-4 weeks, after which there might be one or more periods of elongation of shoots before the buds for next year's growth are developed (Armson 1964). Alternatively, new buds sometimes flush in the same season in which they were laid down. Such development, termed lammas growth, often occurs after soil moisture levels have been recharged following the dry conditions that to some extent curtailed the spring flush (Sutton 1969a). Lammas growth becomes less common with older seedlings as the expanding root system exploits an increasingly large volume of soil (Sutton 1969a).

The terminal shoot of white spruce is glabrous; branchlets, also, are usually without hairs, "characteristically glabrous, while those of Engelmann spruce have a short, crisp pubescence" (Taylor 1959), sometimes slightly puberulous, and whitish-grey to yellowish (Hosie 1969) or white-yellow to yellow-brown, becoming glossy (Krüssmann 1985). In the material examined by Garman (1957) in interior British Columbia, "true" white spruce was entirely glabrous, but the internode of Engelmann spruce was "uniformly covered with straight, stiff, short hairs, sometimes appearing glandular tipped". However, in the overlapping ranges of white spruce and Engelmann spruce in southeastern British Columbia and adjacent Alberta, Taylor (1959) found that of 21 trees bearing typical white spruce cones, 11 had pubescent twigs and 10 had glabrous twigs.

Habit, i.e., the general appearance and arrangement of shoots, varies somewhat, but Owens et al. (1977) in their British Columbia study described sexually mature white spruce in terms that would apply through much of the range of the species: "Primary branches from upper regions of the crown were horizontal to somewhat ascending, whereas smaller secondary branches were usually drooping. Branches in lower regions of the crown usually drooped more, especially on trees not grown in the open. Lateral buds formed along the entire length of the shoot but usually were more abundant in the distal portion."

Branches frequently are male or female with respect to sex of strobili naturally produced (Marquard and Hanover 1984a).

Epicormic branching

Epicormic branches (*epicormics*) are shoots that originate from dormant or adventitious buds on the tree bole. They are common on relatively few conifers, but fir (*Abies* L.) species are among these. Epicormics tend to develop when exposure of the bole to light is suddenly increased, as by thinning or green pruning, and may be a response to the altered physiological balance occasioned thereby. Epicormics present a problem only where the objective is to produce knot-free wood. As long as the production of common lumber grades of white spruce was accepted as adequate, the culture of relatively knot-free trees was of little interest. However, after Berry (1964) showed that pruning of white spruce would be profitable under favourable market conditions, Berry and Innes (1967) set out to ascertain the extent to which epicormic branching of white spruce is associated with pruning and thinning. Epicormics were observed developing in a 25-year-old plantation after crown thinning and pruning in 1962. Thinning had reduced basal area in three areas, in each of which, plus a control, 150 crop trees per acre were pruned to a height of 17 feet (5.2 m). Most branches pruned were dead, but an average of about 13% of live crown length was removed. All other trees were pruned to head height. Pruning took place in late summer, thinning the following winter. In 1965, epicormics were found on crop trees in all of eight permanent plots, with two in each of the four areas. Their frequency of occurrence was clearly correlated with treatment intensity. Thinning increased not only the number of crop trees developing epicormics but also the number of epicormic shoots per tree (Table 3.4).

Table 3.4. Epicormic branching on crop trees as related to residual basal area per acre [hectare].

Residual basal area (ft^2/ac) [m^2/ha]	Trees with epicormics (%)	Epicormics per crop tree with epicormics (number)	Epicormics per acre [ha] (number)
162 (control) [37]	8	3.2	40 [16.2]
140 [32]	25	4.2	157 [63.5]
110 [25]	50	5.4	405 [164]
80 [18]	55	7.1	587 [237.6]

Shoot elongation

The apex of the elongating white spruce shoot is small and domed (Cecich and Miksche 1970, Cecich et al. 1972). Vegetative buds of white spruce become mitotically active in the spring, largely in response to rising temperatures, and Owens et al. (1977) found that mitotic activity in reproductively mature white spruce in interior British Columbia began 6 weeks earlier in trees at an elevation of 500 m than at 1,000 m. At Rhinelander, Wisconsin, Cecich et al. (1972) examined terminal vegetative shoot tips of 4-year-old white spruce collected on alternate days from 9 June through 8 August. Cataphyll (bud scale) primordia were produced throughout June (Figure 3.3A). Cytohistological zonation became evident in late June, when vacuoles developed in the apical initials and central mother cells. The apex became conical on 28 June (Figure 3.3B), 2 weeks before the mammillary apex (Figure 3.3C) became evident. Needle primordia were not identified until early July (Figure 3.3D).

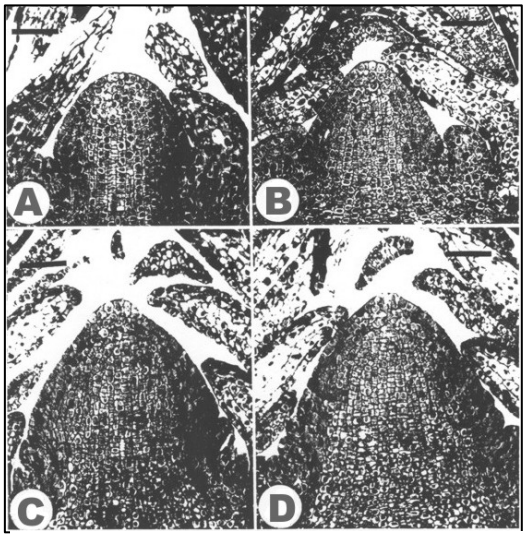

Figure 3.3 Morphogenetic changes in the vegetative shoot apex of white spruce during ontogeny. (A) – Apex was small, dome-shaped during shoot elongation in June. (B) – Apex changed from a small dome to a cone in late June. (C) – The mammillary apex was evident on July 10. (D) – Leaf primoridia were identified by mid July. Line = 100 µm.

Needle and cataphyll primordia "appeared to be identical under the microscope" and "the only way to detect the change from cataphyll to leaf primordia was by numbers": there was only one pair of primordia on the flank or peripheral zone of the apex during cataphyll formation in May and June, and the beginning of leaf initiation could be demarcated when more than one pair of primordia were present (Cecich et al. 1972). The timing of these morphogenetic events agreed closely with that reported in earlier work by Vanden Born (1963) and Cecich and Miksche (1970).

Cecich et al. (1972) also determined deoxyribonucleic acid (DNA), nuclear and cytoplasmic ribonucleic acid (RNA), nuclear and cytoplasmic proteins, and histone fractions of nuclear proteins. The relative amount of DNA per cell varied both in time and among the cytohistological zones of the shoot apex (Cecich et al. 1972). During ontogeny, relative levels of DNA peaked in the central mother cell zone and peripheral zone, but not in the apical initial zone. However, Cecich et al.'s (1972) graphs (Figure 3.4) do not indicate the variability of observations, which impairs their usefulness in establishing patterns of relative amounts of constituents in various zones of the shoot apex.

Shoot elongation in each of 2 years of observation was characterized by more or less similar smooth sigmoid curves, slow during the first month, rapid during the second month, and slow again during the third month (Owens et al. 1977). Flushing occurred during the same week in both years on shoots from all sides and at both of two heights sampled within the crowns. Temperature sums correlated best with percentage of shoot elongation when the end of vegetative bud dormancy was used as the starting date and 5°C was used as the threshold temperature. Generally, though, if the end of vegetative bud dormancy is known, the number of days thereafter is almost as accurate as the more complex use of temperature sums in predicting the percentage of shoot elongation or stage of vegetative bud development. Section 3.2 has more on phenology. Shortly before the end of shoot elongation, the apical meristem undergoes differentiation to produce either leaves, bracts, or sporophylls, instead of the cataphylls it produces during shoot elongation (Owens et al. 1977).

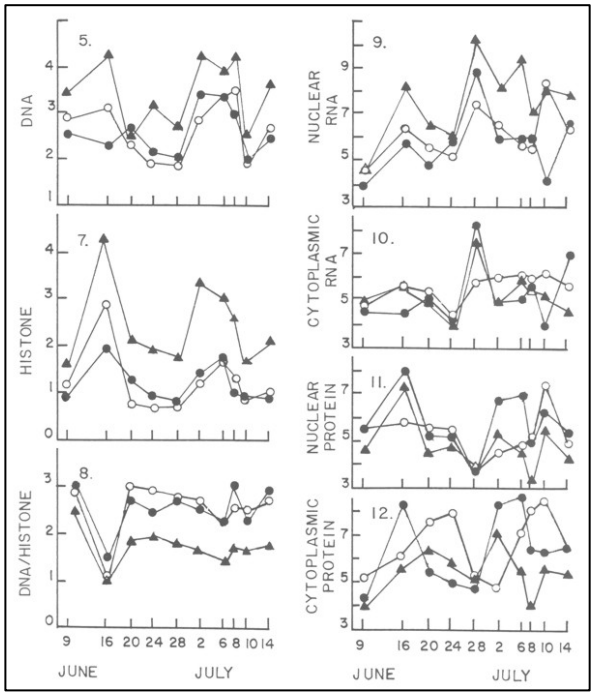

Figure 3.4 Relative amounts of DNA, histones, RNA, and total proteins in the apical initial zone – ●, central mother cell zone – ○, and peripheral zone – ▲, during ontogeny.
Tabular and statistical data on file at the Institute of Forest Genetics. Graph 5. the apical initials did not show a peak on June 16. Graph 7. Histones followed the same pattern as DNA, except for the increase in the apical initials on June 16. Graph 8. The DNA/histone ratio was generally constant, except on June 16. Graph 9. Nuclear RNA generally increased during ontogeny. Graph 10. Cytoplasmic RNA was relatively stable during ontogeny, except for a significantly higher peak on June 28. Graph 11. There was no discernable pattern to nuclear proteins. Graph 12. Cytoplasmic proteins in the apical initials and central mother cells were cyclic but out of phase with each other. (from Cecich et al. [1972]).

Owens et al. (1977) observed that the mitotically active vegetative apex of white spruce varied in size and shape during the growing season but retained essentially the same cytohistological zonation at all stages. At the summit of the apex was a layer of apical initials, usually slightly enlarged, that underwent infrequent periclinal and anticlinal divisions. Directly below was a cup-shaped zone of enlarged central mother cells, which divided in all planes infrequently, giving rise to the pith rib meristem directly below and lateral to the peripheral zone. Both the pith rib meristem and the peripheral zone consisted of small, actively dividing cells during the growing season, giving rise to the pith and lateral appendages, respectively. The surface layer of the peripheral zone was the protoderm which divided both anticlinally and periclinally.

Leaf primordia in the dormant bud showed no tissue differentiation, but the pattern of future tissues was indicated by differences in cell size and staining characteristics (Owens et al. 1977). Anastomosing strands of procambium formed a eustele in the bud axis and extended into the leaf primordia. The most distal of the leaf primordia were smaller than proximal leaf primordia.

Bud-scale initiation occurs during shoot elongation. Owens et al. (1977) found that when dormancy ended, cells began to divide first in the leaf primordia, then, in order, in the peripheral zone, rib meristem, and apical zone of the apex. Cell division in the peripheral zone marked the onset of bud-scale initiation. Completion of bud-scale formation coincided with the end of shoot elongation.

Initiation of the first bud scales reduced the width of the apex, and the apex became a narrow dome. Apical height and width then increased gradually. Mitotic activity differed among the major apical tissues, but within them mitotic activity remained rather uniform throughout the early stage of bud-scale initiation. The peripheral zone (where bud scales arise) was most active, the apical zone least so, while the rib meristem was intermediate. The apex widened rapidly during the final 2 weeks of bud-scale initiation with increased mitotic activity in the peripheral zone and, to a lesser extent, in the rib meristem also. The apex became broadly conical, and zonation became more distinct during late bud-scale initiation. Increases in RNA and cytoplasmic protein in July preceding the appearance of leaf primordia in the shoot apex of white spruce led Cecich et al. (1972) to speculate that these increases might trigger the transition of vegetative apices to reproductive apices.

In white spruce younger than those used by Owens et al. (1977), Pollard (1973) at Chalk River, Ontario, found that bud scale development was well advanced at the beginning of shoot extension, with about 20 scales or scale primordia distinguishable by the end of the first week in June; and the transition from bud scale to leaf initiation occurred between 11 and 24 July. Until the end of September, leaf initiations averaged six primordia per day in each of 10 provenances. Differences among provenances developed thereafter and were correlated with tree height differences. Development of a large complement of needle primordia seemed to depend on an ability to prolong leaf initiation; latitude of provenance origin did not account for observed differences.

Axillary bud initiation occurred within the vegetative buds during early bud-scale initiation, 1-2 weeks after dormancy ended (Owens et al. 1977). Frequent cell divisions occurred in the axils of some of the elongating leaf primordia forming a small buttress. Cells divided on either side of each axillary primordium, as viewed in transverse section, giving rise to two oppositely arranged prophylls, which elongated and arched over the apex, though remaining small compared with later, spirally arranged bud scales. The axillary apex enlarged and within 4 weeks developed zonation similar to that described for the terminal apex. All axillary primordia along the shoot axis were initiated at the same time, but some became latent and ceased further development after about half of the final number of bud scales had been initiated. Latent buds occurred most frequently in the axils of the most proximal leaves; and the frequency of latent buds decreased acropetally along the shoot.

Leaf initiation followed bud-scale initiation and began when shoot elongation was complete (Owens et al. 1977). The change was preceded by a marked increase in apical width but with only a slight and gradual increase in apical height and mitotic activity. Some of the larger apices developed a mammillary apex. The first leaf primordia were rapidly initiated acropetally from the broadened peripheral zone, producing a series of small, rather uniform buttresses on the

lower flanks of the apex. About 75% of the final number of leaves were initiated quickly during a 6-week period in the early fall. Apical zonation was most prominent both immediately preceding and during initiation of the first leaves. During the last 3 weeks of early leaf initiation, the mitotic activity of the apex decreased and the rapid rate of leaf initiation exceeded the rate of apical enlargement; leaf primordia encroached on the summit of the apex, reducing it to a broad conical shape by mid-September. As a result of cell divisions within the active rib meristem and cell enlargement in the future pith, the entire embryonic shoot axis elongated during early leaf initiation.

Leaf primordia continued to be initiated until the apices became dormant in late fall (Owens et al. 1977). During that time, the mitotic activity of the apices continued to decrease, while cell divisions and cell enlargement continued in the leaf primordia and embryonic shoot axis subjacent to the rib meristem. Even after the apices became dormant, cell division continued to occur within the leaf primordia for 2 more weeks. Apical zonation became indistinct during late leaf initiation and remained so throughout the winter.

Owens et al. (1977) found that, in both years of their study and at both sites (in interior British Columbia), leaf initiation began about August 1st, coincidentally with the cessation of shoot elongation. In a subsequent study at Smithers, British Columbia, and in an earlier study in Ontario (Fraser 1962b), lateral shoot elongation ended and leaf initiation also began about August 1st.

The consistency of those findings led Owens et al. (1977) to suggest that the end of lateral shoot elongation could be used as an easily visible indicator of the important morphogenetic changes within the buds, when bud scales cease to be initiated and leaf initiation begins. Further, Owens et al. (1977) noted that the coincidence of these events over the wide distribution of white spruce also suggests that cessation of shoot elongation depends more on photoperiod than on temperature, as in Norway spruce (Heide 1974a, b).

Attenuation of one or more of the basal scales of buds, at least for terminal leaf buds, occurs variously in the spruces, with the long-pointed scales curving over the top of the bud and capping it (Garman 1957). A *fimbriate* (fringe) of long awl-shaped scales is characteristic of black spruce (*Picea mariana* (Mill.)) B.S.P.). The buds of black spruce examined by Garman in interior British Columbia, were surrounded by fringed and hairy, long-pointed scales arranged in two basal rows: “At nine control locations for white spruce, seven stations had trees with one long-pointed bud-scale in the basal ring of scales; at the other two stations the number varied either on different trees or within the same tree. In Engelmann spruce, bud-scales with long points varied from zero to three at five places, and at four others all basal bud-scales were broadly acute and keeled, but none of them long-pointed.” The variability in the buds of both white and Engelmann spruces is too great to use in species identification, though Garman (1957) found that “the long-pointed scale is far more frequent in white spruce than in Engelmann spruce, and occurred in 19 out of 27 intermediate variants.”

Vegetative bud dormancy, as indicated by the absence of mitosis in the buds, lasted for 6-7 months in trees studied by Owens et al. (1977) in regard to shoot elongation and bud development.

3.1.2 Needles

White spruce needles are usually straight (Hosie 1969) but have also been described variously as “incurved” (Dallimore and Jackson 1961) and “often curved” (Taylor 1959). Engelmann spruce needles are curved (Hosie 1969). The needles end in an acute or roundish horny, moderately sharp-pointed tip. White spruce needles are rather stiff, firmer than those of Engelmann spruce (Taylor 1959), and are easily rolled between fingers. Needles are 15-22 mm long, with considerable variability in length on the same tree, and, at least in one study, not significantly different in length between the north and south sides of the crown (Taylor 1959). On trees of low vigour, needles may be no longer than 10 mm and persist for as few as 2 years (cf. Armson 1958). On well grown trees, needles typically persist for 4 or 5 years, and exceptionally up to 10 years. Needles are normally green or, particularly on especially vigorous trees, glaucous blue-green (Munsell 7.5GY6-7-7/1-4). Needle colour is affected by nutrient stress; for seedlings subjected to severe deficiencies of single nutrient elements in solution-culture, white spruce needles were yellow-green to yellow under N-deficiency, green or yellow-green when young but distinctly purple-fringed and becoming increasingly purple with age under P-deficiency and chlorotic with some green near the base under K-deficiency (Swan 1960, Morrison 1974). In the field, chlorotic or greenish-yellow (Munsell 10Y5-6/6) foliage is typical of N-deficiency (Sutton 1968); and solarization, especially when direct sunlight is augmented by reflection from snow cover, often causes temporary loss of green coloration of foliage exposed above snow. Ronco (1970) described the development of chlorosis in shade-tolerant Engelmann spruce seedlings that were exposed to direct sunlight after planting, and he ascribed the cause to solarization rather than to nitrogen deficiency. Toumey (1924) mentioned the opinion held by some that “individuals of a species growing in the coldest part of their range are of a deeper color and the foliage is more likely to be tinged with brown”. Toumey (1924) observed “that the leaves of white spruce in Quebec are more closely pressed against the axis than is characteristic of this species farther south”. The needles are mostly quadrangular in section (Brayshaw 1960), though Taylor (1959) described white spruce needles as “tending to be dorsiventrally flattened or triangular in section”.

Stomata

Stomata occur on all four sides of needles, variously reported as arranged in four to six, or six to eight rows on each of upper and lower surfaces (Sargent 1898), or two to three stomatal lines above and three to four beneath (Krüssmann 1985). Guard cells “unlike any previously described” have thickened upper and lower walls, which, in the region of the stoma are separated by two extremely thin, flexible membranes, which collapse when the stoma opens (Marco 1939). In material from interior British Columbia, Garman (1957) found little difference between species in the total number of rows of stomata in each leaf, but reported a “more or less consistent” difference in the number of lines on the upper surface of leaves, the number varying from a low for white spruce through Engelmann to a high for Sitka spruce. As the upper surface of needles is not always longitudinally concave, and as the cross-section at mid-portion of the leaf may be as markedly keeled or angular on the upper surface as on the lower, the upper surface cannot be recognized by these criteria. However, the surfaces can always be identified, because in all native spruces the surface uppermost at the point of attachment to

the stem is invariably flattened to almost one plane, even though at the tip of the needle this surface may be more keeled than the under surface.

Counts of the numbers of stomatal lines on the upper surface of the leaves of all species examined by Garman (1957) in interior British Columbia were made on samples taken from the base of the crown. Observations were confined to needles from the lower branches because in each species a few counts on upper- and lower-crown leaves showed a greater total number of stomata per leaf from the upper crown than from the lower crown. The number of lines on the upper surface of leaves from the top of the tree was not much greater than for leaves from the base of the crown, but the number of lines on the undersides of leaves from the top of the tree was much larger than in needles from the lower crown. A subsequent analysis of British Columbia samples gave the mean number of upper-surface lines as 7.1 for white spruce and 8.0 for Engelmann spruce, but with considerable overlapping (Garman 1957).

The resin canal is median and paired (Wright 1955), though Dorner (1899) termed it single, a discrepancy that might be explained by Marco's (1939) evidence that spruces have two longitudinal, parallel series of resin ducts or cysts, usually, except in tiger-tail spruce (*Picea torano* (Koch) Köhne) and Sitka spruce, located in the lateral angles of the needles adjacent to the dermal tissue; and that zero, one, or two ducts or cysts may be evident in any one cross section. The number of ducts per section is not diagnostically helpful, but diameters are constant enough within species to assist identification (Marco 1939). The discrepancy might also be due to variation of resin canal position with age of tree. For example, Roller (1966) has shown that, in *Abies* species (another member of the Pinaceae), the position of resin canals moved from peripheral to medial with increasing age of tree. The odour of crushed foliage has been described variously as pungent (Harlow and Harrar 1950), polecat- or skunk-like (Sargent 1898), “fétide du putois” (Lacassagne 1934), rank (Jackson 1948, Forestry Branch 1961), fetid (Brayshaw 1960, den Ouden and Boom 1965), and pleasantly aromatic (Sutton 1968). Seasonal fluctuations in free amino acid concentrations occur (Kim and Glerum 1995); alanine, serine, aspartic acid, glutamic acid, asparagine, threonine, valine, glutamine, and proline increased in summer, and tyrosine and histidine increased in winter in needles of 3-year-old bareroot white spruce, while tryptophan rose from low concentration in summer to peak in the fall before declining to low concentration by spring; 15 amino acids showed significant (mostly $P = 0.01$) coefficients of determination with photoperiod and daily air temperature together. Seasonal changes also take place in the organization of leaf cells (Lewis and Tuttle 1923). Ligno-suberized cells form a protective layer toward the needle base, immediately distal to which is the one-cell-thick abscission layer. Excepting the secondary walls of abscission layer cells, all primary and secondary walls of cells in the abscission zone contain lignin; abscission is a mechanical process without previous chemical breakdown of cell walls (Facey 1956).

Small hair-like outgrowths (*trichomes*) develop from the white spruce needle epidermis, but not from black spruce needles, offering a means of distinguishing between these species, even as very young seedlings (Templeton n.d.).

Yeh and Arnott (1986) found that needle serration was greatest at the distal end of needles located in the midsection of the seedling stem.

One 11-m-tall, 36-year-old white spruce at Chalk River in eastern Ontario carried 5.25 million needles of all ages (Fraser et al. 1964).

Pulvini

The peg-like leaf base characteristic of the spruces has received little attention in the literature, but Garman (1957) described their arrangement on material in interior British Columbia. When viewed on the upper side of branchlets, where they are straight, the pulvini "have upper angles to 90 degrees with the axis of the twig. The amount of spread to the outer point of leaf attachment is about 1 millimetre, but may be more and is often less in different specimens. Length varies in the same specimen, depending on the rate of growth of the internode, but the spread, which is a combination of length and angle, is more or less characteristic for these species. In white spruce practically all the specimens measured had a spread of less than 1 millimetre associated with an angle mostly of 45 degrees, but with some less than 45 degrees. Sixty-five per cent of Engelmann spruce had a spread of 1 millimetre or more, and angles of more than 45 degrees and mostly over 60 degrees."

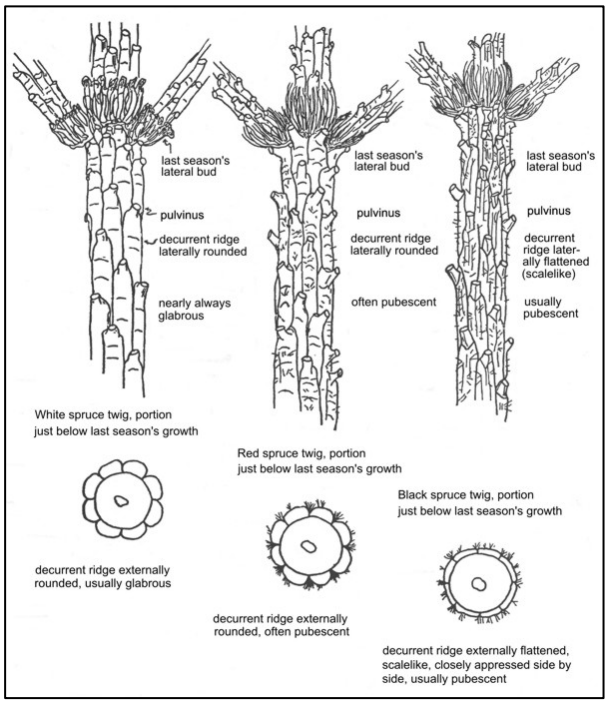

Figure 3.5 Underside of twigs and cross sections of white, red, and black spruces showing section of decurrent ridge. (after Gordon 1952)

Decurrent ridges

The twig surface is composed of a series of decurrent ridges that run longitudinally along the twig (Gordon 1952). Prolongation of the pulvini, i.e., the decurrent bases of the leaves, creates a pattern in cross-section, which varies with species (Garman 1957). Both white spruce and red spruce (*Picea rubens* Sarg.) have ridges that are laterally rounded. The ridges of white spruce are relatively larger than those of red spruce, and are quite glabrous. Black spruce has flattened ridges, which give the twig the deceptive appearance of being an almost smooth cylinder from which project the pulvini and needles (Figure 3.5). Twigs of the current year do not show these characteristics as well as do twigs 1-2 years old.

3.1.3 Buds

Budscales

The buds of white spruce on well-grown shoots are ovoid, about 6 mm long, blunt, and enclosed by non-resinous outer budscales that are shorter than the bud. Budscale margins are ragged and out-curled (Farrar 1995). Engelmann spruce buds are similar, but with slightly reflexed, long-pointed outer scales.

Dormant buds

The dormant bud was described by Owens et al. (1977) as consisting of a thick layer of tightly packed budscales that enclosed the embryonic shoot bearing all the leaf primordia for the next season. The dormant stem apex was domed to conical, and averaged 147 µm high and 298 µm wide. Apices from the upper crown were often, but not consistently larger than those from the middle of the crown. The apical zone consisted of irregularly arranged, vacuolate cells that were slightly larger than subjacent cells. Pith cells extended to just below the apical zone, leaving a rib meristem only a few cells thick. The basal portion of the apical zone and the rib meristem were surrounded by a narrow peripheral zone.

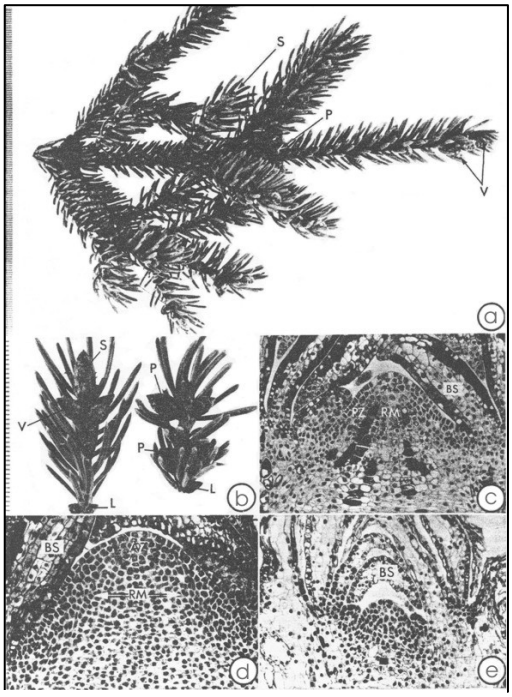

Figure 3.6(a) Dominant white spruce branch showing vegetative (V), seed-cone (S), and pollen-cone (P) buds. (b) Twigs showing dormant vegetative, seed-cone, pollen-cone and latent (L) buds. Scale in millimetres is shown on the left. (c) Median longitudinal section of a potentially vegetative bud collected in mid-July, just before differentiation, showing bud scales (BS) and the apex with an apical zone (AZ), peripheral zone (PZ), rib meristem (RM), and files of cells containing phenolic compounds. × 100. (d) Median longitudinal section of an apex which is differentiating into a cone apex in late July showing the broad rib meristem enclosed by the broad peripheral zones. × 100. (e) Median longitudinal section of a latent bud collected in August showing the small apex with indistinct zonation. × 100. (from Owens and Molder 1977).

As illustrated by Owens and Molder (1977), the phenology of vegetative shoot, seed-cone, and pollen-cone development in white spruce begins with winter dormant vegetative buds and shoots (Figure 3.6). The state of winter dormancy is a convenient starting point for looking at the life cycle of white spruce in a sexually mature tree. The formation of bud dormancy in woody plants and the associated development of cold hardiness are stimulated by short-day photoperiod (Reid et al. 1991). Pollen-cone buds and seed-cone buds develop, after shoot extension ceases (Nienstaedt and Zasada 1990), during the summer and early fall of the year before flowering, pollination, and seed dispersal (Owens and Molder 1977). Terminal cones form at the tips of shoots that were initiated as axillary buds the previous year. Those buds initiated first budscales then leaves and became dormant in the fall. After a period of chilling temperatures, needed to fulfil dormancy-breaking requirements (Reid et al. 1991), and during shoot elongation the following spring, the shoot apex initiates budscales and, as shoot elongation ceases, the apex differentiates into a vegetative, seed-cone, or pollen-cone apex (Owens and Molder 1977). Jablanczy (1971) noted as well that in “adult” trees budscale formation occurs concurrently with primordia elongation. The renewed cell division in floral buds in spring begins before bud elongation becomes evident (Owens and Molder 1979).

Axillary cones develop from axillary primordia initiated in spring within enlarging vegetative buds (Owens et al. 1977). The axillary primordia enlarge and initiate bud scales during

elongation of the parent shoots. As elongation comes to an end, some axillary buds initiate either bracts or microsporophylls rather than needles. Axillary and terminal cone buds differentiate concurrently and follow the same sequence of development.

Floral primordia, male and female separately on the same tree (Nienstaedt 1958), are differentiated the year before flowering and seed dispersal, when shoot elongation ceases (Nienstaedt and Zasada 1990). Flower buds can usually be distinguished from vegetative buds in late summer (Nienstaedt 1958, Eis 1967b, Fraser 1962b). Very rarely, a bisexual primordium is produced (Santamour 1959). In British Columbia, the differentiation of reproductive buds takes place during the second half of July over such a wide range of sites as to suggest that the process might occur at about the same time over a much wider part of the range.

Typically, female strobili are confined to vigorous shoots in uppermost whorls and internodes of the tree crown, and male strobili to less vigorous shoots in the middle portion of the crown (Eis and Inkster 1972). Both sexes are borne in the transition zone, but the general separation of male and female strobili within a crown serves to limit self-fertilization. The distribution of sexuality suggests control by a hormonal gradient.

Vegetative buds

The two phases in the formation of a bud are: bud initiation, i.e., the production of budscales; and bud development, i.e., the formation and accumulation of needle primordia in association with the maturation of budscales (Templeton et al. 1991). According to Templeton et al., the formation of buds concludes a period of shoot elongation, though, as Owens et al. (1977) observed in British Columbia, vegetative buds with light green budscales develop during shoot elongation. By late summer, the buds become what is variously described as “broad and pointed”, and “ovoid and obtuse”. The mature winter bud is surrounded by thin glabrous and scarious (membranous) scales, which do not project beyond the tip of the bud. The lower scales are keeled and have a very fine tip; upper scales loosely appressed and obtuse (Krüssmann 1985). Though usually loose, scales are sometimes recurved and sometimes tight, and are brown or chestnut-coloured. They serve to protect the underlying embryonic shoot (Figure 3.7), which has a central, pithy core covered with needle primordia (Templeton et al. 1991) (Figures 3.8, 3.9). Although described by Owens et al. (1977) in British Columbia as “slightly resinous”, vegetative buds are generally described as “non-resinous” (cf. Lewis and Dowding 1924, Templeton et al. 1991).

There are many similarities with Norway spruce (*Picea abies* [L.] Karst.), described by Romberger (1966).

Distal leaves on the shoot commonly almost enclose and obscure the vegetative bud (Owens et al. 1977), but the investiture of terminal buds by needles is very variable in pattern and degree. A conical arrangement of chaffy scales “rises on the inner side, about 3 mm. beyond the apical cluster of young leaves” (Lewis and Dowding 1924).

A spirally arranged group of buds in the axils of the most proximal leaves on a shoot normally remain as small latent buds on branches in the upper crown, or develop as pollen cones on branches in the lower crown (Owens et al. 1977).

Vegetative buds and shoots of spruces (*Picea* A. Dietrich) pass through three phases of development: a dormant, resting phase; a period of shoot elongation and budscale formation; and leaf primordial formation. The duration of each phase may vary within a species. Terminal vegetative bud morphogenesis and shoot development in white spruce seedlings were described by Pollard (1973; 1974a, b).

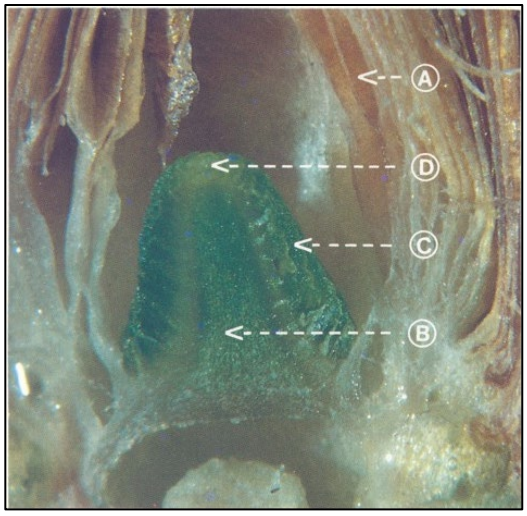

Figure 3.7 A mature Norway spruce bud. "A bud is composed of several parts. The bud scales (A) serve to protect the delicate underlying tissues of the embryonic shoot. The embryonic shoot has a central core called the pith (B) that is covered with needle primordia (C). New needle primordia are initiated at the edges of the apical meristem (D). Needle primordia enlarge the following year to form new needles on the shoot." (Templeton et al. 1991).

Floral buds

White spruce is monoecious; male and female strobili normally occur separately on the same tree. Either pollen cones or seed cones can differentiate from either axillary or terminal apices after completion of budscale initiation, which coincides with completion of lateral shoot elongation (Owens and Molder 1979b). Differentiation refers to the change from budscale initiation to bract of microsporophyll initiation, with the development of apices distinguishable as seed-cone, pollen-cone, or vegetative (Owens and Molder 1979b).

Various cultural and hormonal treatments have enhanced flowering in conifers, and within the Pinaceae a mixture of the less-polar gibberellins A_4 and A_7 ($GA_{4/7}$) has been most successful in promoting strobilus production. Species, age of tree, and crown position can profoundly influence the results obtained (Marquard and Hanover 1984a, b). Two experiments to test the effect of $GA_{4/7}$ on strobilus production in white spruce were conducted by Marquard and Hanover (1984b), the first with a $GA_{4/7}$ concentration of 500 mg/L, the second with $GA_{4/7}$ 250mg/L. Three treatments were factored with four treatment times and five crown positions. Male flowering was not affected by treatment, but female strobilus production was significantly affected by treatment, as well as interaction with crown position and time of treatment. Marquard and Hanover felt justified to recommend that $GA_{4/7}$ treatments to enhance female flowering be carried out after shoots have elongated from 15% to 75% of their final length. Together with the results of the study by Owens et al. (1977), this window of opportunity for effective use of $GA_{4/7}$ would last about 5 weeks and provide adequate latitude in treatment time for large-scale treatment of seed orchards.

$GA_{4/7}$ treatment was generally ineffective in enhancing female strobilus production on branches in the uppermost crown (whorl 1 and internode 1). Marquard and Hanover (1984b) suggested that this lack of response might result from an endogenous chemical gradient or translocation

of chemical within the crown, the uppermost whorl and internode of 8- and 9-year-old white spruce being the crown regions where female strobili production is most prolific (Marquard and Hanover 1984a).

Marquard and Hanover (1984b) found a negative relationship between female strobili production and $GA_{4/7}$ concentration, but Marquard (1983) reported a positive relationship in juvenile white spruce.

In rare instances, however, white spruce cones with male and female strobili have been found, possibly induced by drought (Santamour 1959). Bisexual flowers, mostly only one or sometimes a few on a tree, had been reported in most genera of the Pinaceae, before the discovery of numerous bisexual flowers on *Picea likiangensis* var. *montigena* (Masters) Chen in the spring of 1958 prompted Frank Santamour Jr., USDA Forest Service geneticist at the Morris Arboretum, to survey all 25 available spruce species growing in the Philadelphia area; bisexual cones were found on 11 individual trees distributed among seven of the 17 species producing flowers that year (Table 3.5).

With the exception of those of Himalayan spruce (*Picea smithiana* the bisexual cones were similarly structured, with male tissues on the lower portion of the cone and the female tissues in various proportions occupying the tip. The bisexual cones were found in all but the topmost parts of the crown. Santamour suggested that the bisexual cones found in 1958 probably resulted from the severe drought of 1957 rather than a formerly unnoticed annual phenomenon. In their study of sexual zonation in the crown of 8- and 9-year-old white spruce, Marquard and Hanover (1984a) observed five hermaphroditic strobili in the transitional zone whorl-2 and whorl-3 branches of one tree.

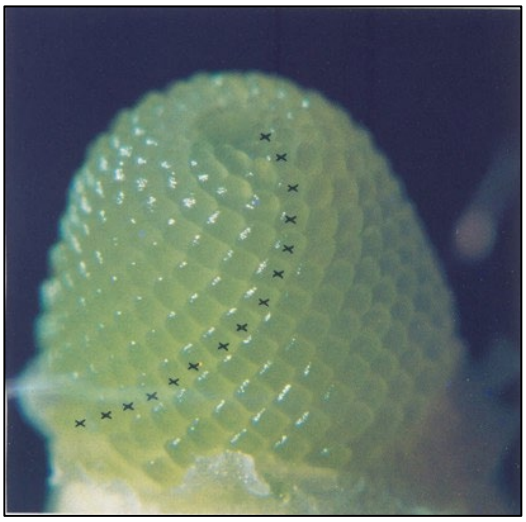

Figure 3.8 Rows of needle primordia. "*Count the needle primordia within a short row.* Viewing the embryonic shoot from the side, two types of vertical rows of primordia can be seen spiralling from the base to the tip of the embryonic shoot. The short rows run more directly up the side of the apex and contain fewer primordia. Conversely, the long rows contain more primordia and spiral more gradually up the side of the apex. The mathematical series with few exceptions, there being 8 short and 5 long rows, 13 short and 21 long rows, or 21 short and 13 long rows. This bud has 15 primordia per short row." (Templeton et al. 1991).

