# Effect of companion species on the growth of jack pine (*Pinus banksiana*)

MARIE-HÉLÈNE LONGPRÉ, YVES BERGERON, AND DAVID PARÉ[1]

*Groupe de recherche en écologie forestière, Université du Québec à Montréal, C.P. 8888, Succ. A, Montréal, PQ H3C 3P8, Canada*

AND

MARTIN BÉLAND

*Groupe de recherche en écologie forestière, Université du Québec à Montréal, C.P. 8888, Succ. A, Montréal, PQ H3C 3P8, Canada*

*and*

*Unité de recherche et de développement forestier de l'Abitibi-Témiscamingue, Université du Québec en Abitibi-Témiscamingue, C.P. 700, Rouyn-Noranda, PQ J9X 5E4, Canada*

Received October 21, 1993

Accepted April 6, 1994

LONGPRÉ, M.-H., BERGERON, Y., PARÉ, D., and BÉLAND, M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can. J. For. Res. **24**: 1846–1853.

The growth and yield of jack pine (*Pinus banksiana* Lamb.) was studied in even-aged stands of three types: pure jack pine, jack pine mixed with paper birch (*Betula papyrifera* Marsh.), and jack pine mixed with trembling aspen (*Populus tremuloides* Michx.) growing on moderately well-drained glaciolacustrine clay soils in the southern tip of the Clay Belt of northwestern Quebec. Site index, average DBH, and average height of jack pine, and the availability of nutrients in the forest floor were compared among stand types. No differences were found in the height growth of jack pine among stand types. However, diameters of jack pine in mixtures with paper birch were significantly greater than in either pure stands or in mixtures with aspen despite the fact that both mixed stand types showed higher forest floor pH and greater concentrations of exchangeable calcium and magnesium than the pure stands. These results, together with the pattern of height growth of the three species, suggest that the beneficial effect of paper birch on the diameter growth of jack pine is caused mainly by a reduction in the competition for light among individual jack pine trees. The silvicultural implications of the results are discussed.

LONGPRÉ, M.-H., BERGERON, Y., PARÉ, D., et BÉLAND, M. 1994. Effect of companion species on the growth of jack pine (*Pinus banksiana*). Can. J. For. Res. **24** : 1846–1853.

La croissance et le rendement du pin gris (*Pinus banksiana* Lamb.) ont été étudiés dans des peuplements de pins gris purs, des peuplements de pins gris mélangés à du bouleau à papier (*Betula papyrifera* Marsh.) et des peuplements de pins gris mélangés à du peuplier faux-tremble (*Populus tremuloides* Michx.). Ces peuplements équiennes se trouvaient tous sur des argiles glacio-lacustres modérément bien drainées dans la portion sud de la ceinture d'argile au nord-ouest du Québec. L'indice de qualité de station du pin gris, son DHP moyen, sa hauteur moyenne ainsi que la disponibilité des éléments nutritifs dans la couverture morte ont été comparés d'un type de peuplement à l'autre. Aucune différence n'a été trouvée dans la croissance en hauteur des pins gris des trois types de peuplements. Toutefois, le diamètre de ces derniers s'est avéré significativement plus élevé dans les peuplements mélangés avec du bouleau à papier que dans les peuplements purs ou mélangés à du peuplier faux-tremble, bien que les deux types de peuplements mélangés aient présenté un pH de la couverture morte et des concentrations en calcium et magnésium échangeables significativement plus élevés que ceux des peuplements purs. Ces résultats, combinés au patron de croissance en hauteur des trois espèces en cause, suggèrent que l'effet bénéfique du bouleau à papier sur la croissance en diamètre du pin gris est principalement causé par une réduction de la compétition pour la lumière parmi les pins gris. Les implications sylvicoles des résultats sont discutées.

## Introduction

The productivity of forest stands is controlled by abiotic and biotic factors. The effects of abiotic factors on forest productivity are generally well known, especially the permanent site factors (e.g., topographical and pedological site characteristics) (Pawluk and Arneman 1961; Wilde et al. 1964; Shetron 1972; Carmean 1975; Hamilton and Krause 1985; Schmidt and Carmean 1988; Klinka and Carter 1990; Brisson 1992). However, the role of biotic factors, such as forest competition, has received less attention.

