Review article

Ecophysiology and field performance of black spruce *(Picea mariana)*: a review

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Summary — This paper presents a literature review of black spruce (*Picea mariana* [Mill] BSP) ecophysiology concerning the response of net photosynthesis and stomata to changes in environmental factors. Current knowledge on root growth, mineral nutrition and response to high temperature, CO_2 enrichment and climate change, frosts, water stress and flooding are also covered. The review ends with an overview of stand establishment and field performance of planted seedlings. The authors highlight the need for research on the long-term effects of multiple stresses, such as climate change and air pollution on the black spruce ecosystem.

Picea mariana / ecophysiology / photosynthesis / environmental stress

Résumé — Écophysiologie et performances des plants de l'épinette noire. Revue. *Cet article présente une revue de littérature de l'écophysiologie de l'épinette noire (Picea mariana [Mill] BSP) mettant l'accent sur les facteurs environnementaux qui affectent la photosynthèse nette et la réponse des stomates. Cette revue offre une mise à jour sur l'état actuel des connaissances sur la croissance racinaire, sur la nutrition minérale, ainsi que sur la réponse de la plante aux températures élevées, à l'augmentation en CO2 atmosphérique et aux changements climatiques, aux gels, au stress hydrique, et à l'engorgement des sols. Finalement, l'article rapporte différents résultats concernant la régénération naturelle et la performance des plants de l'épinette noire en site de reboisement. Les auteurs soulignent l'importance de poursuivre les recherches sur les effets à long terme de stress multiples comme la pollution de l'air et les changements climatiques sur l'écosystème de la pessière noire.*

Picea mariana / écophysiologie / photosynthèse / stress environnemental

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INTRODUCTION

Black spruce, *Picea mariana* (Mill) BSP, is
the principal constituent of the North Amer-
ican boreal forest. Although slow growing,
it is an important source of high-quality fibre
for the Canadian pulp and paper industry.
Its range includes most of Canada and the
northern United States (fig 1), where it grows
on a wide variety of mineral and organic soils
(Heinselman, 1957; Morgenstern, 1978;
Cauboue and Malenfant, 1988; Sims *et al*,
1990). Black spruce is moderately shade
tolerant (Sims *et al*, 1990) and is less aggres-
sive than other boreal species such as bal-
sam fir (*Abies balsamea* L [Mill]) or white
birch (*Betula papyrifera* Marsh). It can grow
under conditions of low nutrient availability,
and can therefore outcompete other species
on nutrient-poor sites (Lafond, 1966).

As with all plant species, the growth of
black spruce seedlings or trees is a function
of how physiological processes respond to
the physical environment. Knowledge about
such responses is important for the contin-
uing improvement of forestry practices in the
boreal forest and for the assessment of the
impact of climatic changes that are predicted
to take place in that ecosystem.

Black spruce physiology has been rela-
tively well studied in Canada, with a more
limited number of ecophysiological studies
of the species under natural conditions car-
ried out in the last few years. To our know-
ledge, the last review on black spruce phys-
iology dates back to the *Black Spruce
Symposium* held in 1975 (Canadian Forestry
Service, 1975). Although genetic research
has been and is still actively being carried
out on black spruce, we decided to omit
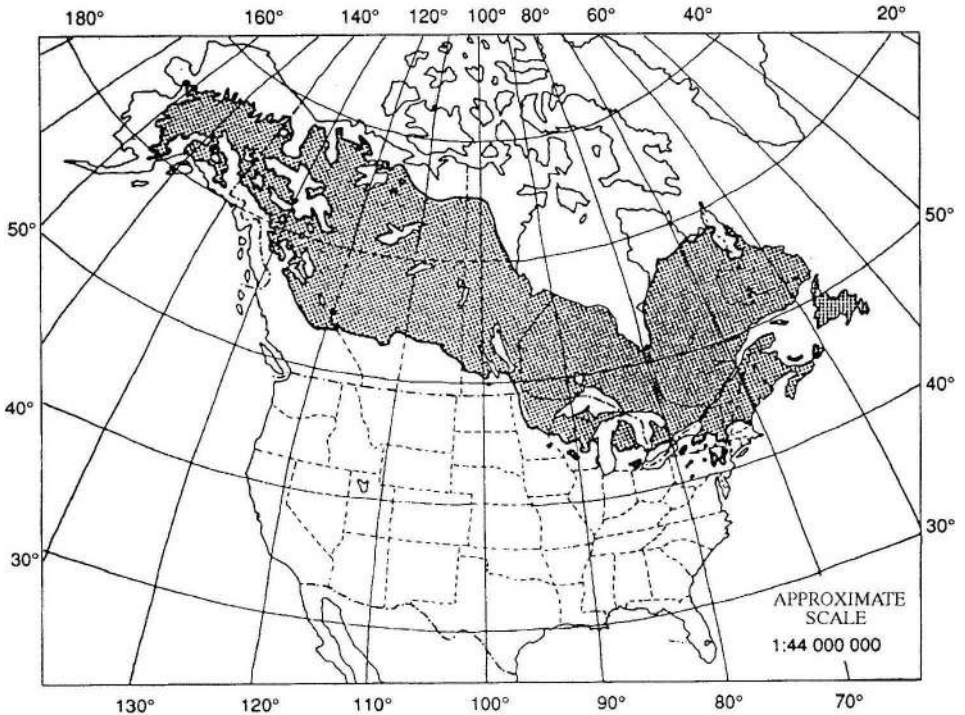detailed coverage of this topic from our

Fig 1. Natural distribution of black spruce (by permission of Les publications du Québec).

review. Several studies have reported genetic variations in black spruce regarding clinal variation (Morgenstern, 1975; 1978; Fowler and Mullin, 1977; Park and Fowler, 1988; Chang and Hanover, 1991), cone characters and foliar flavonoids (Parker *et al*, 1983; Stoehr and Farmer, 1986), allozyme variation (Yeh *et al*, 1986; Desponts and Simon, 1987), heterozygosity (Park and Fowler, 1984), genotypic stability of provenances (Khalil, 1984), inherent variation in 'free' growth in relation to number of needles (Pollard and Logan, 1976), heat tolerance (Colombo *et al*, 1992) and mineral nutrition (Maliondo and Krause, 1985; Mullin, 1985). Additional work has failed to find evidence of ecotypic variation in black spruce (Wang and Macdonald, 1992, 1993; Zine El Abidine, 1993; Zine El Abidine *et al*, 1994). The reader should refer to the specific studies for additional information on these topics. Details on the autecology and silviculture of black spruce are given in Black and Bliss (1980), Cauboue and Malenfant (1988), Sims *et al* (1990) and Jeglum and Kennington (1993).