Table 3.5. Bisexual cones found in Santamour's 1958 survey of spruce in the Philadelphia area. (after Santamour 1959).

***Picea* species**	**Number of trees**	**Bisexual conelets/tree**	**Pollen abortion**	
			Normal cones %	**Bisexual cones %**
asperata	2	c.50, 500+	1	10
balfouriana	1	25	–	–
glauca	3	c.10	1	–
montigena	2	500+	2	40
retroflexa	1	13	6	16
smithiana	1	24	4	35
wilsonii	1	33	–	52

Reproductive buds are differentiated quite rapidly, during the course of about a week, after the cessation of shoot growth, the year prior to flowering and seed dispersal (Eis 1967b, Owens and Molder 1977). In British Columbia, differentiation occurs over a wide range of sites during the last half of July, suggesting that the process occurs at about the same time throughout much of the species' range (Nienstaedt and Zasada 1990). Development of reproductive buds continues for 8-10 weeks in parallel with shoot maturation. By late August in interior British Columbia, reproductive buds of white spruce can be distinguished macroscopically by their size and shape, but dissection is needed to determine definitively whether a bud is male or female (Eis 1967b). In the same area, male buds become dormant around 1 October about 2 weeks before female buds and the vegetative buds (Owens and Molder 1977).

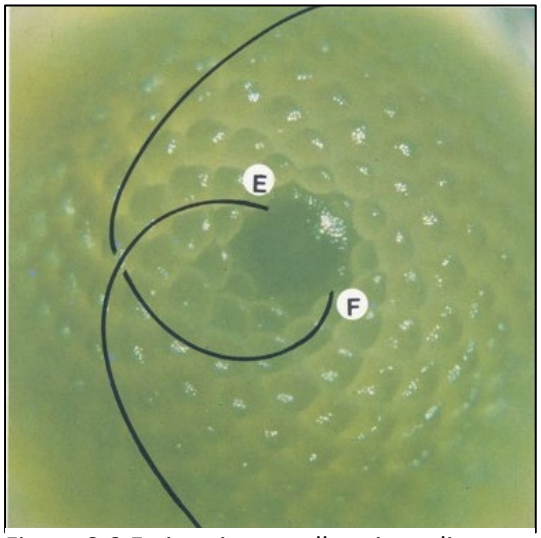

Figure 3.9 Estimating needle primordia. "To estimate the total number of needle primordia in a bud, first calculate the average number of primordia by counting the primordia in 2 or 3 short rows. Next, observe the embryonic shoot from above, and count the number of short rows of primordia spiralling out from the apical dome. The total number of primordia in the buds equals the product of the average number of primordia per row multiplied by the number of rows. The bud shown here has 13 short rows (E) with an average of 15 primordia per row and therefore contains a total of (13 x 15) 195 needle primordia. A long row is indicated for comparison (F.)." (Templeton et al. 1991).

Gibberellins will promote precocious and enhanced flowering in the conifers, but whereas any of the bioactive gibberellins tested have promoted flowering in the Cupressaceae and Taxodiaceae, only the mixture of $GA_{4/7}$ or GA_9+$GA_{4/7}$ has been highly florigenic in the Pinaceae (Reid et al. 1991). Scions from the upper crown of old Norway spruce, after grafting onto young seedlings, produced abundant female flowers after 3 years (Müller-Stoll 1947), far earlier than seedlings would have done in the natural course of events. No male

flowers were produced, reflecting the rarity of male flower production in the upper crown, from which the scions were collected.

3.1.4 Flowers

Flowering age

Precocious flowering, producing cones and viable seed, has been observed in the field on 4-year-old white spruce (Sutton 1968), viable seed has been obtained from a 13-year-old tree (Zasada and Gregory 1969), and good cone crops have been produced by 20-year-old plantation white spruce (Nienstaedt 1957). However, over much or most of the general range substantial flowering and seed production probably begins no earlier than 30 years of age. Significant seed production begins in 45- to 60-year-old mixedwood white spruce in Manitoba and Saskatchewan (Rowe 1955). In general, cone and seed production reaches a maximum in dominant trees 60 or more years of age. Seed production of white spruce on harsh sites occurs later and more reluctantly, with possible "distress" flowering excepted. Cone-bearing by dominant white spruce continues well into the second century of life and probably beyond (Zasada and Gregory 1969). Engelmann spruce seed production reaches a maximum on dominant trees 45-50 cm in diameter between 200 and 250-years-old (Oosting and Reed 1952, Garman 1957).

3.1.4.1 Female flowers

Female flowering is influenced by nutrition, phytohormones or phytohormal balance, and various cultural treatments that induce changes in nutrition and/or phytohormones. Weather, too, exerts influence that can be decisive: *Picea* flowering was virtually non-existent in central New Brunswick in 1985 (Fowler et al. 1988). Fertilization with ammonium nitrate (Holst 1959) and calcium nitrate (Pharis et al. 1986) promoted female flower production, as did application of gibberellins to elongating shoots (Pharis and Kuo 1977, Pharis 1979, Cecich 1985, Pharis et al. 1986). Root-pruning promoted flowering of white spruce (Holst 1959, Ho 1982, Marquard and Hanover 1985). The floral response of 6-year-old white spruce was evaluated after treatment with gibberellins $GA_{4/7}$, naphthaleneacetic acid, and root pruning (Marquard and Hanover 1985). $GA_{4/7}$ was generally, though not significantly (P= 0.05) more effective as a single treatment than root-pruning in promoting female flower production, and though root-pruning did positively influence flower production, no consistent synergistic effect was noted. However, both $GA_{4/7}$ and root pruning were significant as main effects in each of two experiments (Table 3.6), and Marquard and Hanover judged that the combination of the two treatments would be likely to give the biggest increase in female flowering in white spruce. The effect of treatment did not carry over into the following year.

Table 3.6. Main effects of $GA_{4/7}$, NAA, and root-pruning on female strobilus production (mean number per tree) of white spruce. (after Marquard, and Hanover 1985).

Main effect	Experiment 1	Experiment 2
$GA_{4/7}$ (mg/L)		
0	2a[a]	68a
50	11ab	124b
500	16b	113b
NAA (mg/L)		
0	8a	109 ns
25	14b	94
Root-pruning		
Control	5a	81a
Root-pruned	14a	123b

[a] Within columns, means not followed by the same letter differ significantly (P = 0.05) by Duncan's multiple range test; ns = not significant (P = 0.05).

Female cone production in 10-year-old white spruce in field conditions was significantly (P = 0.05) depressed by night-interrupted short-duration exposures of leading shoots to red light; this was interpreted as indicating that white spruce is a short-day plant with respect to flowering (Durzan and Campbell 1979).

Cone buds may develop from terminal apices that have been vegetative for at least one year or from newly-initiated axillary apices on newly elongated shoots (Owens 1986). At maximum receptivity, the erect female flowers have reflexed scales 20-25 mm long, and are either deep red, yellow-green, or green, but of uniform color on individual trees (Nienstaedt and Zasada 1990). The bracts are denticulate (minutely dentate). Flowers are 3-4 cm long and are more abundant in the upper region than in other regions of the crown, often abundant in the upper few whorls of the crown. On 17-year-old grafts, the most productive whorl was fourth from the top, and the zone producing female buds averaged 6.4 whorls (Nienstaedt 1981). In light crop years, cones were concentrated in the upper whorls to a greater extent than in intermediate or heavy crop years. The scales are widely separated during receptivity. They close shortly after pollination and the cones gradually become brown and dull.

The “large cone crops” produced by white spruce only a few feet high after planting on infertile sand in upstate New York were presumably an expression of the “distress” phenomena; those spruce not already dead all showed pronounced symptoms of stagnation (Heiberg and White 1951).

Cones

Cones become pendant 2-4 weeks after pollination during the period of fastest cone growth. When young, cones are yellowish green ("diagnostic", according to Wright [1955]), pale green, sometimes with reddish tinge (Forestry Branch 1961) or, for var. *albertiana*, either vivid, waxy green or strong reddish brown on the side of cones exposed to sun, and green on the shady side (Crossley 1953). At maturity, cones are brown or light tan, pendent, cylindric, 1.2-2.0 cm in diameter (Figure 3.10), and, with different lengths on the same branch, 3.5-5.0 cm long (Krüssmann 1985). The variety interior white spruce (*Picea glauca* var. *albertiana* S. Brown) has cones shorter and broader than those of white spruce. Although one open-grown 75-year-old white spruce in northern Minnesota in one year produced 271,000 viable seeds from 11,900 cones (Roe 1952), and 25 white spruce produced an average of 8,000 cones per tree in one seed year in southern Ontario (Tripp and Hedlin 1956), while one dominant interior white spruce, with its narrower crown, will typically produce no more than 3,000 cones, even in an excellent seed year (Alden 1985). Cones are formed of close-fitting scales (loose-fitting in Engelmann spruce [Hosie 1969]) directed apically, and arranged spirally about the central rachis. Each scale is subtended by a bract (Figure 3.11) that is appressed to its outer convex surface, and the inner concave surface, at its base, bears two seeds, each in a shallow depression (Tripp and Hedlin 1956). The scales are thin, soft, and flexible, not brittle to the touch as in black and red spruces, and are straight or slightly rounded and entire (smooth) at the margin. The firm, smoothly rounded scales of white spruce are closely appressed when the cone is wet, whereas in Engelmann spruce the scales are thin and flexible, apically crisped or erose, seldom rounded, and not closely appressed when the cone is wet.

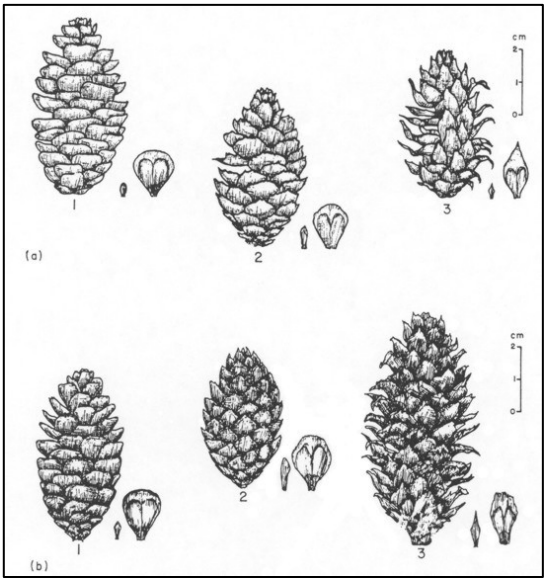

Figure 3.10 Extremes and intermediate forms of the spectrum of variation in cone morphology in (a) the white–Engelmann spruce complex and (b) the white–Sitka spruce complex in British Columbia. Note the long bract of the intermediate form (B2) from the white–Sitka complex, A1) 6 miles north of Williams Lake, latitude 52°12', elevation 2700 ft; (A2) 13 miles south of Merritt, latitude 50°00', elevation 3300 ft; (A3) 13 miles northwest of Kamloops, latitude 50°47', elevation 5200 ft; (B1) 67 miles east of Smithers, latitude 54°20'. Elevation 2800 ft; (B2) 43 miles east of Terrace, latitude 54°57', elevation 700 ft; (B3) 89 miles northwest of Terrace, latitude 55°02', elevation 500 ft. (after Roche 1969).

In studies by Garman (1957) in interior British Columbia, cone length for 80% of samples ranged from 43 to 58 mm in Engelmann spruce and 38 to 53 mm in white spruce, which is a non-significant difference. The white spruce cones were often somewhat conical as a result of a contraction of the small scales at the tip of the cone, whereas Engelmann cones tended to be oblong and usually blunt on top. Garman noted that the Engelmann cone when dry is soft and elastic, the scales lying close to the axis being thin and flat; while green, the scales tend to dry and shrink at the tips, causing them to wrinkle and partly separate from each other at the tips.

The white spruce cone is rigid even when open because the scales stand out at a wide angle from the axis of the cone and are thick and curved.

One white spruce cone 46 mm long from a young tree in interior British Columbia yielded the following data (Table 3.7). The ratio of bract length to scale length was examined for its potential value as an index to help differentiate among spruce species; but the averages for Engelmann control samples were .34, .39, and .43, and those for white spruce were .37, .38, and .39.

The ratio of width to length of cone scale was found to be a useful ("highly significant") aid to identification of species (Garman 1957). Cone scale length by itself is not particularly useful, because cone size, and therefore scale length, is governed not only by genetic factors but by ecologic influences. The average ratio for 66 white spruce specimens was .81, with 80% falling between .89 and .73. Fewer specimens (24) of Engelmann spruce averaged .62, with 80% between .69 and .54. The cone scales of white spruce are more broad than long; those of Engelmann spruce have the broadest part of the scale below the middle. Garman cited photographic evidence in support of his statement that the cone scale is always longer than broad in all Canadian species of spruce. If the breadth of the scale approaches equivalence with the length, the specimen will have other characters that identify it as either white spruce or black spruce.

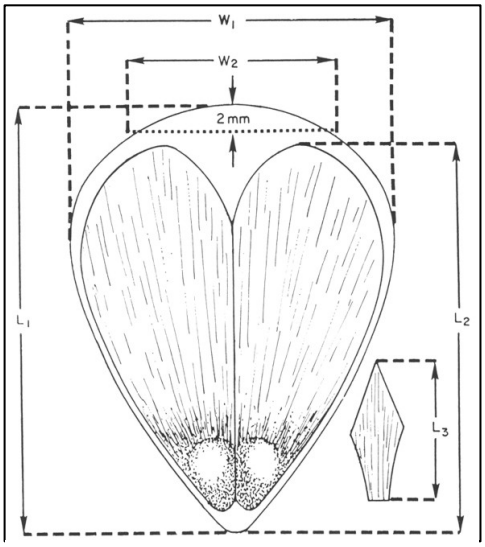

Figure 3.11 Diagrammatic representation of spruce scale and bract showing five basic measurements (after Roche 1969).

Table 3.7. Means of measurements on five scales and five bracts from mid sections of the upper (distal), central, and lower (proximal) thirds of the cone. (after Garman 1957).

	Upper	Central	Lower
Scales			
Length (mm)[a]	13	14	12
Width (mm)	9	11	11
Width: length	.69	.79	.92
Bracts			
Length (mm)	5	5	5
Bract length: scale length	.38	.36	.42

[a] Conversion of measurements to mm from original inches gives ratios that differ slightly from those reported by Garman.

The cone scales of white spruce are obovate-triangular to almost orbicular. The scales are stiff and the margin entire; the apex is flat to round, and being stiff, is slow to erode after maturity. The bracts are usually spatulate. Engelmann spruce scales are elliptical and often narrowed to the base; they are flexible, and the margin is erose to wavy. The apex is also wavy and often

appears truncate. It is thin and papery, and erodes readily when old. The bracts are lanceolate and usually long and acute at the apex.

Cones become soft to the touch a week before major seed cast; softness of cone to the touch, color of testa (seed coat), and brittleness of seed, are more reliable than color as indices of cone maturity (Crossley 1953). Cones, which open at maturity, are usually quite pitchy (Dobbs et al. 1976). Scales of open cones are spread almost at right angles and are easily crushed (Hosie 1969). In Dobbs et al.'s (1976) guide to cone collecting in British Columbia, and in the revision by Eremko et al. (1989), white spruce and Engelmann spruce are treated together as interior spruce. Seed collected within the zone of hybridization between white spruce and Engelmann spruce in middle elevations of the Rocky Mountains, and between white spruce and Sitka spruce in north-coastal British Columbia, are not now labelled separately by species but merely designated as being of "spruce complex" origin (Morgenstern 1990).

Cone induction

The association between cone abundance in nature and above-average temperatures at the time of cone-bud differentiation the previous summer has long been noted in conifers, including *Picea* (Chalupka 1975, Olsen 1978). Heat treatment of potted propagules has successfully promoted flowering in Sitka spruce (Tompsett and Fletcher 1977), Norway spruce (Olsen 1978), and Engelmann spruce (Ross 1985). Other stress-inducing treatments, including drought, root pruning, and excess and deficiency of nitrogen, have been sought to promote cone induction.

That root growth would seem to be retarded by such treatments elicited the suggestion that the treatments might curb the export from the root system of a chemical inhibitor of flowering, perhaps root-synthesized cytokinins (Dunberg 1979, Philipson 1983), but the involvement remains unsubstantiated (Ross 1991a, b). The results of Ross' experiments did not support the hypothesis that heat promotes flowering in white spruce by retarding the number of actively growing roots, but rather implicated the shoot as the primary receptor for the heat effect. Only heat applied to shoots promoted flowering, and the effect was independent of soil temperature and root activity. Ross found that a daytime temperature of about 30°C was near optimal for promotion of male flowering in potted white spruce grafts, and there was little difference in the production of seed cones at polyhouse temperatures of 20°, 25°, and 30°C. Temperature requirements for flowering may differ between male and female. Heat applied to shoots promoted only male flowering (barely at $P = 0.057$) in the 1985 experiment and only female flowering in the 1987 experiment. Five hours at 20°C per day sufficed to effect differentiation of seed-cone buds, and this was realized in 1985, but not in 1987 when ambient temperatures were lower. Ten hours at 30°C per day maximized production of pollen cones.

Following a lack of success in promoting early and enhanced flowering in various species of the Pinaceae using the most readily available gibberellin A_3 (GA_3), notwithstanding the ready induction by GA_3 of early and enhanced flowering in members of the Cupressaceae and Taxodiaceae, research by Pharis, Ebell, Rediske, Cade, and Ross led to the correlation of flowering in several Pinaceae species with enhanced endogenous concentrations of "less polar" gibberellins (i.e., gibberellins with few or no hydroxyl groups which exhibit a non-polar chromatographic mobility)(Pharis 1978). Field testing of some of the less polar gibberellins began

in the early 1970s, and obtained success in promoting flowering with $GA_{4/7}$ mixture in several members of the Pinaceae, including white spruce and Norway spruce. However, although promotion of flowering in the Pinaceae became possible, the technique was not simple. Additional cultural treatments, such as girdling, fertilization, water stress or root pruning might also be needed on some sites to secure the response to the hormone. The timing of GA_3 treatment may also vary with location (Pharis 1978).

The promotion of female and male strobilus production using $GA_{4/7}$ combined with promotive cultural treatments was one of two aspects of a program to decrease the breeding period for white spruce. Greenwood et al. (1988) used 3- to 4-year-old white spruce grafts initially averaging 57 cm in height. Greatest success (30 female strobili per graft) was obtained with 500 mg/L of $GA_{4/7}$ in a solution of 5% ethanol with Aromox C/12 (0.01%–0.02% active ingredient), sprayed on to drip point. Using the same technique, Adams (1990) increased white spruce female strobili production to two to 10 times that of untreated controls; male strobili production generally increased but not to statistically significant levels. Greenwood et al. (1988) found no statistical significance between two environments in their effect during shoot elongation on flowering of potted white spruce grafts, but $GA_{4/7}$ significantly ($P < 0.05$) promoted female flowering in both environments after $\sqrt{n+1}$ data transformation (Table 3.8; Greenwood et al. 1988). In 8- and 9-year-old white spruce, Marquard and Hanover (1984a), using $GA_{4/7}$ as a foliar spray, increased female strobili production 6.2-fold and male strobili production 2.4-fold on branches in the transitional zone; on male zone branches, female strobili were induced and male strobili production increased 6-fold (Figure 3.12).

Table 3.8. Effect of environment on number of ♀,♂ per ramet (clones flowering, %) for white spruce in 1987. An equal number of ramets were either left in the greenhouse throughout the shoot elongation and $GA_{4/7}$ application, or moved into the greenhouse from a shade frame for the last half of the GA application period (Greenwood et al. 1988).

♀, ♂		$GA_{4/7}$	Control
Outdoor mid-May to mid-June,	♀	23 (70%)	1 (10%)
thereafter greenhouse	♂	28 (60%)	1 (10%)
Continuous greenhouse	♀	23 (70%)	8 (30%)
	♂	16 (50%)	3 (10%)

Flower induction with gibberellin “is now being used routinely to promote flowering in both the greenhouse and in the seed orchard” at J.D. Irving’s Sussex Tree Nursery, New Brunswick (Adams 1990).

Flowering in potted grafts of white and Engelmann spruces was maximized by cool (ambient) temperatures and moderate water stress during active shoot elongation, followed by 3 weeks of heat treatment (>20°<30°C) and adequate water in a polyhouse (Ross 1985, 1988a; Ross et al. 1988). Under ambient temperatures the following spring, the induced cones developed normally and yielded high quality pollen and seed. The use of heat to force early shedding of pollen resulted in abnormally small cones and reduced yield of pollen and seed (Ross 1988b).

Use of foliar $GA_{4/7}$ sprays to promote flowering can damage interior spruce especially under droughty and/or hot conditions. If the $GA_{4/7}$ spray is allowed to dry and remain on the foliage, the residue surfactant (Aromox C-12/W) seems to slowly break down the cuticle. However, foliage rinsed with water 4 days after each $GA_{4/7}$ treatment minimized injury without reducing the flowering response (Eastham, Hollefreund, and Ross unpublished, cited by Ross et al. 1988).

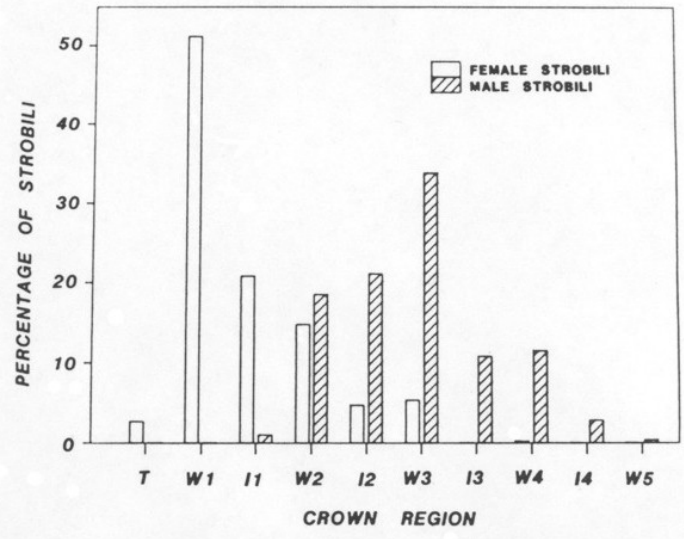

Figure 3.12 Vertical distribution of female and male strobili in relation to crown position of 8- and 9-year-old white spruce. T indicates terminal leader, W1 indicates the uppermost nodal whorl, and I1 indicates the uppermost internode.

Promotion of flowering by gibberellins

Exogenous application of $GA_{4/7}$ is known to stimulate flowering in species of the Pinaceae (Pharis and Kuo 1977, Ross et al. 1983), and direct injection into the stem of Sitka spruce produced large numbers of pollen and seed cones (Philipson 1984); the injection technique is easy to use and is more economical than spray application in the amount of gibberellins needed.

Experiments on three populations of white spruce in the Lake States examined interrelationships between calendar date and response to application of exogenous $GA_{4/7}$ (Cecich 1985). In one experiment, trees sprayed with $GA_{4/7}$ between 7 May and 1 July produced significantly more ovulate (24) and staminate (17) strobili than the controls (one ovulate, no staminate). Trees sprayed between 8 July and 9 September produced no strobili. Another experiment determined that sprayed application of $GA_{4/7}$ to ramets in May produced significantly ($P \leq 0.02$) more strobili, both ovulate and staminate, than did spraying in June. There was no significant ($P \leq 0.05$) flowering response, ovulate or staminate, among the 10 clones, which showed considerable variability. For instance, while two ramets of one clone sprayed in May yielded 61 staminate strobili, four clones produced no staminate strobili. In a third experiment, ramets of early- and late-flushing clones were sprayed with five weekly applications of $GA_{4/7}$ in June at a time when white spruce meristems in the Lake States differentiate to become vegetative or reproductive (Cecich et al. 1972, Marquard and Hanover 1984a). The foliar treatment may not have been fully utilized by the time of meristem differentiation near the end of shoot elongation (Cecich 1985), even though June treatment significantly increased the production of ovulate and staminate strobili (Table 3.9).

Table 3.9. Total number of strobili on early- and late-flushing white spruce clones (six ramets each) after spraying with $GA_{4/7}$.

Early-flushing					Late-flushing				
Ovulate			Staminate		Ovulate			Staminate	
Clone	Control	$GA_{4/7}$	Control	$GA_{4/7}$	Clone	Control	$GA_{4/7}$	Control	$GA_{4/7}$
1	0	1	0	0	6	0	0	0	0
2	0	19	5	58	7	0	71	0	6
3	0	0	0	0	8	0	83	0	118
4	0	30	0	16	9	0	138	0	0
5	0	10	19	158	10	0	151	3	52
Total	0	60*”	24	232**	Total	0	443**”	**3**	176**

* and ** differ significantly from controls, P ≤ 0.05 and 0.01, respectively.
” Significantly different from each other (P ≤ 0.05).

Promotion of flowering by girdling

Girdling has been used in adjunction with growth regulator treatment to stimulate flowering in the Pinaceae. While often ineffective by itself, girdling can increase flowering in lightly flowering trees and enhance the stimulation effected by $GA_{4/7}$ (Ross and Pharis 1976).

Promotion of flowering by root pruning

When promoted by root pruning, flowering in conifers is typically accompanied by an inhibition of shoot elongation in the year of treatment. However, the responses by white spruce grafts to root pruning and drought, and to root pruning applied at different stages of root and shoot development in separate experiments suggested that root pruning does not simulate drought (Ross 1991b). Differences in midday needle water potentials between root-pruned and non-root-pruned grafts were small and short-lived. Furthermore, root pruning promoted only female flowering, whereas drought inhibited only male flowering. Ross concluded that the flowering response to root pruning does not depend on a reduced rate of shoot elongation.

Effect of fertilization on flowering

Fertilization with NPK of a low-nutrient boreal forest ecosystem in Yukon Territory for 9 years had no effect on cone production of white spruce (Turkington et al. 1998).

Cone development

Maturation continues after embryos reach anatomical maturity (Winston and Haddon 1981, Zasada 1973). The embryo will fill its cavity well before the seed is mature (Eremko et al. 1989), and cone dry weight generally increases. Seed quality depends on the weather during maturation, with cold or short growing seasons producing immature seed with poorly developed embryos (Zasada 1973, Zasada et al. 1978). In general, the heavier the seed production, the higher the seed quality. But, at least in floodplain stands in interior Alaska, production is not necessarily related to total basal area, basal area of white spruce, number of living white spruce stems/ha, average dbh of all trees, or average height of dominant trees (Youngblood and Max 1992).

Cones ripen in August or September of the first season, 2-3 months after pollination (USDA Forest Service 1948, Cram and Worden 1957), and as much as 90% of the seed is released by the end of October (Roe 1946). Cones have been produced in quantity by trees only 10-15 years old (Wright 1964); 2,973 female cones were counted on 994, 10-year-old white spruce that were 140-260 cm tall, near Kemptville, Ontario, at latitude 45°N (Durzan and Campbell 1979). However, in general, trees younger than about 30 years of age do not produce seed in quantity (USDA Forest Service 1948, Stiell 1955). "Optimum" production occurs only in trees double that age (Fowells 1965), though Roe (1948) in northeastern Minnesota found germinable seeds in cones on white spruce 13 years after planting, and Sutton (1968) reported precocious fruiting on one white spruce in the first growing season after outplanting as 2+1 stock. In mixedwood stands in Manitoba and Saskatchewan, white spruce are generally 45-60 years old before the onset of substantial cone production (Rowe 1955). At higher latitudes, cone production typically does not occur until trees are older. The age at which conifers begin to flower and fruit may be influenced strongly by mineral nutrition (Sweet and Will 1965).

Seed years, cone crop periodicity

Over much of the range, some cones are produced every year, but are produced prolifically, in "seed years", only every 2-6 or more years (Sutton 1968). The phenomenon of widespread and synchronous production of large seed crops at variable intervals is called *masting* (Peters et al. 2005). The production of white spruce cones varies annually, and depends on such factors as tree age, weather experienced during the previous year, previous cone and seed crops, and other factors (Matthews 1963). In propitious conditions, white spruce can have good to excellent cone and seed crops in alternate years, as noted by Zasada (1986) in Alaska, but good seed years never occur in successive years, in part because strobili are formed in lateral buds that would otherwise form the vegetative shoots that carry cones (Nienstaedt and Teich 1972).

While the periodicity of seed crops can vary among sites (Zasada 1986), the seed year phenomenon in white spruce tends to occur regionally over very large areas; the cone-laden crowns of emergent white spruce trees become vulnerable to breakage by quite moderate wind stress. There seems little doubt that seed years are a response to previous weather. Specifically, they seem to be related to hot, sunny, dry weather at the time of bud differentiation the previous year (Nienstaedt 1981). Lakari (1921), quoted by Büsgen and Münch (1929), stated that in Finland a seed year for Norway spruce and Scots pine (*Pinus sylvestris* L.) follows 2 years after a hot dry summer, though this was not found in Saxony by Zimmerman (cited by Büsgen and Münch as "not yet published"), who traced out the seed years of the spruce and the weather of the 2 years previous to each, finding no relation between the weather and seed production. Vagaries of weather would seem to account for the irregularity and unpredictability of seed year occurrence. In Alaska, for instance, although white spruce "can have good-to-excellent cone and seed crops in alternate years" (Zasada 1986), "good seed years may be 10 or 12 years apart" (Zasada 1976). Gill (1973, 1974) observed that good seed years appeared to be few in interior Alaska and the Mackenzie Delta.

In the Duck and Porcupine Mountains of Manitoba, there were 12 seed years between 1911 and 1951 (Rowe 1955). In north central interior British Columbia, the period 1954 through 1961

included two seed years and one year with a moderate crop (Arlidge 1967). The following 10 years produced only one seed year and one moderate cone crop (Dobbs 1972 citing a personal communication from S. Eis[6]). Engelmann spruce in Montana west of the continental divide produced five seed years and eight fair cone crops in a period of 21 years (Boe 1954). East of the divide, there were two seed years and four fair cone crops in the same period. The annual cone crops for 15 individual white spruce trees in one stand near Fairbanks, Alaska, were reported by Zasada (1980) (Table 3.10).

Table 3.10. Annual cone crops for 15 white spruce in a stand near Fairbanks, Alaska; cone counts made from a fixed point for each tree (after Zasada 1980).

Tree	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978
1	1	500	0	750	82	0	500	0	450	220
2	3	1,100	0	1,600	0	0	600	0	700	5
3	0	1,300	0	500	125	0	375	0	500	10
4	0	700	0	650	46	2	275	0	250	0
5	0	550	0	300	26	0	225	0	260	0
6	12	585	0	500	43	0	225	0	300	30
7	20	415	0	350	15	0	200	0	100	0
8	8	775	0	525	45	0	175	0	150	25
9	0	420	0	650	22	5	425	0	250	50
10	18	360	0	575	10	0	85	0	100	75
11	90	271	0	575	0	0	50	0	300	1
12	1	400	0	525	0	0	175	0	200	0
13	6	850	0	125	0	0	0	0	10	0
14	0	900	0	300	147	1	275	0	450	0
15	29	470	0	325	17	0	65	0	73	12

Day (1970) observed that in the subalpine forest of Alberta, spruce seedfall was “very satisfactory and uniform” after shelterwood logging in fall 1964, even though the seed year was rated “poor” by local foresters: “The abundance of seedfall in a poor year is caused by the shelterwood which always appears to supply adequate seed.” In the “poor seed year” of 1964, seedfall was estimated in numbers of sound seed as 998,000/ha in one block, 613,000/ha in the other.

In the 1950 seed year in southern Ontario, Tripp and Hedlin (1956) found an average of more than 8,000 cones per tree; two-thirds of the trees sampled produced no cones the following year, and none of the others had more than a few hundred cones. Roe (1952) in Minnesota reported 11,900 cones with 271,000 viable seed on one open-grown 75-year-old white spruce.

[6] Canadian Forest Service, Victoria, B.C.

3.1.4.2 Male flowers

By late summer, male flower buds can be recognized morphologically (Winton 1964d). The male buds are first to reach a state of dormancy (about 1 October at Prince George, British Columbia), and the female and vegetative buds become dormant about 2 weeks later (Owens and Molder 1977). Primordia of reproductive strobili continue to develop late into the fall, long after vegetative meristems have ceased growth (Eis 1967b). Male (polleniferous) and female (ovuliferous) strobili overwinter in the mother-cell stage (Nienstaedt 1957). Cell division and growth resume in the spring before bud elongation is detectable. Flowering takes place in May (USDA Forest Service 1948), June (Forestry Branch 1961) or July (Hustich 1950), depending on geographical location and climate. Flowers appear on cone-like strobili having a central axis bearing spirally arranged, spore-bearing, leaf-like microsporophylls. Pollen cones generally develop from small axillary, or from small terminal apices on less vigorous, proximal shoots (Owens and Molder 1977); they are commonly abundant in the axils of the most proximal needles, and are more abundant in lower than in other parts of the crown.

Before pollen dispersal, male flowers are red or pale red, and succulent to the extent that a substantial drop of liquid can be squeezed from the conelet, which is 10-12 mm (Nienstaedt and Zasada 1990) and occasionally up to 15-20 mm long prior to the release of pollen (Sutton 1968). Just before the pollen is ready to be shed, the conelet becomes yellow and almost dry when squeezed; this is the best time to collect pollen (Nienstaedt and Zasada 1990). A moisture content five to six times dry weight drops precipitously prior to pollen dispersal. After the pollen has been shed, the conelet quickly turns brown and drops off.

Staminate flowers on white and black spruces as well as on balsam fir offer food and shelter to budworm larvae. When staminate flowers are unusually abundant, as in the spring of 1960 in the Lake Kedgwick in the Gaspé–Lower St. Lawrence region of Quebec, budworm larval development and survival are enhanced (Blais 1961). Favourable weather conditions can then facilitate major spreading of infestations.

Pollen

The average grain size of white spruce pollen is larger than that of any of the other North American spruces, but differentiation between pollen of white spruce and that of black spruce is complicated by variability in pollen size and morphology. Separation has been attempted on the basis of grain size (Wilson and Webster 1942), morphology (Richard 1970), and linear discriminant analysis of size measurements (Birks and Peglar 1980). Problems with discriminant analysis were pointed out by Hansen and Engstrom (1985), who found that separation based on four morphological characters, especially including the shape and internal reticulation of the saccus, gave results similar to those obtained by the numerical method.

Minimum, mean, and maximum total lengths found by Griffin (1950) and Guennel (1949–50) were: 88 µm, 101 µm, 108 µm; and 92.4 µm, 98.3 µm, and 104.4 µm, respectively. Guennel, measuring parallel to lines of attachment, found wing depth averaged 78.5 µm, and Griffin reported minimum, mean, and maximum wing depths as 25 µm, 29 µm, and 33 µm; clearly, differences can be large.

The grain size of white spruce pollen overlaps with that of *Abies*, but is generally larger (Potzger 1943–1944), and whereas *Abies* and *Pinu*s have distinct re-entrant angles between wings and tube cell, *Picea* pollen does not (Guennel 1949–50).

Pollination

In British Columbia, pollination takes place 6-8 weeks after bud elongation, depending on elevation (Owens and Molder 1979b), and meiosis occurs during this period about 3 weeks ahead of peak pollen shedding. The duration of flowering is less than a week, but pollen shedding overlaps with receptivity of the female flower (Wright 1953; Nienstaedt 1957, 1958). At St. Paul, Minnesota, meiosis in one white spruce was observed to begin on 22 April 1961 and in another on 21 April 1962, in each instance 5 days after the mean daily temperature rose to about 10°C. In the same 2 years, 2 days later than meiosis began at St. Paul, meiosis began in a white spruce near Cromwell, Minnesota, after a period of 10 days in which the mean daily temperature reached 4.4°C (Winton 1964b). Winton interpreted these results to mean that meiosis had about the same heat requirement in the two areas. The time of pollen shedding and female receptivity is undoubtedly temperature-dependent and, while year-to-year variation might be as much as 4 weeks (Nienstaedt and Zasada 1990), pollen dispersal in southern areas is usually earlier than in northern areas, even though peak dispersal can occur on the same calendar date over a north-south range of 15 or more degrees of latitude (Nienstaedt 1958, Zasada et al. 1978). Pollen has a markedly diurnal pattern of dispersal dependent on temperature, humidity, and wind (Zasada et al. 1978). The period of peak pollination coincides with female receptivity and can be severely impacted by rain or frost (Nienstaedt 1958, Maini 1966, Zasada 1971). The peak usually lasts about 3-5 days in May, June, or July, depending on geographic location and climate.

Female flowers at peak receptivity are erect, have widely separated scales, and are 20-25 mm long; the color, uniform for a given tree, varies from green to deep red. The scales close shortly after pollination. Cones become pendant during the following 2-4 weeks while growth of the cone is most rapid.

Interference in the reproductive processes in plants by acid rain decreasing pollen viability, disrupting fertilization, decreasing fruit or seed production, and reducing germinability of seeds has been bruited as a potentially serious problem, particularly in conifers already under budworm stress in eastern North America (Sidhu 1983). However, an experiment in Newfoundland found that simulated acid rain of pH 3.6 or more (less acid) produced no adverse effects on white spruce germination and pollen tube growth. In pollen washed with acid rain and germinated on normal agar medium, rain of greater acidity (pH 3.0 and 2.6 tested) reduced germination by less than 30%. When agar was prepared with acid rain of pH 3.6 or greater acidity, germination was reduced further and pollen tube growth was strongly inhibited. Sidhu concluded that washing of pollen by acid rain of pH > 3.6 during the release and transportation stage would have very little effect on either pollen germination or pollen tube growth. Precipitation data for May through July in 1980 and 1981 at selected locations in Newfoundland show that pH was lower than 4.0 less than 1% of the time. The likelihood of there being any

effect is further reduced by the release of most white spruce pollen when the atmospheric relative humidity is less than 70% (Owens and Molder 1979b).

3.1.5 Fertilization and embryo development

Fertilization occurs 3-4 weeks after pollination (Mergen et al. 1965, Owens and Molder 1979a), and maximum size, maximum water content, and maximum fresh weight are reached by midsummer. The final size may vary considerably from year to year, depending on weather of the previous year and during cone expansion (Zasada et al. 1978).