Many studies concerning the productivity of mixed forest stands have been conducted in mixture of nitrogen-fixing tree species and non-nitrogen fixing species (Tarrant 1961; Tarrant and Trappe 1971; Binkley 1983, 1984, 1991; Hendrickson and Burgess 1989; Brozek 1990). Most productivity studies concerning mixtures of non-nitrogen-fixing tree species have been conducted in Europe and revealed a variety of trends.

Some studies indicate that the presence of birch in coniferous stands can improve forest productivity (Jonsson 1962; Jensen 1983; Mielikäinen 1985; Tham 1988). Studies from Finland have shown that the productivity of stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) in mixture with birch was similar or superior to that of pure stands (Frivold and Mielikäinen 1990). Moreover, under certain conditions, mixed stands are financially more valuable than pure stands (Valsta 1988; Valsta and Mielikäinen 1987). On the other hand, the total volume of mixed stands is frequently less than the volume of pure stands of the locally most productive species (Burkhart and

[1]Author to whom all correspondence should be addressed.

Printed in Canada / Imprimé au Canada

Tham 1991). The lack of well-designed long-term studies on the productivity of mixed forest and the poor understanding of the mechanisms controlling forest productivity in mixed stands do not allow forest managers to prescribe forest mixture as a means of increasing site productivity (Lanier 1992).

These examples illustrate that a tree species can react differently in pure and mixed stands. According to Kelty (1992), two major mechanisms can explain the growth modification of a species according to stand composition. These mechanisms are competitive reduction and growth facilitation or inhibition. In the first case, the two species utilize the same resource differently. Consequently, the competition is reduced and is less than competition in pure stands and the environmental resources are used more efficiently. For example, a more complete use of available light may be obtained in mixed stands having a stratified canopy where a sun-adapted species occupies the high-light environment of the overstory and a shade-adapted species occupies the low light of the understory. In some cases, the productivity of these stands may surpass the productivity of pure stands of each species (Assmann 1970; Wierman and Oliver 1979; Kelty 1989; Binkley et al. 1992).

Furthermore, competitive reduction could also occur below ground with species differences in root structures and root depths as well as with preferences for different nutrient forms or different efficiencies of using nutrients (McKay and Malcolm 1988; Brown 1991; Morgan et al. 1991).

The second mechanism, growth facilitation or inhibition, implies that a species influences positively or negatively the growth of another associated species. Allelopathy between species is often suggested as a mean of growth inhibition, although it is very difficult to demonstrate this mechanism in natural conditions (Heilman and Stettler 1985; Binkley 1991; Brown 1991).

The growth improvement of a species by another one is often the result of an increased availability of soil nutrients. Generally, this increase is the result of the presence of nitrogen-fixing species or the presence of broad-leaved species that increase litter decomposition rates, although some conifers seem to lead to better N availability than some hardwoods (Binkley and Valentine 1991; Gower and Son 1992). Because it has a higher content of nutrients, lower concentration of polyphenols and lignin, and a higher surface/weight ratio, broad-leaved litter usually decomposes more rapidly than most conifer needles and assures a quick recycling of nutrients (Perry et al. 1987; Bockheim et al. 1991; Morgan et al. 1991). This suggests that nutrient cycling could be accelerated and stand productivity improved by keeping a certain proportion of broad-leaved species in conifer stands (Beaudet 1990).

Most of the studies concerning the productivity of jack pine (*Pinus banksiana* Lamb.) have been conducted in pure or almost pure stands (Pawluk and Arneman 1961; Chrosciewicz 1963; Plonski 1964; Boudoux 1978; Schmidt and Carmean 1988; Carmean and Lenthall 1989; Leary and Smith 1990). The stand tables available for this species have also been derived from pure stands. The prediction of the productivity of mixed stand from these tables is, therefore, questionable.

The objective of the present study was to determine if the growth of jack pine is different in mixed and in pure stands growing on similar sites. Site index, mean DBH, mean height, mean volume, and nutrient availability in the forest floor were compared among mixed and pure jack pine stands.