The objective of the current review is to provide an update on research results on the ecophysiology and field performance of black spruce, with an emphasis placed on the regeneration phase. The major topics of this review are the response of net photosynthesis and stomatal conductance to certain environmental parameters, such as light and temperature. Also covered are transpiration, root growth, mineral nutrition, overall responses to specific environmental stresses. The last section covers field performance.

NET PHOTOSYNTHESIS

As in all tree species, the rate of photosynthesis in black spruce is influenced by environmental factors such as light, temperature, atmospheric humidity, CO_2 concentration, soil water availability and phenology (Kozlowski *et al*, 1991). Some factors, such as atmospheric humidity deficit, affect photosynthesis indirectly through stomatal effects. Others, like temperature, have a more direct effect on the biochemistry of photosynthesis. However, many factors have both a direct and an indirect effect, making cause and effect interpretation more uncertain. We have retained 3 factors that act directly on photosynthesis: light, temperature and the age of the needles.

Measured maximum rates of net photosynthesis for black spruce, all units converted (table I), vary from about 0.03 μmol g^{-1} (needle dry weight) s^{-1} for trees in the field, to 0.036 μmol g^{-1} s^{-1} for seedlings in the field, to 0.1 μmol g^{-1} s^{-1} for seedlings in the greenhouse, to 0.17 μmol g^{-1} s^{-1} for seedlings in irrigated and fertilized exterior sand beds (table I). Most measurements reported here were performed on unshaded 1-year-old or current-year needles.

Light response

Figure 2 shows light response curves on sunlit lateral branches of black spruce trees at air temperatures between 13 and 20°C
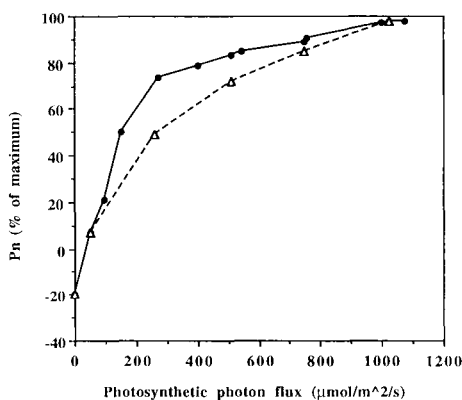

Fig 2. Effect of photosynthetic photon flux on net photosynthesis (% of maximum) (Vowinckel *et al*, 1975 (●); Black and Bliss, 1980 (△)).

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Table I. Values of transpiration (T), needle or stomatal conductance to water vapour (g_{sw}), net photosynthesis (P_n) and water use efficiencies (WUE) measured in various field and laboratory experiments.

Studies	T^* ($\mu mol\ g^{-1}\ s^{-1}$)	g_{sw}^* ($mmol\ g^{-1}\ s^{-1}$)	P_n^* ($\mu mol\ g^{-1}\ s^{-1}$)	WUE ($mol\ CO_2/mol\ H_2O$)
Vowinckel et al, 1975[t,f]			0.012–0.022	
D'Aoust, 1978a[s,l]	30–90		0.08	
Black and Bliss, 1980[s,l]			0.03	
Hom and Oechel, 1983[t,f]			0.015–0.03	
Grossnickle and Blake, 1986[s,f]		1.5		
Blake and Sutton, 1987[s,f]		1.4	0.036	
Zwiazek and Blake, 1989[s,l]		0.3**	0.015**	0.004
Macdonald and Lieffers, 1990[t,f]		0.58**	0.027**	0.002
Dang et al, 1991[t,f]		0.1–0.38	0.029	0.001–0.003
Tan et al, 1992a,b[s,l]	2.7**	0.11	0.013	
Wang and Macdonald, 1993[s,l]		0.65–2.5	0.007–0.056	0.0007–0.003
Yue and Margolis, 1993[c,l]			0.07	
Bernier, 1993[s,f]	20–50	1.3		
Zine El Abidine, 1993[s,l]	50	2.0	0.1	0.006
Zine El Abidine et al, 1993b[s,b]	80	3.0	0.17	

* All values have been converted to molar units per unit needle dry mass per unit time. Assumed values of specific leaf area, air temperature and atmospheric pressure used in the conversions are 100 g cm^{-2}, 15°C and 1 000 mb, respectively. ** Average measurements. All other values are reported maximums. [c] Rooted cuttings; [s] seedlings; [t] trees; [b] exterior planting beds; [l] laboratory conditions; [f] field conditions.

(Vowinckel et al, 1975) and on greenhouse seedlings (Black and Bliss, 1980). Vowinckel et al (1975) reported light saturation at 1 000 μmol m^{-2} s^{-1} for mature trees in the field. Work on seedlings under controlled or semi-controlled conditions has yielded values ranging from about 1 000 μmol m^{-2} s^{-1} to as low as 200 μmol m^{-2} s^{-1} for very young stock under optimal growth conditions (table II). This variability in response shows that the light response curve of photosynthesis in black spruce is dependent on the amount of chlorophyll per unit of illuminated leaf area (Leverenz, 1987). Growth conditions evidently play a major role in the level at which photosynthesis becomes light saturated.

The light compensation point for black spruce is reached around 35–50 μmol m^{-2} s^{-1}, although a compensation point as high as 100 μmol m^{-2} s^{-1} has been measured under warm conditions in actively growing young stock (table II). Yue and Margolis (1993) reported a significant effect of temperature on this value with measurements ranging from 5 μmol m^{-2} s^{-1} at 5°C to 27 μmol m^{-2} s^{-1} at 30°C in rooted black spruce cuttings.
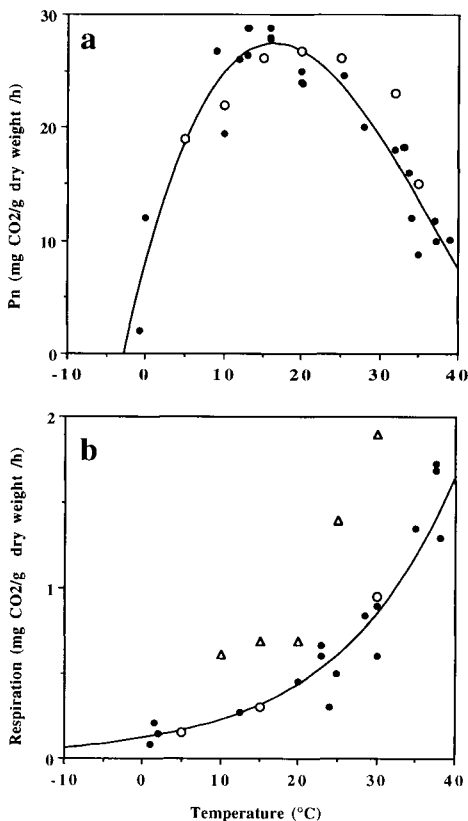
Temperature