The primary period of embryo growth occurs after cones reach maximum size. Cotyledons appear in mid to late July, and embryo development is completed in August (Mergen et al. 1965, Rauter and Farrar 1969, Owens and Molder 1979b, Zasada 1988). Seed development can vary from year to year by as much as 3 weeks, presumably in response to weather variation (Caron et al. 1989, 1993). The influence of elevation of site also presumably depends on differences in weather.

3.2 Phenology

The times of recurring natural phenomena in white spruce are affected by several factors and vary greatly. Geographical location and related climatic variation obviously have great influence. In this respect, the effect on white spruce phenology is likely to exceed the variation in balsam fir (*Abies balsamea* (L.) Mill.) for which Lamb (1915) has shown differences of at least a month in the onset of phenological activities between the northern and southern parts of its range. Physiography and microclimate also have strong phenological consequences. Even on apparently homogeneous sites, the time of flushing among young white spruce within a local population may differ by 2 weeks or more (Nienstaedt 1964, Stoeckeler 1965). Planting position can also influence flushing time. Sutton (1969a), for instance, found that whereas most of the 4-year-old white spruce planted near Ottawa, Ontario, on two planting positions had flushed by 28 May, 30% of the spruce in the third planting position still had not flushed (Table 3.11; Sutton 1969a).

Table 3.11. Influence of planting position on time of flushing of white spruce. Observations on 4-year-old trees close to Ottawa, Ontario, on 28 May 1968 (after Sutton 1969a).

Planting position	Trees not flushed (%)
Grass sod	2 a[a]
Overturned spoil	3 a
Furrow bottom	30 b

[a] Within the column, values not followed by a letter in common differ significantly (P = 0.001) by t-test.

While trees in northern latitudes on high-elevation sites may begin growth developments later in the spring and stop sooner than trees in southern latitudes or at low elevations, development during the middle of the growth cycle occurs at more or less the same time in most regions (Owens and Molder 1984). Coates et al. (1994) showed the phenology of growth and the time of flushing of white and Engelmann spruces in British Columbia, along with comparative data from eastern North America and Alaska (Table 3.12).

Terminal and lateral shoot elongation occurs over a short period of time and growth is usually complete by the end of July or early August (Owens et al. 1977, Harrison and Owens 1983).

Cessation of height growth is related to declining day length (Owens et al. 1977) and may be a response to the onset of fall frosts (Pollard and Ying 1979). Premature budset by northern latitude or high-elevation populations of interior spruce grown in coastal nurseries can be overcome by artificially extending day length (Arnott 1979).

Table 3.12. Phenology and periodicity of growth. (after Coates et al. 1994).

Species	Location and elevation	End of dormancy	Start of shoot elongation	Flushing	End of shoot elongation	Dormancy of vegetative buds	Source
white	Prince George 500 m	2nd week April	early May	late May to early June	early August	mid- to end of October	Owens et al. 1977
white	Prince George 1,000 m	end May	mid-May		early August	mid-to end of October	Owens et al. 1977
Engelmann	Prince George 1,400–1,670 m	mid-April	late May	late June	late July	mid-October	Harrison and Owens 1983
white	provenances from eastern Canada and USA	end April to end May					Blum 1988
white	Alaska			June 28			Nienstaedt and Zasada 1990

Height increment

As well as macro and microclimates, age of tree, fertility, dormancy requirements, intra-specific and intra-progeny variation, previous photoperiod experience, and seed source affect amount and rate of height growth. Patterns of height growth may differ appreciably between young seedlings and mature trees (Wareing 1956), or even between 1-year-old and 4-year-old plants (Nienstaedt 1966). Kozlowski and Ward (1957) in Massachusetts found that 3-year-old white spruce seedlings in a fertile forest nursery flushed on 20 April 1954, 5 days later than Norway spruce. Height growth of both species ceased on 18 August, after quite different growth patterns; for example, although white spruce had flushed later than Norway spruce, initial height growth was much more rapid in white spruce, completing 5% of the season's increment by 23 April, 18 days before Norway spruce reached the same stage. However, white spruce took until 1 August to complete 95% of its height increment, whereas Norway spruce had already reached that stage 25 days earlier. Holst (1956) noted that Norway spruce might be considered an oceanic species, adapted to relatively mild winters and unstable spring weather. Some provenances of white spruce might qualify similarly, but more continental provenances have low chilling requirements to break physiological dormancy, with low temperatures maintaining dormancy thereafter until spring (Winton 1964a). A chilling requirement of 4-8 weeks at 36°-40°F (2.2°-4.4°C) for white spruce was suggested by Nienstaedt (1966), depending on developmental stage and age when chilling is begun. The rapidity with which height growth can proceed once it has started was regarded by Kozlowski and Ward (1957) as evidence of great dependency on carbohydrate reserves manufactured during the prior year.

Flushing of white spruce in the Lake States begins in early to mid-May, and shoot elongation ends by early July (Cecich and Miksche 1970, Nienstaedt and King 1970, Nienstaedt 1974). Late flushing clones completed 95% of shoot elongation by 1 July, 10 days later than for early flushing clones (Nienstaedt and King 1970). There was no significant year-to-year change in a period of 4 years, in that all clones in their study completed 95% of growth between 18 June and 7 July, and the period of growth was similar for both early- and late-flushing clones (Nienstaedt 1974).

In a forest nursery at Grand Rapids, Minnesota, Winton (1964c) observed two flushes of growth on 3-year-old transplants of white spruce and three flushes on 2-year-old transplants of black spruce. Nearby mature white spruce plantation trees flushed only once, in May, but new flushes of growth were produced on 1-year-old seedlings in the nursery up to 24 August. At Orono nursery, Ontario, Armson (1964) found three distinct patterns of height growth in first- and second-year seedlings of white spruce: (a) height growth completed for the season in the first week of June, (b) an initial period of height growth similar to (a) but followed 2-4 weeks later by a second period of height growth, and (c) indeterminate height growth continuing through July. Armson's (1960, 1965, 1966) data from Ontario for 2+0 nursery-grown white spruce show that differences in amount and period of height growth may result from differential fertility. Non-fertilized white spruce seedlings ceased height growth early in July but seedlings fertilized with ammonium nitrate and superphosphate continued height growth through mid-July. Moreover, fertilized trees showed a second period of height growth, not from lammas flushing of previously-set buds, but from extension of shoots on which terminal buds had not set. Patterns of height growth shown by Armson's fertilized white spruce were similar to those reported by Kozlowski and Ward (1957) for 3+0 white spruce on fertile nursery soil.

Winton (1964c) observed that 2- and 3-year-old transplants of white and black spruces in the Blandin Nursery at Grand Rapids, Minnesota, had three and two flushes of growth, respectively, in 1960. Nearby white spruce approaching maturity made only one flush of growth, but among 1-year-old seedlings in the nursery, some new flushing took place up to 24 August. Also, while 4- and 5-year-old white and black spruces in the greenhouse flushed in 1962 twice and thrice, respectively, no terminal growth occurred in 1963. The effect of lammas activity in nursery- or field-grown white spruce on height increment in the following year seems not to have been evaluated; but in nursery-grown jack pine (*Pinus banksiana* Lamb.), lammas growth did not significantly depress height growth the following year in the field (Rudolf 1964).

A pronounced deficiency of rainfall in the period of height growth of spruce will retard or curtail height growth (Cook 1941). If height increment has been thus curtailed, replenishment of soil moisture levels later in the summer will often, as in eastern Ontario and northern New York State in 1964, be followed by profuse lammas activity in young white spruce. With Norway spruce, Farrar (1961) found that lammas activity decreased with age, and casual observation suggests that white spruce behaves similarly. Farrar also found that disposition towards or against lammas activity was not consistent for given trees or seedlots, interpreting this as indicating that lammas activity is not genetically controlled. A reduction of lammas activity with age would reflect an increasing ability of a tree, as it becomes established, to achieve its growth potential as its root system exploits an increasingly large volume of soil. Nienstaedt (1966) noted

that 4-year-old white spruce, unlike younger stock, are unable to grow indeterminately in response to long photoperiods.

Two photoperiodic treatments caused large differences in the form and development of two provenances of white spruce soon after germination (Vaartaja 1957). Dependence of the onset of full or nearly full dormancy on short photoperiods was demonstrated in both provenances. In northern latitudes under large seasonal extremes of photo-climate, the photoperiods can efficiently control the onset of dormancy. Without this mechanism, an incidental warm period would favour fast-growing but non-hardy ecotypes. Photoperiodic responses of provenances from more southerly parts of the range cannot be assumed to be identical with those of northern provenances (Vaartaja 1954).

When white spruce seedlings were grown under continuous light, “the plants repeatedly formed resting buds and then flushed again immediately. When white spruce does not go through a normal dormancy after resting bud formation, the lateral buds tend to flush first, thereby decreasing apical dominance” (Campbell and Durzan 1976).

Phenology of older trees

The period of height growth of older white spruce in Maine began between 17 May and 3 June in a 3-year period and lasted about 12 weeks, with 90% of the growth occurring in the first 6 weeks (Baldwin 1931). In 1933 at Keene, New Hampshire, white spruce began and ceased height growth in mid-May and 23 July (Kienholz 1934).

At the Petawawa Forest Experiment Station, Chalk River, Ontario, in 1960 and 1961 Fraser (1962a) studied the growth of the leader and four lateral branches in each of 18 whorls of a white spruce about 9 m high. The terminal bud of the leader began to swell by mid-May in 1960. Shortly afterwards, growth began basipetally in the apical buds of the lateral branches. The grand period of growth of the leader was from late May to mid-July. The lower laterals ceased extending by mid-June, and the upper laterals by early July. Results in 1961 were similar.

Near Stephentown, New York, at an elevation of 430 m, white spruce flushed on 19 May 1940, 5 days ahead of Norway spruce (Cook 1941). Height growth continued until 24 July, 2 days longer than that of Norway spruce. In the course of 5 years, periods of seasonal height growth of individual white spruce varied from 46 to 76 days, and the earliest dates of initiation and cessation were 4 May and 2 July (Cook 1941). Height growth rates for white spruce reached a maximum in the Hudson Highlands of New York concurrently with those of red pine (*Pinus resinosa* Ait.) and European larch (*Larix decidua* Mill.) (Tryon and Finn 1937).

In a phenological study of 19 native tree species in northeastern Minnesota, initial bud activity of white spruce occurred between 4 April and 15 May, and initial leaf activity between 17 May and 9 June (Ahlgren 1957). Comparative figures for black spruce were 12 April and 15 May (bud), and 2 June and 19 June (leaf). Swelling of vegetative buds and white spruce frequently overlapped in time with flowering and usually followed a rise in maximum temperature to 21°C or more after minimum temperatures had remained above freezing for more than a week.

The average date of flushing of white spruce in the Upper Peninsula of Michigan is 25 May; elongation begins 2 days earlier and continues for 65 days to the end of July (Nienstaedt 1957).

In the Prairie Provinces, where low precipitation and high summer temperatures induce severe plant water stresses (Nienstaedt 1957), the period of height growth is shorter than in eastern parts of the continent. Leader growth usually begins in mid-May in the Edmonton AB, area, and is completed by the middle of June (Lewis and Dowding 1924). In Manitoba and Saskatchewan, white spruce flushes "about June 1" (Rowe 1955). The period of height increment of sapling white spruce was about 48 days during a 5-year period at Riding Mountain Forest Experimental Area, Manitoba: mean air temperature during the 2 weeks preceding flushing averaged 51°F (10.6°C) each year (Jarvis et al. 1966); height increment was greater in warm, moist weather than in weather that was hot and dry. However, as Jarvis et al. (1966) noted, "most terminal growth occurs at night and the rate is influenced directly by night temperature".

White spruce flushes 5-10 days in advance of black spruce in Manitoba and Saskatchewan (Rowe 1955). A similar differential has been observed in Minnesota (LeBarron 1948) and also obtains in Ontario. This accords with Winton's (1964b) observation that black spruce has a much higher heat requirement for the initiation of microsporogenetic meiosis than has white spruce.

At Kananaskis, Alberta, one white spruce flushed on the 140th day of the year 1940, the 124th day of 1941, and the 144th day of 1942 (Sayn-Wittgenstein 1961).

White spruce grown in Florida from Lake States' seed under natural and long-day photoperiods flushed simultaneously in the spring, but plants that had received the long-day treatment had much longer periods of height growth (Watt and McGregor 1963). This indicated to Watt and McGregor that, once chilling requirements have been satisfied, initiation of growth is controlled by temperature, rather than by photoperiod. Winton (1964b) produced evidence supporting this view; only 6% of the white spruce under natural photoperiod produced a second flush, but 15% of trees in the long-day treatment did so.

As well as weather- and climate-controlled variation in times of flushing, different specimens of white spruce (Nienstaedt 1964, Stoeckeler 1965) may vary by 2 weeks or more in the time of flushing within a local population, planted or natural, on apparently homogenous sites. This variation in the time of flushing is of great importance in determining susceptibility to spring frost on any given site. Usually ascribed to genetic control, it may often reflect contributory differences in soil-volume exploitation by roots, differences in soil fertility and soil moisture, or both.

Diameter increment

"The beginning of cambium activity is brought to the notice of the practical man as that period of the life of the tree during which the bark may be easily stripped from the wood" (Büsgen and Münch 1929).

In 1950, radial increment began in white spruce at Chalk River (45°58'N, 77°31'W) on 11 May but not until 29 May at Cedar Creek (50°15'N, 93°15'W), Ontario (Belyea et al. 1951); radial growth for the season was half-completed by 13 June at Chalk River, 10 July at Cedar Creek. However, Fraser's data (1956; 1962b) show that even within a 5-year period there can be differences of 13 days in the onset of growth between trees on different sites in the same area and same year (Table 3.13).

Table 3.13. Dates of initiation and duration (days) of diameter growth at breast height for white spruce at Chalk River, Ontario[a] (after Fraser 1962b).

Moisture regime (Hills 1952)	1955	1956	1957	1958	1959
1 (dry)	May 13 (67)	June 2 (67)	May 16(76)	May 1 (99)	May 13 (110)
2 (fresh)	May 18 (63)	June 2 (60)	May 20 (72)	May 14 (95)	May 14 (101)
4/5 (wet)	May 20 (47)	June 2 (49)	May 21 (78)	May 14 (88)	May 18 (95)
1 to 5	May 16 (63)	June 2 (63)	May 16 (76)	May 10 (99)	May 14 (99)

[a] Note: The summer of 1955 was very dry; another drought occurred in June to July 1959.

Gregory and Wilson (1968) compared cambial activity of white spruce in Alaska and New England and noted that the season for cambial activity was much shorter in Alaska (65°N) than in New England (43°N), though producing annually the same number of tracheids. Cambial activity was studied in 45- to 50-year-old trees near College and at Petersham, Massachusetts, by sampling at frequent intervals through the growing seasons of 1964 to 1966, pieces containing wood, cambium and bark, from dominant, intermediate, and suppressed trees. In these, the number of potential dividing cells in the cambial zone were counted, and the rate of cell division estimated by determining the percentage of cambial zone cells in mitosis for trees of different degrees of vigour (annual tracheid production) from each region during the early summer period of relatively constant mitosis activity. Within each region, cambial zone number was dependent on, and mitosis independent of, tree vigour. Rate of tracheid production was higher in the Alaska trees because of their high rate of cell division.

Flowering and fruiting

In two white spruce trees at St. Paul, Minnesota, meiosis began on 22 April 1961 and 21 April 1962, in each instance 5 days after the average daily temperature rose to about 10°C, and a white spruce near Cromwell, Minnesota, in the same 2 years began meiosis 2 days later than those at St. Paul after a period of 10 days in which the average daily temperature reached 4.4°C (Winton 1964b). Winton interpreted these results to mean that meiosis had about the same heat requirement in the two areas.

Flowering takes place in May (USDA Forest Service 1948), June (Forestry Branch 1961), or July (Hustich 1950) depending on geographical location and climate. Male and female flowering overlap in time, and are completed within 2-5 days (Wright 1953, Nienstaedt 1957, 1958).

3.3 Seed

Seeds are small (2.5-5.0 mm long), oblong, and acute at the base. Determinations of the average number of sound seeds per white spruce cone have ranged from 32 to 130 (Waldron 1965, Zasada and Viereck 1970). Owens and Molder (1984) suggested that an average of 30 full seeds per cone might be closer to the mark for British Columbia, although Eis and Craigdallie (1981) estimated an average of 8-20 seeds per cone for interior spruce in British Columbia. Based on 245,052 cones from nine locations in Ottawa Valley, Ontario, Wang and Haddon (1975) reported a great variation in the number of white spruce filled seed per cone: averaged 20.4, and ranging from 14 to 28. Certainly, values vary greatly among trees, regions, and years. In a random collection of Ontario white spruce cones, Tripp and Hedlin (1956) found an average of 140 seeds per cone, 92 of them centrally located; the seeds in the apical and basal parts of cones were infertile. The percentage of sound seed in the central zone varies from year to year, but is often about 50%, according to Tripp and Hedlin's data. According to the National Tree Seed Centre's white spruce seed yield data, the average seed per cone was 33 in 1971, 12 in 1972 in Ontario, and 33 in 1972 for seed from British Columbia.

White spruce grafts of northern Alberta origin made in 1979 and outplanted (three or four ramets of 12 to 17 clones) at four locations in Alberta and British Columbia in 1981 and 1982, which steadily increased percentage flowering from 23% in 1983 to 91% in 1987, produced 0 to 18.3 sound seeds per cone for 1985 and 1986 (Dhir and Schilf 1988). The 1986 seed crop at the local Grande Prairie site had clonal means for average number of seeds per cone varying from 1.8 to 11.6, mean 6.2; clonal differences were statistically significant.

Common causes of empty seed are lack of pollination, abortion of the ovule, and insect damage. Zasada (1980) stressed the effect of temperature on seed development. Two general effects of temperature are noteworthy: (1) death caused by subfreezing temperatures, and (2) the particular susceptibility of developing cones at the time of pollination. The first effect has been observed in Alaska. The second effect is more subtle and occurs when summer temperatures are not warm enough for developing seeds to mature. The phenomenon, which is a well-documented serious problem in northern Scandinavia, has also been observed in Alaska at higher elevations and in some areas north of the Arctic Circle.

The average weight per individual seed varies from 1.1 to 3.2 mg (Hellum 1976, Zasada et al. 1978). Youngblood and Safford (2008) reported great variation in numbers of seeds per kilogram: from 298,000 to 884,200 for white spruce. Hellum (1976) reported a range of 312,000-909,000 for white spruce. In British Columbia, Owens and Molder (1984) cited averages of 513,000 and 480,000 cleaned seeds per kg for white spruce and Engelmann spruce, respectively. Weight per 1,000 seeds in three consecutive years was 2.65, 2.09, and 2.43 g, with germination percentages of 30, 26.5, and 42, respectively (Rubanik and Parshina 1978). Based on the National Tree Seed Centre's record of 2605 seedlots (unpublished data, 2012), the average 1,000 seed weight is 2.27 g, ranging from 1.05 to 4.05 g.

Each seed is clasped by a thin wing two to four times as long as the seed. Seed and wing are appressed to the cone scale. Embryo and megagametophyte are soft and translucent at first; later the endosperm becomes firm and milky white, while the embryo becomes cream-colored

or light yellow. At maturity, the testa darkens rapidly from light brown to dark brown or black and mature seed "snaps in two" when cut by a sharp knife on a firm surface (Crossley 1953).

The sorting of germinable and non-germinable seeds by the incubation-drying-separation (IDS) method varied by white spruce seedlot in ease of application (Edwards et al. 1988): for some seedlots, sorting was easier before the seeds were stratified, whereas in other seedlots sorting was more effective after stratification. Other tests showed that IDS-sorted seeds returned to cold storage retained their viability well into a second year; even after 2 years of storage, decreases in germination were usually less than 10% (Edwards et al. 1988).

Seed maturation

Seeds mature within cones. Good seed can be obtained from cones collected before natural seed dispersal begins only if seed ripening is complete or well advanced. The effect is well illustrated by the results of a study in Newfoundland (Table 3.14). White spruce cones reached their maximum size after 800 growing degree days (GDD). Cone moisture content decreased gradually after about 1,000 GDD, but, contrary to Cram and Worden's (1957) suggestion, was not precisely related to seed ripeness. Significant (P = 0.05) reductions in yield of full seeds, seed size, and seedling yield were incurred from cones harvested prior to 1,100 GDD. Mosseler and Tricco (1991) found that maturation of white spruce cones was slower than that of black spruce cones; but an earlier study (Curran et al. 1987), also in central Newfoundland, had indicated the reverse. Be that as it may, GDD accumulations may well be a useful index of seed maturation.

Collection, extraction, and sowing procedures are well described in the *Woody Plant Seed Manual* (Bonner and Karrfalt 2008) and *Seeds of Woody Plants in the United States* (Safford 1974). Spruce seeds are more sensitive to adverse storage conditions than are those of pines and may lose viability if not extracted promptly (Allen 1957, Heit 1961, Schopmeyer 1974).

Recommended collection standards are given by Eremko et al. (1989): seven filled seeds/half cone, lustrous light brown cone color, opaque, firm storage tissue resembling coconut meat, glossy pale to dark brown seedcoat, light brown seed wing with a dark stripe along one edge, and a firm yellowish embryo occupying 90% of the cavity.

Cone colour also can be used to help determine the degree of maturation, but cones may be red, pink or green (Teich 1970). If cones are to be collected, their development should be monitored closely during the late stages of maturation so as not to miss the optimum collection period. The quality of white spruce seed collected two to four weeks prior to natural seedfall can be improved by holding them at 4°-10°C in ventilated storage. Collection and storage dates and conditions influence germination requirements and early seedling growth (Zasada 1973, Edwards 1977, Winston and Haddon 1981).

Table 3.14. Average cone and seed traits for white spruce cones collected in Newfoundland in 1988 on five separate occasions at intervals of 100 growing-degree-days; mean n = 24 trees/cone collection (after Mosseler and Tricco 1991, see publication for standard errors of the means).

	Average growing degree days accumulated by cone harvest date				
Cone, Seed Traits	**782.7**	**877.6**	**985.0**	**1104.4**	**1228.2**
Full seeds/cone (F)	7.4	15	18.3	21.5	17.4
Empty seeds/cone(E)	54.0	45.8	44.2	46.0	54.3
Ratio F:E	99.7	28.5	3.4	2.9	3.0
Weight 1,000 full seeds (g)	2.114	2.591	2.828	2.994	3.030
Cone dry weight (g)	0.87	0.91	0.95	0.93	0.93
Cone moisture (%)	30	31	33	35	41
Seedling yield (%)[a]	7	14	27	55	57

[a] Percentage of seedlings produced from 45 full seeds and surviving at 6 weeks of age.

A bushel (35 L) of cones, which may contain 6,500-8,000 cones, yields 6-20 ounces (170-567 g) of clean seed (USDA Forest Service 1948). In Canada, there are 165,000 white spruce cones in a hectoliter, ranging from 80,000 to 428,000 cones, which yielded an average of 72,687 g of clean seed, ranging from 176 to 18,124 g (unpublished data, National Tree Seed Centre, 2012).

Seed ripeness

Dormancy in white spruce seed has been attributed to an inhibition of embryo development by an influence generated by the seed coat or megagametophyte tissue (Caron et al. 1993). Patterns of maturation and ripening of seed vary among trees in a stand (Caron et al. 1989) and from year to year. Other variability might be associated with provenance; the degree of dormancy in white spruce seed varies considerably among seed sources (Zasada et al. 1978, Edwards 1987).

Seed dispersal

Seed dispersal begins after cone scales reflex with cone maturation in the late summer or early fall of the year of formation. Cones open at moisture contents of 45-70% and specific gravities of 0.6-0.8 (Cram and Worden 1957, Zasada 1973, Winston and Haddon 1981). Weather affects both the initiation and pattern of seed dispersal (Nienstaedt and Zasada 1990), but cone opening and the pattern of seed dispersal can vary among trees in the same stand (Zasada 1986). Even after dispersal has begun, cold, damp weather will cause cone scales to close; they will reopen during dry weather. Most seed falls early rather than late, but dispersal may continue through fall and winter (Zasada 1986), even into the next growing season (Rowe 1953). Roe (1946) found that about 80% of the seed was shed within 5 weeks after cones opened and that a further 13.5% fell during the ensuing month.

Seed dispersal occurs mainly in late summer or early fall (Waldron 1965), though Dobbs (1976) found that one-third of the medium to heavy seed crop in a stand of white spruce in central British Columbia in 1970 had not been dispersed by the end of October. The quality of the seed remaining longer in the cone was described by Crossley (1953) as not inferior in viability to seed

dispersed earlier, but both Waldron (1965) in Manitoba and Dobbs (1976) in British Columbia found that the seed released during peak seedfall was of higher quality than seed dispersed later. Nienstaedt and Zasada (1990) cited Waldron's (1965) statement that both early- and late-falling seeds are less viable than seeds falling during the peak period.

White spruce seed is initially dispersed through the air by wind. Both the initiation and pattern of seed dispersal depend on the weather (Nienstaedt and Zasada 1990), but these can vary among trees in the same stand (Zasada 1986). A few seeds are usually dispersed in August through much of the range, but most seeds fall in September (Waldron 1965, Dobbs 1976, Zasada and Viereck 1970, Zasada et al. 1978, Zasada 1985), and some seed falls in winter (Zasada 1986). Small amounts of white spruce seed are normally dispersed beyond 100 m from the seed source, but exceptionally seeds have been found more than 300-400 m from the nearest seed source (Zasada 1986). Similar dispersal distances for white spruce seed in Manitoba and Saskatchewan were cited by Rowe (1955).

The duration and distance travelled by an individual seed in its initial flight through the air depends on atmospheric conditions at the time of dispersal (Zasada and Lovig 1983), and the interaction of the seed and its wing with the airflow. If the rate of fall of white spruce seed is about 1.2 m/sec, as was determined for red spruce seed by Siggins (1933), then seed from the top of a tree 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). The seed of white spruce averages only about half the weight of red spruce (Safford 1974), however, and, notwithstanding Galileo, can be expected to fall more slowly and travel further than red spruce seed. Thereafter, seed may be blown long distances skittering or skating over snow crust or ice cover (Dobbs 1976). But in general, the amount of seed reaching a given area decreases rapidly with distance from the seed source. In a particular case, at 50, 100, 200, and 300 m distances from the seed source stand, the seed rain was determined as amounting to only 7, 4, 0.1, and 0%, respectively, of the seed falling inside the stand (Dobbs 1976, Zasada 1985).

White spruce recolonizing after an intense fire in the balsam fir-white birch climax region in northwestern Quebec occurred up to 2,000 m from a seed source (Galipeau et al. 1997).

Seed dispersal as measured by seed-trapping varies with seed year and from day to day. In Manitoba, Waldron (1965) found a maximum annual total seedfall of 1400/m^2 (59% filled) during a 10-year period. The seed rain exceeded 290/m^2 (40-71% filled) in 5 of the 10 years, and in 3 years the seed rain was less than 10/m^2 (2-36% filled). In Alaska, Zasada (1980) reported a maximum total seed rain of 4,000/m^2 in one stand over a period of 13 years; it exceeded 1000/m^2 in 3 years, 400/m^2 in 2 other years, and fewer than 100/m^2 in the remaining years. The amount of seed received and retained within a given area will vary with forest floor conditions in that area and its surroundings.

Waldron (1963) determined seedfall of 6.4 kg/ha, about 3.6 million seeds, between early August and late November 1961, from a "moderate" cone crop in a stand of mature white spruce in Riding Mountain Experimental Area, Manitoba. Seedfall in that same stand during a 10-year period totalled 28.9 million seeds/ha, 57% of them sound. Half of the total number of sound seeds falling during the decade fell in the heavy seed year of 1960 (Waldron 1965). Total

annual seedfall varied from 14 million to 25,000 seeds/ha. The percentage of sound seed each year ranged from 2 to 71%, and low values were generally associated with poor seed years (Waldron 1965). After a shelterwood cutting to favour spruce in mature stands of the pine-spruce phase in the Crowsnest Forest, Alberta, white spruce seedfall was estimated at 998,000/ha in the "mainly spruce" block and 613,000/ha in the "mainly pine" block, even though the seed year was rated "poor" by local foresters (Day 1970). Dominant and co-dominant white spruce in Waldron's (1965) study on the Riding Mountain, Manitoba, produced virtually indistinguishable average annual total and sound seedfall from 1954 through 1963 (Table 3.15). Far fewer intermediate trees produced cones, and those that did produced only half as much seed per tree as did more dominant trees.

Table 3.15. Average annual total and sound white spruce seedfall (thousands of seeds per tree), Riding Mountain Experimental Area, Manitoba (after Waldron 1965).

	All trees		Cone-bearing trees	
Crown class	**Total**	**Sound**	**Total**	**Sound**
Dominant	11	6	20	11
Co-dominant	10	6	19	11
Intermediate	3	2	10	5
Suppressed	1	<1[a]	6	3

[a] >1 in original

The dispersal of white spruce seed through trembling aspen forests was investigated by Stewart et al. (1998) by releasing artificial seed (confetti) from different heights on a meteorological tower, and also by determining the distribution of spruce regeneration along transects radiating from small, isolated patches of mature spruce seed trees. As might be expected, mean dispersal distance of confetti increased with height of release, and was influenced by whether the aspen bore leaves or not. Before leaf fall, most confetti landed close to and in all directions around the tower; after leaf fall, no confetti landed upwind of the tower, with peak densities occurring 15 m downwind. The rate of decrease in regeneration density with distance from patches of mature, seed-bearing white spruce was much less than that observed in the confetti release experiments. Regeneration densities were significantly greater downwind than in other directions, perhaps indicating the importance of stronger than average northwest, west, and southwest winds in dispersal of spruce seed. Modelling the observed distribution of regeneration suggested that long-distance (>250 m) dispersal might be important in maintaining a white spruce presence in the fire-prone boreal forest of western Canada.

Alexander and Edminster (1983) found that seed dispersed into clearcut openings in the central Rocky Mountains, Colorado, in stands of Engelmann spruce amounted to about 40% of the seedfall in the uncut stand and reached into the opening by up to 30 m, 10% as far as 90 m, and about 1% as far as 180 m. In central British Columbia, white spruce deposited 236,000 sound seeds/ha in 1 year to a distance of 220-300 m from the source (Dobbs 1976). In northwestern Ontario, Bell (1991) considered 46-62 m to be the maximum distance to which "adequate" quantities of white spruce will spread from a seed source. An insignificant amount of seed is dispersed by squirrels and rodents (Alexander 1958).

In nature, cones may fall in the year of their formation after seed dispersal (Kenety 1917), but some may remain on the tree for 1 or 2 years and still contain a modicum of viable seed (Roe 1952, Rowe 1953).

Seed dormancy

After Downie and Bewley (2000) postulated that dormancy may be imposed through a metabolic block in reserve mobilization, they set out to identify any impediment to raffinose family oligosaccharides (RFO) mobilization in dormant relative to nondormant seeds of white spruce. In order of abundance on a molar basis, desiccated seeds contain primarily sucrose and the first three members of the RFOs, raffinose, stachyose and verbascose. Upon radicle protrusion at 25°C, the contents of RFOs decreased to low amounts in all seed parts, regardless of prior dormancy status, and sucrose was metabolized to glucose and fructose, which increased in seed parts. During moist chilling at 4°C, RFO content initially decreased, stabilized, and then increased. In seeds that did not complete germination, the synthesis of RFOs at 4°C favoured verbascose, so that at the end of 14 (nondormant) or 35 (dormant) weeks, verbascose contents in megagametophytes exceeded the amount initially present in the desiccated seed. This was also true in the embryos of the dormant seedlot. In seed parts from both seedlots after months of moist chilling, stachyose amounts exceeded raffinose amounts. Upon radicle protrusion at 4°C, RFO contents decreased to amounts most similar to those present in seeds that completed germination at 25°C. Hence, the RFOs are utilized as a source of energy, regardless of the temperature at which white spruce seeds complete germination. The similarity of sugar contents in seed parts between dormant and nondormant seeds that did not complete germination persuaded Downie and Bewley (2000) that differences in sugar metabolism are probably not the basis of dormancy in white spruce seeds.

Seed dormancy in white spruce has also been attributed to an inhibition of embryo development by an influence effected by the seed coat or megagametophyte (Caron et al. 1993). Seed dormancy and post-harvest seed ripening were found in seed from all of 18 trees tested, but among the trees there was considerable variation (Caron et al. 1989). Patterns in maturation and ripening might vary from year to year, depending on weather, and other variability might be associated with provenance. Whereas seeds from 1984 cones stored for 6 weeks matured during storage and gave improved germination percentage and germination rate, seeds in cones collected from the same trees in 1988 had already attained maturity before the cones were collected, so that cone storage improved neither germination percentage nor germination rate (Caron et al. 1993). However, seed dormancy was present in both years.

Some white spruce seed lots show internal dormancy. Fresh mature seed of many species of conifers is naturally protected against fall germination by an internal dormancy. Some period of stratification is generally necessary to overcome that dormancy. Using fresh seed of local eastern Ontario provenance, Santon (1970) determined the effects of stratifying white spruce seed (Table 3.16).

Table 3.16. Effect of stratification on germination % of fresh white spruce seed (after Santon 1970).

Weeks of stratification	Germination % (after 60 days)[a]	% of best treatment
4	62.0a[b]	100
3	52.8a	85
2	54.8a	88
1	33.5b	54
0	4.8c	8

[a] Values reported for 60 days, but virtually identical for 45 days.
[b] Values of germination % differ significantly (P = 0.05) by Duncan (1955) multiple range tests unless followed by the same letter.

At one time, stratification at temperatures just above freezing in moist peat and sand was generally recommended for seed of white spruce (other than var. *albertiana*), for 60-90 days prior to sowing (USDA Forest Service 1948). However, Hellum (1968) showed that cold stratification decreased germination with increased duration of stratification, increased differences among seedlots, and produced inconsistent rates of germination. Also, contrary to the stated (USDA Forest Service 1948) differences in stratification requirements between the typical element and var. *albertiana*, seedlots that in all probability included typical element white spruce (Lesser Slave Lake origin) and the variety (southwestern Alberta origin) did not differ sufficiently in either germination or early growth to justify cold stratification for any of the samples (Hellum 1968). Certainly, some seedlots will germinate during stratification in fewer than 60 days (Rudolf 1950). In fact, while the seeds of most species of *Picea* germinate promptly without pretreatment (Schopmeyer 1974), the degree of dormancy in white spruce seed varies sufficiently with seed source to warrant routine testing of each seedlot by both stratified and non-stratified germination tests to determine the need for stratification (Zasada et al. 1978, Edwards 1987, International Seed Testing Association 1996). In the Prairie Provinces, stratification has not normally been required (Hocking 1972), but the uniformity of germination in some instances has been increased by cool, moist treatment in peat at 4.5°C for 21 days (Carlson 1983). Results from cold-soaking at 5°C for 7 or 14 days have in some cases been about as good as those obtained with 60- or 90-day stratification (Rudolf 1950). In another case, complete germination required cold-soaking for 30 days (Crossley and Skov 1951), but that seed was 13 years old, of unspecified provenance, and possibly not of typical element white spruce. However, prechilling at 3°-5°C for 21 days, which gives good results in both laboratory and nursery (Cram 1951, Wang 1974), is recommended by the International Seed Testing Association (1985); it is used operationally for all spruce seedlots at the Surrey Seed Centre, British Columbia (Bowden-Green 1988). Wang and Berjak (2000) noted that studies on white spruce seeds combining accelerated ageing with vigour testing and the use of moist chilling indicated that the cold treatment “consistently facilitated better germination than if chilling was not used”.

The beneficial effect of moist chilling may be attributed to the operation of inherent repair mechanisms (Wang and Berjak 2000), which, according to Roberts and Ellis (1982), require moisture contents greater than 25% in the presence of oxygen to be activated. Wang (1987)

found that natural restitution of intracellular damage in white spruce seed was possible at temperatures of 2°-4°C, and studies on physiologically dormant white spruce seeds showed that moist chilling accelerated that rate of germination. Germination is sluggish at temperatures of less than 15.6°C (Heit 1949, McLeod 1953).

Lengthy stratification is important where nursery soil temperatures are less than optimal. To facilitate sowing, seeds should be surface-dried at the end of stratification.

Hybrid seed may need treatment similar to that recommended for Engelmann spruce. Pre-testing to determine seedlot characteristics is highly desirable.

Recommended procedures for long-term storage of spruce seed were described by Simpson et al. (2004).

Germination

The period of germination under field conditions is mid-May through early August. Given adequate moisture, seeds will germinate as soon as soil surface temperatures are warm enough. Germination is mostly complete by early July. Some white spruce seed is able to retain viability even after several cycles of wetting and drying (Zasada and Gregory 1969, Waldron 1966, Hellum 1972b). Spring-sown seeds germinate rather later than seeds fall-sown the previous year. White spruce germinants developing after the middle of July have less chance of surviving than do germinants originating earlier in the growing season (Hellum 1972a, Ganns 1977, Zasada et al. 1978).

However, two basic patterns of white spruce seed germination have been observed in interior Alaska (Zasada 1980). In one pattern, germination begins in mid-late May and occurs with little or no interruption over a 3–4-week period, with 90% or more of germination occurring by late June. The second basic pattern begins as in the first pattern, but is interrupted by adverse conditions in June or early July, resuming in late July or early August with the onset of more favourable conditions. Low temperatures are thought to depress the first germination peak at high elevations (Zasada 1980).

Experimentation to determine cardinal temperatures for the germination of white spruce seed of six provenances showed that temperatures below 7.2°C and above 35°C virtually eliminated germination; and the germination response to temperature was influenced by the environment of the seed collection area (Fraser 1971) (Table 3.17).

Table 3.17. Lower (LCT), optimum (OCT), and upper (UCT) cardinal temperatures (°C) for laboratory germination 28 days after seeding (after J.W. Fraser 1971).

Provenance	Latitude N	LCT[a]	OCT[b]	UCT[c]
Davie Lake, B.C.	54°32′	7.2	12.8–15.6	32.2
Moosonee, Ontario	51°16′	7.2	12.8–15.6	32.2
Acadia, New Brunswick	46°00′	10	18.3–23.9	35.0
Petawawa, Ontario	46°00′	10.0	18.3–21.1	35.0
Napanee, Ontario	44°08′	10.0	18.3–21.1	32.2
Chilson, New York	43°5′	10.0	12.8–18.3	29.4

[a] Temperature below which germination was essentially nil.
[b] Temperature at or within which maximum germination occurred.
[c] Temperature above which germination was essentially nil.