## Study area

The study area is located in the southern portion of Hébécourt township, Quebec (48°30′N, 79°30′W), where the forest originated from a large fire in 1923 (Dansereau and Bergeron 1993). The stands are thus even aged. The area is located at the southern tip of the Clay Belt of northwestern Quebec and is included in the ecological region of the Amos lowlands, which is characterized by glaciolacustrine clay deposits originating from the presence of the proglacial Lakes Barlow and Ojibway (Vincent and Hardy 1977).

The study region is located at the southern limit of the Boreal Forest (Rowe 1972), within the balsam fir (*Abies balsamea* (L.) Mill.) – paper birch (*Betula papyrifera* Marsh.) domain (Thibault and Hotte 1985). The regional climate is cold and continental with a mean annual temperature of 0.4°C and annual precipitation of 800–900 mm, falling mostly during the growing season (Environnement Canada 1982). Although the average frost-free period is 147 days per year, the risk of frost persists throughout the year (Wilson 1973).

The sites where jack pine is found vary between two extremes: thin organic soil on rock and moderately to well-drained lacustrine clay deposits with a high base content (Bergeron et al. 1982).

## Methods

### *Sampling design*

To minimize the effect of abiotic factors, the study sites were all selected on a similar site type: moderately well-drained glaciolacustrine clay. The ecological mapping of the area (Béland et al. 1992*a*) was used for site selection.

Three stand types were selected: (*i*) pure jack pine stands, (*ii*) mixture of jack pine and trembling aspen (*Populus tremuloides* Michx.), and (*iii*) mixture of jack pine and paper birch. Five 400-m$^2$ square plots were selected per stand type, and the 15 plots were well distributed over the 5-km$^2$ study area. In the mixed stands, the proportion of stems (greater than 10 cm) of each species was approximately 50%.

In each plot, a soil profile was described to verify the ecological site type. This was done with the use of a site type classification key adapted to local conditions (Béland et al. 1990). The DBH of all trees was measured and the height of jack pine trees was estimated with a clinometer.

Stem analysis was used, as described by Zarnovican (1985), to determine the site index for jack pine. This index is determined by the average height of dominant and codominant jack pine trees at age 50. The height of trees is perhaps the best estimate of the productivity of the site because it is less sensitive to stand density than other attributes (Carmean 1975; Spurr and Barnes 1980; Monserud et al. 1990).

Three dominant jack pines per plot were selected for stem analysis. They were chosen according to the following criteria: they had to be free-growing trees having no evidence of past suppression or top injury and their DBH had to rank at precisely the 97 percentile rank among the other jack pine trees. The selected trees were cut at the ground level and disks were sampled at 0.4 m, at 1.3 m, and at each subsequent metre until the diameter outside bark was less than 2 cm.

The width and number of growth rings were measured in 5-year intervals on each disk using computerized data acquisition for radial growth, as described by Zarnovican et al. (1988), to calculate the diameter, height, and volume in relation to age. The average total height of the thee trees at 50 years total age on each plot was considered to be the indicator of site quality.

Stand volume was estimated using a two-entry equation for jack pine and a one-entry equation for aspen and paper birch (Perron 1979).