Figure 3 show the temperature response of net photosynthesis and dark respiration in black spruce. Net photosynthesis stays at 90% of optimal or above at temperatures between 15 and 25°C. Zine El Abidine (1993) found optimal temperatures for net photosynthesis of around 24 to 27°C for fertilized seedlings in sand beds. High opti-

Table II. Light compensation and saturation points, as well as optimum temperature, for net photosynthesis measured in various field and laboratory experiments.

Studies	Compensation point ($\mu mol\ m^{-2}\ s^{-1}$)	Saturation point ($\mu mol\ m^{-2}\ s^{-1}$)	Temperature (°C)
Vowinckel et al, 1975[t,f]	35	1 000	13–15
D'Aoust, 1978a[s,l]	100	200	15–25
Manley and Ledig, 1979[s,l]	68	>1 000	21
Black and Bliss, 1980[s,l]	30	1 000	15
Yue and Margolis, 1993[c,l]	5–27	300–400	
Zine El Abidine et al, 1993b[s,b]	50	400–600	24–27

[c] Rooted cuttings; [s] seedlings; [t] trees; [b] exterior planting beds; [l] laboratory conditions; [f] field conditions.

Fig 3. Influence of temperature on **(a)** net photosynthesis and **(b)** respiration (Vowinckel et al, 1975 (●); D'Aoust, 1978a (O); Black and Bliss, 1980 (Δ)).

mum values can be found in seedlings reared under high temperatures (Manley and Ledig, 1979). Although dark respiration decreases with decreasing temperature, cool nights (10 versus 20°C) have been found to reduce overall growth in greenhouse seedlings (Lord et al, 1993), suggesting a carry-over effect of cool temperatures either on the photosynthesis apparatus or on the stomata.

Age of needles

Needle retention on black spruce varies from 5 to 7 years in southerly reaches of the boreal forest in Quebec (CH Ung, Canadian Forest Service, Quebec Region, personal communication) to 13 years in central Alaska (Hom and Oechel, 1983), and up to 30 years under subarctic conditions (Chapin and Van Cleve, 1981). Different needle age classes differ in their photosynthetic capacity. Using ^{14}C labelling on whole branches of P mariana trees of interior Alaska, Hom and Oechel (1983) showed that needles maintained 40% of maximum photosynthetic rate after 13 seasons of growth. The nutrient use efficiency (the amount of CO_2 fixed per unit nutrient content) decreased with needle age and was more pronounced for nitrogen than for phos-

phorus (Hom and Oechel, 1983). The decrease in the photosynthetic activity of older needles has been attributed to decreased stomatal and mesophyll conductances, accumulation of wax in stomatal cavities, and nonreversible winter chloroplast degradation (Jeffre et al, 1971; Ludlow and Jarvis, 1971). Increasing needle longevity appears to maximize the photosynthetic return per unit of nutrient invested in the needles (Chapin and Van Cleve, 1981; Hom and Oechel, 1983).

STOMATAL CONDUCTANCE (g_s)

Stomatal conductance is influenced by several environmental factors, the most important being light, atmospheric humidity deficit, needle temperature and soil water availability (Grossnickle and Blake, 1986; Roberts and Dumbroff, 1986; Blake and Sutton, 1987; Zeiger et al, 1987; Grossnickle, 1988; Blake et al, 1990; Zine El Abidine, 1993). It was formerly thought that these environmental factors controlled stomatal opening solely via hydraulic signals that could be quantified by measuring the xylem water potential. We now know from recent research that stomata integrate signals from a wider variety of sources, including hormonal fluxes from drying roots (Davies and Zhang, 1991), in such a way as to prevent large fluctuations in the plant water status (Meinzer and Grantz, 1991). However, this expanded view of stomatal function has yet to shed light on how internal water status information is translated into stomatal responses, as well as which physical measure of plant water status is most physiologically significant (Schulte, 1992).

Maximum reported values of stomatal conductances to water vapour for black spruce, all units converted, range from 0.58 mmol g^{-1} s^{-1} for mature trees in the field to 1.5 mmol g^{-1} s^{-1} for seedlings in the field to 3.0 mmol g^{-1} s^{-1} for irrigated and fertilized seedlings in exterior sand beds (table I). Stomatal conductance influences net photosynthesis by controlling the amount of CO_2 that can enter the mesophyll. Recent work with black spruce seedlings has shown that this effect is not linear, with stomatal limitation to net photosynthesis becoming important only at low values of stomatal conductance (Stewart et al, 1994).

Light response

In many tree species, maximal stomatal conductance is reached when the light level reaches about 10% of full sunlight, or about 200 µmol m^{-2} s^{-1} (Hinckley et al, 1978). Measurements on fertilized black spruce seedlings in outside sand beds (Zine El Abidine, 1993) show near maximum conductance at light levels closer to 100 µmol m^{-2} s^{-1}. The rise in conductance with increasing light level is also much more rapid in black spruce than in either white spruce (Picea glauca [Moench] Voss) or jack pine (Pinus bankslana Lamb) (Grossnickle and Blake, 1986), indicating the greater shade tolerance of this species.

Light interacts with other environmental parameters as well in its influence of the stomata. The slope and maxima of the stomatal conductance–light relationship of black spruce is influenced by atmospheric humidity deficit (Grossnickle and Blake, 1986) and soil dryness (Wang and Macdonald, 1993) as these parameters appear to control the maximum value of stomatal conductance.

Effect of atmospheric humidity

The atmospheric humidity deficit, or more accurately the difference between atmospheric humidity inside the needle and in the outside air, has a major influence on the stomatal opening of black spruce and other

boreal conifers (Grossnickle and Blake, 1986). Stomata are usually open under low humidity deficits and close as the air becomes drier. Reported responses of black spruce stomata are quite variable (*eg*, Grossnickle and Blake, 1986; Blake and Sutton, 1988; Zine El Abidine, 1993), and highly dependent on other physiological or physical parameters (Blake and Sutton, 1988). Overall, however, absolute humidity deficits (AHD) greater than 12–14 g m^{-3} cause significant closure of the stomata.