In laboratory germination testing, International Seed Testing Association (1996) recommends 21-day double tests, with 21-day prechill and no chill and germinates at alternating temperatures of 30°C with light for 8 hours, and 20°C at night in darkness for 16 hours.

Exogenous applications of ascorbic acid (AA) were known to increase the conversion frequency of somatic embryos of white spruce. To determine whether ascorbic acid alters purine metabolism during the early phases of embryo germination, Stasolla et al. (2001a) investigated the relative rates of purine salvage and degradation by following the metabolic fates of exogenously applied [8-14C] adenine, [8-14C] adenosine, and [8-14C] inosine, as well as the activities of several key enzymes. They demonstrated that both the salvage and the degradation pathways operate during germination. Specifically, adenine and adenosine were mainly salvaged to nucleotides and nucleic acids, whereas an appreciable amount of inosine was degraded to CO_2 and ureides. Comparisons of purine metabolism between control and AA-treated embryos showed that exogenous applications of ascorbic acid enhanced the ability of the embryos to take up adenine and adenosine throughout the germination period. Furthermore, the higher enzymatic activities of adenosine kinase and adenine phosphoribosyltransferase were responsible for the larger proportion of adenine and adenosine being salvaged in AA-treated embryos compared with control embryos. Thus, there was a positive correlation between the ability to anabolize purine precursors and successful embryo conversion.

Ashihara et al. (2001a) looked specifically at pyrimidine metabolism at various stages of somatic embryo development in white spruce. The contribution of the de novo and the salvage pathways of pyrimidine biosynthesis to nucleotide and nucleic acid formation and the catabolism of pyrimidine was estimated by the exogenously supplied [6-14C] orotic acid, an intermediate of the de novo pathway, and with [2-14C] uridine and [2-14C] uracil, substrates of the salvage pathways. The de novo pathway was very active throughout embryo development. More than 80% of [6-14C] orotic acid taken up by the tissue was utilized for nucleotide and nucleic acid synthesis in all stages of this process. The salvage pathways of uridine and uracil were also operative. Relatively high nucleic acid biosynthesis from uridine was observed,

whereas the contribution of uracil salvage to the pyrimidine nucleotide and nucleic acid synthesis was extremely limited. A large proportion of uracil was degraded as $^{14}CO_2$, probably via beta-ureidopropionate. Among the enzymes of pyrimidine metabolism, orotate phosphoribosyltransferase was high during the initial phases of embryo development, after which it gradually declined. Uridine kinase, responsible for the salvage of uridine, showed an opposite pattern, since its activity increased as embryos developed. Low activities of uracil phosphoribosyltransferase and non-specific nucleotide phosphotransferase were also detected throughout the developmental period. These results suggest that the flux of the de novo and salvage pathways of pyrimidine nucleotide biosynthesis in vivo is roughly controlled by the amount of these enzymes. However, changing patterns of enzyme activity during embryo development that were measured in vitro did not exactly correlate with the flux estimated by the radioactive precursors. Therefore, other fine control mechanisms, such as the fluctuation of levels of substrates and/or effectors may also participate in the real control of pyrimidine metabolism during white spruce somatic embryo development.

Results obtained by Stasolla et al. (2001b) suggest that although both the salvage and de novo pathways operate in germinating white spruce somatic embryos, their contribution to the enlargement of the nucleotide pool appears tightly regulated as germination progresses. The metabolic fate of [2-14C] uracil and [2-14C] uridine, intermediate metabolites of the salvage pathway, as well as [6-14C] orotic acid, a central metabolite of the de novo nucleotide biosynthesis, was investigated to ascertain changes in pyrimidine metabolism in germinating white spruce somatic embryos. An active uridine salvage was found to be responsible for the enlargement of the nucleotide pool at the inception of germination. Uridine kinase, which catalyses the conversion of uridine to uridine monophosphate (UMP), proved to be very active in partially dried embryos and during the early phases of imbibition. The contribution of uracil to the nucleotide pool was negligible since a large amount of radioactivity from [2-14C] uracil was recovered in degradation products. As germination progressed, the decline of the uridine salvage pathway was concomitant with an increase of the de novo biosynthetic pathway. The central enzyme of the de novo pathway, orotate phosphoribosyltransferase, showed increased activity and contributed to the larger amount of orotate being anabolized.

3.4 Seedling development

Seedlings are most susceptible to injury during the first year following germination. Survival through the first growing season and the following dormant season is affected by the time at which germination occurs, as this will determine the time available for growth and the range of conditions to which the seedling is exposed during the first year (Zasada 1980). In one case, white spruce seed that germinated in May/June showed 54% and 48% survival through the first summer and winter, respectively; comparable survival for seedlings that germinated in July were 83% and 20%, and for August germination 71% and 16%. Seedlings arising from late germination have little time in which to die before winter, but they are not well equipped to survive the winter.

In the greenhouse, seed sown and covered with plastic and sacking germinated and developed radicles up to 13 mm long within 5 days (personal observation). Under Growlux illumination

18 hours per day, and with watering every second day, seedling roots up to 2 cm long developed within a further 14 days. Cotyledons numbered seven or six in 75% of cases, and five or four in 25%.

White spruce exhibits two forms of shoot growth: (1) indeterminate ("free") and (2) determinate. After germination, growth occurs in an indeterminate manner, with new needles developing continuously from primordia initiated at the apex (Pollard 1974b). The onset of short-day photoperiods brings indeterminate growth to an end, whereupon bud scales are formed. New needle primordia are then initiated and accumulated inside the bud ready for deployment the following spring, both in Norway spruce (Korody 1937) and white spruce (Jablanczy 1971).

Thereafter, according to Jablanczy (1971), seedling white spruce exhibit five growth phases: primordial shoot elongation of preformed stem and needles, beginning at the time of bud burst; free growth of additional non-preformed stem with new needles on it; bud scale formation for the terminal bud "as during the first phase on old trees"; and primordial shoot formation starting immediately after the formation of bud scales and proceeding intermittently throughout the fifth, overwintering, phase (Figure 3.13). Jablanczy (1971) stated that indeterminate growth is the sole growth mode in germinants and is "typical on young seedlings", though, as Pollard (1974b) noted, there is no doubt that the overwintering bud rather than free growth is the major determinant of growth for the following season. Pollard commented that, in his experience, indeterminate growth after flushing in second-year seedlings was more characteristic of black spruce than of white spruce. Logan (1969) and Jablanczy (1971) postulated that the free-growth phase gradually diminishes and is lost by about 5-10 years after germination. Nienstaedt and Zasada (1990), however, noted that their observations suggested that it would be "extremely rare" in seedlings older than 5 years. Pollard (1974b) also commented on the tendency of free growth to become less pronounced in older seedlings and to disappear when seedlings are flushed under a short-day (8 hour) photoperiod.

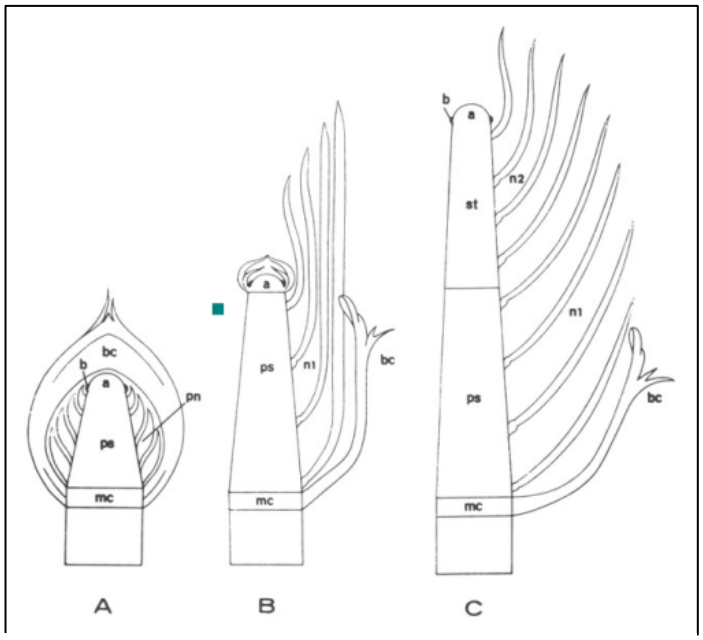

Figure 3.13 Comparison of shoot development from the spring primordium (A), in mature trees (B, after Korody 1937) and young seedlings (C) Legend: bc–bud scale coat, b–buttress, a–apex, pn–primordial needle, ps–primordial stem, mc–medullary cavity, st–stem portion formed by free growth, n2–needles formed *de novo*.

First-year seedling height influenced terminal bud development in an investigation by Pollard (1974b). The effect apparently depended on the age (6 through 16 weeks in increments of

2 weeks) when buds were initiated (Figures 3.14, 3.15). A 1 cm advantage in height resulted in 35 additional primordia in seedlings initially 6 weeks old, but only six primordia in seedlings initially 16 weeks old. Pollard (1974b) suggested that the similarity between the two families of regressions in those two figures indicates correlation between the number of needles initiated and subsequent height growth (in germinants).

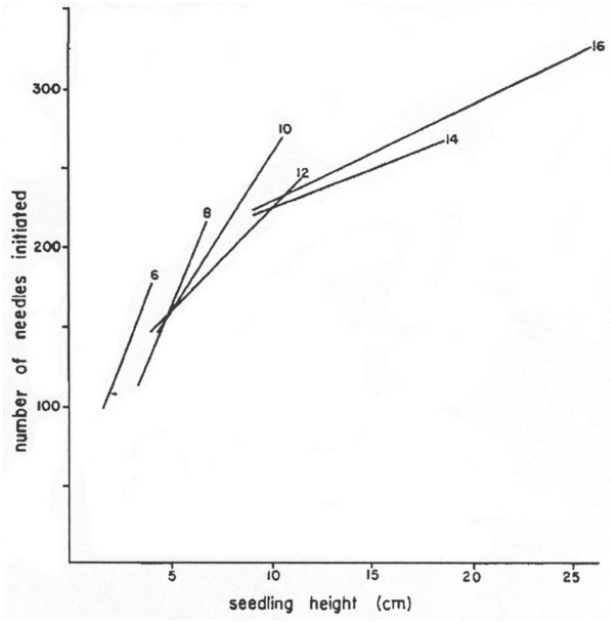

Figure 3.14. The influence of seedling size (height) on needle initiation in different age groups (6-16 weeks) of white spruce. For regression equation parameters see Pollard 1974b

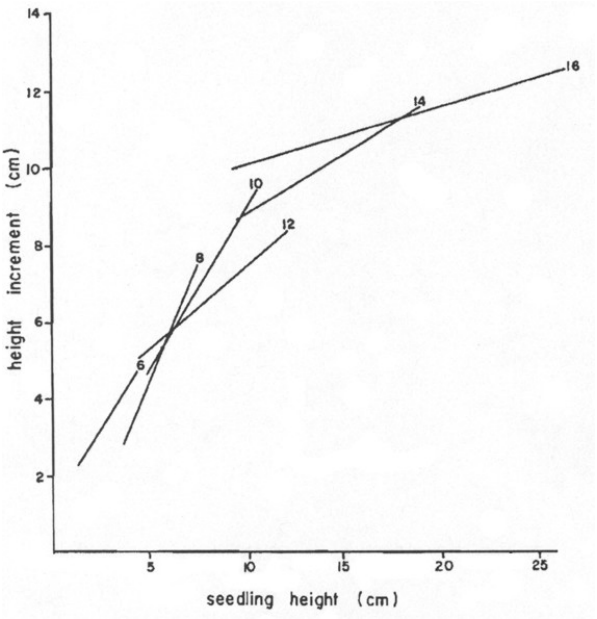

Figure 3.15. The influence of seedling size (height) on subsequent increment (height) in different age groups (6-16 weeks) of white spruce. For regression equation parameters see Pollard 1974b.

Growth of seedlings in the nursery is much more rapid than that of natural regeneration. At St. Williams Nursery, at about 43°N in southwestern Ontario, the growth curve of white spruce in the first growing season, though curvilinear, does not diverge greatly from linearity; in the second growing season, the curve is linear even through November (Armson 1960). The relationships between dry weight and chronological time (R = 0.99) and dry weight and degree days (R = 0.97) were significant (P = 0.01). After germination, first-year growth of the various component organs (cotyledons, hypocotyl dry weight and the logarithm of root dry weight was linear, but for the second year of growth, the curvilinear relationship indicated that the rate of shoot growth was decreasing in relation to the rate of root growth during the second growing season.

In undisturbed forest, decayed stemwood provides the most favourable seedbed for seedling germination and survival. Seedlings have access to a dependable supply of moisture (Place 1950), and, because they tend to be positioned somewhat above the general level of the forest floor, are less subject to smothering by leaves or minor vegetation. The position of seedlings on rotted wood, logs or stumps, also tends to confer other advantages compared with the general forest floor: more light, higher root zone temperatures, and better mycorrhizal development (Baldwin 1927, Mork 1933, Rowe 1955). Phelps (1940) reported that a survey in the Porcupine Hills, Manitoba, found that 90% of all spruce seedlings were rooted in rotted wood. Mineral soil seedbeds are receptive, too, and are generally moister and more readily rewetted than the organic forest floor.

Growth rates of naturally regenerated seedlings are generally higher on mineral soil seedbeds than on rotted wood, which though favourable with regard to moisture is less so in relation to nutrient supply. In the Porcupine Hills Forest Reserve, Manitoba, 7-year-old white spruce averaged 61 cm on a mineral soil seedbed, but only 14 cm on rotted wood (Rowe 1955). Root development was also stronger on mineral soil seedbeds, where one 7-year-old seedling on a very moist site had lateral roots 90 cm long and a taproot 15 cm deep, and another seedling on a drier site had 40-cm laterals and a taproot of more than 60 cm. In contrast, the root systems of seedlings on rotted wood were weakly developed, and tended to remain within the rotted wood, showing little sign of exploiting the mineral soil beneath (Rowe 1955). Even after site preparation, a white spruce seedling might commonly attain a total height of no more than 5 cm or so after three growing seasons (Rowe 1955). Growth in nurseries is much faster.

Hypocotyl

Hypocotyls of 6-week-old white spruce seedlings were red (Munsell Color Chart 2.5R 4/8) (Fowler 1966).

Cotyledons

Cotyledons, the foliar portion or first leaves of the embryo, are horizontal, almost straight (Fowler 1966) in the germinant. The number of cotyledons varies but in my experience is commonly six or seven, occasionally as few as four. In one study, cotyledons numbered seven or six in 75% of germinants, five or four in 25%.

Dallimore and Jackson (1961) noted that “cotyledon number varies from 4 to 15”, possibly referring to the genus.

3.5 Root system form

The root system of white spruce is highly variable (= highly adaptable, cf. Wagg 1964, 1967), responding to a variety of edaphic factors, especially soil moisture, soil fertility, and mechanical impedance. On soils that limit rooting depth, the root system is plate-like, but it is a common misconception to assume that white spruce is genetically constrained to develop plate-like root systems irrespective of soil conditions (Sutton 1969b). In the nursery, or naturally in the forest, white spruce usually develops several long "running" roots just below the ground surface (Mullin 1957); often four to six of these major lateral roots, commonly called *long roots*, are distributed irregularly around the tree. Asymmetrical root systems are common and unrelated either to crown symmetry or topography (Eis 1970). The ratio of length of major laterals to tree height reached a maximum of 4:1 in white spruce 3-4 years old (Eis 1970). Sinker roots (Sutton and Tinus 1983) are invariably present (Sutton 1968), though described by Eis (1970) as "infrequent and short", and are rarely longer than 20 cm. Mean total length of roots of white spruce excavated four or five growing seasons after outplanting in eastern Ontario varied with site: 1706 cm and 405 cm on clay sites, 1,275 cm and 2,288 cm on loam sites, and 2,906 cm on a sand (Sutton 1968); in 10-year-old white spruce in interior British Columbia, the total length of roots averaged 165 m (Eis 1970). Place (1952) found that 1-year-old seedlings of white spruce raised in sand flats of medium sand had rooted more aggressively and with greater variability than had red or black spruces. But the 2-year performance of red spruce in a small experiment in southern New Brunswick was rather better against eastern bracken fern (*Pteridium aquilinum* ssp. *latiusculum* (Desvaux) Hultén ex R.T. Clausen) competition than that of white spruce (Place 1952).

The structure of the tracheids in the long lateral roots of white spruce was found to vary with soil nitrogen availability (Krasowski and Owens 1999). Seedlings were grown in soil at three levels of nitrogen (10, 50, and 125 ppm N) and dormant first-order laterals with intact tips were sampled. Root diameter and surface area occupied by the xylem. In the two higher nitrogen treatments, secondary root development was more advanced near the root tip than in the low nitrogen treatment. Non-conducting space within the xylem occupied 10-13% of its cross-sectional area. Tracheids of the primary xylem were larger, and had larger lumens but thinner cell walls than those of the secondary xylem. Tracheids of low nitrogen seedlings had smaller total cross-sectional area, less lumen, and less cell wall surface area than in the other treatments. Tracheid diameter means were between 19-20 µm in the high and medium nitrogen and 15.2 µm in the low. The range was 4.5-51.3 µm. Tracheid length was not significantly affected by N level; the mean length was 1,000 µm, with a range of 110-3,530 µm. Pit-border diameters, which ranged between 4.1 and 20.6 µm (mean 10-11 µm), were also unaffected by N treatment. If the capacity for axial water transport in spruce roots is affected by soil nitrogen availability it would be by its impact on conduit diameter and possibly on the pit-membrane pore sizes, but not by changes to conduit length and the size of the pit membrane surface area (Krasowski and Owens 1999).

The root systems of Siberian spruce (*Picea obovata* Lede.) and several associated species on four mountainous sites in northern Siberia characteristically develop a superficial layer of adventitious roots above the main roots in response to permafrost (Yarmishko and Dem'yanov

1983). White spruce develops similar root systems on soils where depth penetration by roots is limited.

Even the root systems of naturally regenerated seedlings are quite commonly deformed, especially where soil and site conditions produce slow growth, impede root penetration, and promote incipient smothering of small seedlings. Development of the roots of natural seedlings, as of the tops, is apparently stronger on mineral soil than on decayed wood. Seedlings examined by Rowe (1955) on a very moist burned area, lightly shaded by young aspen, had extensively developed lateral roots. One 7-year-old seedling had roots extending 90 cm from the base of the stem, though the tap root penetrated only about 15 cm; on drier sites, downward development was greater, and, for instance, the tap root of a typical 7-year-old seedling penetrated more than 60 cm, while lateral root spread was only 40 cm. In contrast, the root system development of young white spruce growing on decayed wood in shaded forest stands was weak; roots tended to grow along lines of decay in logs and stumps, and there was little sign of seedling roots leaving the decayed wood for the soil beneath (Rowe 1955). Decayed wood usually holds more available moisture than ordinary forest floor humus (Place 1950). The wood of white spruce seems to be more suitable as a seedbed than that of aspen because of its greater retentivity of moisture owing to bark and wood characteristics. Furthermore, there is no great drain by other plants on the moisture supply as plants of relatively few other species seem able to grow on rotted wood. These seedlings also have the advantage of a somewhat elevated position which tends to prevent smothering under hardwood leaves in the fall, and generally improves light and probably temperature (Mork 1933) conditions compared with adjacent forest floor, while the generally prominent development of mycorrhizae among seedlings growing on decayed wood confers protection from damping-off fungi (Baldwin 1927).

Root systems of 12-year-old white spruce growing on a research site at Wonowon, British Columbia, within the boreal white and black spruce biogeographic zone, were excavated from mineral-capped inverted mounds and compared with those growing in untreated ground (control) to determine whether they were developing root systems of adequate size and structure to support the maturing tree (Heineman 2000). Mound seedlings were larger than seedlings growing in the untreated control and their root systems were also proportionally larger. Mound seedlings had more and larger structural roots (main laterals) than control seedlings; they had a greater number of roots of all sizes. Roots were distributed evenly around the stems of both mound and control seedlings. The average depth of main lateral roots (3-5 cm) and their average spread from the stem (150 cm) were similar for seedlings of both treatments. The roots of mound seedlings readily egressed beyond the mound environment, except where mounds were located in hygric depressions.

Instances where 60- to 80-year-old white spruce had practically eliminated birch and poplar from mixedwoods “apparently through root competition” were attributed by Rowe (1955) to the extensive shallow lateral roots from which “sinkers” descend, which “gives spruce the advantage over the deeper-rooted hardwoods in competition for moisture descending from the surface”.

The system of shallow lateral roots has lured some observers to assume that the root system of white spruce is shallow in its entirety. Many writers have believed rooting depth to be under rather rigid genetic control, and spruces are widely regarded as having shallow, plate-like, root systems. White spruce has been so described by Cheyney (1942), Westveld (1949), Forestry Branch (1961), Mullin (1963), and Farrar (1995); and *Picea* generally by Toumey (1929) and Edlin (1949). Place (1955) observed that "Spruce and Fir often seem to remain very shallow-rooted throughout their lives regardless of the morphology of the soil profile". Kenety (1917) considered spruces to be characteristically shallow-rooted, and pines characteristically deep-rooted, right from the seedling stage, though the data presented in support of this view seem mainly to reflect initial growth-rate differences between spruce and pine.

Many other workers have emphasised the great variability in root system form of spruces. Pulling (1918) referred to the rigid adherence to specific root system forms in tamarack, jack and white pines, and black spruce, but he also noted that "the shallow-rooted white spruce" showed considerably greater plasticity in root system form. In fact, white spruce is similar to Norway spruce, which Hartmann (1951) studied and about which he concluded that "on all sites with easily permeated soil through which oxygenated water continually percolates, Spruce generally develops a deep-seated heartroot system", whereas on sites with average surface-soil dryness and downward increasing soil moisture, long tap and heart roots develop. Bornebusch (1931) had previously noted that Norway spruce, "ordinarily regarded as shallow rooted", rooted deeply on some Danish heaths. Similarly, Wilton (1964) observed that the root system of white spruce in Labrador is fairly deep and surprisingly windfirm. I have observed white spruce rooting to depths of more than 1.2 m in upland mixedwoods on deep fertile loams in Ontario, as did Stoeckeler (1938) in Manitoba in calcareous soils at two widely separated locations. Vigorous roots of white spruce planted 3 years earlier as 3+0 stock on a fertile Lucas silt loam (Cline 1961) in upstate New York that were traced to a depth of 92 cm showed every sign of going deeper (Sutton 1967). Wagg (1967) found four root system forms among 30- to 90-year-old white spruce in Alberta and the Northwest Territories of Canada: elongated tap root, restricted tap root, monolayered, and multilayered, and "a myriad of intervening forms".

The fact is that spruces are *not* characteristically shallow-rooted. That reputation stems partly from the easily observed surface laterals that are almost invariably present, but mainly from their ability to occupy sites where edaphic limitations restrict rooting to surface layers. When a spruce on such a site is blown over, the great plate-like root system is commonly thrown up to stand vertically, an arresting and remarkable sight, but typical only in certain circumstances.

The first response from someone asked to describe roots would commonly be that "roots grow down". Undoubtedly some do, but horizontal growth is much more usual, and upward growth is by no means uncommon. White spruce planted in furrows about 25 cm deep in loamy fine sand 50-168 cm deep over silty clay loam in the Hiawatha National Forest in Michigan's Upper Peninsula developed roots into mixed surface soil and organic material ridges formed by furrowing: "Large roots often grew upward into the ridges" (Day and Rudolph 1974).

Roots

A geotropic radicle emerges from the seed and becomes a tap root, which Eis (1970) observed to persist as a strong tap root mostly in root systems that were asymmetrical or possessed of few lateral roots, as also noted by Rowe (1964). With age, lateral roots become increasingly prominent, and the tap root decreases in prominence, but root system form is greatly influenced by soil texture and soil fertility (Sutton 1969b). On loamy sand, white spruce rooting was very shallow, but the root systems of white spruce on silty clay loam were "generally profusely branched with as many as 40 or 50 vertical roots over 1 in [2.5 cm] in diameter" (Paine 1960), while the roots of white spruce in soils with permafrost near the surface commonly develop ovoid cross sections, the result of greater secondary thickening on the upper side (Benninghoff 1952). The adaptability of white spruce root systems enables them to function in soils with permafrost at shallow depth (Pulling 1918), though "limitations imposed on the anchoring functions of tree roots in such soils are obvious and are demonstrated by the relative ease with which the trees are overturned" (Benninghoff 1952). Heterorhizy (Sutton and Tinus 1983) is expressed in the development of both "long" and "short" roots (Wilcox 1964): long roots are sharp-pointed, white, shining, turgescent when first formed, relatively long, sparsely branched, relatively fast-growing during one or more periods of sustained growth, and capable of secondary growth; short roots are non-woody and of determinate growth. Root hairs may or may not occur; no specific reference to root hairs in white spruce has been found, but Engler (1903) determined that, in Norway spruce, root hairs were sometimes present, and sometimes not. Mycorrhizae are common, and play an important nutritional role, especially in regard to phosphorus, for spruce growing on certain soils of moderate or low fertility.

Unless fertilized adequately with phosphorus, the inhibition of mycorrhizal development in coniferous seedlings growing in fumigated soil is reflected in poor growth and low levels of plant P (Henderson and Stone 1970). In the absence of mycorrhizae, young seedlings seem able to take up P only when it is present in inorganic form at high concentration in the soil solution (Campagna and White 1969). In those circumstances, good growth does not depend on mycorrhizae. White spruce seedlings grown with superphosphate fertilizer added to fumigated soil showed very good growth and color, and good root system development, but without mycorrhizae (Campagna and White 1969). The dramatic effect on the growth and appearance of white spruce seedlings growing on sand that tested zero for P after spontaneous development of mycorrhizae is noted in Section 4.7, Nutrition.

The basic specific gravity of root wood is usually less than that of stem wood (Timell 1986). In Norway spruce, at least, coarse and fine roots differ anatomically in that the tracheids in coarse roots are shorter, have smaller cross sections and thicker cell walls than tracheids in fine roots (Eskilsson 1969).

A modified form of sprouting has occasionally been observed to occur in white spruce. New shoots can form in the vicinity of the branch-stem junction on stumps 8-12 cm in diameter, provided that living branches are present on the stump (Zasada 1986).

The rooting of stem cuttings within the genus *Picea* has long been considered difficult, but there is considerable variation among species. Girouard (1970) took short (5 cm) and long

(10 cm) stem cuttings from 2+2 seedlings of white, black, red, and Norway spruces, and found that after 11 weeks short cuttings gave significantly (P= 0.05) higher per cent rooting for all species than did long cuttings, but that cutting length had no effect on the mean number of roots formed per cutting after 11 weeks. White and black spruces differed little from each other and were intermediate between Norway spruce, "always the easiest" to root, and red spruce, the most difficult. These results might require reassessment in view of Girouard's (1972) subsequent demonstration of significant variation in the rooting ability (95.2–3.3%) of stem cuttings from clones of a superior provenance of white spruce.

In an Italian study, cuttings taken monthly from 4-year-old dwarf Alberta spruce (*Picea x albertiana* S. Brown) showed pronounced seasonal changes in rootability and in the activity of one or more endogenous rooting substances (Tognoni and Lorenzi 1972, Tognoni et al. 1977). Rooting was poor among cuttings taken through the winter from October through January and then increased to a maximum in cuttings taken in April. Similar results had been reported for blue spruce (*Picea pungens* Engelm.) (Thimann and Delisle 1942) and Douglas-fir (*Pseudotsgua menziesii* (Mirb.) Franco) (Roberts and Fuchigami 1973). Tognoni and co-workers confirmed an earlier finding that white spruce contains an acidic fraction or fractions that have growth-inhibiting activity as tested with wheat coleoptiles, and root-promoting activity as tested with mung bean cuttings. Tognoni et al. (1977) thought it probable that abscisic acid (ABA) was the major active substance in the acidic fraction, but, while ABA has been known to stimulate the rooting of cuttings (Chin et al. 1969, Basu et al. 1970). Tognoni et al. (1977) could not reconcile the seeming anomaly in their work that both activities in the acidic fraction for root promotion and growth inhibition were highest in the November cuttings when rooting was virtually nil.

Natural layering in white spruce has been reported on shallow soils in Minnesota (Cooper 1911); on sandy loam with a 5 cm coniferous litter layer in New York (Katzman 1971); in a poorly-stocked 35- to 40-year-old plantation in New York (Stone and McKittrick 1976); eastern Ontario (Bannan 1942); and an open old-field stand in Nova Scotia (Stone and McKittrick 1976). However, it is common only near the treeline (Zasada 1986), e.g., where layering has been reported in open stands on the east coast of Hudson Bay and James Bay by Hustich (1950), Maycock (1968), and Payette and Boudreau (1972). Larsen (1965), however, observed layering to be common in apparent white × black spruce hybrids and "rarely if at all" in white spruce. The usual location of the layering root origin "is just outward (distal) of old terminal bud scars at the site of the 'medullary crown' or 'collenchyma plate' in the pith, that marks the terminal bud base" (Stone and McKittrick 1976). The position of the terminal bud in white spruce is marked in the pith by a crown of thick-walled cells, above which the pith cells are in regular longitudinal rows, and below which they are disordered and more or less broken down to form a cavity (Lewis and Dowding 1924). For layering to occur, live lower branches must persist in close and stable contact with soil. Bannan (1942), for instance, searching widely for layered white spruce in eastern Ontario, found very few, for although many trees had branches to the base, "these were rarely covered by soil and hence little opportunity was provided for rooting". Furthermore, while layering ability may vary among individual trees, both genetically and otherwise, the trait has evident survival value in habitats where regeneration by seed is uncommon.

The ease with which white spruce develop adventitious roots is further evidence supporting the view that white spruce, in the appropriate conditions, is able to regenerate by layering. In a study of deep planting in New York, half of the 3+0 white spruce that were planted 5 or 10 cm deeper than they had been growing in the nursery developed adventitious roots within 14 weeks after planting (Sutton 1968). The adventitious roots originated most commonly from the buried stem, but in several cases a root originated on a former lateral shoot that was buried at planting.

Artificial air-layering of white spruce, investigated by removing needles from a 3-15 cm band near the base of 1-year-old branches, girdling near the middle of the needle-free band, enveloping the band with moist sphagnum fortified with various growth regulators at various concentrations, and initiating treatments at various times during the growing season, occurred without significant difference attributable to either the species of growth-regulator or the position of branch on the tree (Feucht et al. 1961). Significant differences were observed in rooting capacity among 15 white spruce trees, each of which had six branches prepared for air-layering; nine of the trees yielded rooted marcots. Time of application of air-layer treatment significantly affected rooting; air-layers applied on May 1 produced more rooted stems in 100 days than did those applied in April, May, July, and August. Mean root length at the end of 100 days was significantly greater for air-layers applied June 1 than those applied in April, May, June, and August; and air-layers applied April 1 and May 1 developed mean root lengths greater than did air-layers applied July 1 and August 1 (Table 3.18).

Feucht et al. (1961) compared rooting levels with local temperature data and found that there was “a critical period for the initiation and development of roots at the beginning of the treatment period”. Rooting was relatively poor when “maximum and minimum daily mean temperatures” exceeded 80°F (26.7°C) or were lower than 60°F (15.6°C) at the time the air-layers were applied. Rooting was greatest when air-layers were applied at the beginning of May, when temperatures were averaging 70°-75°F (21.1°-23.9°C) with a very gradual increase to temperatures above 80°F (26.7°C). Mean root length, however, seemed to be “favoured by higher temperatures and hindered when temperatures decreased during the treatment period” (Feucht et al. 1961). Temperatures *inside* the air-layer wrappings were not reported and seem not to have been measured. Survival and continued growth of rooted air-layers planted in September was 100% after 70 days; those planted in July had a survival rate of 52% after 130 days. These data on air-layering, while somewhat ambiguous, nevertheless show patterns of rooting propensity and within-species variation in rooting. Armson (1960) found “no definite indication of periodicity in the growth of the roots” of 2-year-old white spruce in either of two growing seasons.

Studying the response of the stem and structural roots of white spruce to an increase in wind exposure, Urban et al. (1994) measured ring widths in the roots and stems of trees in a 120-year-old boreal mixedwood stand (control) and at the edge of a road built through the stand 16 years previously (released). Response indices were calculated by subtracting the ring indices of control trees from those of the released trees, and allocation indices were calculated by subtracting the ring indices of stems from those of roots. The change in allocation between

stem and root was examined by subtracting the indices of control trees from those of released trees. Urban et al. (1994) found that the rate of stem diameter growth remained unchanged for 3-9 years, whereas root diameter growth increased, suggesting that preferential root growth occurred for some years following increased exposure, which might help stabilize trees against increased wind exposure.

Table 3.18. Mean rooting results of white spruce air-layers 100 days after application (after Feucht et al. 1961).

	Application				
	April	**May**	**June**	**July**	**August**
Total rooted[a]	5.6*	8.2*	5.8*	0.6*	3.0*
Percent rooted	12.44	18.21	12.88	1.33	6.66
Roots/rooted marcot	2.82	3.60	4.60	3.00	3.75
Mean root length mm	10.84**	13.43**	20.96**	4.06**	4.58**

[a] As reported by Feucht et al. (1961), who also stated "225 air-layers per time", the first and second rows pose difficulties: values in the row marked "total rooted" can be obtained by expressing second-row values as percentages of 225, i.e., reversing column one designations. But the difficulty remains that "total rooted" can hardly be anything but integers. * and ** indicate P = 0.05 and P = 0.01 significances, respectively.

Mycorrhizae

Mycorrhizae most commonly occur on roots high in carbohydrates, which normally only occurs if protein synthesis is lagging behind carbohydrate synthesis, e.g., where a moderate shortage of available soil nitrogen and phosphate obtains (Russell 1961).

Higginbotham and Navratil (1987) inoculated white spruce and lodgepole pine (*Pinus contorta* Dougl. ex Loud) seedlings with the ectomycorrhizal fungus, deceiver (*Laccaria laccata* (Scopoli) Cooke), which were then grown under 340 or 600 ppm CO_2 for 18-19 weeks. Plant growth, numbers of infected root tips and total non-structural carbohydrates were measured. Enhanced CO_2 increased biomass production in uninoculated seedlings, but there were no differences in plant size in inoculated trees. Root:shoot ratios in inoculated seedlings were greater than those in uninoculated trees regardless of CO_2 concentration. *Laccaria* aggressively colonized roots of both species, and virtually all root tips of seedlings grown in inoculated soil became infected.

Among white spruce seedlings naturally regenerating in four interior Alaskan floodplain communities, essentially all short roots were infected with mycorrhizal fungi throughout the growing season, but long lateral roots were largely non-mycorrhizal (Krasny et al. 1984). The observations were made only on seedlings showing no evidence of browsing, and on ones from 2-20 cm in height prior to the growing season in which the study was begun. The number of mycorrhizal root tips per seedling increased more than four times in the 1981 growing season in the open community, compared with two times in the willow (*Salix*) and less than that in the alder (*Alnus*) and spruce communities, though those differences did not attain statistical significance. Long root growth was also much greater in the open community than in the others. Krasny et al. (1984) noted that other investigators, using laboratory seedlings of other coniferous species have reported varying levels of infection in response to varying

environments, although in field observations of Norway spruce by Mikola and Laiho (1962), and Orlov (1960), all absorbing roots were infected by mycorrhizal fungi.

Much experience from tropical areas show that mycorrhizal fungi can effect dramatically increased growth of conifers, and it has been possible to demonstrate that it is chiefly phosphorus that the mycorrhizal fungi can make more available (Björkman 1970). Typically mycorrhizal fungi do not produce laccase or proteinase, whereas litter-decomposing fungi or white rot fungi have an enzyme system conferring the ability to break down complex humus compounds, thereby releasing nitrogen, which becomes available to plants. Lundeberg (1970) found that suede bolete (*Boletus subtomentosus*) can occur in several physiological races with varying ability to break down humic compounds.

Björkman (1942), working with pine and suede bolete, determined that the fungus was able to make nitrogen available to pine in forest soil, but that "this ability did not manifest itself when the plants were shaded and when illumination constituted the growth limiting factor"; mycorrhizal formation which occurred during full illumination ceased entirely in one-quarter light. Heavy fertilization or highly fertile growing media also negate mycorrhizal formation.

The number and diversity of ectomycorrhizal root tips decreases dramatically 1-3 years after clearcut logging (Harvey et al. 1980, Hagerman et al. 1999).

Patterns of ectomycorrhizal colonization of interior spruce seedlings planted in cut blocks of three sizes (0.1, 1.0, and 10 ha) and in uncut forest in the Engelmann Spruce–Subalpine Fir (ESSF) wet-cold (wc2) biogeoclimatic variant in southern interior British Columbia were studied by Hagerman et al. (1999). The richness and diversity of ectomycorrhizal flora that had developed after 13 weeks were significantly greater in forest plots and in plots located 2 m from the forest edge as compared with plots located more than 16 m into the cut block. One year later, the study was repeated with the same results. No differences in any of the diversity measures were detected between the cut blocks of different sizes. Proximity to an overstorey obviously had more influence than size of cut block. In cut blocks lacking mycelial connections with live trees, excised ectomycorrhizal roots may not be an important inoculum source for planted seedlings, since early stage fungi, including E-strain, *Mycelium radicis atrovirens* (MRA) and *Bebeloma*-like strains (presumably originating from spore inoculum), are the most common mycorrhizal associates.

3.6 Stem

Diameter

Breast-height diameters of white spruce in excess of 1 m have been reported (Table 3.19), and while individual ecological conditions and life history determine the size reached by individual stems, there is no doubt that the species has the potential for producing stately trees of impressive size.