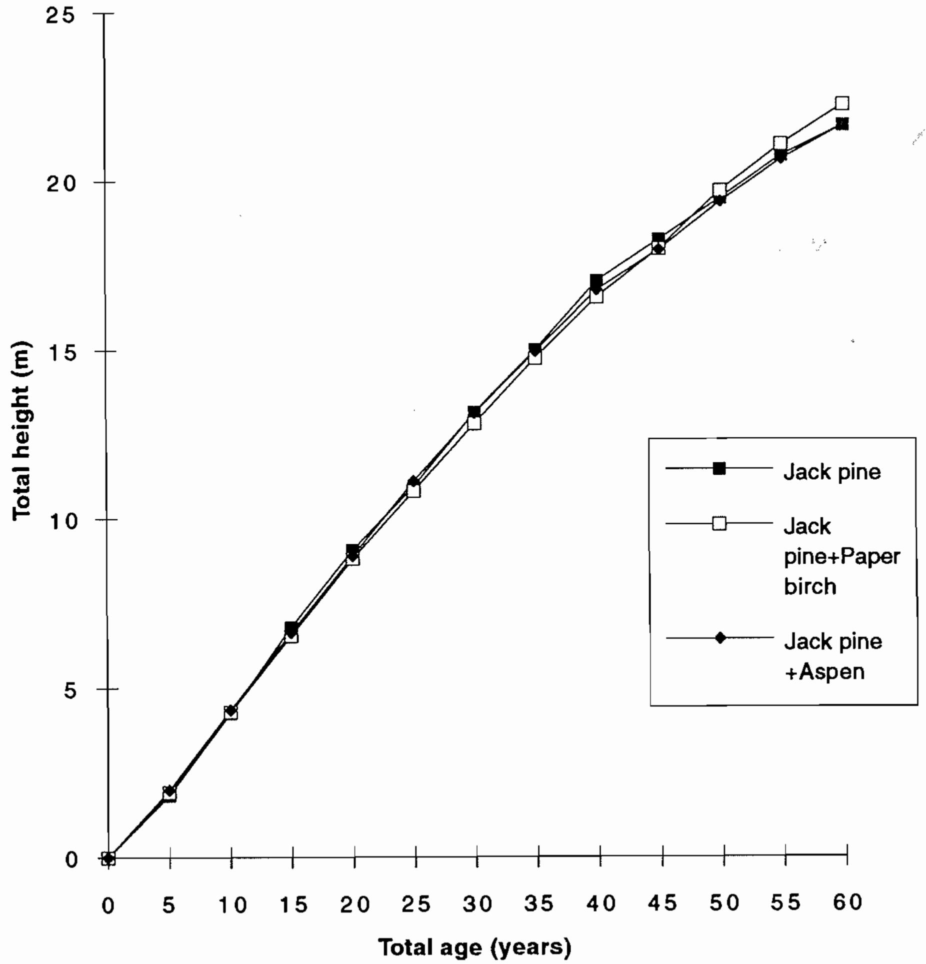


FIG. 1. Average height-growth curves of jack pine for the three stand types sampled.

TABLE 1. Variations of jack pine site index for the three stand types sampled ($p$ = 0.8159)

| Stand type | $N$ | Range | SD (m) | Mean (m) |
|---|---|---|---|---|
| Jack pine | 15 | 17.3–23.6 | 1.4 | 19.5*a* |
| Jack pine + paper birch | 15 | 17.3–21.0 | 1.0 | 19.7*a* |
| Jack pine + aspen | 15 | 16.9–21.3 | 1.2 | 19.4*a* |
| Total | 45 | 16.9–23.6 | 1.2 | 19.5 |

NOTE: Values followed by the same letter do not differ at the 0.05 level.

TABLE 2. Confidence intervals of the estimated parameters of the Korf function for the three stand types sampled

| Stand type | $A$ | $k$ | $n$ |
|---|---|---|---|
| Jack pine | 43.6–230.2 | 1.8–3.8 | 1.3–1.5 |
| Jack pine + paper birch | 84.3–645.7 | 1.5–2.7 | 1.2–1.3 |
| Jack pine + aspen | 52.8–251.4 | 1.8–3.4 | 1.2–1.4 |

*Sample preparation and chemical analysis*

Ten samples from the forest floor were taken in each plot. These samples were analysed individually. They were air dried and then sieved through a large (2-cm mesh) screen. This procedure permitted us to homogenize the material and to remove coarse fragments.

The samples were analysed for pH in double-distilled water (McKeague 1978), for Bray II extractable P (McKeague 1978), and for 1 M $NH_4NO_3$ exchangeable cations (Stuanes et al. 1984). Available N was determined by incubating 2-g (dry weight) samples in the dark at 20°C for 42 days at a water content equivalent to 50% of the field capacity. A polyethylene film was used to limit evaporation. Samples were weighed and the water content was adjusted biweekly. Mineral N ($NH_4$ and $NO_3$) was extracted with 2 M KCl. Mineralizable N was estimated as being the difference between the sum of $NO_3$-N and $NH_4$-N before and after incubation. This method provides an estimate of the substrate quality for net N release under controlled comparable conditions (Binkley and Hart 1989; Vitousek and Denslow 1986). Cations were determined by atomic absorption and anions as well as $NH_4$ by flow-injection colorimetry (Tecator FIA Star 5020 Analyzer).