Xylem water potential (ψ_x)

Under low levels of AHD (2.0–10 g m^{-3}), stomatal conductance decreases as ψ_x becomes more negative. At higher AHD levels, there is little relation between ψ_x and conductance as AHD itself becomes limiting. In the field, Blake and Sutton (1988) observed that values of stomatal conductance in newly planted black spruce declined rapidly as water potential fell below −0.5 MPa. Stomatal closure of black spruce trees can occur at a ψ_x of about −1.3 MPa (Wolff *et al*, 1977; Grossnickle and Blake, 1986; Blake and Sutton, 1987), although Zine El Abidine (1993) measured stomatal conductance of up to 2.4 mmol g^{-1} s^{-1} at that level of ψ_x. In that study, extrapolation of the boundary line suggests a stomatal closure around −2 MPa. Although they grow naturally in moist soils and cool humid boreal forests, black spruce seedlings or trees can reach a midday xylem water potential of −2 MPa or lower (Wolff *et al*, 1977; Bernier, 1993; Zine El Abidine, 1993).

Soil drought and growth regulators

Root tips in drying soils produce abscisic acid (ABA), a growth regulator that influences stomatal conductance and regulates different developmental processes (Davies

and Zhang, 1991). Increases in needle ABA content in relation to high water stress have been negatively correlated with stomatal conductance or transpiration in several tree species (Blake and Ferrell, 1977; Hinckley *et al*, 1978; Newville and Ferrell, 1980; Johnson and Ferrell, 1982; Hogue *et al*, 1983; Johnson, 1987), including black spruce (Roberts and Dumbroff, 1986).

ABA concentration is a sensitive indicator of stress intensity and can reach 3.63 µg g^{-1} dry weight during severe water stress in black spruce (Roberts and Dumbroff, 1986). Even after rewatering, the delay of a few days in the recovery of stomatal conductance suggests the presence of residual ABA or ABA metabolites in the vicinity of the guard cells (Roberts and Dumbroff, 1986; Johnson 1987). Such a residual effect can be exploited with exogenous ABA. Pretreatment of black spruce seedlings with ABA or synthetic analogs (Blake *et al*, 1990) has been shown, through its effect on stomatal conductance, to promote more favourable water potentials, enhanced water retention and increased survival after outplanting (Marshall *et al*, 1991).

Water stress preconditioning

When subjected to successive episodes of water stress, stomata of black spruce seedlings will undergo changes in behaviour. Zwiazek and Blake (1989) found that water stress preconditioning of black spruce seedlings increased stomatal sensitivity to subsequent water stress. Zine El Abidine (1993), however, found the opposite, *ie* a decrease in stomatal sensitivity to water stress following preconditioning, a result similar to what has been found for Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) (van den Driessche, 1991). This apparent contradiction in results may stem from differences in the length or in the intensity of the preconditioning stress, or from

differences in other uncontrolled variables. What is clear, however, is that stomatal mechanisms in black spruce are dynamic and are able to acclimate to a changing environment.

TRANSPIRATION

Transpiration rates of plants are governed by leaf-to-air conductances and humidity gradients, as well as by total leaf area at the plant or canopy level and root-level hydraulic conductances. Current theories suggest that internal physiological processes link with external physical processes to regulate water loss and plant water status (Meinzer and Grantz, 1991). Such structural regulation leads to canopy-level values of transpiration that appear decoupled from stomatal dynamics (Meinzer and Grantz, 1991).

Measurements on well-watered black spruce seedlings inside a well-ventilated cuvette (minimal boundary-layer resistance) show maximum rates between 50 and 90 μmol g^{-1} s^{-1} (D'Aoust, 1978a; Zine El Abidine, 1993). Midday values from natural and planted seedlings on a boreal clear-cut averaged 20 μmol g^{-1} s^{-1}, with a maximum value of 50 μmol g^{-1} s^{-1} (PY Bernier, unpublished data). We could find no data on daily water use by black spruce seedlings or trees. Our best estimate for seedlings based on peak rates cited above would be about 5 g H_2O g^{-1} d^{-1} under warm sunny conditions. At the canopy level, Lafleur (1992) measured evapotranspiration rates of about 0.1 mm h^{-1} from a subarctic black spruce stand. McCaughey (1978) obtained peak values of about 1 mm h^{-1} over a balsam fir stand located at a slightly lower elevation than nearby black spruce stands in the Laurentian highlands, north of Quebec City. On-going experiments under the large-scale BOREAS program (Sellers et al, 1993) should yield values over a broader range of sites and environmental conditions.

ROOT GROWTH

In general, root growth of black spruce seedlings is slower than that of other boreal conifers (Grossnickle and Blake, 1986). Mature trees appear to maintain similar characteristics: fine root production has been measured at 113 g m^{-2} for black spruce compared with 366 gm^{-2} for white spruce (Van Cleve et al, 1983). Root biomass in an old black spruce site was estimated at 1 230 g m^{-2} and comprised only 15% of total tree biomass (Tryon and Chapin, 1983). Root growth is usually superficial with long trailing roots progressing at the mineral soil–organic layer interface, or in the surface organic layers in organic soils (Sims et al, 1990). Mechanical stability of single trees is poor (Sims et al, 1990), but that of dense stands is good because of the interlocked architecture of the root system (Smith et al, 1987).

Root growth declines during the period of shoot growth, as shoot growth itself uses most of the stored and current photosynthates. At other times of the year, soil temperature is the major regulator of root growth (Lawrence and Oechel, 1983a,b) although its effect on growth is more pronounced in large roots than in fine ones (Tryon and Chapin, 1983). For root diameters ranging from 0.5 to 1.5 mm, root growth of black spruce reaches its optimum at 20°C and stops when soil temperature drops below 5°C (Tryon and Chapin, 1983). Black spruce appears to maintain active root growth later in the fall in peatlands than eastern larch (Larix laricina [DuRoi] K Koch), although it is unclear whether this difference is due to a greater tolerance to cold temperatures or to flooding (Conlin and Lieffers, 1993).