Tree-ring growth in white spruce was sampled along two transects through the boreal forest. One extended from near the southern limit of the boreal forest in Alberta to near the northern limit in the Northwest Territories, and the other from near the southern limit to near the northern limit of the boreal forest in Manitoba. The project was undertaken to examine growth

in relation to climatic variation. Stands of a minimum age of 200 years were selected because "older trees are more sensitive to variations in climate and longer chronologies provide better tree-ring data for studying past climates". Jozsa et al. (1984) commented that the availability of white spruce became a problem north of 54°N in Manitoba "contrary to technical information in the literature". Jozsa et al. expected a clear pattern of continuum of growth trends with age in chronologies from south to north, but while the growth trend curve was flatter for northern sites, this was neither marked nor consistent. Ring width trend lines changed little from pith to bark except for the most southerly (Riding Mountain) line in Manitoba, where the average ring width dropped "dramatically" from about 3.4 mm near the pith to 1.5 mm at 50 years of stand age. For the next 70 years, the average ring width dropped from 1.5 to 0.9 mm. The Duck Mountain and Suwannee River ring width trend lines were remarkably similar even though they are 550 km apart on the north–south transect, but this might be a fortuitous compensation resulting from the elevational difference between the sites. Only the Le Pas site showed a positive trend, with rings gradually widening with increasing age in the juvenile wood zone. From the pith to age 30, the average ring width increased from about 1 to 1.75 mm, and then decreased to about 0.6 mm at age 160. Strong climate-tree growth relationships were indicated by numerous common marker years, by strong cross-dating between randomly selected individual cores, and by high correlations between tree-ring chronologies for sites hundreds of kilometres apart.

Current mean annual ring width among dominant white spruce in 31-year-old plantation white birch on dry sandy soil in Quebec was closely related to the mean monthly precipitation during June, July, and August of the preceding year (Gagnon 1961).

Age reached

White spruce can live for several hundred years. Ages of 200-300 years are commonly attained throughout much of the range, and Dallimore and Jackson (1961) estimated the normal lifespan of white spruce at 250-300 years. Jeffrey (1964) found stems older than 240 years in the Lower Liard River area, and Lacate et al. (1965) found stands older than 240 years along the Lower Peace River. Horton (1956b) gave the maximum lifespan of white spruce in Alberta as 400 years or more (Horton 1959). Slow-growing trees in rigorous climates are also capable of great longevity. White spruce 6-10 m high on the shore of Urquhart Lake, Northwest Territories, were found to be more than 300 years old (Hare and Ritchie 1972), and Tremblay and Simon (1989) recorded white spruce up to 390 years of age in the coastal belt along Richmond Gulf, Hudson Bay. White spruce at 67°30'N, 115°30'W in the forest-tundra was found by Jozsa et al. (1984) to have a stand age of 500 years. From the Mackenzie River delta, Giddings (1947) reported counting a 589-year sequence of annual rings, an indeterminate number of rings short of the center, in 6.5 inches (16.5 cm) of radius of a white spruce. Two neighbouring trees yielded cores of 476 and 490 rings. Clearly, individuals are capable of great longevity with little reflection of this in the sizes reached. Giddings (1962) affirmed that spruces nearly 1,000 years old are found well north of the Arctic Circle in northwestern Canada but provided no specific evidence. As

Robinson[7] put it, “Since the trees remain alive in practically a condition of hibernation and there are few tree diseases in the far north some trees reach very old ages”.

Bark

The bark of mature white spruce is scaly or flaky, gray-brown (Brayshaw 1960) or ash-brown (Harlow and Harrar 1950), but silvery when freshly exposed. Resin blisters are normally lacking, but the Porsild spruce (*Picea glauca* var. *porsildii* Raup)[8] has been credited with having smooth resin-blistered bark (Hosie 1969). However, Daubenmire (1974) expressed reservations (“allegedly distinct”) about this before noting that a smooth bark with resin blisters in Engelmann spruce had not yet been recognized as a biotype even in species descriptions.

White spruce bark is mostly less than 8 mm (Hale 1955) and not more than 9.5 mm thick (Chang 1954). Bark thickness of standing white spruce and Engelmann spruce can be estimated from Smith and Kozak's (1967) regression equation of double bark thickness (DBT) on diameter outside bark, constant 0.149, regression coefficient 0.044 (Haygreen and Bowyer 1989):

$$DBT = 0.149 + (0.044 \times DOB),$$

where both DBT and DOB are expressed in inches, or:

$$DBT = 0.378 + (0.044 \times DOB),$$

where both DBT and DOB are expressed in centimetres. Once DBT is known, bark volume (BV) as a percentage of total volume (TV) of wood plus bark can be calculated (Dobie and Wright 1975):

$$BV \text{ as } \% \text{ of } TV = 100\ (DOB^2 - DIB^2)/DOB^2,$$

where DOB is diameter outside bark, DIB is diameter inside bark, and DIB = DOB - DBT. Similarly, bark volume can be calculated as a percentage of wood volume. The bark volume reported by Harkin and Rowe (1971) for 62-year-old “spruce” 10.7 cm in diameter was 12.06%, but only 9.26% for 112-year-old spruce 22.1 cm in diameter. The specific gravity (green volume) of inner, outer, and whole bark was given as 0.45, 0.50, and 0.47, respectively (Smith and Kozak 1971).

Smith and Kozak (1971) reported moisture contents of 104% and 50% for white spruce inner and outer bark, respectively.

White spruce may be distinguished unfailingly from black spruce, even on those poor sites where there may be close resemblance between the two species, by the color of newly exposed bark, which is light and silvery or pinkish in white spruce, olive or brownish yellow in black spruce (Kenety 1917, Brayshaw 1960).

[7] J.M. Robinson, Canadian Forest Service, Ottawa, personal communication 17 September 1969.

[8] Editor’s note (Phippen 2022); this species is now accepted as interior spruce (*Picea* × *albertiana* S. Brown) but was left unchanged in the document as the author described it (https://data.canadensys.net/vascan/taxon/22114).

Table 3.19. Size reportedly attained by white spruce.

Citation	Location	Height		Diameter at breast height	
		Average (m)	Maximum (m)	Average (cm)	Maximum (cm)
Brunet 1866	Saguenay, Quebec	21–24	40–43		
Brunet 1866	Rimouski, Quebec		49[a]		122[a]
Sargent 1898	East of Rockies	18–21	46	61	
Sargent 1922		rarely 18–21		61	
Dame and Brooks 1901	New England	12–23		30–61	
Nisbet 1905		rarely >14–15		30–61	
McElhanney 1940, 1951		15	30	46–61	122
Bowman 1944	northern Michigan	21–24		40–51	
Hyland 1946	Maine	18–21	37	46–61	102
Peattie 1950			46	91–122	
Fernald 1950				45	
Lutz 1953	Alaska interior		26–30	51–61	
Wright 1955					
Seely 1956 cited by Nienstaedt 1957	Peace River, Alberta		56[b]		
Horton 1958	Wood Buffalo National Park		>46		
Petrides 1958		15–18		30–61	
Sutton 1958 unpub.	Manitouwadge, Ontario		36[b]		62[b]
Ontario L&F 1959	Geraldton, Ontario (109 years)		36[b]		67[b]
	(105 years)		35[b]		82[b]
Forestry Branch 1961		24	37		48
Dallimore & Jackson 1961		15–21	21–30	28–38[c]	86–117[c]
Streets 1962			30		97
Mitchell 1963		30–40	46	61	91
Jeffrey 1964	Lower Liard River		34[b]		74[b]
Lacate et al. 1965	Lower Peace River	37 (222 years)			
Eis 1965	Interior British Columbia		46		71
Robinson[d] 1969	Peace River delta		56[b]		

[a] Brunet measured this tree (160 feet): he called it *Picea nigra* var. *grisea* (gray spruce), but, since red spruce does not occur in the Rimouski area and in view of its size, it seems likely to have been white spruce.

[b] Measured individual.

[c] At ground level.

[d] J.M. Robinson, personal communication, 17 Sept. 1969, Can. For. Serv., Ottawa, Ontario: "The very large white spruce stands in the Peace River delta are easily explained. Soil auger borings showed that the soil consisted of layers of rich silts interspersed with layers of organic matter. Evidently each year's crop of annual plants was covered by the silts of the spring floods. A check of the exposed riverbank showed that this mixture of organic matter and silts was at least twelve feet [3.7 m] deep. ... Here one tree reached a measured height of 183 feet [56 m] and several were over 160 feet [49 m]."

Cambium

The vascular cambium is the lateral meristem that constitutes the secondary vascular tissues (Esau 1953). Located between the xylem and phloem, the vascular cambium of white spruce contains cells of two kinds: long, radially flattened, tangentially tapered, spindle-shaped (fusiform) initials; and relatively small, cuboidal ray initials (Gregory 1971). Both give rise by periclinal division to radial files of cells comprising the secondary xylem and phloem. The fusiform initials give rise to all the cells of the xylem and phloem that are arranged with their long axes parallel to the long axis of the stem, thus forming the vertical systems of xylem and phloem (Esau 1953). The ray initials give rise to the ray cells and form the horizontal system of xylem and phloem.

Cambial derivatives in both xylem and phloem are arranged in radial files that are easily traceable to their point of origin in the cambial zone. Cambial zone cells are inactive throughout winter. Vernal reactivation occurs rather abruptly, at least in Alaska, where seasonal patterns are accelerated through a relatively short growing season (Gregory and Wilson 1968, Gregory 1971). A useful terminology of cambial activity was presented by Wilson et al. (1966).

Both xylem and phloem are formed by tangential (periclinal) divisions of cambial initials, with xylem cells towards the interior of the axis, phloem towards the periphery. To accommodate increasing stem thickness, the number of cells tangentially increases by the division of fusiform initials, which enlarge notably along their tangential diameters. Division is mostly by the development of oblique radial divisions. Multiplication of fusiform initials in the cambium takes place by anticlinal divisions of the pseudotransverse type (Bannan 1963). After division, the daughter initials elongate by tip growth, and the cycle of elongation and multiplication continues as radial and tangential growth proceeds. Bannan's (1963) data obtained from the peripheral growth at breast height of white spruce trees 15-50 cm in diameter, show that pseudotransverse divisions took place at a more or less uniform rate of slightly less than one per cm of xylem increment when the annual rings were 2-9 mm wide, but at a sharply increasing rate as ring width fell below 2 mm.

Gregory and Wilson (1968) observed 45- to 50-year-old white spruce in Alaska (64°51'N, 147°44 W) and Massachusetts (42°31'N, 72°05'W) and found trees of comparable age, crown class, and annual radial growth. The radial number of dividing cells in the cambial zone (NCZ) was similar at both places, appearing to reach a maximum of about 15; but the mitotic index (MI) i.e., the percentage of cambial zone fusiform cells in mitosis, or the rate at which those cells divide, was twice as high in the Alaskan trees as in the Massachusetts trees. The rate of tracheid production is determined by NCZ and MI. At both places, the onset of cambial activity appeared to be related to temperature; the first mitoses were observed after 11 cumulative-growing-degree days (the accumulated sum of the degrees by which daily mean temperatures exceed 6°C). The period between the first and last mitoses was 95 days in Alaska, 145 days in Massachusetts.

Tumours on white spruce trees in coastal Maine have been reported to produce up to 800 cells radially in a single growing season, even though the NCZ remained about 15 (Gregory and Wilson 1968).

The relationships between length of wood cells, width of annual rings, and frequency of pseudotransverse divisions in fusiform cambial cells of several *Picea* species, including white spruce, were investigated by Bannan (1963).

In white spruce that were tilted at an angle of 45°, Yumoto and Ishida (1982) found that cambial activity ceased early in the fall on the upper side of the stem but was still continuing on the lower side of the tilted stem as late as mid-December. As noted by Timell (1986), the findings reported by Yumoto et al. (1982) for the rate of formation of compression wood in titled white spruce trees is more in accord with what is known about the formation of normal conifer wood, e.g., more rapid cell division in July than in August.

Coniferin became detectable in the cambium of white spruce at an early stage of reactivation, just before resumption of cell-division activity, thereafter accumulating until lignification of the first-differentiating earlywood tracheids became histochemically detectable (Savidge 1990).

Wood

The single most revealing property of wood as an indicator of wood quality is specific gravity (Timell 1986), as both pulp yield and lumber strength are determined by it. Specific gravity is the ratio of the mass of a substance to the mass of an equal volume of water; density is the ratio of a mass of a quantity of a substance to the volume of that quantity and is expressed in mass per unit substance, e.g., grams per millilitre (g/cm^3 or g/ml). The terms are essentially equivalent as long as the metric system is used. Upon drying, wood shrinks and its density increases. Minimum values are associated with green (water-saturated) wood and are referred to as *basic specific gravity* (Timell 1986).

Wood density is determined by multiple growth and physiological factors compounded into "one fairly easily measured wood characteristic" (Elliott 1970).

Age, diameter, height, radial growth, geographical location, site and growing conditions, silvicultural treatment, and seed source, all to some degree influence wood density. Variation is to be expected. Within an individual tree, the variation in wood density is often as great as or even greater than that between different trees (Timell 1986). Variation of specific gravity within the bole of a tree can occur in either the horizontal or vertical direction.

Unlike most of the conifers, spruces tend to increase wood density towards the top of the tree above a point ½ to ¾ of total stem length where the density is the least. This type of variation has been demonstrated in white spruce, Engelmann spruce and black spruce (Okkonen et al. 1972), as well as Norway spruce (Nylinder 1953).

Compression wood is almost always heavier than corresponding normal wood. For white spruce, Perem (1958) found the specific gravities of green compression wood and normal wood were 0.387 and 0.316, respectively, a ratio of 1.22, and of air-dry compression wood and normal wood 0.392 and 0.332, respectively, with a ratio of 1.18.

Timell's (1986) monumental treatise on compression wood deals with gymnosperms generally, and, while the spruces are not the prime focus, Timell makes clear the fact that the occurrence and characteristics of compression vary among *Picea* species and coniferous genera.

Compression wood has been observed to form under moderate gravistimulus more readily in white spruce than in red pine (Rendle 1956).

Sampling of wood density in eastern Canada found the normal range for white spruce to be "about 0.34 to 0.39…although one exceptional stand of white spruce of very slow growth was found with mean density well above 0.44" (Hale and Prince 1940). Kennedy et al. (1968) also investigated wood density of eastern Canadian tree species, and Alemdag (1982, 1984) examined wood density of 28 species of tree, including white spruce, in Ontario. Oven-dry density determinations among white spruce in Alberta, Saskatchewan, and Manitoba were reported by Singh (1984) (Table 3.20). The weighted average wood density of 957 white spruce in these studies is 0.360 g/cm^3.

Table 3.20. White spruce wood density values (g/cm^3) found in various investigations are compared; oven-dry except where green noted (after Singh 1984).

Hale and Prince (1940)	Chang and Kennedy (1967)	Kennedy et al. (1968)	Jessome (1977)	Alemdag (1982)	Alemdag (1984)	Singh (1984)
.34-.39[a]	.335[b]	.353	.354	.386	.383	.404
.441[c]	.310[d],	.358[e]				.313-.527[f]
n = 285	n = 232	n = 204	n = 43	n = 77	n = 56	n = 60

[a] Normal range
[b] Green specific gravity
[c] Maximum
[d] Green specific gravity, mean of 9 "superior" trees
[e] Green specific gravity, mean of 15 "inferior" trees
[f] Range

Climate might be expected to affect the growth rate and quality of wood (Hale and Prince 1940). The sum of Thornthwaite's (1931) monthly coefficients of thermal efficiency (the T-E ratio) provides the T-E index, which is a measure of climatic rigor in temperature provinces ranging from tropical to frost:

Province	T-E index
Tropical	128 +
Mesothermal	64–127
Microthermal	32–63
Taiga	16–31
Tundra	1–15
Frost	0

When Hale and Prince (1940) plotted their data to show white spruce wood density in stands from regions of the various indices of summer concentration, they found a general relationship between indices of summer concentration and wood density. Density increased from a low of 0.345 at the lowest concentration of thermal efficiency (about 60%) to a density greater than 0.370 for a higher degree of summer concentration (about 67%). This tendency suggests that

the wood density of white spruce would be highest in the western section of the range, under the influence of continental climate conditions.

The ratio between oven-dry mass and green mass was determined by Alemdag (1982) for 77 white spruce trees, drawn from two areas in Ontario (Table 3.21).

Table 3.21. Oven-dry mass/green mass ratios in white spruce, n = 77 (after Alemdag 1982).

Component	Ratio
Stem wood	0.561
Stem bark	0.469
Live branches	0.555
Twigs and needles	0.461
Whole tree	0.538

The wood of white spruce is light, soft, not exceptionally strong, straight-grained and very pale yellow. Samples taken at breast height have varied from 256 kg/m^3 (Gonzalez 1987) to 505 kg/m^3 (Maeglin 1973); and averaged 360 kg/m^3 for 23 collections across Canada and four from the United States (Gonzalez 1990). Heartwood is barely distinguishable from sapwood (Sargent 1922). Annual rings are distinct, and resin canals are distinctive and visible with hand lens (Brunet 1866).

The relative density of white spruce was determined, based on green volume, for a sample of plus trees in New Brunswick and Nova Scotia. White spruce had a mean density of 0.366 with a standard deviation of 0.033 (Morgenstern et al. 1990). Correlations between density and dbh:age ratio were significant (P = 0.01).

Average tree wood density data published by Alemdag (1984) superseded all values previously published by that author.

Volumetric shrinkage from green to oven-dry moisture content, based on green dimensions, was reported as 11.3% (Jessome 1977).

Haygreen and Bowyer (1989) reported mechanical properties of United States and Canadian white spruce used in the United States (Table 3.22).

Table 3.22. Mechanical properties of white spruce wood used in the United States and Canada (after Haygreen and Bowyer 1989)[9].

Character	USA-grown	USA- grown	Canadian origin	Canadian origin
Moisture condition	green	dry	green	12%
Specific gravity	0.33	0.36	0.35	
Modulus of rupture (psi)	5,000	9,400	5,100	9,100
Modulus of elasticity (mil psi)	1.14	1.43	1.15	1.43
Work to max load (in.-lb/in.^{3})	6.0	7.7		
Impact bending (in.)	22	20		
Max crushing strength parallel to grain (psi)	2,350	5,180	2,470	5,360
Compression perpendicular to grain (psi)	210	430	240	500
Shear parallel to grain (psi)	640	970	670	980
Max tensile strength (psi)	220	360		
Side hardness (lb)	320	480		

“Acid-susceptible” wood, i.e., wood that becomes very brittle on treatment with aqueous acid, occurs naturally in white spruce (Yorston 1942, Timell 1986). Such wood averaged 4.4% in a large number of logs destined for sulfite pulping. More than half of the acid-susceptible wood was associated with compression wood, and it was particularly common in regions located between outer bands of compression wood and the pith (Green and Yorston 1939). Macromechanical damage was not involved, for kraft pulps prepared from acid-susceptible wood had normal fibre lengths and normal strength properties, but acid sulfite pulp from acid-susceptible wood was weaker in burst, tear, and tensile strengths than pulp from normal wood.

When exposed to 100% relative humidity, oven-dry compression wood (Timell 1986) of white spruce adsorbed only 88% of the moisture adsorbed by oven-dry normal wood (Perem 1958, 1960), 29.5% vs. 33.5% of oven-dry wood. Green wood shrinks when oven-dried (Table 3.23).

[9] Editor’s note (Phippen 2022); the values in this table were not converted to metric and were left as the author presented it.

Table 3.23 Shrinkage of white spruce and Engelmann spruce wood from green to oven dry (after Mullins and McKnight 1981).

	Shrinkage green to oven dry based on dimensions when green (%)		
Species	**Radial**	**Tangential**	**Volumetric**
White spruce	3.2	6.9	11.3
Engelmann spruce	4.2	8.2	11.6

Chang and Kennedy (1967) pointed out that a fast growth rate in spruce had been commonly associated with low wood specific gravity (Hale and Fensom 1931, Hale and Prince 1940, Aldridge and Hudson 1958, Keith 1961, Hale 1962), but although Chang and Kennedy, from their study of 232 white spruce trees sampled from 29 plots at six locations in southern Ontario, confirmed a negative correlation between specific gravity and growth rate, the effect was minor in relation to the increased volumes associated with fast growth rates. Some trees had ring widths up to 85% wider than the average, but still had average specific gravity.

The methods used in ascertaining various strength properties and in assessing the physical characteristics of various Canadian commercial timbers, including white spruce, were described by Wakefield (1957). The strength and related properties of woods grown in Canada, including white spruce, and the machining properties of 16 eastern Canadian woods, including white spruce, have been reported by Kennedy (1965) and Cantin (1965), respectively.

Mechanical properties were listed for white and Engelmann spruces in the USDA Wood Handbook (USDA Forest Service 1974, Table A-4-3). (Table 3.24).

Table 3.24. Mechanical properties of white and Engelmann spruces (after USDA Forest Service 1974 and Mullins and McKnight 1981); values in the first line for each species are from tests of green material; those in the second line are adjusted from the green condition to 12% moisture content.

Specific gravity	**Static bending: Modulus of rupture**	**Static bending: Modulus of elasticity**	**Compression parallel to grain, maximum crushing strength**	**Compression perpendicular to grain–fibre stress at proportional**	**Shear parallel to grain maximum shearing strength**
	kPa	**kPa**	**kPa**	**kPa**	**kPa**
White spruce					
.35	35,000	7,900	17,000	1,600	4,600
	63,000	1,000	37,000	3,400	6,800
Engelmann spruce					
.38	39,000	8,600	19,400	1,900	4,800
	70,000	10,700	42,400	3,700	7,600

The wood of white spruce resembles that of black spruce closely enough to have resulted in the practice described by Roth and Fernow (1895): "'Black' and 'white spruce', as applied by lumbermen, usually refer to narrow and wide ringed forms of the black spruce (*Picea nigra* [=*Picea mariana* (Mill.) B.S.P.])".

Coniferin, the primary storage reserve for guaiacyl lignin monomers in conifer stems, was quantified by Savidge (1990) using gas chromatography (GC) and GC-mass spectrometry (GS-

MS) in stem and leaf tissues of white spruce and three other conifers. Coniferin was not detected in leaf tissues at any stage of development, nor was it detected in dormant stem tissue. Coniferin appeared in the cambium just before resumption of cell-division activity, thereafter accumulating until lignification of the first-differentiating earlywood tracheids became histochemically detectable.

Height

In 1672, at Poscataway, New England, Josselyn reported seeing a spruce log "brought down to the water-side by our mass-men [i.e., mast cutters] of an incredible bigness, and so long that no skipper durst ever yet adventure to ship it: But there is lyes and rots". Individual white spruce of up to 56 m in height have been measured (Table 3.19).

Branch wood

Branches have a denser wood than the stem because of their narrower growth rings and because of the almost universal presence on their underside of compression wood (Timell 1986). The average specific gravity of the entire branch is influenced strongly by the proportion of compression wood present, and the density of branch wood is higher in *Picea* than in *Pinus*. The density of branch wood decreases towards the branch tip.

Root wood

Root wood has received relatively little attention, but in Norway spruce, at least, coarse and fine roots differ anatomically in that the tracheids in coarse roots are shorter, have smaller cross sections and thicker cell walls than tracheids in fine roots (Eskilsson 1969).

3.7 Asexual reproduction = Vegetative reproduction

The traditional methods of vegetative propagation are rooted cuttings or rooted needle fascicles (also known as brachyblasts, short shoots, or dwarf spurs), and grafting. The rooting capacity of cuttings (ramets) in most conifers generally decreases markedly with increasing age of the parent plant (ortet) (Thorpe and Biondi 1984). Percent rooting, speed of rooting, length and number of roots produced, and survival and growth in and after the year of rooting all decline in cuttings, particularly when the parent plant is more than 10 years old (Girouard 1974). In many species, rooted cuttings from branches tend to maintain bilateral symmetry and horizontal growth habit (plagiotropy) until, after various periods of time, the terminal meristem changes to radial symmetry and vertical (orthotropic) growth ensues. The reversal to normal growth often displays intraclonal and interclonal variations, and is erratic and unpredictable. These factors tend to undermine one of the main aims of vegetative propagation, which is to multiply trees old enough to have demonstrated superior characteristics (Thorpe and Hasnain 1988).

A modified form of sprouting occurs to a limited extent in white spruce. New shoots can form in the vicinity of the branch-stem junction on stumps (8-12 cm diameter stumps observed to sprout in this way) provided that living branches are present on the stump (Zasada 1986).

Layering / cloning

To some degree, members of the genera *Picea* and *Abies* possess the ability to multiply by layering, the rooting, whether natural or not, of an undetached branch (a "layer") lying on or partially buried in the rooting medium, becoming capable of independent growth. Among the

spruces, layering is particularly important in black spruce (Cooper 1911, Fuller 1913). An early report of layering in Norway spruce was Loudon's (1844) citation of James M'Nab, who in *The Gardener's Magazine* wrote: "From the pendent habit of the lower branches of the spruce (*Picea excelsa* Link) [Norway spruce] some curious anomalies are occasionally found in its habit of growth. The shoots next the ground, when they have attained a considerable length, naturally rest on the soil at their extremities; and the soil being kept moist by the shade of the branches, these often root into it; and the points of their shoots taking a vertical direction, a series of new trees are formed in a circle around the old tree.

Although Nienstaedt (1957) stated that layering in white spruce had not been recorded, a claim repeated by Fowells (1965), additional contrary evidence accumulated (cf. Maycock 1968, Katzman 1971, Payette and Boudreau 1972, Stone and McKittrick 1976, Elliott 1979, Densmore 1980), and earlier evidence was uncovered (cf. Cooper 1911, Fuller 1913, Bannan 1942, Hustich 1950) so that Nienstaedt and Zasada (1990) could affirm that "Vegetative reproduction [in white spruce] from layering is common at some latitudinal treeline sites in Canada and Alaska... and probably is an important means of maintaining the stand when sexual reproduction is limited or nonexistent because of climatic conditions". Layering in white spruce in the sub-arctic gives rise to candelabra-form clumps, just as in black spruce (Payette and Boudreau 1972). Of seven sites established by Elliott (1979) in the forest–tundra ecotone in the Ennadai–Kasba Lake region (about latitude 60°N) in southwestern District Keewatin, Northwest Territories, Canada, three have a component of white spruce; layering was frequent at two sites and occasional at one. The two sites occupy esker crests, where white spruce has a krummholz life form. At the third site, a mixed grove of white and black spruces and larch occupy a ravine. Macrofossils associated with the current stands suggest that forest cover was more extensive.

Layering in white spruce, though certainly less common through much of the range than in black spruce, occurs in circumstances that provide stable contact between branch and a suitable rooting medium. Cooper's (1911) report may be the first documentation. During the course of ecological studies on Isle Royale, Lake Superior, Cooper, as well as finding layering to be fairly common in upland black spruce and abundant in black spruce and tamarack in bogs among rapidly growing sphagnum, also noted that "Specimens of white spruce were found upon nearly bare rocks, whose lowest branches, covered with a thin mantle of humus, had developed the layering habit to such an extent that the parent had become entirely surrounded by a group of daughter trees." Cooper noted that layering may take place at any stage in the life of the balsam fir, so that the layered branch may be only a few years younger than the parent and not very perceptibly smaller.

Two features of Cooper's (1911) conclusions occasion surprise. First, their neglect for so many decades. Secondly, their accuracy: "From the material here presented we gather that the habit of natural layering among coniferous trees is common and widely distributed, though its importance appears to have been generally overlooked, at least in this country; that it is particularly characteristic of the closely related genera *Picea* and *Abies*, but is found in many other genera, among which are *Larix* Mill., *Thuja* L., *Pinus* L., *Pseudotsuga* Carrière, *Chamaecyparis* Spach, and *Cryptomeria* D. Don; that it is most prominent in northern and

mountain regions, and that it occurs more frequently and attains more striking development with increasing latitude and altitude; that its best development is found at the extreme limit of the forest–the arctic tree line and the mountain timberline". Zasada (1986) affirmed that layering in white spruce and tamarack is common near the treeline in Alaska.

In the far north, the density of trees originating from layering may reach 1830/ha (Densmore 1980).

Air-layering

Air-layering, also termed *marcottage*, or Chinese layering (propagation by gootee and by mossing-off) has been practised from time immemorial on many species of plants, especially in Asia. However, the first published report of air-layering in white spruce seems to be that by Feucht et al. (1961). The technique of air-layering induces root development on an undetached aerial portion of a plant, commonly by wounding it, treating it with a rooting hormone, and enveloping it in moist rooting medium under a waterproof wrapper, the portion so treated becoming capable of independent growth when planted after separation from the parent plant (Sutton and Tinus 1983).

In exploratory studies, Feucht et al. (1961) examined the effect on the response of 6-year-old white spruce to attempted air-layering using seven growth-promoting hormones, each applied in a talcum powder carrier. The talc preparations were well mixed with sphagnum and applied in 20 g lots to branches prepared by removing needles in a 13-15 cm band near the base of the 1-year-old wood and removing a complete ring of bark 2 mm wide. The pre-weighed sphagnum was wrapped around the girdled branch and covered with polyethylene plastic sheet. "Little" rooting resulted within 75 days, and further attempts were confined to applications of rooting hormone in aqueous solution. Also, in the subsequent field trials the branches were not girdled but wounded with a V-shaped notch on the abaxial side of the stem. Treatments were applied monthly from April through August to top, middle, and bottom whorls of 9- to 12-year-old white spruce: 5 ml of 0.5 ppm 2,4,5-T (2, 4.5-trichlorophenoxyacetic acid), 100 ppm NAA (naphthaleneacetic acid), 100 ppm 4-TNA (4-trinaphtheneacetic acid), 1,000 ppm IPA (indolepropionic acid), and distilled water. The treated branches were severed from the parents after 100 days and planted in rooting mixture. Neither hormone nor position of branch on the tree had significant effect, but time of application did (Table 3.25).

Table 3.25. Mean rooting of white spruce air layers 100 days after application (after Feucht et al. 1961).

	Date of application (225 branches/date)				
	April	**May**	**June**	**July**	**August**
Total rooted	5.6c[a]	8.2d	5.8c	0.6a	3.0b
% rooted	12.44	18.21	12.88	1.33	6.66
Roots/branch	2.82	3.60	4.60	3.00	3.75
Root length	10.84b	14.43b	20.96c	4.06a	4.58a

[a] Within rows, values not followed by the same letter differ significantly, at the P = 0.05 level in row 1, P = 0.01 level in row 4.

Rooting was greatest in air-layer treatments applied in May, when air temperatures were averaging 21°-24°C, rising gradually to 27°C and above. Mean root length appeared to be favoured by higher temperatures and hindered when temperatures decreased during the treatment period. All the rooted air-layers planted in September survived and continued growth, whereas only 52% of those planted in July were still alive 130 days after planting.

Cuttings

Picea, long believed to be difficult to propagate from stem cuttings (Feucht et al. 1961), has been found to produce adventitious roots reasonably well provided the stock plants are young (Girouard 1975). Early experimentation (1939–1942) on rooting of conifer cuttings in Ontario was carried out and described by Farrar (1939) and Farrar and Grace (1940; 1942a, b), who showed that Norway spruce cuttings taken during October through April could be rooted in appreciable numbers and propagated in a greenhouse. The same authors subsequently showed that cuttings of white spruce and white pine could also be rooted (Smith 1985).

The Super Seedling Program initiated by R.M. Rauter of the Ontario Forest Research Branch at Maple, and conducted at six Ontario forest tree nurseries, selected the tallest seedling in the nursery beds, with one super tree out of every 100,000 seedlings, to provide cuttings that would assay the genetic quality of the parent material. Superior clones would be identified, and field tests could be established within 5 years of nursery selection, only half the time needed for conventional controlled pollination tree improvement programs (Rauter 1974).

Cuttings of white spruce and Shrenk's (*Picea schrenkiana* Fisch. & C. A. Mey.) spruce and their hybrids were found to root well (Rauter 1971).

Girouard (1975) determined percent rooting values and numbers of roots formed per rooted cutting in experiments with cuttings from 2+2 stock at Valcartier, Quebec, involving three propagation dates (mid-August, early November, and late April), three types of cutting (terminal shoot, basal cut; lateral shoot, basal cut; and lateral shoot, heel of bark), and four species, including white spruce (Table 3.26; Girouard 1975). Cuttings from lateral shoots rooted more readily than did those from terminal shoots, and mid-August propagation was just as successful for white spruce as later propagation, in contrast with the other species in which mid-August propagation was less successful, significantly so for red spruce. White spruce cuttings prepared with a heel of bark rooted significantly less well than did cuttings lacking a heel. Propagation dates had very little effect on the number of roots formed per white spruce cutting.

The account by Coates et al. (1994) captures the essence very well for interior spruce, which is unlikely to differ materially from white spruce in general: "Interior spruce can be successfully propagated from cuttings (Nienstaedt and Teich 1972, Nienstaedt and Zasada 1990, Russell and Ferguson 1990). Rooting ability varies with age of the donor plant and from tree to tree, but, in general, is considered too poor for practical use by the time trees are 10-15 years old". Girouard (1974), among others, had found earlier that rooting ability decreased rapidly as the age of the ortet increases beyond 10 years. Cuttings taken from lateral shoots root more readily than cuttings from terminal shoots (Girouard 1975). Rooted lateral branches must undergo a period of adjustment as they change from a plagiotropic (creeping) form to an orthotropic

(upright) form. Rooting ability can be increased in older trees if the scions are first grafted to vigorous rootstock (Holst et al. 1969). White spruce cuttings rooted more readily in spring than during the winter (Tognoni et al. 1977). In working on the rooting of Sitka spruce cuttings, Coutts and Bowen (1973) found that roots of two different kinds were produced depending on auxin level.

The strong influence of photoperiodic induction on the rooting of cuttings of several spruces was documented by Rubanik and Parshina (1972); cuttings from plants 8-15 years of age were taken in definite phenological phases, planted in unheated greenhouses, and exposed to the following photoperiods: (1) natural lighting, (2) natural lighting supplemented by 100w incandescent lighting at night, i.e., light 24 hours daily, and (3) daylight 8 hours daily, with 16 hours of special shading. Root growth was noted in autumn, and observations were made over a period of 3 years. Supplementary lighting had a positive effect on the rooting of cuttings from all spruce species studied: Norway spruce for all propagation times; blue spruce for winter cuttings before the start of shoot growth; for Schrenk's spruce during the terminal phase of growth, the appearance of winter buds, and lignification of shoots; and for Siberian spruce during the terminal phase of growth and the appearance of winter buds. During the budding phase, supplementary light increased rooting percentage in all spruce species, and the short day length decreased rooting in almost all instances. Spring was the best time for propagating cuttings.

Techniques for producing plantable rooted cuttings (stecklings) in British Columbia were described by Russell and Ferguson (1990). The technique was developed to increase the availability of genetically improved planting stock, and to reduce genetic variability of stock used in research trials. First, trees from which to take cuttings are grown from genetically improved seed collected from a seed orchard. The donor seedlings are grown for 9 months under high light intensity and wide spacing, and are pruned regularly to produce a bushy form. After hardening for 1-3 months, each tree is sacrificed to yield 50 short (3-6 cm) cuttings, which are dipped in rooting hormone powder (indole-butyric acid and talc), then inserted into standard styroblock containers. The containers kept for 6-8 weeks in an environment designed to promote rooting: 15°-20°C bottom heat, high relative humidity and air temperatures of not less than 12°C. Rooting takes place during this time and the stecklings are then treated like standard nursery seedlings.

Techniques for large-scale production of interior spruce rooted cuttings from genetically superior families were investigated by Russell (1987, 1988). Of particular interest were methods of bulking up families, rooting techniques, comparisons between seedlings and rooted cuttings, and genetic variability in rooting. Seedlings were raised under accelerated growth regimes from seed from genetically superior families in combination with hedging for 8 months. Cuttings are taken when laterals are just setting buds. Rooting success exceeded 90%, with no significant variation in rooting among families.

Two outplantings with family structure to compare seedlings and rooted cuttings were planned for the Prince George in the spring of 1988 (Russell 1988).

Table 3.26. Percent rooting of stem cuttings of *Picea* and mean number of roots formed per rooted cutting, as affected by cutting type, species and planting date, after 11 weeks in the propagation bed.

			Species				
Planting Date	**Type**	**Cutting type**	***P. abies***	***P. glauca***	***P. mariana***	***P. rubens***	**Mean**
Mid - August	**Per cent rooting of cuttings[a]**	Terminal shoots, basal cut	54.0 bc	77.0 de	55.0 bc	11.0 a	49.3
		Lateral shoots, basal cut	66.0 cde	81.0 e	71.0 de	16.2 a	58.5
		Lateral shoots, heel of bark	64.0 bcd	55.0 bc	49.0 b	20.0 a	47.0
		Mean	61.3	71.0	58.3	15.7	51.6
Early November		Terminal shoots, basal cut	93.0 cd	68.0 b	82.0 bc	41.0 a	71.0
		Lateral shoots, basal cut	99.0 d	85.0 cd	91.0 cd	67.0 b	85.5
		Lateral shoots, heel of bark	93.0 cd	37.0 a	86.0 cd	45.0 a	65.3
		Mean	95.0	63.3	86.3	51.0	73.9
Late April		Terminal shoots, basal cut	76.0 ef	65.0 bcd	62.0 bcd	53.0 abc	64.0
		Lateral shoots, basal cut	100.0 g	72.0 cde	94.0 fg	79.0 ef	86.0
		Lateral shoots, heel of bark	88.0 efg	40.0 a	64.0 bcd	48.0 ab	60.0
		Mean	88.0	59.0	73.3	60.0	70.1
Mid - August	**Mean number of roots formed per rooted cutting[a]**	Terminal shoots, basal cut	5.9 d	5.8 d	4.2 c	1.6 a	4.4
		Lateral shoots, basal cut	6.0 d	3.6 bc	4.3 c	2.0 a	4.0
		Lateral shoots, heel of bark	2.8 ab	2.6 ab	1.9 a	2.1 a	2.3
		Mean	4.9	4.0	3.5	1.9	3.6
Early November		Terminal shoots, basal cut	6.0 d	4.0 d	4.1 c	3.3 bc	4.4
		Lateral shoots, basal cut	6.2 d	3.8 c	3.3 bc	3.4 bc	4.4
		Lateral shoots, heel of bark	3.0 abc	1.9 a	2.5 ab	1.8 a	2.3
		Mean	5.1	3.3	3.3	2.8	3.6
Late April		Terminal shoots, basal cut	8.3 ef	5.3 c	7.5 de	4.4 bc	6.4
		Lateral shoots, basal cut	10.1 f	4.4 bc	6.1 cd	5.0 c	6.4
		Lateral shoots, heel of bark	2.7 ab	2.2 a	3.1 ab	2.5 a	2.6
		Mean	7.0	4.0	5.6	4.0	5.1

[a] At any one date, values followed by at least one letter in common are not significantly different from each other at the 5% level by Tukey's Honestly Difference Test (Steel and Torrie, 1960).

3.8 Grafting

White spruce can be grafted with consistent success by using 8-10 cm scions of current growth on thrifty 4- to 5-year-old rootstock (Nienstaedt and Teich 1972). Before greenhouse grafting, rootstocks should be potted in late spring, allowed to make seasonal growth, then subjected to a period of chilling outdoors, or for about 8 weeks in a cool room at 2°C (Nienstaedt 1966).