*Numerical analysis*

Tree growth parameters and soil analyses were subjected to a one-way analysis of variance (ANOVA) to test for differences among stand types. When a significant difference was detected at the 5% level, the Ryans' $Q$ multiple-range test (Day and Quinn 1989) was used to determine the difference among stand types. The average height-growth curves of jack pine per stand type were fitted to the growth function of Korf (Zarnovican 1979). This nonlinear regression allows the estimation of tree height with age and is expressed as

$$\text{Height} = A \exp\left(\frac{k}{1-n}\right) \text{age}^{(1-n)}$$

This function produces an S-shaped curve with an inflection point. Parameters $n$ and $k$ define the position of the inflection point, while parameter $A$ defines the position of the asymptote.

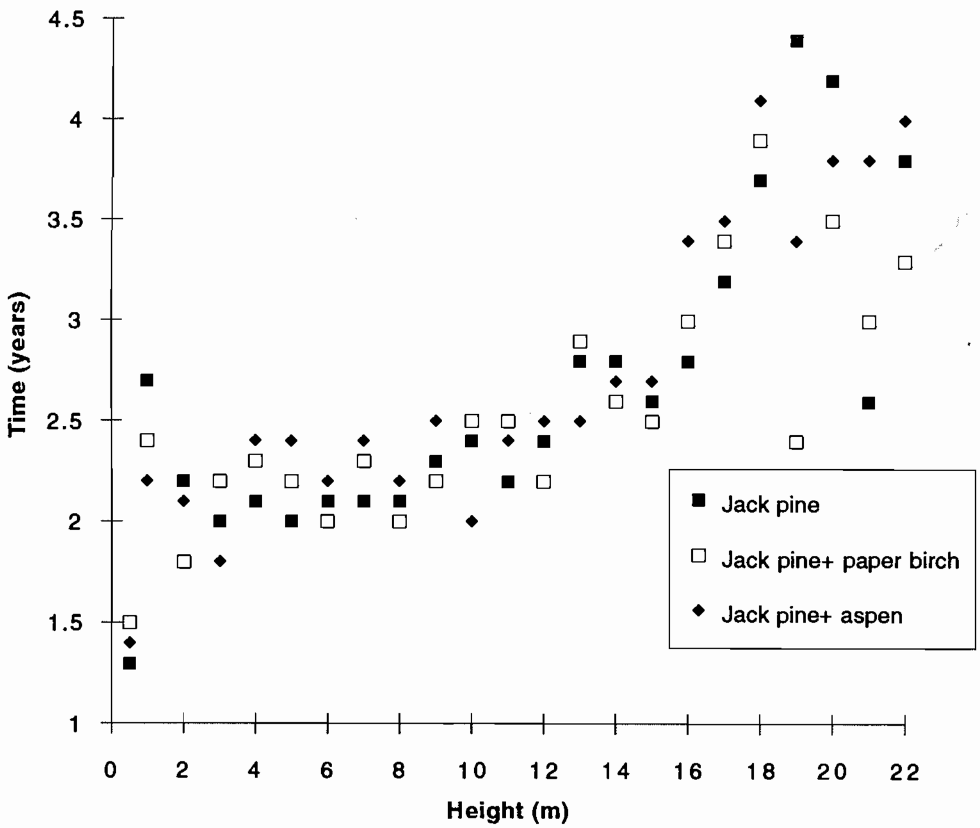


FIG. 2. Variation in the time required between each metre of jack pine height growth for the three stand types sampled.