Several other factors can also affect root growth of black spruce trees. Prévost and Bolghari (1990) found that root penetration decreased with increasing soil bulk densities. Bulk densities of 0.85 and 1.05 g cm^{-3}

favoured deep root penetration, whereas densities of 1.25 and 1.45 g cm^{-3} restricted root elongation. Bernier (1993) reported that, in containerized seedlings planted in mineral soil, most of the increase in root mass during the first field season took place inside the low-density peat plug, with only 10% of the new root mass developing outside the plug. In forested bogs, rooting depth is strongly correlated with depth to water table (Lieffers and Rothwell, 1987). Seed provenance, needle damage, or other factors influencing tree vigour also affect root growth.

MINERAL NUTRITION

In the nursery, black spruce seedlings respond very well to nitrogen fertilization. Optimal growth of the seedlings has been observed at a substrate nitrogen concentration of 250 to 350 ppm (D'Aoust, 1980). Weekly fertilization of containerized black spruce seedlings is usually determined by the target biomass. Recommended final needle concentrations (% oven dry weight) for 2-year-old containerized seedlings are 1.61%, 0.27%, and 1.00% in N, P, and K, respectively (Langlois, 1990). Minimum critical needle concentrations have been estimated at 1.20%, 0.14%, 0.30%, 0.10%, and 0.09%, for N, P, K, Ca, and Mg, respectively (Morrison, 1974). Increased N supply increases amino-acid concentrations such as proline, glutamine acid, and arginine (Kim *et al*, 1987). Improved nutritional status through exponential fertilization in the nursery also increases growth of black spruce seedlings after outplanting (Timmer *et al,* 1991).

Once outplanted, nursery-grown seedlings must adapt to a much poorer soil environment. Comparing natural and planted black spruce seedlings during 2 growing seasons, Munson and Bernier (1993) found that the seasonal patterns of N, P, and K concentration in needles of the planted seedlings reflected early dilution in the nutrient-rich tissues, and, later in the growing season, growth limitation. Nutrient use efficiency of planted seedlings tended to increase with acclimation to the site.

In the field, growth of black spruce appears largely N-limited. The cool and humid conditions of the boreal forest, plus the presence of tanins in the needle litter, favour the accumulation of organic matter and the slow decomposition by soil microorganisms (Waring and Schlesinger, 1985). Root C/N for black spruce stands ranges from 303 to 347 gC/gN (Van Cleve *et al,* 1981; Auclair and Rencz, 1982). In addition, within the boreal forest, black spruce grows on sites with greater nutrient limitations than either white spruce or white birch (Van Cleve and Harrison, 1985). Site-to-site variations in nitrogenase activity in a subarctic black spruce forest depend largely on lichens with nitrogen-fixing phycobionts and on the moss cover (Billington and Alexander, 1983). Mosses in particular have a high retention capacity for nutrients, particularly phosphorus, and compete effectively with black spruce for that resource (Chapin *et al*, 1987).

Treatments that increase nitrogen availability in the forest, such as drainage, thinning or fertilization increase the growth of black spruce. In a 50- to 60-year-old black spruce stand, the N-fertilization treatments accompanied by thinning and drainage increased foliar N concentration and content of current needles (Mugasha *et al,* 1991). In another trial 15 years after N-fertilization, the total volume increases ranged from 3 to 9 m^3 for an application of 112 kg N/ha and from 11.5 to 12.5 m^3 for 448 kg/ha (Weetman *et al,* 1980). Older needles of *P mariana* can act as a sink for nutrient and carbon storage during nongrowth periods (Chapin and Kedrowski, 1983).

In nature, black spruce forms mycorrhizal associations with several ectomycorrhizal

fungi such as *Hebeloma crustuliniforme* (Bull ex St Am), *Laccaria bicolor* (Maire) Orton, *Hebeloma cylindrosporum* Romangnési, and *Telephora terrestris* Ehrh ex Fr. The presence of *H crustuliniforme* in the rhizosphere helps black spruce seedlings use protein as a nitrogen source (Abuzinadah and Read, 1986). Mycorrhiza also help black spruce compete with the moss cover for nutrients (Chapin *et al*, 1987). Inoculation of containerized black spruce seedlings with *L bicolor* improves growth when the seedlings are supplied with limited amounts of nitrogen (Gagnon *et al*, 1988). Short-root density of black spruce is also improved by inoculation with *L bicolor*, *H cylindrosporum*, and *T terrestris* (Stein *et al*, 1990; Browning and Whitney, 1991). Changes in the architecture of root systems by ectomycorrhizal fungi can improve mineral nutrition and drought tolerance of host plants (Lamhamedi *et al*, 1991, 1992a,b), The extramatrical phase of ectomycorrhizal fungi has also been shown to act as a link for carbohydrate and nutrient transfer between adjacent trees or seedlings of various species (Newman, 1988). Such interplant transfers plays a role in the establishment of black spruce regeneration.

RESPONSES TO ENVIRONMENTAL STRESSES

In boreal ecosytems, black spruce seedlings or trees are subjected to different environmental stresses including flooding, heat stress, water stress, and frost. This section looks at whole plant responses to specific stresses rather than focussing on a specific physiological function or mechanism.

Flooding

In the boreal forest, flooding imposes a triple constraint on tree growth, that of low oxygen availability, low nutrient availability, and low root zone temperature (Van Cleve *et al*, 1981; Lieffers and Rothwell, 1986). Tolerance to flooding and low soil temperatures are ecological characteristics that allow black spruce to dominate lowland boreal forests (Crawford, 1976; Larsen, 1982). Studies examining the tolerance of boreal conifers to flooding show that black spruce seedlings are more tolerant to flooded soils than white spruce, Sitka spruce (*P sitchensis* [Bong] Carr), Scots pine (*P sylvestris* L) and European larch (*Larix decidua* Mill) (Zinkan *et al*, 1974; Crawford, 1976; Levan and Riha, 1986).

Although black spruce is more tolerant to flooding than most other boreal conifers, its survival and growth are negatively affected by flooding in peatlands (Payandeh, 1975; Dang and Lieffers, 1989). Root tips do not survive prolonged flooding and show little growth into flooded soil (Levan and Riha, 1986), where oxygen concentrations can drop below an apparently critical level of 2.0 ppm (Zinkan *et al*, 1974). Crawford (1976) observed an increase in accumulation of ethanol and malic acid in flooded tree roots. The production of malic acid and the use of starch enable the roots to respire at low oxygen concentrations through glycolysis (Crawford, 1976).