A method of grafting white spruce of seed-bearing age during the time of seed harvest in the fall was developed by Nienstaedt et al. (1958). Scions of white spruce of two ages of wood from 30- to 60 year-old trees were collected in the fall and grafted by three methods on potted stock to which different day-length treatments had been applied prior to grafting. The grafted stock were given long-day and natural-day treatments. Survival was 70-100% and showed effects of rootstock and post-grafting treatments in only a few cases. Photoperiod and temperature treatments after grafting, however, had considerable effect on scion activity and total growth. The best post-grafting treatment was 4 weeks of long-day treatment followed by 2 weeks of short-day treatment, then 8 weeks of chilling, and finally long-day treatment.

Since grafts of white spruce put on relatively little growth in the 2 years after grafting, techniques for accelerating the early growth were studied by Greenwood et al. (1988) and others. The cultural regimes used to promote one additional growth cycle in 1 year involve manipulation of day length and the use of cold storage to satisfy chilling requirements. Greenwood et al. took dormant potted grafts into the greenhouse in early January then gradually raised the temperature during the course of a week until the minimum temperature rose to 15°C. Photoperiod was increased to 18 hours using incandescent lighting. In this technique, grafts are grown until elongation has been completed, normally by mid-March. Soluble 10-52-10 fertilizer is applied at both ends of the growth cycle and 20-20-20 during the cycle, with irrigation as needed. When growth elongation is complete, day length is reduced to 8 hours using a blackout curtain. Budset follows, and the grafts are held in the greenhouse until mid-May. Grafts are then moved into a cooler at 4°C for 1,000 hours, after which they are moved to a shade frame where they grow normally, with applications of fertilizer and irrigation as in the first cycle. Grafts are moved into cold frames or unheated greenhouse in September until January. Flower induction treatments are begun on grafts that have reached a minimum length of 1.0 m. Repotting from an initial pot size of 4.5 L to 16-L containers with a 2:1:1 soil mix of peat moss, loam, and aggregate.

In one of the first accelerated growth experiments, white spruce grafts made in January and February that would normally elongate shortly after grafting, set bud, and remain in that condition until the following spring, were refrigerated for 500, 1,000, or 1,500 hours beginning in mid-July, and a non-refrigerated control was held in the nursery (Greenwood et al. 1988). After completion of the cold treatment, the grafts were moved into the greenhouse with an 18-hour photoperiod until late October. Height increment was significantly ($P = 0.01$) influenced by cold treatment. Best results were given by the 1,000-hour treatment (Table 3.27; Greenwood et al. 1988).

Table 3.27. Effect of chilling treatment on height increment of terminal shoots of white spruce grafts (after Greenwood et al. 1988).

	Elongation and number of grafts flushing					
	7/11/85		28/11/85		19/12/85	
Chilling duration (hours)	Elongation (cm)	Flushed (# of 15)	Elongation (cm)	Flushed (# of 15)	Elongation (cm)	Flushed (# of 15)
0	0.0	0	1.5	3	2.3	6
500	0.2	2	1.2	2	1.3	3
1,000	7.4	15	7.6	15	7.6	15
1,500	2.7	13	5.1	13	5.1	13

The refrigeration (cold treatment) phase was subsequently shown to be effective when applied 2 months earlier with proper handling and use of blackout curtains, which allows the second growth cycle to be completed in time to satisfy dormancy requirements before January (Greenwood et al. 1988).

3.9 Tree improvement (breeding and heritability)

A genetically variable population and a method of selecting genetically superior individuals provide the basis for tree improvement by breeding. In essence, a tree improvement program sets out to isolate and evaluate the genetic component of variation in one or more characters of interest. Through various techniques, the variation is channelled within a restricted population towards an accumulation of characteristics having economic or other sought advantages (Heaman 1967). In the simplest procedure, cycles of selection reduce the available population in a particular direction to enhance desirable traits, then breeding from selections to expand the population with improved characteristics. Breeding strategies vary with species and objectives, but all use mating designs to generate information and new material. Choice of a suitable breeding strategy and mating design is a key decision in any breeding program. Kiss (1986) used a two-level design in British Columbia to study variation within and between separate populations of white spruce, both within British Columbia and from eastern North America.

The breeding program for white spruce initiated in 1986 by the Canadian Forestry Service in the Maritimes employed two kinds of mating: polycross, to test clones for general combining ability; and pair-mating, to generate material for second generation selections (Fowler et al. 1988).

Newton's (2003) systematic review of yield responses of white spruce and three other North American conifers to forest tree improvement practices indicated that correct provenance-progeny selection could yield juvenile height growth gains of about 12% at 20 years for white spruce, and a corresponding merchantable productivity (mean annual merchantable volume increment) gain of 26% at 50 years for plantations established at nominal initial densities on medium-to-good quality sites. Also, preliminary estimates derived from individual case studies indicated that first generational selection strategies for white spruce could increase merchantable productivity by approximately 20% at 45 years.

Controlled crossing

The controlled crossing program for British Columbia, announced at the 19th Meeting of the Canadian Tree Improvement Association in August 1983, created four breeding units (B.U.), one for each of the three British Columbia selection units (Prince George, Prince Rupert, and East Kootenay), and one for material assembled from various sources in eastern North America (Kiss 1984). Each of the British Columbian B.U.s contained 10 previously tested trees. The other B.U. contained 10 random trees. A total of 40 parents were thus included. Two levels of crossing were accommodated: within B.U.s (half diallel with selfs and five reciprocal crosses in each diallel), and among B.U.s. In addition, each tree from a given B.U. was crossed with two trees of each of the other three breeding units. All 390 matings were completed (Kiss 1988). Matings for second generation breeding production commenced in 1987. The top 50% of the tested trees in each of the three selection units were used for further breeding, the selection units being kept separate. The trees were randomized into groups of four. Half diallel crosses were carried out in each group. Full-sib progeny trials will determine the best two crosses in each group incorporating all four parents (Kiss 1989).

Holst and Teich (1969) studied narrow- and broad-crowned white spruce for their ability to produce fast-growing, single-leadered progeny by open pollination. They calculated height and leader number by regression and analysis of variance. Slender-crowned plus trees (which were 4% taller than the broad-crowned control trees) produced progeny 4% taller than the progeny of broad-crowned trees. Stands also differed in the height of their progeny; the best were 18% taller than the worst. Leader number varied significantly among progeny of different stands but not between progeny of parents from the same stands. There was no parent-progeny correlation in branch length. Heritabilities of height and leader number were calculated by parent-progeny regression and by variance component analysis. Parent-progeny regression resulted in a heritability of 9% for height, indicating that plus-tree selection would be effective. Variance component analysis resulted in single tree heritability of 11% ± 3% for height and 9% ± 4% for leader number. On a family basis, these heritabilities were as high as 91% and 85%. The positive correlation of parent height with progeny height indicated that only plus trees should be progeny-tested in a program for growth rate improvement in white spruce (Holst and Teich 1969).

Nienstaedt and Riemenschneider (1985) tested 92 progenies from Ontario, Michigan, Minnesota, and Wisconsin on two sites in Wisconsin and one site in each of Michigan and Ontario. They determined heritabilities for the 9- and 15-year-old trees for individual tests and in a combined analysis of the U.S. tests. They compared nursery performance with 9- and 15-year heights in the U.S. tests. Heritabilities, which were greatest on the least productive site, increased markedly between the ages of 9 and 15 years. No systematic trends were detected between test sites and the heritabilities of progenies grouped on the basis of climatic origins.

Most tree breeding strategies involve repeated cycles of testing, selection, and breeding. During the initial stage of an improvement program, genetic material is secured by the selection of parent trees in natural populations.

Rudolf's (1959b) classification of subject matter of research projects relating to forest tree improvement is still a useful vignette of this field of investigation in regard to white spruce:

A. Selection and testing of variation
    1. Natural variation
        a. Among races (ecotypes)
        b. Among stands
        c. Among individuals
    2. Induced variation
        a. By recombination
        (1) Interspecific hybridization
        (2) Intraspecific hybridization
        (3) Selfing
        b. By mutation
            (1) Physical treatments (e.g., radiation)
            (2) Chemical treatments (e.g., colchicine)

B. Utilization of selected variants for planting by production of
    1. Clonal lines
    2. Seed
        a. Seed production areas
        b. Seed orchards
    3. Registered seed

C. Applications of genetics in silviculture and management of naturally produced stands

D. Fundamental genetic studies
    1. Mode of inheritance
    2. Reaction range
    3. Experimental taxonomy
    4. Evolution

E. Supporting sciences and special techniques
    1. Botany
        a. Physiology
            (1) Flower induction
            (2) Vegetative propagation
            (3) Nutritional studies
            (4) Photoperiodism
            (5) Thermoperiodism
            (6) Chemistry
            (7) Drought resistance
            (8) Phenology
        b. Cytology
            (1) Chromosome numbers
        c. Taxonomy
        d. Morphology and anatomy
            (1) Flower primordia
            (2) Wood characteristics
                (a) Density
                (b) Fibre length
                (c) Fibril angle
                (d) Heartwood, sapwood
                (e) Compression wood
        e. Ecology
        f. Pathology
    2. Zoology
        a. Entomology
    3. Biometry
    4. Special techniques
        a. Controlled pollination
            (1) Pollen collection
            (2) Pollen storage
            (3) Bagging
            (4) Methods
        b. Climbing gear
        c. Nursery techniques

Tree breeding programs for white spruce begin with the selection of superior trees emphasizing stem form and branching characteristics, together with a requirement of above-average height and diameter growth. Selection programs in Canada were initiated first in Ontario (Carmichael 1960) and British Columbia (Heaman 1967). In Nova Scotia, the plus-tree selection stage for white spruce was completed by 1987 (Morgenstern and Mullin 1988). In 1994, the Canadian Forest Service, in collaboration with the ministère des Ressources naturelles du Quebec's Centre de bouturage de Saint-Modeste, began to evaluate 150 full-sib families using seedlings and cuttings (Beaulieu 2002); 5 years after planting, the best 25 full-sib families had an average height of 2 m, 22% greater than the controls, and, based on Bolghari and Bertrand (1984) yield

tables, would produce 350 m^3/ha in plantations at 2.5m spacing on fertile sites after 45 years, 80 m^3/ha more than plantations using unimproved sources.

Seedling seed orchards are established and rogued on the basis of half-sib progeny tests (Dhir and Vincent 1978). In the selection and breeding of spruce in the interior of British Columbia, species designation is ignored within breeding zones for practical purposes (Kiss 1971, 1986) in favour of “interior spruce” (see section 1.7.4).

By 1988, the British Columbia Ministry of Forests had established 12 interior spruce seed orchards totalling 36.3 ha in the southern interior zone with an additional seed orchard of 7.4 ha under development (Konishi et al. 1988). Seed produced in four of these orchards in 1985 and 1986 totalled 7.0 kg, which yielded 1.7 million plantables. Supplemental mass pollination was used to enhance seed yield and genetic quality of these early crops.

Selections are made by one of several techniques (Ledig 1974, Morgenstern 1983), often the comparison tree selection method, in which measurements of a candidate tree are compared with those of several neighbouring trees. The comparison tree method is most effective for traits with high heritability, or in even-aged populations with low environmental variation and where the coefficient of relationship among the candidate and comparison trees is low. Cheliak et al. (1985) recommended strict avoidance of the comparison-tree technique for white spruce in Ontario after they had confirmed that white spruce trees within a radius of about 30 m were related. In New Brunswick, selected white spruce had 9.9% phenotypic superiority over comparison trees (New Brunswick Tree Improvement Council 1985, reported by Morgenstern and Mullin 1988).

The time and cost of plus-tree selection for white spruce in New Brunswick and Quebec ranged from 2.0 to 9.6 days per tree at costs ranging from $160 to $1,118; mean values were 5.3 days and $558 (Morgenstern 1983).

All selection methods attempt to exclude relatives in the same breeding population so as to avoid the inbreeding depression associated with consanguineous mating. The average relationship in natural stands in central New Brunswick approximates that of half-sibs (Park et al. 1984), and, on the assumption that widely separated trees are less likely to be related than are neighbours, most parent-tree selection programs require selected trees to be located no closer than a specified minimum distance. For white spruce in eastern Ontario, Cheliak et al. (1985) recommended a minimum separation of 65 m.

Seed source studies can delineate regions or stands to obtain promising genetic material for tree improvement. The breeding value of trees selected from natural stands should also be evaluated in well-replicated progeny tests before inclusion in a breeding program. In theory at least, allele frequency differences among samples of populations or families are manifested in trait mean values when grown in uniform environments.

The breeding interval (i.e., the number of years between grafting and final seed) for white spruce can be reduced from 13 years with field culture and no treatments to 7 years with greenhouse culture and growth acceleration ($GA_{4/7}$) (Greenwood et al. 1988).

The main obstacle to rapid progress in genetic improvement of forest trees is the period required for testing and evaluating (Magnussen and Yeatman 1988). The time between generations can be reduced greatly by environmental manipulation to accelerate growth and induce early flowering (Bongarten and Hanover 1985), but short generation times can be used to full advantage only if the characteristics determining future performance can be recognized at an early age. Genetic correlations between juvenile and mature characteristics must be sufficient to support early selection and set realistic limits to the proportion that may be selected to obtain an expected gain.

Genetic gain

There are three approaches to the achievement of genetic advance in tree-breeding (Holst and Teich 1969). The first applies where plus-tree selection is so efficient that selections do not have to be tested individually; the second, where plus-tree selection is so ineffective that testing could be of random trees; and the third, where plus-tree selection is effective, but where testing is required to confirm the value of selected trees and to provide material for continued improvement. Holst and Teich (1969) found that plus-tree selection in white spruce is both effective and relatively cheap compared with progeny tests, but that the two methods nevertheless complement each other. They suggested that plus-tree selection followed by progeny testing is more effective than either method by itself.

White spruce family tests from open pollination at four locations in New Brunswick provided estimates of individual-tree heritability for height of 0.089 and 0.091 at ages 6 and 11 years from seed. Estimates of genetic gain ranged from 4.1% to 5.3%, depending on desired spacing and family selection intensity in the seedling seed orchards (Steeves 1988). Gain estimates from a similar study in Nova Scotia were slightly lower (Veen 1988).

The genetic gain at rotation age arising from juvenile selection can be estimated by formulae provided a number of assumptions are made (Magnussen and Yeatman 1988). Selection before one-half of the economic rotation age will result in considerably greater genetic gain per unit of time than selection at maturity. Under favourable conditions, selection age is less than one-tenth of the rotation age.

3.9.1 Genetic engineering, transgenic breeding

The terms transgenic, genetically engineered, and genetically modified all mean the same thing when applied to plants, including trees. A transgenic tree is one that has had one or more specific genes artificially added or removed to create a unique gene combination with the aim of improving the performance of the tree. The goal of transgenic breeding is to produce trees with particularly desirable traits, e.g., faster growth, better wood fibre quality, herbicide tolerance, increased resistance to damage by insects, diseases, or environmental stresses. Improvement by traditional tree breeding would take decades.

The introduction of foreign genes (transgenes) or the transformation of plants is routine for many annual crop species, but transgene research on forest trees is less advanced. Field trials of transgenic trees, including poplar and spruce hybrids, were established to determine the stability and variation of the transgene expression. In transformations mediated by

Agrobacterium tumefaciens with the gene uidA coding for the protein ß-glucuronidase (GUS), expression of the GUS reporter gene is detectable by blue coloration or other quantitative assays after the tissue is supplied with an appropriate enzymatic substrate. In field trials of several transformed lines of white spruce, the highest level of GUS activity and the least variation in GUS expression occurred with in vitro plants (Ellis et al. 1996). As plants were transferred to greenhouse, cold frame and field conditions, the levels of GUS expression decreased while variation in expression among the different lines increased, possibly due to differences in relative growth rates, plant structure, and leaf anatomy of plants in the different environments (Pilate et al. 1997).

Genes can be moved into host tree cells by a variety of techniques: A naturally occurring soil bacterium can be used to shuttle genes, genes can be micro-injected by means of a tiny needle, or a gene can be introduced into a cell by electroporation, whereby the gene is punched through an evanescent electrically made hole in the cell wall. Particle bombardment, another technique, can shoot the cell with microscopic bullets coated with the new gene.

Hodgetts et al. (2001) reported the development of 13 primer pairs that allowed the unambiguous amplification of 15 microsatellite (simple sequence repeat [SSR]) loci in white spruce. Fourteen of these loci were polymorphic in trees sampled at three geographically separated regions of western Canada (Alberta and Saskatchewan). Segregation analysis carried out on these loci confirmed a Mendelian inheritance pattern for all except two loci, which showed significant segregation distortion. All of these primer pairs amplified SSR loci in at least one of the other *Picea* species tested: black, red, Norway, Colorado, Sitka, and Engelmann spruces. This set of markers will be useful for the management of these species and the improvement of commercially important traits.

A cDNA encoding a 14-3-3 protein was isolated from white spruce (Lapointe et al. 2001). The corresponding polypeptide contains several motifs that are conserved in this type of protein and is predicted to be 260 amino acids in length. Multiple banding in Southern blot analysis suggests that the gene encoding this cDNA is, in fact, part of a small family of genes. Wounding and chitosan treatment of spruce plants followed by Northern blot analysis indicates that these stimuli caused the accumulation of 14-3-3 mRNA. In addition, cell suspension cultures treated with methyl jasmonate showed up-regulation of 14-3-3-encoding mRNA. Chitosan and methyl jasmonate are both signalling molecules in the activation of plant-defence response genes. It is suggested that this 14-3-3 protein may play a role in the pathogen defence response of coniferous trees.

3.9.2 Tissue culture

Tissue culture is often used as a generic term encompassing both organ culture and cell culture.

Micropropagation

Micropropagation, which is defined as the art and science of plant multiplication in vitro, allows large numbers of plants to be produced from small pieces of the stock plant in relatively short periods of time. Depending on species, a shoot tip, leaf, lateral bud, stem, or root tissue supplies the initial piece of tissue, and in most cases the original plant is not destroyed in the

process. Micropropagation includes: stock plant care, explant selection and sterilization, media manipulation to obtain proliferation, rooting, acclimation (acclimatization), and growing on of liners.

Purpose

Whereas traditional methods of vegetative propagation tend to be unsuited to mass production in breeding programs, cell culture has potential for enormous multiplication rates (Thorpe and Hasnain 1988). While a rooted cutting can produce a single plant from which, some years later, further cuttings can be taken, even the most limited cell culture system (resting buds) can produce several axillary and adventitious shoots, both of which can in turn be induced to form additional axillary and/or adventitious shoots, often within weeks. Clonal propagation lends itself to the rapid production of large numbers of uniform plants of selected qualities.

Methods

Asexual multiplication of plants by tissue culture can be achieved by: (1) enhancing axillary bud breaking, (2) production of adventitious buds, and (3) somatic embryogenesis.

Plantlet formation

Plantlet formation by adventitious budding involves at least four phases: (1) induction of shoot buds on the explant, (2) development of these buds into shoots and their multiplication, (3) rooting of the developed shoots, and (4) the hardening of the plantlets. The hypocotyls and epicotyls of white spruce have been used as explants for micropropagation via adventitious budding (Patel and Thorpe 1986). The formation of adventitious buds is influenced by many factors, including the inoculum, the medium, the culture conditions, the organ serving as tissue source, the physiological and ontogenetic age of the organ, the season in which the explants were obtained, the size of the explant, and the quality of the plant contributing the explant, including in some cases the kind of pretreatment applied prior to the collection of explants. Rumary and Thorpe (1984), who selected epicotyl explants 27-29 days after germination of white spruce seeds, found that the number of seedlings useful for experimentation was maximized (77%) by giving the seed a 5-day cold (5°C) treatment after planting in agar.

The second phase of plantlet formation involves the development of the nodular tissue formed during the bud induction phase into shoots with primary needles. The formation of true shoot apices with juvenile leaf primordia generally requires transfer onto a medium with altered nutritional and/or phytohormonal levels, often with the inclusion of activated conifer-derived charcoal.

Rooting usually requires treatment with auxin, usually indole butyric acid. Often the levels of mineral salts and sucrose in the medium have to be reduced. The aim is to minimize the formation of callus at the base of the shoot. Where much callus is formed, roots often arise in the callus and a functional root/shoot junction may not be obtained.

Plantlets are hardened to survive the transfer to greenhouse and finally the field. Rooting under non-sterile conditions facilitates hardening. In contrast, sterile rooting often produces plantlets with inadequate or inoperative waxy cuticles and stomata.

Somatic embryogenesis

Micropropagation of trees can also be achieved via the formation of somatic embryos (Lu and Thorpe 1987). The process of plant regeneration by somatic embryogenesis has four main phases, beginning with a plant embryo excised from a seed. The excised embryo or explant is placed in an initiation medium for about 6 weeks to develop characteristically white, fluffy, translucent embryogenic tissue, which proliferates indefinitely as long as it remains in the initiation medium. Clumps of the embryogenic tissue are transferred to a maturation medium containing the plant growth regulator in which, after about another 6 weeks, mature somatic embryos, resembling embryos found in seeds, begin to appear on the clumps. Individual mature somatic embryos are germinated in a nutrient medium, roots and shoots developing similarly to those produced from plants germinating from seeds. The plants propagated by somatic embryogenesis are variously termed emblings, somatic seedlings, or somatic embryo-derived plantlets. After the emblings have formed primary needles and roots, they are transplanted into soil and raised to term in a normal greenhouse culture.

Somatic embryogenesis avoids the difficult and lengthy process of rooting of shoots and provides a means for rapid mass-propagation. Also, embryogenic suspensions obtained from embryogenic callus can provide embryogenic protoplasts, useful in genetic engineering.

Since 1985, somatic embryo formation and subsequent plantlet regeneration has been successful in several coniferous species, including white spruce (Fowke and Hakman 1988, Lu and Thorpe 1987, Thorpe and Hasnain 1988), though only a small percentage of the somatic embryos continued to develop into complete plantlets. Lu and Thorpe (1987) dissected immature embryos out of female white spruce cones collected 8 July - 19 August and cultured them in a basal medium prepared with von Arnold and Eriksson's (1981) salts, vitamins, and carbohydrates (AE) plus 500 mg/L casein hydrolysate, 100 mg/L glutamine, and 100 mg/L myo-inositol; the hormones N6-benzyladenine (BA, µM) in combination with 5 or 10µM 2,4-D, MCPA, or picloram were then tested. Areas of embryogenic callus (EC) became visible on the hypocotyls of the cultured immature embryos 1 week after the start of culturing. EC continued to proliferate and eventually covered the zygotic embryo. The transparent and mucilaginous callus consisted of elongated cells and pockets of small densely cytoplasmic embyrogenic cells. Within 2 weeks, somatic embryos with embryonal heads and long suspensors, typical of zygotic embryos, began protruding from the callus. The percentage of embryos forming callus varied with the collection date of the female cones. Little or no callus developed on embryos excised from cones collected on 8 July, and the highest percentage forming callus was obtained from material collected 2 weeks later, decreasing thereafter with increasing maturity of the embryos. The percent embryogenic callus formation was also influenced by the species of auxin; the highest percent was observed on picloram-containing medium, while MCPA and 2,4-D were about equally less effective at equal concentrations (Table 3.28). Somatic embryos did not develop beyond globular stages on the induction medium. Without auxin in the basal medium, or with 2,4-D or 2iP, a few somatic embryos developed to the cotyledon stage but then stopped growing, while others developed a little further but turned brown after 4 weeks.

Table 3.28. Effects of auxin species *in vitro* response of immature embryos of white spruce collected on various dates; values are percentage of explants producing embryogenic callus and somatic embryos (after Lu and Thorpe 1987).

		Collection Date					
Auxin	**Concentration (µM)**	**July 15**	**July 22**	**July 29**	**August 5**	**August 12**	**August 19**
2,4-D	5	17	42	25	19	18	9
	10	38	50	33	25	20	17
MCPA	5	16	41	26	17	11	10
	10	26	43	39	30	17	17
picloram	5	33	67	50	36	27	9
	10	25	61	43	20	21	20

Lu and Thorpe (1987) used four approaches to promote development of somatic embryos and promote plantlet regeneration: (1) incorporation of ABA into the embryo development medium, (2) increased osmolarity of the embryo development medium, (3) transfer of somatic embryos to different germination media, and (4) the use of vermiculite saturated with liquid one-third Schenk and Hildebrandt's (1972) media (SH) or one-third SH solidified with agar or agarose to enhance plantlet growth. However, as with Norway spruce (Hakman and von Arnold 1985), white spruce somatic embryo development was not improved by the addition of ABA. Somatic embryos developed further on media with higher sucrose, the embryonal head becoming white and dense, the embryo then elongating and the cotyledons being initiated. The cotyledons became green soon after their formation and the hypocotyl and radicle became red. More somatic embryos developed on media containing 6% sucrose than on 3% sucrose media. As many as 33 embryos in different stages of maturation were observed on one piece of callus. Similar results were obtained when sorbitol replaced 3% of the sucrose in the medium, suggesting that the effect of the higher sucrose concentration on embryo development was osmotic.

Mature somatic embryos had to be transferred to germination medium for plantlet regeneration (Lu and Thorpe 1987). Among the five media tested, one-third SH gave best results; AE did not support germination of the embryos. Both the cotyledon and the embryo axis started to elongate on germination medium, and roots with root hairs appeared about 10-14 days after transfer to that medium. Shoot development was slower than that of roots, shoots not appearing until 3-4 weeks after transfer to the germination medium. Growth of plantlets improved on liquid one-third SH supplied to vermiculite, or gelled with agarose.

Contribution of the adenine, adenosine and inosine salvage to purine nucleotide and nucleic acid biosynthesis during white spruce somatic embryo maturation was determined by Ashihara et al. (2001b) using in situ assays with [8-14C] adenine, [8-14C] adenosine and [8-14C] inosine. The salvage of adenine and adenosine was high during the initial stages of embryo maturation, characterized by rapid cell proliferation, but it declined upon further embryo development. Inosine salvage activity was always much lower than that observed for adenine and adenosine.

Consistent with these results, activities of adenine phosphoribosyltransferase (APRT) and adenosine kinase (AK) measured in the embryo extracts in vitro were much higher than the activity of inosine kinase (IK) during all stages of embryo development. Utilization of adenosine and inosine for nucleotide and nucleic acid synthesis was found to be regulated by the enzymes AK and IK, as the pattern of their activities was very similar to the activity of adenosine and inosine salvage, estimated with exogenously supplied precursors. However, little correlation between salvage of adenine and activity of APRT was found throughout somatic embryo maturation. As no adenosine nucleosidase activity was found in white spruce embryos, adenosine, but not adenine, seems to be the major end product of adenylate catabolism, and becomes the predominant substrate for purine salvage in vivo. Thus, adenosine salvage appeared to have the most important role in white spruce embryos. Studies on the metabolic fate of [8-14C] adenine and [8-14C] adenosine suggest that turnover of adenine nucleotides is rapid, as some of them are utilized for nucleic acid synthesis. In contrast, most of [8-14C] inosine taken up by the embryos seems to be directly catabolized by the conventional purine catabolic pathway via ureides in all stages of embryo maturation.

Iraqi and Tremblay (2001) examined the role of sucrose in the medium on the maturation of black and white spruce somatic embryos (M-286 and G-316, respectively). A maturation medium containing 6% sucrose, which hydrolyzed into glucose and fructose, gave significantly more embryos than a medium containing 3.16% each of glucose and fructose. Preventing the complete sucrose hydrolysis by a daily transfer of the tissues onto fresh medium significantly decreased the yield of somatic embryos compared to when sucrose was allowed to complete its hydrolysis. This reduction was not due to the manipulation of the tissues during the transfer, since a daily in situ transfer did not affect embryo production. To verify if the better embryo production observed on a medium containing 6% sucrose was due to the increasing osmotic pressure of the medium, this increasing osmotic pressure was simulated with a sequence of media containing different concentrations of glucose and fructose. Unexpectedly and for both species, this simulation did not improve somatic embryo production, which remained similar to the one obtained on constant osmotic pressure. Embryos produced in the different treatments were analysed in terms of sucrose, glucose, fructose, starch levels and protein content. The embryo carbohydrate content was independent from the carbohydrate used in the maturation medium. However, embryos grown in 6% sucrose and allowed to hydrolyse during the maturation period contained significantly more soluble and insoluble proteins than embryos grown in any other treatment. Furthermore, embryos with a higher protein content also exhibited a higher epicotyl appearance frequency.

The kinetics of ethylene biosynthesis and its effects during maturation of white spruce somatic embryos were studied by El-Meskaoui et al. (2000) with the objective of determining the role of ethylene in the maturation of white spruce somatic embryos. They examined the effects of: (1) 1-aminocyclopropane-1-carboxylic acid (ACC), a direct precursor of ethylene in plant tissue, (2) silver nitrate ($AgNO_3$), an inhibitor of ethylene action, (3) alpha-aminooxyamino acid (AOA), a potent inhibitor of ethylene biosynthesis, and (4) enrichment with ethylene. Ethylene biosynthesis was biphasic and gradually increased during embryo development, whereas

endogenous ACC and N-malonylaminocyclopropane-1-carboxylic acid (mACC) decreased. Addition of ACC or AOA to the culture medium increased or decreased, respectively, ethylene biosynthesis by altering endogenous ACC levels during the culture period. In contrast to AOA and $AgNO_3$, ACC and ethylene enrichment significantly decreased the production of mature somatic embryos and increased the browning of the cultures. However, the structure of the shoot apex in mature cotyledonary stage embryos formed under ethylene enrichment was similar to that in control systems. This showed that a reduction in ethylene benefits maturation of white spruce somatic embryos, a conclusion further substantiated by the finding that the inhibitory effects of AOA were partially reversed by the addition of ethylene.

The isolation of intact, functional RNA from conifer species is not easy, especially from those tissues that are heavily lignified and characterized by a low number of living cells. An efficient procedure for isolating RNA from combined wood and bark tissues of Sitka spruce and white spruce, developed by Melichar et al. (2000), was based on a protocol optimized for the extraction of RNA from pollen and one for the isolation of RNA from woody stems. This protocol does not involve the use of phenol, nor does it need ultracentrifugation. In addition, the protocol overcame the problems of RNA degradation and low yield due to oxidation by polyphenolics and co-precipitation with polysaccharides, both of which are abundant components in conifer bark tissues. The isolated RNA was of high quality and undegraded as gauged by spectrophotometric readings and electrophoresis in denaturing agarose gels. Quality was further assessed through the subsequent use of the RNA in reverse transcription and RT-PCR, indicating that it could be used for a number of downstream purposes including Northern blot hybridization and cDNA library construction. Using this modified protocol, 80-150 µg of RNA was routinely obtained from 1 g of fresh material. This protocol was also used for the isolation of RNA from needles of spruce species, from which 750-950 µg RNA per gram of starting material could routinely be obtained.

The development of somatic embryogenesis procedures has given rise to research on seed storage proteins (SSPs) of woody plants for tree species of commercial importance, i.e., mainly gymnosperms, including white spruce. In this area of study, SSPs are used as markers to determine the embryogenic potential and competency of the embryogenic system to produce a somatic embryo biochemically similar to its zygotic counterpart (Flinn et al. 1991, Beardmore et al. 1997).

Emblings vs. seedlings

Grossnickle et al. (1992) compared interior spruce seedlings with emblings during nursery development and through a stock quality assessment program immediately before field outplanting. Seedling shoot height, root collar diameter, and dry weight increased at a greater rate in seedlings than in emblings during the first half of the first growing season, but thereafter shoot growth was similar among all plants. By the end of the growing season, seedlings were 70% taller than emblings, had greater root collar diameter, and greater shoot dry weight. Root dry weight increased more rapidly in seedlings than in emblings during the early growing

season, but this relationship reversed during the latter half of the growing season, so that seedlings and emblings had roots of similar dry weight at the end of the growing season.

During fall acclimation, the pattern of increasing dormancy release index and increasing tolerance to freezing was similar in both seedlings and emblings. Root growth capacity decreased then increased during fall acclimation, with the increase being greater in seedlings.

Assessment of stock quality just prior to planting showed that: emblings had greater water use efficiency with decreasing predawn shoot water potential compared with seedlings; seedlings and emblings had similar water movement capability at both high and low root temperatures; net photosynthesis and needle conductance at low root temperatures were greater in seedlings than in emblings; and seedlings had greater root growth than emblings at 22°C root, but root growth among all plants was low at 7.5°C root temperature.

Growth and survival of interior spruce 313B Styroblock® seedlings and emblings after outplanting on a reforestation site were determined by Grossnickle and Major (1992). For both seedlings and emblings, osmotic potential at saturation (ψsat) and turgor loss point (ψtip) increased from a low of -1.82 and -2.22 MPa, respectively, just prior to planting to a seasonal high of -1.09 and -1.21 MPa, respectively, during active shoot elongation. Thereafter, seedlings and emblings (ψsat) and (ψtip) declined to -2.00 and -2.45 MPa, respectively, at the end of the growing season, which coincided with the steady decline in site temperatures and a cessation of height growth. In general, seedlings and emblings had similar ψsat and ψtip values through the growing season, and also had similar shifts in seasonal patterns of maximum modulus of elasticity, sympalstic fraction, and relative water content at turgor loss point.

Grossnickle and Major (1992) found that year-old and current-year needles of both seedlings and emblings had a similar decline in needle conductance with increasing vapour pressure deficit. Response surface models of current-year needles net photosynthesis (P_n) response to vapour pressure deficit (VPD) and photosynthetically active radiation (PAR) showed that emblings had 15% greater P_n at VPD of less than 3.0 kPa and PAR greater than 1000 µmol $m^{-2}s^{-1}$. Year-old and current-year needles of seedlings and emblings showed similar patterns of water use efficiency.

Rates of shoot growth in seedlings and emblings through the growing season were also similar to one another. Seedlings had larger shoot systems both at the time of planting and at the end of the growing season. Seedlings also had greater root development than emblings through the growing season, but root:shoot ratios for the two stock types were similar at the end of the growing season, when the survival rates for seedlings and emblings were 96% and 99%, respectively.

4. PHYSIOLOGY / NUTRITION

4.1 Introduction

4.11 Dormancy

Typically, temperate woody perennial plants require chilling temperatures to overcome winter dormancy (rest). The effect of chilling temperatures depends on species and growth stage (Fuchigami et al. 1987). In some species, rest can be broken within hours at any stage of dormancy, with either chemicals, heat, or freezing temperatures, effective dosages of which would seem to be a function of sublethal stress, which results in stimulation of ethylene production and increased cell membrane permeability.

Dormancy of various kinds is expressed in white spruce (Romberger 1963). Dormancy is a general term applicable to any instance in which a tissue predisposed to elongate or grow in some other manner does not do so (Nienstaedt 1966). *Quiescence* is dormancy imposed by the external environment. *Correlated inhibition* is a kind of physiological dormancy maintained by agents or conditions originating within the plant, but not within the dormant tissue itself. *Rest* (winter dormancy) is a kind of physiological dormancy maintained by agents or conditions within the organ itself. However, physiological subdivisions of dormancy do not coincide with the morphological dormancy found in white spruce and other conifers (Owens et al. 1977). Physiological dormancy often includes early stages of bud-scale initiation before measurable shoot elongation or before flushing. It may also include late leaf initiation after shoot elongation has been completed. In either of those cases, buds that appear to be dormant are nevertheless very active morphologically and physiologically.

White spruce, like many woody plants in temperate and cooler regions, requires exposure to low temperature for a period of weeks before it can resume normal growth and development. This “chilling requirement” for white spruce is satisfied by uninterrupted exposure to temperatures below 7°C for 4-8 weeks, depending on physiological condition (Nienstaedt 1966, 1967). Nienstaedt and Zasada (1990), on the basis of results from several studies (e.g., Holst 1956, 1962, Fraser 1962a, Nienstaedt 1966, Logan and Pollard 1976) assessed the chilling requirements of white spruce at 2°C for 6 weeks.

Powerful as are the physiological effects of exposure to chilly temperatures on species such as white spruce that have chilling requirements, chilling is not an absolute requirement. Long photoperiods can compensate for chilling (Nienstaedt 1966). Initial results indicated that to break dormancy of 1-year-old and 2-year-old white spruce seedlings under 13-hour day length, a period of 6-8 weeks of chilling is required if begun in July, or 4-6 weeks if begun in September (Rudolf 1959a). Long-day treatments compensated fully for lack of chilling in the July series but were less effective in the September series. Interaction between chilling and photoperiod is also indicated by the observation that the effect of chilling is reinforced by darkness (Holst 1962).

Unchilled white spruce treated with long-day (20-hour) photoperiods take 2-4 weeks longer to flush than do chilled but otherwise similar white spruce, and the first 2 weeks of chilling treatment are relatively more effective than subsequent additional days of chilling. Treatment

with long-day (18- to 20-hour) photoperiods compensates at least in part for lack of chilling; photoperiods of 13 hours have no compensating effect.

Nienstaedt (1966) found that grafts from 30-year-old trees required somewhat less chilling than 4-year-old plants. The effects of many short chilling treatments are not cumulative; during the early part of dormancy release, a warm period can reverse the effect of a preceding cold period (Romberger 1963); the date at which effective dormancy release begins may therefore vary considerably from year to year (Nienstaedt 1966). Below a certain threshold, the effectiveness of chilling is not a function of temperature; all temperatures below the threshold are equally effective (Samish 1954).

Other definitions of dormancy

The definition of classical dormancy is weak, in that it describes neither seedling anatomy nor morphology (Lavender 1985). Other definitions that might be appropriate for coniferous seedlings are based on mitotic activity in buds, and on resistance to stress, or "hardening off". Owens and Molder (1973) termed Douglas-fir buds "dormant" when there is no mitotic activity of cells of buds. In some species, e.g., Douglas-fir (Hermann 1967), deep dormancy (maximal stress resistance) coincides quite well with dormancy as defined by mitotic activity, but poorly with classical dormancy.

4.2 Light

Plants can react to light in any or all of several ways: phytomorphogenesic, mediated by changes in the quality and quantity of the ambient light environment; phototropic, mediated by the direction of the incident light; and photoperiodic, mediated by day-length (light/dark cycling).