TABLE 3. Total stand basal area and average DBH, height, and volume for jack pine in the three stand types sampled

| Stand type | Total basal area ($m^2$/ha) | DBH (cm) | Height (m) | Volume ($m^3$/tree) |
|---|---|---|---|---|
| Jack pine | 35.9*a* | 18.6*b* | 21.3*a* | 0.263*b* |
| Jack pine + paper birch | 35.1*a* | 22.8*a* | 22.0*a* | 0.418*a* |
| Jack pine + aspen | 35.8*a* | 19.8*b* | 21.1*a* | 0.298*b* |
| *p* | 0.9015 | 0.0177 | 0.0612 | 0.0150 |

NOTE: Values followed by the same letter do not differ at the 0.05 level.

The numerical analysis were all performed on the SAS software (SAS Institute Inc. 1985).

## Results

### *Stem analysis*

Site-quality index for jack pine varied considerably among stands, ranging from 16.9 to 23.6 m at 50 years (Table 1). These values testify to the high potential productivity of jack pine, in pure or mixed stands, on clay soils. No significant differences in site index were found among stand types (Table 1). The average height-growth curves for each stand type were also similar (Fig. 1) as confirmed by the overlapping confidence intervals of the estimated parameters of the Korf function (Table 2). Moreover, the average period of time required for each metre of height increment was similar among stand types (Fig. 2). An ANOVA revealed that there were no significant differences ($p < 0.05$) among stand types in the time required for each metre of height growth (results not shown). These results indicate that height-growth dynamics are comparable in both mixed and pure stands during the course of stand development.

TABLE 4. Total merchantable stem volume of jack pine, paper birch, and aspen and total stand volume ($p$ = 0.4357) for the three stand types sampled

| Stand type | Total merchantable stem vol. ($m^3$/ha): Jack pine | Paper birch | Aspen | Total stand vol. ($m^3$/ha) |
|---|---|---|---|---|
| Jack pine | 1544.678 | 18.363 | 0 | 1563.091*a* |
| Jack pine + paper birch | 1094.081 | 394.975 | 15.253 | 1504.309*a* |
| Jack pine + aspen | 783.521 | 2.988 | 747.970 | 1534.479*a* |

NOTE: Values followed by the same letter do not differ at the 0.05 level.

### *Volume production*

No significant differences were found among stand types for total basal area, total merchantable stem volume, and average height of jack pine (Tables 3 and 4). On the other hand, average DBH for jack pine and the volume per jack pine tree were significantly greater in stands containing

TABLE 5. Forest floor properties for the three stand types sampled

| | Jack pine | Jack pine + paper birch | Jack pine + aspen | *p* |
|---|---|---|---|---|
| pH | 4.7*c* | 4.9*b* | 5.3*a* | 0.0001 |
| Ca (mequiv./100 g) | 21.3*c* | 25.4*b* | 37.1*a* | 0.0001 |
| Mg (mequiv./100 g) | 4.3*b* | 5.0*a* | 5.4*a* | 0.0136 |
| K (mequiv./100 g) | 2.6*a* | 2.9*a* | 2.8*a* | 0.6387 |
| P (µg/g) | 115.3*a* | 121.3*a* | 104.3*a* | 0.6899 |
| Mineralization (µg/g) | 877.0*a* | 1055.8*a* | 753.9*a* | 0.2131 |
| Nitrification (µg/g) | 7.6*b* | 113.2*a* | 92.4*a* | 0.0469 |

NOTE: Values followed by the same letter do not differ at the 0.05 level.