Flooding greatly influences the diurnal pattern of water relations of black spruce. Grossnickle (1987) found reduced diurnal fluctuations of g_s and ψ_x in flooded black spruce compared with nonflooded seedlings. The reduction in g_s in response to flooding is accompanied by a decrease in photosynthesis and transpiration (Zaerr, 1983; Levan and Riha, 1986). The flooding of roots reduces root hydraulic conductivity, which can increase water stress and xylem injury. Flooding also decreases mineral nutrition and hormonal levels in trees (Kozlowski and Pallardy, 1979; Kozlowski 1984; Grossnickle, 1987). Recovery of g_s after flooding may take several days (Grossnickle, 1987).

Drainage of peatlands improves rates of net assimilation, foliar nitrogen concentration, water use efficiency, and mesophyll conductance (g_m) (Macdonald and Lieffers, 1990). Drainage of peatlands can increase soil temperatures and improve substrate aeration, changes that can influence the early timing of photosynthetic start-up and the growth of trees. Wang and Macdonald (1993) found that seedlings grown at low substrate temperatures (8°C at 5 cm below the surface) were smaller and showed lower P_n, g_s and g_m than those at higher substrate temperatures (20°C).

Heat stress

High temperatures at the soil surface can occur for brief periods on boreal planting sites during the summer, reducing physiological processes of young seedlings and possibly causing serious damage (Seidel, 1986; Lopushinsky and Max, 1990). The exposure of seedlings to high temperatures causes cell membrane damage, protein and enzyme denaturation and the accumulation of toxic nitrogenous compounds that can cause mortality (Stathers and Spittlehouse, 1990; Colombo *et al*, 1992). The sensitivity of black spruce seedlings varies with tissue age and ontogeny. Current-year shoots are more sensitive than older shoots; actively growing seedlings are more sensitive than dormant ones (Koppenaal and Colombo, 1988). The susceptibility of black spruce seedlings to direct and indirect damage increases exponentially with increasing temperature and length of exposure (Colombo and Timmer, 1992). The exposure of plants to high temperatures (47°C for 30 min) induces the synthesis of heat shock proteins (HSP) which play a role in the acquisition of thermotolerance (Colombo *et al*, 1992). Preconditioning black spruce seedlings to heat shock (pretreated for 6 d at 38°C for 3 h per d) can increase their tol-erance to high temperatures (Koppenaal *et al*, 1991).

Water stress

Black spruce seedlings are more sensitive to water stress than other boreal conifers (Grossnickle and Blake, 1986; Blake and Sutton, 1988; Grossnickle, 1988). In the field, part of this sensitivity is due to the shallow and slow-growing root system (Grossnickle and Blake, 1986; Bernier, 1993), while another part is related directly to physiological processes. Sensitivity to water stress is not static over time as water relations components change in concert with shoot phenology both in seedlings and in mature trees (Colombo, 1987; Zine El Abidine *et al*, 1994). Sensitivity to water stress increases dramatically from bud break to the middle of the period of shoot elongation, and decreases progressively thereafter (Zine El Abidine *et al*, 1994). During the period of maximum sensitivity, a high evaporative demand can induce turgor loss even under conditions of high soil water availability (Zine El Abidine, 1993). Drought tolerance mechanisms of black spruce have been related to the phenological state of the seedlings (Buxton *et al*, 1985; Roberts and Dumbroff, 1986; Colombo, 1987; Blake *et al*, 1991).

Maintenance of turgor during drought is achieved mainly through osmoregulation, the passive and sometimes active accumulation of osmotically active molecules within the cell in response to water stress (Turner and Jones, 1980; Morgan, 1984). Sugars and amino acids are the major constituents of osmoregulation in expanded leaves of many species with sugars being apparently dominant in black spruce (Zwiazek and Blake, 1990a; Tan *et al*, 1992a,b). Concentrations of several amino acids in the free amino-acid pool also vary greatly during drying (Cyr *et al*, 1990). Large

increases in the concentration of proline in response to both moderate and severe drought were also observed in black spruce, suggesting a role for proline in the stress adjustment mechanism protecting enzymes from heat denaturation (Paleg *et al,* 1981; Cyr *et al,* 1990).

The degree of active osmotic adjustment is influenced by the degree of stress pre-conditioning. Zwiazek and Blake (1990a) found that the osmotic potential of precon-ditioned black spruce seedlings was lower than that of unconditioned plants before and during subsequent exposure to osmotic stress with polyethylene glycol (PEG). The difference in osmotic potential between non-stressed preconditioned and unconditioned plants was attributed to an active accumu-lation of soluble carbohydrates in the pre-conditioned seedlings. In addition to carbo-hydrate and amino-acid accumulation in response to water stress, Zwiazek and Blake (1990a) also observed an increase in major organic acids in drought-stressed black spruce. Tan *et al* (1992a,b) revealed that faster- and slower-growing black spruce progenies differed in osmotic adjustment and changes of soluble carbohydrates and amino acids under osmotic stress. Recently, however, Zine El Abidine (1993) found no such active osmoregulation in his precon-ditioned black spruce seedlings. The use of 3 prolonged drying cycles by Zine El Abidine (1993) instead of the short preconditioning with polyethylene glycol (PEG) of Zwiazek and Blake (1990a) might explain the differ-ences in results. PEG can also be absorbed by treated plants and affect their physio-logical processes (Lawlor, 1970).

Zwiazek and Blake (1990b) found that black spruce seedlings stressed with PEG leaked more electrolytes than unstressed plants. Leakage under stress was less in preconditioned than in unconditioned seedlings. Preconditioning and osmotic stress also halved sterol concentrations in the shoots from 1.96 mg g^{-1} dry weight in controls to 0.83 mg g^{-1} dry weight in treated seedlings. The sterols identified were sito-sterol, stigmasterol and campesterol. Zwiazek and Blake (1990b) showed that sterol/phospholipid ratios varied markedly depending on the severity of water stress and suggested that the decrease of this ratio during water stress could indicate an important mechanism contributing to stress tolerance. In a later study, these same authors showed that the electrolyte leak-age method detected membrane injury in black spruce with greater sensitivity than other methods such as the electrical impedance and xylem sap methods (Zwiazek and Blake, 1991).

Frosts and frost tolerance

Black spruce trees in the boreal forest must be able to grow in the summer in spite of occasional radiative frosts, and survive the winter in spite of air temperatures that can drop to −40°C or below. Cellular membranes in black spruce are very permeable and permit rapid transport of water out of living cells, preventing formation of intracellular ice crystals (Glerum, 1976).