The seasonal variation in the daily duration of daylight (photoperiod) also has important effects on plant growth. White spruce exhibits two forms of shoot growth, indeterminate (free) and determinate. After germination, shoot growth is indeterminate, with new needles developing continuously from primordia initiated at the apex of the growing point (Pollard 1974b). The onset of short-day photoperiods as day length decreases brings indeterminate growth to an end. Bud scales are formed, and new needle primordia are initiated and accumulated inside the bud, ready for deployment the following spring (Jablanczy 1971). The free-growth phase diminishes in subsequent years and generally disappears within 5 years (Nienstaedt and Zasada 1990).

For those studies of micro- and meso-climate dealing with the amount of solar radiation intercepted by plane surfaces of various slopes and aspects, Gloyne (1965) presented a method for calculating the angle of incidence of the direct beam of sunlight on a plane surface of any slope and aspect.

Light in the nursery/greenhouse

In Wisconsin, both white spruce and black spruce grew continuously under long-day illumination during the second growing season, until terminal buds formed shortly after the end of a supplemental light treatment (Watt and McGregor 1963). White spruce under long-day illumination averaged twice the height increment of spruce under the natural day length

treatment. White spruce seedlings of the same provenance, grown in two locations widely separated by latitude (Wisconsin and Florida), did not differ significantly in total height or total weight, but the stem diameter of the Florida-grown plants was greater than that of the Wisconsin stock.

Light in the field

Once the cotyledons have been raised by the elongation and upward arching of the hypocotyl, they expand and force their way out of the seedcoat. Concurrently, the primary photosynthetic organs start to function. Initial light requirements are very low. Photosynthesis increases with increasing light intensity up to saturation point, perhaps somewhere between 25% and 50% of full sunlight on a clear day, beyond which net photosynthesis does not increase with further increase in light intensity. In field experimentation in interior British Columbia, rates of photosynthesis in white spruce and interior spruce seedlings reached maxima at between 20% and 30% of full sunlight (Binder et al. 1988, Bassman 1989). Height growth of white spruce seedlings up to about 10 years old is promoted by increasing light only up to about 50% of full sunlight (Gustafson 1943, Logan 1969). However, beyond the thicket stage, white spruce height growth is greatest at full light intensity (Logan 1969, Eis 1970), possibly because of increasing self-shading of foliage in crowns of increasing size.

Needles of shade-grown seedlings differ from those of unshaded seedlings and have higher photosynthetic capacity, a feature that is more pronounced at low intensities. Shade needles function efficiently in weak illumination. However, the fact that shade foliage of white spruce maintains higher rates of photosynthesis than sun foliage even at relatively high light intensities is probably of little practical consequence, as shaded foliage in natural conditions is rarely exposed to illumination greater than 10% of full sunlight (Clark 1961).

Understorey white spruce beneath established stands in the *Picea glauca–Viburnum–Rubus pubescens* association of the Lower Boreal Cordilleran Ecoregion of Alberta received 14-40% of incoming light through hardwood-dominated canopies, compared with only 5-11% light through white spruce-dominated canopies (Lieffers and Stadt 1994). Competing bluejoint reedgrass (*Calamagrostis canadensis* (Michaux) Palisot de Beauvois) and fireweed (*Chamaenerion angustifolium* (L.) Scopoli) decreased in cover and height with decreasing light transmission. Both species were reduced greatly compared with open-grown conditions, and both were virtually eliminated from stands transmitting less than 10% light through the canopy. The annual height increment of white spruce saplings increased from 5 cm at 10% light to 25 cm at 40% light, about equal to full light performance. The number of buds, leader diameter, and the height:diameter ratio also increased with increasing light.

Fundamental to an understanding of forest community dynamics is knowledge of the effects of variation in light on the constituent individuals, especially the seedlings and saplings of the regeneration phase. Both the successional dynamics of species within a region, and the differential success of species across regions, are likely to be more strongly influenced by variation in the performance of juvenile than of mature trees (Kobe 1996). The variation in height and radial growth of saplings of the major tree species in response to variation in ambient light levels across the major forest zones of northern British Columbia was

characterized by Wright et al. (1998). Early- to late-successional forests were sampled in each region, and the species were ordered from most to least shade-tolerant: Pacific silver fir (*Abies amabilis* (Dougl. ex J. Forbes western red cedar (*Thuja plicata* Donn ex D. Don) > western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) ≥ mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) = subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) > black spruce ≥ white spruce > hybrid spruce = interior spruce > lodgepole pine > trembling aspen (*Populus tremuloides* Michx.) > black cottonwood (*Populus trichocarpa* Torr. & A. Gray) = paper birch (*Betula papyrifera* Marsh.). All sites sampled were uniform in topography and soils and represented mesic conditions for the region. They were located in mature stands (>140 years old), in canopy gaps, along edges of old road or trail cuts, in regenerating burns (>30 years old) and associated mature remnants, and in partially cut and clearcut areas. Areas disturbed within the previous 5 years were avoided. Trees were sampled across a gradient of low to high light (Table 4.1). The best growing sample tree per species per light level was always selected. Saplings of all species had measurable radial and height growth rates even at the lowest light levels sampled. In the Boreal Forest Region, there was a strong trade-off between ability to grow at high light versus low light, and the light response curves for radial and height growth were compatible with shade tolerance rankings. For example, low-light growth of subalpine fir was higher than that of white spruce in the Intermontane Boreal region, while growth of lodgepole pine was greater than that of white spruce and subalpine fir in high light. In Sub-boreal forests, radial growth rates of subalpine fir, interior spruce, and lodgepole pine were very similar at light levels below 20% full sun, but growth diverged at progressively higher light levels, with lodgepole pine having the greatest radial and height growth in full sun. But, at low light, leader growth of interior spruce was significantly greater than that of lodgepole pine, with predicted leader lengths of 13 cm for spruce versus 6 cm for pine at 20% of full light. There were shifts in both asymptotic growth and response to low light for the spruces across climatic regions, with response to low light showing the greatest differences. Hybrid spruces in the three temperate zone regions had greater low-light radial growth rates than hybrid, interior, or white spruces in the harsher climates of the sub-alpine, sub-boreal, and boreal regions.

Table 4.1. Mean age, height, and diameter (at 1.3 m) of tree species sampled in each climatic region.

Species	Climatic region	Age (years)	Height (m)	Diameter (mm)
Hybrid spruce	Transitional subalpine	39 (14–152)	2.8 (0.9–7.9)	38 (8–97)
	Wet temperate	25 (9–51)	3.1 (0.6–6.7)	41 (15–94)
	Snowy temperate	34 (9–116)	2.7 (0.8–8.7)	40 (7–111)
	Moist temperate	19 (8–79)	3.4 (0.7–7.6)	43 (3–101)
Interior spruce	Continental subalpine	45 (12–135)	3.1 ((0.7–8.2)	44 (6–133)
	Western sub-boreal	24 (13–51)	2.9 (0.9–6.0)	34 (1–92)
White spruce	Intermontane boreal	48 (13–161)	3.5 (0.5–9.2)	42 (5–96)
	Plains boreal	35 (10–79)	3.2 (0.9–7.6)	34 (7–69)

Note: Data in parentheses are ranges.

Amount of light

Measurements of radiation in physiological ecology are of primary importance because of their role in energy balance determinations and in photosynthesis measurements (Pearcy 1989). The radiant energy incident on a unit surface from all directions is called the *incident radiant flux density* or *irradiance* in SI units of $W \cdot m^{-2}$.

4.3 Temperature

Temperature has a multiplicity of effects on plants depending on a variety of factors, including the size and condition of the plant and the temperature and duration of exposure. The smaller and more succulent the plant, the greater the susceptibility to damage or death from temperatures that are too high or too low. Temperature affects the rate of biochemical and physiological processes, rates generally (within limits) increasing with temperature. However, the Van't Hoff relationship for monomolecular reactions (which states that the velocity of a reaction is doubled or trebled by a temperature increase of 10°C) does not strictly hold for biological processes, especially at low and high temperatures.

At the small, domed apex of vegetative buds of white spruce shoots, cell division begins in the spring, largely in response to rising temperatures (Owens et al. 1977). Newly flushed shoots of white spruce are very sensitive to spring frost (Sutton 1992), and damage can occur regionally (Cayford et al. 1959, Coates et al. 1991). In boreal climates, frost injury can be incurred annually by white spruce that are not protected by some kind of overstorey. Shoot tissue as well as buds and needles can be damaged. Early-flushing provenances or clones of white spruce are particularly susceptible to damage by late spring frost. Even unflushed buds of white spruce can be damaged enough by frost as to render them unable to flush (Harding 1986, Sutton 1992); sometimes, the needles surrounding such aborted buds develop atypically and come to resemble a tufted bottle-brush (Sutton 1992). Such problems can affect natural regeneration but are much more common in artificial regeneration, where overstorey protection is minimal.

Natural frost injury in white spruce has been mimicked artificially in needles (Glerum and Farrar 1965) and stems (Glerum and Farrar 1966). Cold temperatures during growth can interfere with the development of cuticle by maturing needles (Vanhinsberg and Colombo 1990), thus reducing their ability to resist desiccation and winter browning.

Especially important in determining the response of white spruce to low temperatures is the physiological state of the various tissues, notably the degree of "hardening" of dormancy. A natural progression of hardening and dehardening occurs in concert with the seasons (Glerum 1985). While different tissues vary in their ability to tolerate exposure to stressful conditions (roots, for instance, being more susceptible than shoots), white spruce, as with woody plants in general, has necessarily developed sufficient winter hardiness in its various tissues to enable them to survive the minimum temperatures encountered in the distribution range.

In the early 1980s, outdoor-overwintered containerized conifer seedlings commonly suffered heavy losses in Ontario, the trees having been placed outside in the fall while actively growing and before adequate hardening off (Colombo and Gellert 2002). Even mild frosts could damage them, and in some cases entire crops were lost. Methods of frost hardiness testing were developed (Colombo et al. 1984). Testing of stock for readiness for overwinter frozen storage

was necessitated because, even though temperatures for frozen storage are relatively mild (usually -4°C — 2°C), nursery stock requires a high level of frost hardiness to stay healthy during storage.

Seedlings must enter dormancy to become adequately hardy for overwintering. Dormancy begins with the initiation of buds on shoots, following shortening of day length, naturally or otherwise. A sequence of warm short days followed by cool short days will give the best seedling quality for both overwintering and for planting the following summer (Colombo and Gellert 2002). Such seedlings will have large buds, large stem diameters, and low shoot: root and height: diameter ratios (Colombo 1997). After the terminal buds are initiated, seedlings become hardy to -15°C after 4 to 6 weeks. Exposing seedlings to cooler temperatures during hardening can shorten this period, but risks negative side effects if temperatures are too cold shortly after bud formation.

Frost hardiness tests are done by subjecting shoot tips to controlled freezing and assessing the resultant damage using the electrolyte leakage method. In Ontario, the standard test produces results after at least 3 days, but a quick test that provides results after just one day has also been developed (Colombo and Gellert 2002).

Experience in Ontario, Manitoba, and the Maritime Provinces shows that seedlings that have passed two consecutive -15°C frost hardiness tests can usually be safely moved outside as late as the end of October, provided that they do not encounter temperatures lower than about -20°C. The trees also need to have received a period of cold temperature around 5°C in the greenhouse in order to increase root hardiness. Stock is not ready to be moved outside before the stems are brown (lignified), not green to the tip of the stem, or if long white roots are present.

The leaves, cortex, and xylem in twigs, and bud tissues of white spruce from Fairbanks, Alaska, were all found to be hardy to -70°C, but in Engelmann spruce from Colorado the primordial shoot was almost 30°C less hardy than the cortex, which was as hardy as white spruce (Sakai and Larcher 1987). Primordia of winter buds of white spruce survived freeze dehydration, even at -70°C, by extraorgan freezing, i.e., ice segregation from a supercooled organ to a specific space outside, dehydrating the organ (Sakai 1979b).

When water freezes in plants, the consequences for the plant depend very much on whether the freezing occurs intracellularly (within cells) or outside cells in intercellular (= extracellular) spaces (Glerum 1985). Intracellular freezing usually kills the cell regardless of the hardiness of the plant and its tissues (Lyons et al. 1979). Intracellular freezing seldom occurs in nature, but moderate rates of decrease in temperature, e.g., 1°- 6°C/hour, cause intercellular ice to form, and this “extraorgan ice” (Sakai and Larcher 1987) may or may not be lethal, depending on the hardiness of the tissue.

At freezing temperatures, water in the intercellular spaces of plant tissues freezes first, though the water may remain unfrozen until temperatures fall below 7°C (Glerum 1985). After the initial formation of ice intercellularly, the cells shrink as water is lost to the segregated ice. The cells undergo freeze-drying, the dehydration being the basic cause of freezing injury.

The rate of cooling has been shown to influence the frost resistance of tissues (Sakai 1979a), but the actual rate of freezing will depend not only on the cooling rate, but also on the degree of supercooling and the properties of the tissue (Levitt 1980). Sakai (1979a) demonstrated ice segregation in shoot primordia of Alaskan white and black spruces when cooled slowly to -30° to -40°C. These freeze-dehydrated buds survived immersion in liquid nitrogen when slowly rewarmed. Floral primordia responded similarly. Extraorgan freezing in the primordia accounts for the ability of the hardiest of the boreal conifers to survive winters in regions when air temperatures often fall to -50°C or lower (Sakai and Larcher 1987). The hardiness of the winter buds of such conifers is enhanced by the smallness of the buds, by the evolution of faster translocation of water, and an ability to tolerate intensive freeze dehydration. In boreal species of *Picea* and *Pinus*, the frost resistance of 1-year-old seedlings is on a par with mature plants (Sakai and Okada 1971), given similar states of dormancy.

Temperature and root growth

Soil temperature is important for the survival and early growth of newly planted seedlings. Soil temperatures affect the anatomical and morphological character of root systems (Taylor 1983). All physical, chemical, and biological processes in soil and roots are affected not least because of the increased viscosities of water and protoplasm at low temperatures. In general, climates that do not preclude survival and growth of white spruce above ground are sufficiently benign to provide soil temperatures able to maintain white spruce root systems. In some northwestern parts of the range, white spruce occurs on permafrost sites (Gill 1975), and although young unlignified roots of conifers may have little resistance to freezing (Mityga and Lanphear 1971), less than half of the "secondary mature" root system of white spruce was killed by exposure to a temperature of 23.3°C in multiple year experiment with containerized trees from local nurseries in Massachusetts (Havis 1976).

Optimum temperatures for tree root growth range between 10° and 25°C in general (Lyr and Hoffmann 1967) and for spruce in particular (Chalupa and Fraser 1968, Heninger and White 1974, Ritchie and Dunlap 1980, Binder et al. 1988). In 2-week-old white spruce seedlings that were then grown for 6 weeks in soil at temperatures of 15°, 19°, 23°, 27°, and 31°C; shoot height, shoot dry weight, stem diameter, root penetration, root volume, and root dry weight all reached maxima at 19°C.

However, whereas strong positive relationships between soil temperature (5°-25°C) and growth have been found in trembling aspen and balsam poplar (Landhäusser et al. 2001, Tryon and Chapin 1983, Landhäusser et al. 2003), white and other spruce species have shown little or no changes in growth with increasing soil temperature (Turner and Jarvis 1975; Tryon and Chapin 1983; Day et al. 1990; Landhäusser et al. 2001, 2003). Such insensitivity to soil low temperature may be common among a number of western and boreal conifers (Green 2004).

The minimum temperature for tree root growth ranges from just above 0° to 7°C, and while roots of white spruce grow little or not at all in soil cooler than about 5°C, some white spruce root growth has been recorded at temperatures as low as 1°C (Day 1985). However, a minimum of 7° or 8°C may be a more realistic threshold limiting satisfactory establishment of interior spruce in British Columbia (Coates et al. 1994). Soil temperature is particularly important for

newly planted stock. Trees planted in cold soil in spring lack new root growth sufficient to avoid plant water stresses caused by transpirational losses (Sutton 1978). Trees planted into soil too cold to encourage root growth are likely to transpire far more water than they are able to take up, especially if the soil is poorly aerated. Water becomes increasingly viscous with decreasing temperature, and plant tissues also become less permeable to water. Water uptake is restricted (Lopushinsky and Kaufmann 1984, Grossnickle 1988), new roots do not develop, and existing roots do not function effectively (Sutton 1969b). In boreal conifers, cambial activity in roots is initiated only when the temperature of the surrounding soil reaches 10°-13°C (Sutton 1991).

The influence of two levels of soil temperature (10° and 20°C) and flooding on the water relations and morphological development of cold-stored white spruce and black spruce seedlings was studied by Grossnickle (1987). Changes in water flow characteristics occurred for non-flooded seedlings of both species at both soil temperatures over the course of the 42-day experiment. As seedlings of both species underwent a longer exposure to different soil temperature treatments, RSPAC (root–soil-plant–atmosphere continuum) decreased, suggesting that the initial root membrane alterations, if any, were temporary. By day 21, white spruce seedlings showed a large RSPAC difference between soil temperature treatments. RSPAC values were determined from the slopes of the ψ_x by TFD regression lines (Running 1980, Grossnickle and Blake 1985). Needle conductance $g_{\omega\upsilon}$ and transpirational flux density (TFD) were measured with a steady-state porometer. Similar results had been found in other conifer species (Kaufmann 1977, Teskey et al.1984). As spruce seedlings did not show a large RSPAC difference between seedlings at 10°C and 20°C soil temperature treatments, white spruce seedlings were found to be more sensitive than black spruce to soil temperature. Both white spruce and black spruce are found on boreal sites having moderate soil temperatures and better-drained soils, but with decreasing soil temperature and increasing soil moisture, black spruce becomes the dominant species (Viereck et al. 1983).

White spruce seedlings planted after cold storage initially showed greater resistance to water flow through the soil-plant-atmosphere-continuum at 10°C than at 16° or 22°C (Grossnickle and Blake 1985). The resistance to water flow at low soil temperatures can be attributed to the combined effects of increased viscosity of water and increased resistance to water flow through the root. In Grossnickle and Blake's study, the growth of new white spruce roots in the root growth capacity test was poor at all three soil temperatures, no better at 22°C than at 10°C. The relative plant resistance of white spruce seedlings decreased with time, and after 18 days any differences in relative plant resistance at different soil temperatures were due to changes in the viscosity of water, suggesting that the root systems had by then acclimated to the soil temperature treatments. This indicates the importance of allowing a period of time for acclimation, as these membrane changes would seem to be reversible.

Root temperature of 1-year-old Engelmann spruce seedlings in a growth chamber had no effect on net photosynthesis between 10° and 20°C, but stomatal conductance and photosynthesis declined sharply below 8°C. After 7 days at a root temperature of 0.7°C, net photosynthesis and stomatal conductance decreased to 50% and 34%, respectively, of the initial values (DeLucia 1986). Root chilling caused a large decrease in root starch concentration and an increase in

total soluble sugars, more than doubling the ratio of soluble sugars to starch. The accumulation of reducing sugars, which can act as cryoprotectants, is commonly observed in the development of frost hardiness in conifers. An increase in the ratio of glucose to sucrose after root chilling suggests an increase in invertase activity and the production of a low temperature invertase isozyme. Maintenance of adequate sugar supplies to the root tip is important for continued elongation. Continued root growth in spruce at low soil temperatures probably depend on the maintenance of large pools of reducing sugars, particularly glucose.

The constant flux of radiant energy in the biosphere became susceptible to monitoring with the development of inexpensive portable radiometers in the 1950s. Moen (1968) made use of these in measuring thermal radiation from an isolated paper birch tree and an isolated white spruce tree on four clear and calm summer nights at five distances from the base of each tree. The birch was 14 m tall and had a maximum crown diameter of 8.5 m; the spruce was 9.5 m tall and had a crown diameter of 4 m. Radiometers of the type described by Suomi and Kuhn (1958) were placed 45 cm above the ground at distances of the base of each tree of 0.0, 0.2, 0.4, 0.6, and 0.8 times tree height and aligned in WNW direction. Temperatures were converted to Langleys per hour using formula (1) of Tanner et al. (1960). Patterns of radiation flux were similar for both spruce and birch trees. The effectiveness of the crowns in shielding the radiometers in positions 0.0 and 0.2 from the cool night sky was clearly evident. Cooling by radiation was evident in the upward flux in the 0.4, 0.6, and 0.8 positions, which were beyond the crown periphery. The flux appeared to level off beyond the 0.4 position. Moen concluded that the infrared contribution of the crown extended to a distance of about one-half the height of the trees. The additional energy flux under the crown compared with that around the edge influenced the distribution of dew and could affect the distribution of rusts and insect activity.

4.4 Photosynthesis

Photosynthesis is a photochemical process driven by photons absorbed by chlorophyll in the wavelength band from 400 to 700 nm (Gordon et al. 2001). The absorption of most leaves is quite high within that range, and, although the energy content of a 700 nm photon is only 57% that of a 400 nm photon, the photosynthetic rate depends essentially on the number of photons absorbed rather than on their wavelength (Pearcy 1989).

A committee of the Crop Science Society of America proposed the following definitions (Shibles 1976):

> *Photosynthetically active radiation* (PAR): radiation in the 400–700 nm waveband;
>
> *Photosynthetic photon flux density* (PPFD): incident photon flux density of PAR: the number of photons (400–700 nm) incident per unit time on a unit surface, with the SI unit mol $m^{-2}{\cdot}s^{-1}$ as µmol $m^{-2}{\cdot}s^{-1}$ or the non-SI µEinsteins $m^{-2}{\cdot}s^{-1}$;
>
> *Photosynthetic irradiance* (PI): radiant energy flux density of PAR: the radiant energy (400–700 nm) incident per unit of time on a unit surface, with the unit $W{\cdot}m^{-2}$.

Pearcy (1989) commented that definitions for light measurement were likely to undergo further modification.

The process provides the main input of free energy into the biosphere, and is one of four main ways in which radiation is important for plant life (Jones 1992).

Spectral responses of various physiological processes differ; therefore, instruments for measuring them must be appropriately sensitive. Combinations of photocells and filters can approximate the responses needed to measure either irradiance in the PAR or photon irradiance in the PAR. Such instruments are often called photosynthetic energy and quantum sensors, respectively (Jones 1992). Radiometers measure radiant flux density, and pyranometers or solarimeters measure total shortwave radiation incident upon a surface. Photosynthesis does not respond linearly to light, hence the average irradiance cannot be expected to predict CO_2 uptake well. Furthermore, the high irradiance within sunflecks may even cause photoinhibitory damage to the chloroplasts. For many purposes, especially in studies of photosynthesis, the average irradiance on a horizontal surface at any depth in the canopy is not the value of interest (Jones 1992).

The radiation climate within plant communities is extremely variable, both spatially and temporally.

Newly transplanted 3-year-old bareroot white spruce seedlings grown in three levels of absolute humidity difference (AHD), with and without water-stress, showed stomatal conductance to CO_2 as well as net assimilation more than twice as high in the low AHD treatment as in the high AHD treatment (Marsden et al. 1996). Transpiration rates were uniform among humidity treatments, but in the low AHD treatment water use efficiency was more than double that of the high AHD treatment. Water use efficiency was greatest in the low AHD conditions, in the water-stressed seedlings, and immediately after planting. Despite the different levels of photosynthesis there were no differences in the number of new roots produced among humidity treatments.

Maximum photosynthesis of white spruce foliage occurs between 40% and 60% of full sunlight (Man and Lieffers 1997a, b), but maximum growth in stem diameter and volume of conifer seedlings and saplings generally occurs under full light (Eis 1967a, Logan 1969, Comeau et al. 1993, Lieffers and Stadt 1994, Jobidon 2000). Minimum light levels for survival might vary with tree size (Givnish 1988).

White spruce is less adapted to photosynthetic production than balsam fir under low temperature and low light conditions, though white spruce requires less moisture (Clark 1956, 1961). The photosynthetic capacity of spruce foliage reaches a maximum in the year it is produced, and then gradually declines with increasing age (Clark 1961).

While height increment is the most obvious component of growth responding to light, stem diameter and root system development are also affected by the amount of light received by the foliage. Significant response of white spruce stem diameter to increasing light can occur without any increase in height (Brix 1972). Root system development in white spruce is promoted by full light (Shirley 1945, Logan 1969). In Sitka spruce, at least, the rate of photosynthesis was markedly depressed at soil temperatures below 1°C (Turner and Jarvis 1975).

4.4.1 Needle conductance

Environmental and physiological control of needle conductance in bareroot white spruce, black spruce, and jack pine seedlings outplanted on two boreal cutover sites in northern Ontario (one upland, the other a spruce bog) were examined by Grossnickle and Blake (1986). Seedlings were planted in May 1984 and monitored from June through August to examine the influence of photosynthetically active radiation, absolute humidity difference (AHD) between needle and air, and xylem pressure potential on seedling stomatal response. The results indicated that all species had adequate soil moisture for optimal physiological response to the environment during the first growing season. Both spruces had stomata that were very sensitive to atmospheric evaporative demands and plant moisture stress. Stomatal response of the seedlings showed that as absolute humidity deficit between needles and air increased, needle conductance (gwv) decreased in both white spruce and jack pine, but at low AHD white spruce had gwv approximately 35% higher than jack pine (Grossnickle and Blake 1987). In white spruce, gwv decreased as xylem pressure potential became more negative in a predictable curvilinear manner. White spruce reached turgor loss at 88% relative water content. Over the first growing season, white spruce showed osmotic adjustment, with an osmotic potential at turgor loss of -1.27 MPa and 1.92 MPa at the beginning and end of the growing season, respectively. Coupled with greater moisture stress at high AHD and less new root growth in the first growing season than in jack pine, growth of the spruces would be more constrained.

Carbon balance

Mature boreal forest ecosystems are large annual carbon sinks. Bonan (1993) used the Terrestrial Carbon Exchange (TCX) model of the combined energy, heat, moisture exchange, tree photosynthesis and respiration, decomposition, and nitrogen mineralization to examine the physiological controls of the carbon balance of boreal forests. Simulated annual tree production, forest floor decomposition, nitrogen mineralization and soil respiration did not differ significantly from previously published data for nine black spruce, five white spruce, two trembling aspen, two paper birch, and three balsam poplar forests near Fairbanks, Alaska. The output from the model also compared well with data from previously published fertilizer application, soil warming, and litter transplant experiments. Net carbon uptake during tree growth was the largest simulated carbon flux. Bonan suggested that differences in the carbon balance of those forests can be explained in part through key physiological parameters that link photosynthesis, carbon allocation, nitrogen requirements, litter quality, and foliage longevity. The simulations suggested greater variation in those parameters between coniferous and broad-leaved life forms than among species.

4.5 Respiration

4.5.1 Root respiration

Conlin and Lieffers (1993) measured the anaerobic and aerobic CO_2 efflux rates from roots of white spruce, black spruce, jack pine, lodgepole pine, and tamarack at temperatures of 5°C, 15°C, and 25°C. Black spruce showed an anaerobic to aerobic CO_2 efflux ratio, which at 5°C was significantly higher than that of the other species. Tamarack showed highest anaerobic and aerobic efflux rates. Conlin and Lieffers interpreted the data as suggesting that black spruce have higher overall increases in fermentation rates, with onset of anoxia at 5°C, and that

tamarack roots have high fermentation and respiration rates at 5°C, features that may suggest metabolic adaptations to cold, flooded peatland soils. A redox dye test showed O_2 diffusion from roots of the pines and tamarack, this demonstrating some ability to transport O_2 to root tissues and sustain limited respiration under anaerobic conditions. Neither white spruce nor black spruce showed any O_2 diffusion from roots at any temperature.

4.5.2 Root physiology

The potential for modifying the IAA concentration in roots, root growth responses, and outplant survival by the application of plant growth regulators (PGRs), e.g., IBA, NAA, and ethylene or moisture-retaining alginate was investigated in several conifer species, including Engelmann spruce, by Scagel and Linderman (2001). The control of root growth is commonly associated with the PGRs auxin and ethylene. Scagel and Linderman (2001) applied PGR treatments to 1+0 container-grown Engelmann spruce by submerging the root systems for 10 sec in one of Hormogel®, Stim-root® (Plant Products Co. Ltd., Brampton, Ontario), Ethrel® (Rhône-Poulenc, Canada, Inc., Mississauga, Ontario), or alginate (calcium alginic acid, Protanal SF®, (MultiKem Corp., Ridgefield, New Jersey). The Hormogel® treatment was an experimental combination of 500 $mg \cdot L^{-1}$ indolebutyric acid (IBA) and 500 mg L^{-1} naphthalenacetic acid (NAA). Stim-root® treatment consisted of a commercial preparation of IBA at 500 mg L^{-1} applied to roots in a carrier of 5.0% alginate. Ethrel®, a commercial formulation of Ethephon (2-chloroethyl phosphonic acid) is a slow-release ethylene compound that was applied at 50 $\mu g \cdot L^{-1}$ for 10 sec in water. Treatment with alginate consisted of submerging tree root systems for 10 sec in a commercial formulation of 5.0% calcium alginic acid. Control plants were untreated. The root systems of control plants received no treatment. Roots of early-lifted Engelmann spruce had lower levels of free IAA and IAA conjugate 2 weeks after planting than had roots of plants lifted at the normal time. Roots of early-lifted plants grew less during the first 2 weeks after planting than did roots of plants lifted at the normal time, and early lifting decreased tree growth and survival. PGR treatments to roots did not always increase survival among early-lifted spruce.

4.6 Water

For good growth, white spruce needs root access to well-aerated water (Cheyney 1942) and adequate nutrition (Sutton 1968). Soil moisture is of particular importance because it acts on plant growth and function both directly and indirectly through its influence on other factors, such as nutrition, aeration, mechanical impedance, and soil temperature (Eavis and Payne 1969). Soil moisture deficits, a principal cause of poor germination, are conditioned by: the amount and distribution of rainfall; presence of shade; rate of evaporation; depth to water table; soil texture; nature and degree of seed covering; season; and nature and condition of seedbed (Arnott 1974a). Collectively, these are the prime determinants of root system architecture in particular (Sutton 1991) and of whole plant development in general.

Experiments at the Kananaskis Forest Experiment Station showed that germination and survival of white spruce seedlings were unaffected by trenching to preclude root competition for moisture by the residual stands (Table 4.2); the study took place in two stands, one an old, moist, fertile spruce–fir “typical of the better sites” in the Subalpine Region, the other 80-year-old lodgepole pine (Ackerman 1957). The lower number of seedlings and lower survival rates on

the moister more fertile site was attributed to a thick (12.5-30.0 cm) layer of organic matter and severe competition from luxuriant minor vegetation.

Table 4.2. Influence of trenching (= root competition from residual stand) on number of white spruce seedlings and survival rates from seedings of 2000 seed per milliacre (8, 094 per m^2) quadrat on a moist spruce–fir and a dry lodgepole pine site in Alberta (after Ackerman 1957).

Site	Treatment	Number of seedlings		Survival (%)
		1951	1955	
Spruce–fir	Trenching	485 b[a]	108 b	22 b
	No trenching	488 b	117 b	24 b
Lodgepole	Trenching	1648 a	885 a	54 a
	No trenching	1730 a	795 a	46 a

[a] Within columns, values followed by the same letter do not differ significantly (P= 0.05) by analysis of variance.

Insufficient soil moisture causes stress in plants. Reduced turgor pressure and inhibition of cell expansion and growth are early responses to insufficient moisture supply. Unless plant water potential remains high, growth will be slowed or stopped. Extended periods of soil water potentials below -1.5 to -2.5 MPa (-15 to -25 bars) will be fatal to most seedlings (Spittlehouse 1985).

A wide range of moisture conditions can be tolerated by white spruce, but growth is stunted where rooting volume in soil of low fertility is restricted by stagnant water, or where soils are dry and infertile.

Growth of white spruce can be excellent on saturated soils if the water contains nutrients and is not stagnant (Sutton 1968). Flooding for up to a month, especially while trees are dormant, was tolerated well by white spruce; trees in small height classes (e.g., 30-60 cm) were affected more than taller (<3.6 m) trees, but still had a 90% survival rate after flooding for 28 days (Ahlgren and Hansen 1957). Thereafter, mortality increased sharply with increasing duration of flooding, and was complete in all height classes after 48 days. Non-dormant white spruce trees are more susceptible to injury from flooding than are dormant trees (Ahlgren and Hansen 1957, Grossnickle 1987). White spruce is less tolerant of flooding than are black spruce, balsam fir, or jack pine. Roots of young white spruce will barely penetrate soil below a water table, and existing root tips will not survive inundation by a rising water table that lasts for more than a few hours (Levan and Riha 1986).

Water loss from white spruce needles is controlled by the response of the stomata to evaporative demand and soil temperature (Goldstein et al. 1985). The response of stomata to evaporative demand appears to be related both to the sensitivity of stomata to vapour pressure deficit and to reduction of water supply in consequence of low soil temperatures. Goldstein et al. suggested that soil temperature is an important component of treeline water relations, since stomata close under conditions of low soil temperature even when there is ample soil moisture and low or moderate evaporative demand.

The apparent sensitivity of white spruce stomata to vapour pressure deficit, soil temperature, and xylem pressure potential indicates a great ability to avoid the development of low plant water potentials. By curbing transpiration during times when the soil is frozen, this enhances the ability of white spruce to resist winter desiccation damage. The downside of the ability to limit loss of water during the growing season by closing stomata at high xylem pressure potentials and low vapour pressure deficits is the constraint it places on CO_2 uptake and therefore on photosynthesis.

Another strategy for curbing loss of water, investigated by Berg and Chapin (1994), is needle loss as a mechanism of winter drought avoidance in black spruce and tamarack. Xylem (water) pressure potential was measured from October 1987 to June 1988 in Fairbanks, Alaska, where tamarack values averaged about -1.0 MPa, with occasional decreases to -1.5 MPa. Black spruce showed similar values until May, when values dropped to 2.5 MPa. Regression models indicated that desiccation in black spruce responds primarily to cumulative vapour pressure deficit, which becomes severe as spring daylight increases rapidly (R^2 = 80%). White spruce might be expected to behave similarly. In tamarack, the effect of cumulative drought was offset by increased spring air temperatures.

High resistance to the uptake of soil moisture by white spruce seedlings at 10°C soil temperature was observed by Grossnickle and Blake (1985).

Stomata of white spruce seedlings coming out of cold/cool storage seem to lack the normal ability possessed by rapidly growing plants to respond rapidly to changes in photosynthetically active radiation (PAR). The inability of stomata on mature foliage of white spruce to close fully after removal from cold storage would increase water stress in newly planted seedlings.

Low soil temperature, as well as reducing uptake of water also tends to discourage root growth. Markedly decreased root growth was observed in white spruce at soil temperatures below 10°C (Tryon and Chapin 1983). However, root growth of white spruce planting stock after cold storage was not initially greater at soil temperatures higher than at 10°C (Grossnickle and Blake 1985). Also, Boyce and Lucero (1999) have shown that roots play an important part in maintaining foliar water balance in subalpine Engelmann spruce saplings during winter. The water status of small seedlings covered by snow did not change materially while snow cover was maintained, these seedlings having very low rates of transpiration because of high humidities in snowpack air spaces and the consequent small vapour pressure deficits.

Soil water is generally considered to be unavailable to plants at soil temperatures below 1°C. The winter desiccation of needles is thought to limit tree growth and survival within alpine timberline ecotones, but Sowell et al. (1996) found that severed shoots of Engelmann spruce were subject to greater desiccation than were intact shoots, indicating the availability of stem water to needles despite presumably frozen soil, frozen roots, and frozen stems. Boyce and Lucero (1999) confirmed the unavailability of soil water at 5 cm depth under the snowpack during 4 months from late November, and concluded that, because exposed intact saplings had lower water-loss rates than exposed severed trees, and deuterium-labelled water was taken up by the roots, the intact saplings took up water during the winter, either from deep soil layers or from unfrozen pockets in the shallower soil layers.

Significant reductions in needle water content were observed in white spruce, black spruce, and jack pine seedlings in response to a 10-day drought, notwithstanding the apparent maintenance of turgor (Marshall et al. 2000). When the seedlings were re-watered after the drought, jack pine needles regained their original saturated volume, whereas white spruce and black spruce needles did not. Significant drought-induced reductions in turgor-loss volume (i.e., tissue volume at the point of turgor loss) were observed in shoots of all three species, especially jack pine. Repeated exposure to 7 days of drought or treatment with the cytochrome P450 inhibitor paclobutrazol reduced seedling height relative to that of untreated controls in all three species. The reductions in saturated and turgor-loss needle volumes in the seedlings treated with paclobutrazol were comparable with those of seedlings subjected to a 10-day drought. The treatment-induced reductions in shoot and needle water contents enabled seedlings to maintain turgor with tissue volumes close to, or below, the turgor-loss volume of untreated seedlings. Paclobutrazol-treated seedlings subsequently survived drought treatments that were lethal to untreated seedlings.

Water and nitrogen commonly limit plant growth. Dang et al. (2000) investigated the interacting effects of water and nitrogen on plant physiological processes in white and black spruces. Seedlings were grown in a growth chamber for two weeks and then subjected to factorial combinations of two water regimes (drought and non-drought) and two nitrogen regimes (high and low) for 16 weeks, through 28 drought cycles. Rates of photosynthesis, mesophyll conductance, stomatal conductance, and photosynthetic nitrogen-use efficiency were significantly higher in white spruce than in black spruce, but the two species had similar photosynthetic water-use efficiency. White spruce was better able to improve photosynthetic performance under improved water and nitrogen regimes than was black spruce. The finding that stomatal conductance was the primary limiting factor to photosynthesis in seedlings subjected to drought stress seemingly contradicts the results of other studies, e.g., by Teskey et al. (1986) and Dang et al. (1991), but since the sensitivity of mesophyll to drought increased and the sensitivity of stomatal conductance decreased with decreasing nitrogen supply, the plants used in those studies may have been subjected to even greater nitrogen stress than the plants in the low nitrogen treatment in Dang et al.'s (2000) investigation.

White spruce was more responsive than black spruce to water regime, and proved better able to improve photosynthetic performance under improved soil water conditions (Dang et al. 2000). This would confer on white spruce a competitive advantage over black spruce in occupying sites with good soil moisture conditions.

Plant moisture pressure at various soil moisture potentials was determined by Pierpoint (1967) in some coniferous seedlings including white spruce:

Soil Water Potential (atmospheres)	Plant Water Potential (psi)
ca 0.06	60
ca 4.0	200
ca 6.0	225
ca 15.0	260

Pierpoint determined internal moisture pressure using the method described by Scholander et al. (1965).