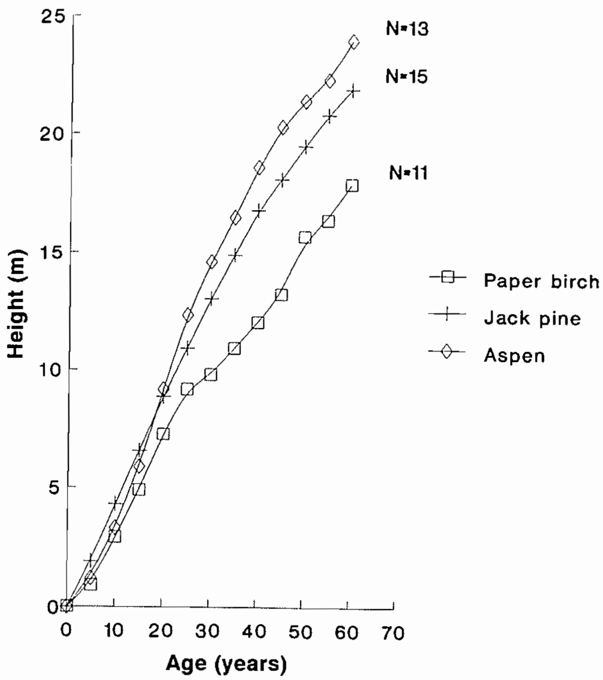


FIG. 3. Average height-growth curves of jack pine, paper birch, and aspen. The jack pine curve is the average of pure and mixed stands; the other curves are from a nearby site with comparable abiotic conditions (Bergeron and Charron 1994).

paper birch than in either pure jack pine stands or in mixtures with aspen.

*Forest floor properties*

Mixed stands had significantly greater pH, exchangeable Ca and Mg, and net nitrification in forest floor samples than pure stands (Table 5). Exchangeable Ca and forest floor pH were significantly higher in mixtures with aspen, followed by mixtures with birch, and finally by pure jack pine stands. Exchangeable Mg and net nitrification were much greater in mixed stands than in pure stands. No significant differences were found among stand types for exchangeable K, extractable P, and net N mineralization.

## Discussion

Our results indicate that the presence of companion species in jack pine stands had little effect on the height growth of jack pine. In fact, neither site index nor average height growth of jack pine showed significant variation among stand types. However, average DBH and the average volume of jack pine trees were significantly greater in stands containing birch. Lafond (1966) observed that jack pine attained its maximal growth in mixture with paper birch and aspen.

In contrast with stands having paper birch, the presence of aspen did not have any significant effect on the volume growth of jack pine trees despite the fact that several forest floor properties were improved by the presence of aspen. The most significant effects associated with the presence of aspen were increased pH and concentrations of exchangeable Ca. Other studies have shown similar effects with respect to the presence of aspen (Alban 1982; Perala 1990; Paré et al. 1993). Our results suggest that on clay soils, the forest floor properties that are modified by the presence of aspen are not critical to the growth of jack pine. This is not surprising because the requirements of jack pine for Ca are low (Rudolph and Laidly 1990) and the clay soil of the study sites contains very high reserves of this element. Other studies have suggested that over the range of conditions where jack pine is found, effective rooting depth of the soil profile has a stronger influence on stand productivity than the concentrations of available nutrients in the soil (Schmidt and Carmean 1988; Béland et al. 1992*b*).

The availability of nutrients in the forest floor of jack pine – aspen mixtures was greater or equivalent to that of jack pine – paper birch mixtures. Nevertheless, it is in mixtures with paper birch that jack pine exhibited the greatest diameter growth. These observations suggest that nutrient availability may not be the key factor controlling jack pine growth in mixed stands and that the availability of light, another limiting resource, should not be overlooked.

Because height growth of companion species was not measured on the study sites, we have used stem analyses that were performed for dominant and codominant aspen and paper birch from a nearby site. Although not perfectly similar, this site has comparable abiotic conditions (moderately well drained glaciolacustrine clay) and the even-aged forest had originated from a contemporary fire in 1916 (Bergeron and Charron 1994). Stem analysis revealed that the height growth of aspen was similar to that of jack pine, while the height growth of paper birch was much slower (Fig. 3). Aspen apparently occupies the same canopy space as jack pine and may, therefore, have conditions of light competition that are similar to that of jack pine. On the other hand, paper birch occupies a lower level in the canopy because of its slower height growth (Fig. 3). A vertical stratification of species in the canopy of mixed paper birch – jack pine stands could, for the pine, reduce interspecific competition for light and allow for greater diameter growth.