Although black spruce is capable of tol-erating some level of frost during the grow-ing season, photosynthesis is impaired. Field experiments show that air temperatures of −4°C kill actively growing shoots and cause large reductions in net photosynthesis and stomatal conductance in 1-year-old needles; air temperatures of −3°C produce no visi-ble damage and impact only moderately on net photosynthesis and stomatal conduc-tance (Dang *et al* 1991, 1992). Full recovery of the photosynthetic apparatus after a sum-mer frost may take several weeks (Pharis *et al,* 1970). Recovery of stomatal control after a frost is accelerated by the exposure of the foliage to direct sunlight through mechanisms that remain unclear (Dang *et al,* 1992).

Growth, bud formation and freezing tolerance in black spruce seedlings are regulated by photoperiod and temperature, as with most boreal conifers, through the involvement of the phytochrome (Pollard and Logan, 1977; D'Aoust, 1978b, 1981; D'Aoust and Trudel, 1984; Grossnickle and Blake, 1985; D'Aoust and Hubac, 1986; Colombo *et al*, 1989; Bigras and D'Aoust, 1992). Generally, the hardening phase of shoot components coincides with the accumulation of food reserves (Glerum, 1976). Roots, on the other hand, harden only in response to low temperature (Bigras and D'Aoust, 1992). Shoots and roots of black spruce differ greatly in their winter frost hardiness. For example, Bigras and D'Aoust (1992) achieved a frost tolerance of −30°C in black spruce shoots, but of only −6.4°C in roots during a controlled experiment. The limited frost hardiness of roots coupled with the superficial rooting habit of black spruce suggests that this species would be vulnerable to episodes of mid-winter snowmelt followed by severe frosts.

Other factors can influence frost hardening in black spruce. Cold temperatures during growth reduce needle cuticularization during needle maturation (Vanhinsberg and Colombo, 1990), predisposing seedlings to desiccation damage during winter. Alternances of warm and cool temperatures during hardening, on the other hand, increase frost hardiness in both roots and shoots (Colombo, 1994). Provenance, soil moisture, and plant nutrient levels also appear to influence frost hardiness of black spruce (Pollard and Logan, 1979; Glerum, 1985).

Early and late frosts are one of the leading causes of seedling mortality in nurseries, particularly in containerized production. Even short-day treatments, commonly used in nurseries to induce growth cessation, bud setting, and frost hardening (D'Aoust, 1981; Bigras and D'Aoust, 1992), can result in earlier spring dehardening and needle flush (Colombo, 1986; Bigras and D'Aoust, 1992,

1993), and therefore increased susceptibility to late frosts. Such a problem has prompted a search for rapid evaluators of frost hardiness. Frost hardiness has been correlated with shoot moisture content (Colombo, 1990; Calmé *et al*, 1993), mitotic index of shoot primordia (Colombo *et al*, 1989), and electrical impedance (Glerum, 1973). The relationship between frost tolerance and shoot water content appears to be independent of cultural practices (Calmé *et al*, 1993). None of these methods has yet emerged as operationally suitable for nursery operators.

Increasing atmospheric CO_2 and climate change

Most of the work on the effect of elevated CO_2 on black spruce has been done at the nursery level, looking at elevated CO_2 as a cultural treatment. In all studies, CO_2 enrichment has resulted in increased needle, stem and root biomass and nitrogen use efficiency (Bégin, 1986; Campagna and Margolis, 1989; Lord *et al*, 1993). Increases in growth have been as high as 41% (Bégin, 1986), although the response of specific morphological parameters depends on the development stage (Campagna and Margolis, 1989). CO_2 enrichment does not appear to affect sugar, starch or total nonstructural carbohydrates, suggesting that black spruce can maintain a strong sink to avoid accumulation of nonstructural carbohydrates under high CO_2 concentrations. CO_2 enrichment has been shown to reduce the late summer frost hardiness of black spruce seedlings (Margolis and Vézina, 1990), but to increase the growth of drought-stressed seedlings (Johnsen, 1993).

Our knowledge on possible responses of the boreal forest ecosystem to climate warming has been derived mostly from mathematical modelling under various scenarios. In general, climate-change models

predict an increase in the nutrient turnover rates of the boreal forest (Pastor and Post, 1988), the general movement of tree species towards northern latitudes (Gates, 1990) and an increased potential for forest fire (Stocks, 1993). As far as we know, the only field experiment on possible effects of climate change on the boreal forest has been that of Van Cleve et al (1990) who showed that a warming of the root zone by 8–10°C above ambient temperature in late summer increased the rate of decomposition of the forest floor and elevated foliar nutrient concentrations. Predictions of northward movements of species are still affected by an apparent lack of knowledge on the exact nature of factors defining the current range of species such as black spruce (Bonan and Sirois, 1992). Further appreciation of effects of climate changes will probably come from physically-based ecosystem modelling (Bonan, 1993).

STAND ESTABLISHMENT AND FIELD PERFORMANCE

Black spruce forests are by and large even-aged, originating from large-scale perturbations such as fires. Over the past few decades, in portions of the boreal forest, clear-cutting has partially replaced such natural agents. Natural regeneration of fire-perturbed areas takes place through the germination of seeds originating from semi-serotinous cones that have survived the fire in scorched tree tops (Millar, 1939). In clear-cuts, regeneration can take place through seeds rained in from adjacent stands or residual trees, or through the growth of layers. Although black spruce layers have long been considered as 'second-class' regeneration, we now know that their growth following release from the mother tree can be as good as that of seedlings (Morin and Gagnon, 1992; Paquin and Doucet, 1992a,b).

Ideal seedbeds for germination vary according to site moisture conditions (Fleming and Mossa, 1994). Germination is generally lower on thick organic matter or moss cover (St-Pierre et al, 1992; Fleming and Mossa, 1994). During and after germination, mosses can act as a reservoir for water and nutrients during drought periods, preventing seedling desiccation (Marek, 1975). During germination, black spruce is more sensitive to water stress than either jack pine or balsam fir (Thomas and Wein, 1985).

Following initial establishment, young black spruce trees can differ greatly in growth and survival as constraints typical of boreal sites such as cold, waterlogged or nutrient-poor soils, and competition from other vegetation limit growth. Local microclimate might also increase the probability of extreme events such as frosts that can reduce annual growth increments and cumulative growth (Glerum and Paterson, 1989). As with most tree species, final tree vigour and root/stem/needle carbon partitioning in mature black spruce are closely related to site quality (Robichaud and Methven, 1991).