4.7 Nutrition

At least 17 elements are known to be essential nutrients for plants. In relatively large amounts, the soil supplies nitrogen, phosphorus, potassium, calcium, magnesium, and sulphur; these are often called the macronutrients. In relatively small amounts, the soil supplies iron, manganese, boron, molybdenum, copper, zinc, chlorine, and cobalt, the so-called micronutrients. Nutrients must be available not only in sufficient amounts but also in appropriate ratios.

The effect of a nutrient deficiency can vary from a subtle depression of growth rate to obvious stunting, deformity, discoloration, distress, and even death. Visual symptoms distinctive enough to be useful in identifying a deficiency are rare. Most deficiencies are multiple and moderate. However, while a deficiency is seldom that of a single nutrient, nitrogen is commonly the nutrient in shortest supply.

Chlorosis of foliage is not always due to mineral nutrient deficiency. Solarization can produce superficially similar effects, though mineral deficiency tends to cause premature defoliation, whereas solarization does not, nor does solarization depress nitrogen concentration (Ronco 1970).

Growth rates of naturally regenerated seedlings are generally higher on mineral soil seedbeds than on rotted wood, which, though favourable with regard to moisture is less so in relation to nutrient supply. Growth of naturally regenerated seedlings is much slower than that of nursery stock. Even on prepared sites, a 3-year-old seedling is commonly no taller than 5 cm (Rowe 1955). In the Porcupine Hills Forest Reserve, Manitoba, the average height of 7-year-old white spruce was 61 cm on a mineral soil seedbed, and 14 cm on rotted wood (Rowe 1955). Root development was also stronger on the mineral soil seedbeds, where one seedling on a very moist site had lateral roots 90 cm long and a taproot 15 cm deep, and another seedling on a drier site had 40 cm laterals and a taproot > 60 cm. In contrast, the root systems of seedling on rotted wood were weakly developed and tended to remain within the rotted wood (Rowe 1955).

Nutrient cycling

Canada's contribution to the International Biological Program (IBP) involved detailed studies of productivity and related processes in several ecosystems. Gordon (1975) presented initial data

for the determination of static pools and seasonal process fluxes for the Canadian IBP forest ecosystem site. Above-ground biomass of the spruce forest was greatest on moist sites, and diminished through fresh, then wet sites, and was least on dry sites. Seasonal variation of foliar nutrient concentrations of red, white and black spruces, compared across a moisture regime catena of fresh, moist and wet sites, indicated that highest concentrations of nitrogen were maintained by white spruce and lowest by red spruce. Foliar phosphorus concentrations of black spruce on wet sites were one-third greater than those for red spruce, which were one-third greater than white spruce; and potassium concentrations in red spruce were generally equivalent to, or greater than the other species.

Nutrient cycling dynamics and productivity of fully stocked black spruce on two principal land types (peat and moist outwash sand), were elucidated by Gordon (1983) and compared with those of two boreal mixedwood ecosystems consisting of white spruce, white birch and trembling aspen of moderate and high productivity. Comparisons were also made with north temperate red spruce ecosystems. Mass budgets indicate that almost half of the total organic pools above- and below-ground are in the standing crops. When these are compared with their respective total organic and mineral soil mass reserves, only that of black spruce on peat is still nearly as great as reserves. Such sites could become vulnerable under full-tree harvesting. The effects of full-tree harvesting on the nutrient pools of these sites are also shown. While simple budgets do not predict replacement times, data from nutrient cycles will. Differences in residence times for nitrogen in red and black spruce ecosystems explain the rapid reappearance of black spruce ecosystems on the outwash sand site after fire. Replacement times also provide estimates of the real tolerances to perturbations such as harvesting. Calculated at steady state input, they are relatively short, at 20 years or less for the richer upland mixedwood sites and longer for black and red spruce sites. However, on acidic tills, outwash sands and peat, replacement times for potassium can extend from 30 to 45 years. Upland mixedwood stands have greater resilience than have black spruce stands on outwash or peat.

Paré (1990) used various field and laboratory methods to characterize nutrient cycling on two mature white spruce sites, one recently harvested site and three, 14-year-old harvested white spruce sites colonized by different plant communities and presenting different intensity of soil disturbance. Study sites were chosen on upland south facing sites and presented conditions of reduced environmental variability. Soil analysis showed no changes in pools of soil nutrient, unless the forest floor was removed. On the other hand, some differences in the dynamics of nutrients were seen: (1) sites where the forest floor was removed showed low N mineralization rates, (2) N mineralization rates appeared faster in the surface soil of the recently harvested site than in mature white spruce sites, and (3) the surface soil of sites regenerating to aspen showed the highest N mineralization rates of all 14-year-old sites. Field soil temperature, and field soil moisture content as well as N and lignin concentrations of the forest floor could not explain the differences in N mineralization rates between sites. This suggests that species colonization may influence N dynamics and that N cycling rate on regenerating sites is controlled by a small pool of rapidly cycling N. The determination of nutrient uptake and return by vegetation growing in the field indicated that nutrient cycling was much faster in 14-year-old aspen stands than on any other regenerating or mature site. The measurement of element

availability with ion exchange resin bags indicated an increased leaching of nitrate, phosphate and sulfate at springtime and the second summer following harvesting. Poor correlations were obtained between conventional soil testing and ion exchange resin bag determinations. Comparisons between field and laboratory nutrient availability indices indicated that sites colonized by sprouting aspen exhibited the highest N cycling rates seen in this study.

4.7.1 Macronutrients

4.7.1.1 Nitrogen

Nitrogen is a major constituent of several of the most important plant substances. For example, nitrogen compounds comprise 40-50% of the dry matter of protoplasm, and it is a constituent of amino acids, the building blocks of proteins (Swan 1971a). The foliage of healthy, nitrogen-sufficient white spruce is deep green, 7.5 GY 5-4/4-2 in the notation of the Munsell Color Co., Baltimore, Maryland. On sites or microsites of low fertility, seedlings are unable to synthesize normal amounts of chlorophyll, and commonly exhibit pale yellow foliage, 2.5 GY 5-6/6. This color, together with smallness of buds and the ready loss of needles 2 or more years old, confers a characteristic appearance on such trees, which are commonly described as “being in check”. The current-year foliage of such trees usually has one or more macronutrients in low concentration, e.g., <1% nitrogen, <0.10% phosphorus, and <0.30% potassium (Sutton 1975). White spruce seedlings grown by Swan (1960) in sand culture without N were very small and pale green, but with very little browning until “imminent death at end of growing season”; with very low N (1.12 ppm), the seedlings were small and pale green, with some purple/brown discolouration at the end of the growing season; and with low N (11.2 ppm), seedlings were smaller than the full nutrient controls, but only slightly paler green. Provisional standards for levels of foliar nutrients in current-year needles of white spruce nursery stock, collected mid-September to mid-November from the upper third of the crown, were suggested by Swan (1971a): 1.10% or less dry matter = acute deficiency; 1.10 - 1.30% = moderate deficiency; 1.50 to 2.50% = sufficient for good to very good growth, and 2.50% or more = luxury to toxic consumption.

White spruce is a relatively nutrient-demanding species; its foliage and fine branches when well grown contain relatively high levels of nutrients (Hendrickson et al. 1987). Even foliar concentrations of 1.3-1.55% nitrogen might indicate moderate deficiency of nitrogen in white spruce in British Columbia (Ballard and Carter 1986). The nitrogen level in bark of branches 0.5-2.5 cm exceeded 5%; foliage and branches smaller than 0.5 cm assayed at 8.64%.

In many boreal forest ecosystems, plant productivity is limited by mineral nutrient availability. Turkington et al. (1998) applied NPK fertilizer over a 9-year period to a low-nutrient ecosystem in Yukon Territory and observed changes in species composition and increased growth rates, but white spruce cone crop production was unaffected.

White spruce seedlings were more responsive to low and high nitrogen treatments than were black spruce seedlings (Dang et al. 2000). High nitrogen treatment increased mesophyll conductance and photosynthesis in both species, but the increase in white spruce was almost twice as high as that in black spruce.

The growth of all organisms depends on the availability of mineral nutrients, and none is more important than nitrogen, which is required in large amounts as an essential component of proteins, nucleic acids, and other cellular constituents, including enzymes. Nitrogen is an essential constituent of chlorophyll, but it influences growth and utilization of sugars more than it influences photosynthesis through a reduction in chlorophyll. There is an abundant supply of nitrogen in the earth's atmosphere—nearly 79% in the form of N_2 gas. However, N_2 is unavailable for use by most organisms because there is a triple bond between the two nitrogen atoms, making the molecule almost inert. In order for nitrogen to be used for growth it must be "fixed" (combined) in the form of ammonium (NH_4) or nitrate (NO_3) ions. The weathering of rocks releases these ions so slowly that it has a negligible effect on the availability of fixed nitrogen. Therefore, nitrogen is often the limiting factor for growth and biomass production in all environments where there is suitable climate and availability of water to support life.

Nitrogen enters the plant largely through the roots. A "pool" of soluble nitrogen accumulates. Its composition within a species varies widely depending on several factors, including day length, time of day, night temperatures, nutrient deficiencies, and nutrient imbalance. Short day length promotes asparagine formation, whereas glutamine is produced under long day regimes. Darkness favours protein breakdown accompanied by high asparagine accumulation. Night temperature modifies the effects due to night length, and soluble nitrogen tends to accumulate owing to retarded synthesis and breakdown of proteins. Low night temperature conserves glutamine; high night temperature increases accumulation of asparagine because of breakdown. Deficiency of K accentuates differences between long- and short-day plants. The pool of soluble nitrogen is much smaller than in well-nourished plants when N and P are deficient, since uptake of nitrate and further reduction and conversion of N to organic forms is restricted more than is protein synthesis. Deficiencies of Ca, K, and S affect conversion of organic N to protein more than uptake and reduction. The size of the pool of soluble N is no guide *per se* to growth rate, but the size of the pool in relation to total N might be a useful ratio in this regard. Nitrogen availability in the rooting medium also affects the size and structure of tracheids formed in the long lateral roots of white spruce (Krasowski and Owens 1999) (See 3.5).

Microorganisms have a central role in almost all aspects of nitrogen availability, and therefore for life support on earth. Some bacteria can convert N_2 into ammonia by the process termed *nitrogen fixation*; these bacteria are either free-living or form symbiotic associations with plants or other organisms (e.g., termites, protozoa), while other bacteria bring about transformations of ammonia to nitrate, and of nitrate to N_2 or other nitrogen gases. Many bacteria and fungi degrade organic matter, releasing fixed nitrogen for reuse by other organisms. All these processes contribute to the nitrogen cycle.

Fertilizer test plots have provided the best evidence for assessing soil nutrient-supplying ability in relation to tree demand. Results from experiments in adult forests across Canada and the adjacent United States support the hypothesis that lack of N generally limits growth of some coniferous species, especially on drier sites (Foster and Morrison 1983). Responses to P and K are reported only occasionally; e.g., red pine on outwash sands abandoned from agriculture,

produced 25-80 m^3/ha of extra wood over 5-10 years after fertilization with K. With many species additional growth is realized when P and/or K are added with N, but generally response is not significantly greater than with N alone. The addition of urea (224 kg N/ha) to natural stands produced, on average, an additional 15.6 m^3/ha of wood over four years with Douglas-fir and 8.5 m^3/ha over 5 years with jack pine. In Douglas-fir and jack pine forests, inverse relationships between site index and response to N have been found, the greatest growth increase being on poorer sites. Average 5-year responses were less with balsam fir, red spruce, white spruce, and black spruce.

Nitrogen fixation

A relatively small amount of ammonia is produced by lightning. Some ammonia also is produced industrially by the Haber-Bosch process, using an iron-based catalyst, very high pressures and fairly high temperature. However, the major conversion of N_2 into ammonia, and thence into proteins, is achieved by microorganisms in the process called nitrogen fixation (or dinitrogen fixation).

Mechanism of biological nitrogen fixation

Biological nitrogen fixation can be represented by the following equation, in which two moles of ammonia are produced from one mole of nitrogen gas, at the expense of 16 moles of ATP and a supply of electrons and protons (hydrogen ions):

$$N_2 + 8H^+ + 8e^- + 16\ ATP = 2NH_3 + H_2 + 16ADP + 16\ P_i.$$

This reaction is performed exclusively by prokaryotes (the bacteria and related organisms), using an enzyme complex termed nitrogenase. This enzyme consists of two proteins—an iron protein and a molybdenum-iron protein. The reactions occur while N_2 is bound to the nitrogenase enzyme complex. The Fe protein is first reduced by electrons donated by ferredoxin, then the reduced Fe protein binds ATP and reduces the molybdenum-iron protein, which donates electrons to N_2, producing HN=NH. In two further cycles of this process (each requiring electrons donated by ferredoxin), HN=NH is reduced to $H_2N\text{-}NH_2$, and this in turn is reduced to $2NH_3$. Depending on the type of microorganism, the reduced ferredoxin which supplies electrons for this process is generated by photosynthesis, respiration or fermentation.

All the nitrogen-fixing organisms are prokaryotes (bacteria). The so-called free-living nitrogen-fixing bacteria live independently of other organisms. Others live in intimate symbiotic associations with plants or with other organisms (e.g., protozoa).

A point of special interest is that the nitrogenase enzyme complex is highly sensitive to oxygen. It is inactivated when exposed to oxygen, because this reacts with the iron component of the proteins. Although this is not a problem for anaerobic bacteria, it could be a major problem for the aerobic species such as cyanobacteria (which generate oxygen during photosynthesis), as well as the free-living aerobic bacteria of soils, such as *Azotobacter* and *Beijerinckia*. These organisms have various methods to overcome the problem. For example, *Azotobacter* species have the highest known rate of respiratory metabolism of any organism, so they might protect the enzyme by maintaining a very low level of oxygen in their cells. Azotobacter species also produce copious amounts of extracellular polysaccharide (as do *Rhizobium* species in culture). By maintaining water within the polysaccharide slime layer, these bacteria can limit the

diffusion rate of oxygen to the cells. In the symbiotic nitrogen-fixing organisms such as *Rhizobium*, the root nodules can contain oxygen-scavenging molecules such as leghaemoglobin, which shows as a pink colour when the active nitrogen-fixing nodules of legume roots are cut open. Leghaemoglobin may regulate the supply of oxygen to the nodule tissues in the same way as haemoglobin regulates the supply of oxygen to mammalian tissues. Some of the cyanobacteria have yet another mechanism for protecting nitrogenase: nitrogen fixation occurs in special cells (heterocysts) which possess only photosystem I (used to generate ATP by light-mediated reactions), whereas the other cells have both photosystem I and photosystem II, which generates oxygen when light energy is used to split water to supply H_2 for synthesis of organic compounds.

Symbiotic nitrogen fixation

The most familiar examples of nitrogen-fixing symbioses are the root nodules of legumes (e.g., peas, beans, clover). *Frankia* is a genus of the bacterial group termed actinomycetes—filamentous bacteria that are noted for their production of air-borne spores. Included in this group are the common soil-dwelling *Streptomyces* species, which produce many of the antibiotics used in medicine. *Frankia* species are slow-growing in culture, and require specialised media, suggesting that they are specialised symbionts. Alder and the other woody hosts of *Frankia* are typical pioneer species that invade nutrient-poor soils. These plants probably benefit from the nitrogen-fixing association, while supplying the bacterial symbiont with photosynthetic products.

White spruce in close competition with alder did not exhibit enhanced levels of foliar nitrogen, presumably a dilution effect with increased biomass, even though soil nitrogen levels were elevated (Doran et al. 2001).

Nitrogen mineralization

The effects of commercial timber harvesting upon nitrogen transformations were evaluated by Gordon and Van Cleve (1983) for the forest floor and mineral soils of mature white spruce forest sites in interior Alaska. Analyses of forest floor incubated *in situ* in mature forest and two recently harvested areas of different ages indicated an ammonium-dominated soil system for the unharvested area. Maximum NH_4-N mineralization rates (300 µg N/100g dry soil/day) occurred in mid-summer and generally declined with the onset of fall. In the harvested areas, rates of NH_4-N accumulation were almost invariably lower than in the uncut area, a consequence of elevated levels of nitrification. Shortly after harvesting, NO_3-N concentrations were extremely high. Thereafter, they declined to levels slightly higher than in the mature forest. Nitrification was strongly enhanced by harvesting, and regular patterns within season were evident. For the youngest clearcut, the combined processes of ammonification and nitrification only occasionally supplied more nitrogen to the site on a daily basis than was supplied to the mature forest site. For the oldest clearcut, the supply from the combined mechanisms was variable and depended on the time since clearcutting.

4.7.1.2 Phosphorus

Like nitrogen, phosphorus is closely concerned with many vital plant processes. It is present mainly as a structural component of the nucleic acids, deoxyribonucleic nucleic acid (DNA) and ribose nucleic acid (RNA), and as a constituent of fatty phospholipids, of importance in membrane development and function. It is present in both organic and inorganic forms, both of which are readily translocated. All energy transfers in the cell are critically dependent on phosphorus.

Phosphorus deficiency can produce symptoms similar to those of nitrogen deficiency (Black 1957), but is much more difficult to diagnose (Russell 1961). Deficiency of phosphorus can be extreme with no obvious indication of cause. For example, seedlings of several species, including Sitka spruce, showed consistently strong responses to phosphorus in very acid tree nurseries in England, even though the only visible symptom of deficiency was a slight lack of lustre in the foliage of some species (Benzian 1965). White spruce seedlings grown by Swan (1960) in sand culture without P, were very small and tinted deep purple. Grown with very low phosphorus (0.62 ppm), seedlings were small and some of the smallest were tinted deep purple. With low phosphorus (6.2 ppm), seedlings were of good colour and rather bigger than the controls that were supplied with 62 ppm P.

Phosphorus uptake may control height growth of white spruce (Armson 1966).

Provisional standards for levels of phosphorus in current-year needles of white spruce nursery stock collected in mid-September to mid-November from the upper third of the crown were suggested by Swan (1971b): 0.11% or less dry matter = acute deficiency; 0.11-0.14% = moderate deficiency; 0.18-0.28% = sufficient for good to very good growth; 0.32% or more = luxury to toxic consumption.

On some soils, the phosphorus nutrition of some conifers, including the spruces, depends on the ability of mycorrhizae to take up, and make soil phosphorus available to the tree, hitherto unobtainable to the non-mycorrhizal root. Seedling white spruce, greenhouse-grown in sand testing negative for phosphorus, were very small and purple for many months until spontaneous mycorrhizal inoculation, the effect of which was manifested by greening of foliage and the development of vigorous shoot growth.

4.7.1.3 Potassium

Unlike other major elements, potassium does not enter into the composition of any of the important plant constituents involved in metabolism (Swan 1971a), but it does occur in all parts of plants in substantial amounts. It seems to be of particular importance in leaves and at growing points. Potassium is outstanding among the nutrient elements for its mobility and solubility within plant tissues. Processes involving potassium include the formation of carbohydrates and proteins, the regulation of internal plant moisture, as a catalyst and condensing agent of complex substances, as an accelerator of enzyme action, and as contributor to photosynthesis, especially under low light intensity.

When soil potassium levels are high, plants take up more potassium than needed for healthy growth. The term *luxury consumption* has been applied to this. When potassium is moderately

deficient, the effects first appear in the older tissues, and from there progress towards the growing points. Acute deficiency severely affects growing points, and die-back commonly occurs. Symptoms of potassium deficiency in white spruce include: browning and death of needles (chlorosis); reduced growth in height and diameter; impaired retention of needles; and reduced needle length (Heiberg and White 1951). A relationship between potassium nutrition and cold resistance has been found in several tree species, including two species of spruce (Sato and Muto 1951).

White spruce seedlings grown in sand culture with 0 ppm potassium were very small, and their brown-tipped, pale-green needles became purple or brown as necrosis developed. In a 0.78 ppm potassium treatment, mortality was 40%, but the survivors, though small, appeared moderately healthy, with yellow tips only on the lower primary needles (Swan 1960). Seedlings provided with 7.8 ppm K ("low potassium") showed normal colour and little mortality, but slightly less height growth than the controls.

Provisional standards for levels of potassium in current-year needles of white spruce nursery stock collected mid-September to mid-November from the upper third of the crown were suggested by Swan (1971a): 0.19% or less dry matter = acute deficiency; 0.19-0.30% = moderate deficiency; 0.45-0.80% = sufficient for good to very good growth; 0.80% or more = luxury to toxic consumption. Heiberg and White (1951) found that deficiency symptoms were likely to develop in white spruce foliage at foliar concentrations of less than 0.15%.

Swan (1960) investigated the influence on white spruce seedlings growing in sand culture of increasing potassium concentration in the nutrient solution while keeping Mg constant (48 ppm) (Table 4.3).

Table 4.3. Potassium and magnesium concentration in white spruce sand-cultured seedlings at different potassium but constant magnesium concentrations (after Swan 1960).

	Potassium in nutrient solution (ppm)			
	0	**0.78**	**7.8**	**78**
K (% dry weight) in aerial portion of seedlings	0.19	0.26	1.20	1.74
Mg (% dry weight) in aerial portion of seedlings	0.34	0.24	0.23	0.22

Parallel investigation of the influence of increasing magnesium concentration in the nutrient solution, constant potassium concentration, produced similar results (Table 4.4). Again, similar results were obtained in other species, including black spruce and jack pine.

Table 4.4. Magnesium and potassium concentration in white spruce sand-cultured seedlings at different magnesium but constant potassium concentrations (after Swan 1960).

	Magnesium in nutrient solution (ppm)			
	0	**0.48**	**4.8**	**48**
Mg (% dry weight) in aerial portion of seedlings	0.06	0.08	0.14	0.25
K (% dry weight) in aerial portion of seedlings	2.05	2.05	1.90	1.51

In both sets of data, it is evident that the concentration of K and Mg increases with increasing concentration of those nutrients in the nutrient solution, but with a concomitant decrease in

the concentration of the other nutrient, rather more evident in Table 4.3 than Table 4.4. Swan (1960) noted that in his experiment, in which potassium was always in plentiful supply, the trend was from abnormally high levels of potassium down to normal levels of potassium.

The aggravation of magnesium deficiency by potassium fertilizing is discussed at some length by Jacob (1958). The magnesium requirement of cultivated plants is influenced by fertilization regime and therein by the antagonistic effect of potassium on the uptake of magnesium. Like hydrogen and ammonium ions, the easily mobile potassium ions also increase the speed of diffusion of the more ponderous magnesium ion. Since the magnesium ion has the lowest speed of diffusion of the various soil cations, its mobility suffers the most on increasing the potassium content of the soil solution, especially with heavy additions of potassium, since then only few magnesium ions oppose the many potassium ions. Bradfield and Peech (1945) found that the uptake of potassium from soil was reduced by applying magnesium to the soil, and that on soils low in potassium this could induce damaging potassium deficiency. Other evidence cited by Jacob (1958) showed that on acid soils a good supply of potassium intensified magnesium deficiency if the fertilizers applied were magnesium-free. The available soil magnesium, it was suggested, was displaced by the potassium and leached, and also, because of ion antagonism, the potassium increased the difficulty of the plant in taking up magnesium. On poor sandy soils, the effect of a magnesium fertilizer was greater the better the plants were supplied with nitrogen and potassium. Similar results were also obtained with seedlings of other species, including black spruce and jack pine.

4.7.1.4 Calcium

Calcium in plants occurs chiefly in the leaves, with lower concentrations in seeds, fruits, and roots. A main function is as a constituent of cell walls. When coupled with certain acidic compounds of the jelly-like pectins of the middle lamella, calcium forms an insoluble salt. It is also intimately involved in meristems, and is particularly important in root development, with roles in cell division, cell elongation, and the detoxification of hydrogen ions. Other functions attributed to calcium are: the neutralization of organic acids; inhibition of some potassium-activated ions; and a role in nitrogen absorption. A notable feature of calcium-deficient plants is a defective root system. Calcium deficiency causes stunting of root systems (Russell 1961). Roots are usually affected before above-ground parts (Chapman 1966).

Provisional standards for levels of calcium in current-year needles of white spruce nursery stock, collected mid-September to mid-November from the upper third of the crown, were suggested by Swan (1971a): 0.05% or less dry matter = acute deficiency; 0.05-0.10% = moderate deficiency; 0.15-0.40% = sufficient for good to very good growth; 0.40% or more = luxury to toxic consumption.

Up to the thicket stage, there is commonly a negative correlation between the concentration of calcium in white spruce foliage and height growth (Sutton 1968). A plausible explanation is that calcium accumulates until the uptake of other nutrients more directly involved in cell division, e.g., nitrogen, phosphorus, and potassium, reaches utilizable levels.

4.7.1.5 Magnesium

The outstanding role of magnesium in plant nutrition is as a constituent of the chlorophyll molecule. As a carrier, it is also concerned in numerous enzyme reactions as an effective activator, in which it is closely associated with energy-supplying phosphorus compounds. Magnesium is very mobile in plants, and, like potassium, when deficient is translocated from older to younger tissues, so that signs of deficiency appear first on the oldest needles and then spread progressively to younger and younger tissues.

Provisional standards for levels of magnesium in current-year needles of white spruce nursery stock collected mid-September to mid-November from the upper third of the crown were suggested by Swan (1971a): 0.04% or less dry matter = acute deficiency; 0.04-0.06% = moderate deficiency; 0.10-0.20% = sufficient for good to very good growth; 0.20% or more = luxury to toxic consumption.

Chlorosis of white spruce foliage has been associated with magnesium deficiency in a Wisconsin nursery, when soil nutrient levels were between 0.0006 and 0.0016 in exchangeable magnesium, and between 0.00385 and 0.00661 in exchangeable calcium. Seedlings showed no sign of deficiency when growing in soil containing 0.0028 to 0.0040 exchangeable magnesium, and 0.010 to 0.016 exchangeable calcium (Voigt et al. 1958). Visual symptoms of magnesium deficiency have been reported in Norway spruce nursery stock having concentrations of foliar magnesium less than 0.05% (Ingestad 1960) and less than 0.072% (Himmelfreundpointner 1966).

4.7.2 Micronutrients

Plants (white spruce included) are able sufficiently to accumulate most trace elements. Some plants are sensitive indicators of the chemical environment in which they grow (Dunn 1991), and some plants have barrier mechanisms that exclude or limit the uptake of a particular element or ion species, e.g., alder twigs commonly accumulate molybdenum but not arsenic, whereas the reverse is true of spruce bark (Dunn 1991). Otherwise, a plant can integrate the geochemical signature of the soil mass permeated by its root system together with the contained groundwaters. Sampling is facilitated by the tendency of many elements to accumulate in tissues at the plant's extremities.

Some elements are more highly concentrated in red and black spruces than in white spruce, and the reverse is true for a few other elements (Dunn 1991).

4.8 Nutrient levels in white spruce planting stock

Sampling protocols for nutrient levels vary among jurisdictions. In British Columbia, sampling of seedlings for nutrient analyses normally takes place in late autumn or early winter, by which time rates of change in nutrient levels have decreased much below those occurring earlier in the growing season (van den Driessche 1984). Whole shoots or entire plants are commonly analyzed for 1+0 seedlings, and with older stock, only needles are sampled.

Chemical analyses of soils and plants can help the nursery manager maintain soil fertility adequate for satisfactory growth of planting stock, mostly by detecting obvious deficiencies rather than by enabling any fine-tuning of fertilization. Cultural regimes that have been

producing stock of desired quality for some years will remain the main governing criteria for the nursery manager.

Nitrogen concentrations in most organs decrease sharply at the beginning of the growing season and then remain more or less uniform during the remainder of the growing season. The phosphorus concentration varied considerably among organs, and in all but the roots there was a great decrease during the first month of the second growing season. However, at about the beginning of August, in both the first and the second growing season, the concentration of phosphorus became very similar in all organs, "which distinguishes this element very strikingly from both nitrogen and potassium" (Armson 1960). Potassium concentrations did not decrease markedly at the beginning of the growing season. As with nitrogen, potassium uptake is generally similar to the curves for relative growth and net assimilation rates during the first and second growing seasons.

Another study at St. Williams Nursery investigated levels and schedules of fertilization of white spruce nursery stock, and found that nitrogen content and concentration responded positively to increased fertilization (Armson 1963), but that foliar phosphorus concentration was not affected significantly by level or timing of application. Contents increased with increasing level of fertilizer. Foliar potassium concentrations showed a general decrease, and contents showed a general increase with an increase in fertilizer level.

At Swastika Nursery in northern Ontario (48°N), white spruce responded much more strongly to late-season fertilization than did pines. At the end of the second year, late-season fertilization had increased growth by 114% and 74% over that of the control (Armson et al. 1963).

Levels of nutrients in young white spruce raised for planting stock are fairly well established in Ontario (Armson and Sadreika 1974) and Quebec (Swan 1960, 1971a). Levels vary with season, stock type, plant part, age, and soil environment. Amounts of nutrients in the soil are important, but the ratios of the various nutrients among those present also exert a strong influence on uptake. Lavender et al. (1990) recommended ranges of soil nutrient levels that are desirable prior to sowing or transplanting in British Columbia nurseries: pH 5.2-5.8, organic matter 3-8%, total Kjeldahl nitrogen 0.20-0.25%, cation exchange capacity 15-20 meq/100 g, phosphorus by Bray I method 100-250 ppm, potassium 78-117 ppm, calcium 1,000-1,600 ppm, and magnesium less than 340 ppm. However, the percentage of nitrogen determined by the Kjeldahl method is largely a function of soil organic matter content and seldom indicates the nitrogen available to plants (van den Driessche 1984).

Cation exchange capacity is an arbitrarily defined concept (Russell 1961). The most common definitions are based on determining the amount of single ions, e.g., Na^{+}, NH_4^{+}, Ca^{++}, or Ba^{++} a soil can hold when the salt solution, usually buffered at about pH 7, is leached through the soil. The pH 8.1 buffer tri-ethanolamine has also been used. On the whole, the four cations give about the same exchange capacity, but the variation is far too great to permit discussion about the cation exchange capacity of a soil at any pH without at the same time specifying the method used.

The nutrient status of good white spruce planting stock is high (Armson and Carman 1961). However, strong nutrient stresses can develop even during the first growing season, and "planting disturbance" may account for some of this. Mobile nutrients may be leached from roots and aerial parts immediately after planting. Then, with the onset of flushing, the developing tissues draw nutrients from old tissues, as well as from the soil. However, the root system has been damaged in lifting, packing, storage, and distribution, and then plunged into an environment typically much less fertile than the nursery soil in which it was raised. On sites that are infertile or highly competitive, there must be impairment of the ability of the root system of a newly planted tree to maintain high nutrient status. The part of the rapid reduction in foliar nutrient concentrations in newly planted white spruce attributable to root damage and disarray is termed the planting disturbance effect. This is not easily separated from the effect of site, but the size of the planting disturbance effect can be inferred from a comparison of nutrient concentrations (at similar stages of phenology) before and after a period of one or more years during which equilibration with site can be expected to have taken place. The depression of foliar concentrations in the year of outplanting below levels achieved in the following year, as illustrated by Sutton (1968) with potassium, may be taken to represent the planting disturbance effect.

Foliage nutrient levels

During the first few years after outplanting, nutrient levels in spruce foliage undergo considerable change. The basic pattern of change in concentration of nitrogen, phosphorus, and potassium in new foliage is for initial maxima to be followed by rapid decreases during the first part of the growing season, then generally continuing to decrease less rapidly (Sutton 1968). However, where a nutrient is in low supply in a soil, there may be a late season increase in the foliar concentration of that nutrient. Potassium concentration in current-year foliage of white spruce in the first and second growing seasons increased between September and November, probably reflecting the nutrient release from dead and dying vegetation, possibly reinforced by late season root growth (Sutton 1968).

The amount of nutrient decrease is influenced strongly by soil type (Table 4.5). Foliage nutrient levels of white spruce vary with the fertility of the growing medium, other growing conditions, and the age and phenological and seasonal stage of the needles. The nutritional status of the foliage reflects the site nutrient regime (Gordon and Van Cleve 1987). The ranges of nutrients in foliage associated with good growth of white spruce vary with many factors including age of plant, with young seedlings generally showing higher levels than older and especially pole-stage and older trees.

Table 4.5. Reduction in phosphorus concentration in current-year foliage of white spruce from June 26 to August 9 of the first growing season after outplanting; average of the same five treatments at each sampling date and on each soil, expressed as percentage of the initial concentration on the P63 Clay(Sutton 1968).

Site	Reduction in P concentration (%)
P63 Clay	26
P63 Loam	55
P63 Sand	63

In established stands in British Columbia, foliage N of 1.55% indicates adequate soil nitrogen, according to Ballard and Carter (1986).

4.9 Phytohormones

Specific hormones and plant growth regulators (PGRs) mediate growth and development (Ross et al. 1983). Endogenous hormone levels are influenced by plant age, cold hardiness, dormancy, and other metabolic conditions; photoperiod, drought, temperature, and other external environmental conditions; and exogenous sources of PGRs, e.g., externally applied and of rhizospheric origin.

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APPENDIX

Scientific name[1]	English Common Name[1]	French Common Name	Original Scientific Name[2]	Original Common Name[2]
Abies amabilis Dougl. ex J. Forbes	Pacific silver fir	sapin gracieux	*Abies amabilis*	amabilis fir
Abies balsamea (L.) Mill.	balsam fir	sapin baumier	Abies balsamea (L.) Mill.	balsam fir
Abies Mill.	fir	sapin	*Abies*	-
Abies lasiocarpa (Hook.) Nutt.	subalpine fir	sapin subalpin	*Abies lasiocarpa* (Hook.) Nutt.	subalpine fir
Alnus Mill.	alder	aulne	*Alnus*	-
Betula papyrifera Marsh.	paper birch	bouleau à papier	*Betula papyrifera*	paper birch
Boletus subtomentosus	suede bolete	bolet tomenteux	*Boletus subtomentosus*	-
Calamagrostis canadensis (Michaux) Palisot de Beauvois	bluejoint reedgrass	calamagrostide du Canada	*Calamagrostis canadensis* (Michx.) Beauv.	-
Chamaecyparis Spach	false-cypress	faux-cypres	*Chamaecyparis*	-
Chamaenerion angustifolium (L.) Scopoli	fireweed	épilobe à feuilles étroites	*Epilobium angustifolium* L.	-
Cryptomeria D. Don	Japanese cedar	-	*Cryptomeria*	-
Laccaria laccata (Scopoli) Cooke	deceiver	clitocybe laqué	*Laccaria laccata*	-
Larix decidua Mill.	European larch	mélèze d'Europe	*Larix decidua* Mill.	European larch
Larix Mill.	larch	mélèze	*Larix*	-
Picea A. Dietrich	spruces	épinettes	*Picea*	spruces
Picea abies (L.) H. Karst	Norway spruce	épinette de Norvège	*Picea abies* (L.) Karst	Norway spruce
	Norway spruce	épinette de Norvège	*Picea excelsa* Link	-
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 likiangensis var. *montigena* (Masters) Chen	-	-	*Picea montigena* Masters	-
Picea mariana (Mill.) B.S.P.	black spruce	épinette noire	*P. mariana* [Mill.] BSP	black spruce
Picea obovata Lede.	Siberian spruce	épicéa de Sibérie	*Picea obovata*	-
Picea pungens Engelm.	blue spruce	épinette du Colorado	*Picea pungens*	-
	blue spruce	épinette du Colorado	*Picea pungens* f. glauca Engelm.)	-
Picea rubens Sarg.	red spruce	épinette rouge	*Picea rubens*	red spruce
Picea schrenkiana Fisch. & C. A. Mey.	Schrenk's spruce	épinette Schrenk's	-	Shrenk

Scientific name[1]	English Common Name[1]	French Common Name	Original Scientific Name[2]	Original Common Name[2]
Picea sitchensis (Bong.) Carrière	Sitka spruce	épinette de Sitka	*Picea sitchensis* [Bong.]	Sitka spruce
Picea smithiana (Wallich) Boissier	Himalayan spruce	épicéa de l'Himalaya	*Picea smithiana* Boiss.	-
Picea torano (Koch) Köhne	tiger-tail spruce	épicéa du Japon	*Picea polita*	-
Picea x albertiana S. Brown	dwarf Alberta spruce	épinette blanche 'Conica'	*Picea glauca* var. *albertiana cv. Conica*	-
Picea x albertiana S. Brown	interior spruce	épinette intérieur	*Picea glauca var. Albertiana* [S. Brown] Sarg.	western white spruce
	interior spruce	épinette intérieur	*P. glauca* var. *porsildii Raup*	Porsild spruce
Picea × lutzii Little	Lutz spruce	épinette de Lutz	*Picea × lutzii*	Roche spruce
Pinus banksiana Lamb.	jack pine	pin gris	*Pinus banksiana*	jack pine
Pinus contorta Dougl. ex Loud	lodgepole pine	pin tordu latifolié	*Pinus contorta* Dougl. ex Loud	lodgepole pine
Pinus L.	pine	pin	*Pinus*	-
Pinus radiata D. Don	radiata pine	pin de Monterey	*Pinus radiata* D. Don	radiata pine
Pinus resinosa Ait.	red pine	pin rouge	*Pinus resinosa*	red pine
Pinus sylvestris L.	Scots pine	pin sylvestre	Pinus sylvestris	Scots pine
Populus tremuloides Michx.	trembling aspen	peuplier faux-tremble	*Populus tremuloides* Michx.	trembling aspen
Populus trichocarpa Torr. & A. Gray	black cottonwood	peuplier de l'Ouest	*Populus trichocarpa*	black cottonwood
Pseudotsuga Carrière	Douglas-fir	douglas de Menzies	*Pseudotsuga*	-
Pseudotsgua menziesii (Mirb.) Franco	Douglas-fir	douglas de Menzies	*Pseudotsgua menziesii* (Mirb.)	Douglas-fir
Pteridium aquilinum ssp. *latiusculum* (Desvaux) Hultén ex R.T. Clausen	eastern bracken fern	fougère-aigle de l'Est	*Pteridium aquilinum var. latiusculum* (Desv.) Underw.	bracken
Thuja L.	cedar	thuya	*Thuja*	-
Thuja plicata Donn ex D. Don	western red cedar	thuya géant	*Thuja plicata*	western red cedar
Tsuga heterophylla (Raf.) Sarg.	western hemlock	pruche de l'Ouest	*Tsuga heterophylla* (Raf.) Sarg.	western hemlock
Tsuga mertensiana (Bong.) Carrière	mountain hemlock	pruche subalpine	*T. mertensiana*	mountain hemlock

[1] Updated Scientific and English names.

[2] Original scientific and English names from the submitted manuscript.

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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.[10]

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