One of the major constraints to black spruce establishment following a perturbation is competing vegetation. Different types of interactions between black spruce seedlings and competitive species have been demonstrated. Allelopathic effects on germination and root and shoot growth of black spruce have been shown with the ericaceous shrub *Kalmia angustifolia* L (Peterson, 1965; Mallik, 1987), causing severe forest regeneration problems in Newfoundland. On moist sites, fast-growing species of *Sphagnum* can smother young seedlings, or force them to produce adventitious roots ever higher up their stems (Sims et al, 1990). Usually, however, shrubs or herbaceous vegetation reduce the growth and survival of natural or outplanted seedlings through their effects on water relations, gas exchange, mineral nutrition, soil and air temperature, and light quantity and quality

(Brand and Janas, 1988; Brand, 1990, 1991; Jobidon, 1992). Light is the dominant factor influencing the performance of outplanted black spruce seedlings under competitive stress (Brand and Janas, 1988; Jobidon, 1992). Shrubs are usually regarded as more serious competitors for light than are herbaceous vegetation, although both types of vegetation use site resources, making them unavailable to seedlings.

In Canada, the control of competing vegetation has been done extensively by using glyphosate, a foliage-active herbicide (Arnup and MacKintosh, 1989). The use of herbicides as a tool for controlling competition has recently come under scrutiny for environmental reasons. Different strategies such as biological control, integrated silviculture, companion species and the use of large seedlings are now under laboratory and field investigation for improving the field performance of planted black spruce stock while minimizing the use of herbicides.

Black spruce is widely used in artificial regeneration programs across Canada and research has gone into relating seedling quality in the nursery to performance in the field. Although operational grading of nursery seedlings is usually based on morphological attributes such as height, root collar diameter, and height/diameter ratio, the relation between such grading and initial field performance of planted black spruce stock is not always clear (Paterson, 1991).

Most research into physiological grading of nursery black spruce seedlings has centered on root growth capacity (RGC) (Sutton, 1980, 1983, 1987, 1990; Burdett, 1987). The growth of new roots increases the absorption of water (Colombo and Asselstine, 1989) and thus improves the establishment of black spruce seedlings after planting. In the field, black spruce seedling survival and growth has been correlated with growth of new roots (Prévost and Bolghari, 1990). Black spruce cannot develop new roots rapidly over the first growing season, especially in dry sites.

The shallow and slow growth of roots of newly planted black spruce seedlings (Armson, 1975; Bernier, 1993) coupled with low soil water availability or stomatal closure at high atmospheric humidity deficits can severely limit water and mineral absorption (Grossnickle and Blake, 1986; Blake and Sutton, 1987; Grossnickle, 1988).

Pre-planting RGC has been correlated with the field performance of black spruce (Sutton, 1983, 1987), as well as that of other conifers such as lodgepole pine (Pinus contorta Dougl), Douglas-fir, western hemlock (Tsuga heterophylla [Raf] Sarg), interior spruce (P glauca – P engelmannii complex) and Scots pine (Ritchie, 1985; Simpson, 1990; Mattsson, 1991; van den Driessche, 1991). However, no relation could be found between RGC and field performance of Norway spruce (P abies [L] Karst) (Mattsson, 1991). In addition, not all types of RGC indices correlate equally well with field performance. Sutton (1987), for example, found poor correlations between field performance and RGC indices based on new root numbers, and good correlations between field performance and RGC indices based on mean length of new roots >1 cm.

Although the relation between RGC and field performance is conceptually simple, its application, and the physiological justification for using 1 arbitrary index over the other, or even 1 set of test conditions over the other, appear more uncertain. In general, RGC can be considered an index of seedling vigour. Final seedling survival and performance will rest, however, on how the seedling can overcome site-specific stresses (Grossnickle, 1988), stresses for which RGC may or may not be critical. In that sense, the integrated assessment approach developed by Grossnickle et al (1991) makes more ecophysiological sense by recognizing implicitly that no one single test will ever correlate well with seedling survival and performance over a broad range of field conditions.

RESEARCH NEEDS

Several major challenges lie ahead in the management of boreal forests in general, and of black spruce stands in particular. The first and most immediate of these is the adequate regeneration of harvested sites. A second one, more long term and hypothetical, and yet possibly more taxing on our resources, is the sensitivity of the boreal forest ecosystem to climatic changes and atmospheric pollution (Harrington, 1987; Zayed et al, 1991; Stocks, 1993).

Growth of planted or natural seedlings is influenced by the presence of woody or herbaceous vegetation. Traditional treatments for competition control have relied heavily on the application of herbicides, a practice that has come under intense public criticism over the past few years. Better management of black spruce regeneration will require increased knowledge of the medium- and long-term impact of herbicide use on seedling growth, either through direct effects on the plant, or through indirect effects such as the impact of herbicides on the microflora and microfauna of the soil. Research is also much needed on the proposed alternatives to herbicide application. Large planting stock, companion species, biological herbicides, increased reliance on advanced regeneration, and all improved silvicultural systems in general are alternatives that will require a greater input of knowledge for their application.

The world's environment is not static as humans have made a significant impact on all its components. The atmosphere in particular is being profoundly altered as CO_2 concentrations increase beyond recorded levels. Global circulation models, however imperfect, all appear to lead to the conclusion that boreal areas will become increasingly warmer and drier (IPCC, 1990; Kurz et al, 1992). Such a prospect creates research needs at 2 levels. The first concerns the fate of the boreal forest ecosystem in general, with black spruce as one of its components. The boreal forest is a major component of terrestrial ecosystems, and its coupling with atmospheric processes is presently being assessed through BOREAS, a large-scale Canada–US research program (Sellers et al, 1993). Although we do not know the exact extent of the changes that will take place, we must estimate the effects of such changes on the components of the boreal forest and their repercussions on the atmosphere.

The second level of research requirements created by the current and predicted changes in atmospheric composition and behaviour is that concerning their impact on forestry practices. For example, over 100 million black spruce seedlings were planted in 1992 in the province of Quebec. Questions regarding the long-term impact of climate change on black spruce plantation should be monitored by establishing field trials. These trials could make it possible to choose genotypes that are best adapted to any changed climatic conditions. Impacts of multiple stresses must be assessed, and improved selection methods for tolerance or resistance to stresses must be designed and implemented.

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