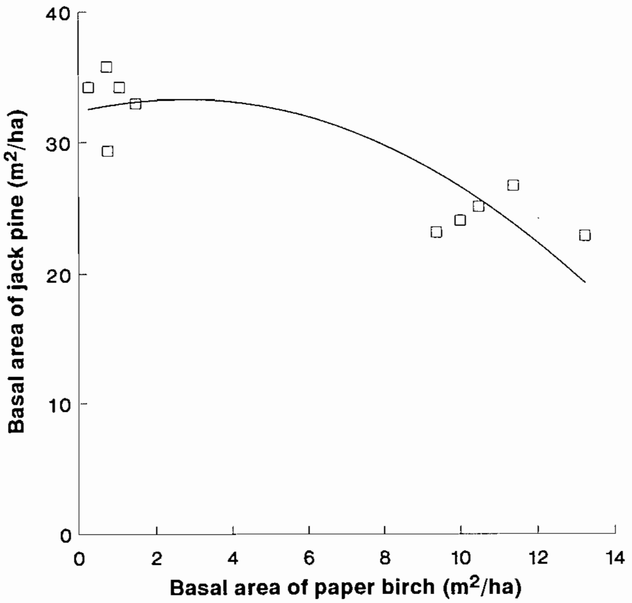


FIG. 4. Relationship between basal area of jack pine and paper birch. Squares represent observed values.

A similar situation has been observed for mixed stands of pine and oak (Biondi et al. 1992).

The significantly greater diameter growth of jack pine trees in mixed stands with paper birch suggests that a certain proportion of birch could be maintained in jack pine stands without causing a reduction in the harvestable volume of jack pine. This implies that the relationship between the basal area (or the volume) of paper birch and that of jack pine is not linear. From our data set, both the number of jack pine per area and the average basal area per jack pine stem can be estimated with linear regressions with the basal area of birch as the independent variable:

$$y_1 = -63.407x + 1200.606, \qquad n = 10,\ R^2 = 0.793,\ p < 0.0005$$

$$y_2 = 0.002x + 0.027, \qquad n = 10,\ R^2 = 0.918,\ p < 0.0001$$

where $y_1$ is the number of jack pine per area, $y_2$ is the average basal area per jack pine stem, and $x$ is the basal area of paper birch. A polynomial equation can be obtained from the combination of these two equations (Fig. 4). This curve suggests that it may be possible to allow as much as 5 $m^2$/ha (basal area) of paper birch in jack pine stands (approximately 15% of the volume) without decreasing the basal area of jack pine. However, these results should be interpreted with caution because these relationships are derived from stands of either almost pure jack pine (95–99% jack pine basal area) and 50% mixture (48–65% jack pine basal area). The model needs to be verified with stands having a range of species proportions before any sivilcultural recommendation should be accepted.

The results obtained in the present study suggest that it may be possible to maintain a certain proportion of companion species in jack pine stands without significantly reducing the volume of jack pine. Additional studies are needed to determine accurately the proportion of companion species that would be allowable. The management of mixed stands may also bring other benefits such as increased biodiversity and wildlife habitat as well as improvement of the soil properties that may affect the growth of future generations of trees.

## Acknowledgements

The authors express their appreciation to Francis Dupuis, Ginette Baril, and Marie-Josée Simard who participated in the fieldwork. This research was funded by the Natural Sciences and Engineering Research Council of Canada, the ministère de l'Enseignement Supérieur et de la Science du Québec (Fonds pour la formation de chercheurs et l'aide à la recherche), the ministère des Forêts du Québec, Canadian Forest Service, Canada and the Unité de recherche et de développement forestier de l'Abitibi-Témiscamingue.

Alban, D.H. 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil properties. Soil Sci. Soc. Am. J. **46**: 853–861.

Assmann, E. 1970. The principles of forest yield study. Pergamon Press, Oxford.

Beaudet, R. 1990. Effet d'une présence accrue de bouleau à papier (*Betula papyrifera* Marsh.) sur les caractéristiques et la fertilité la couverture morte d'une sapinière boréale âgée de 40 ans. Mémoire de maîtrise, Université Laval, Québec, Canada.

Béland, M., Brais, S., and Harvey, B. 1990. Guide à l'identification des dépôts de surface et des classes de drainage pour l'Abitibi-Témiscamingue: première approximation. Unité de recherche et de développement forestier de l'Abitibi-Témiscamingue, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda.

Béland, M., Bergeron, Y., Harvey, B., and Robert, D. 1992*a*. Quebec's ecological framework for forest management: a case study in the boreal forest of Abitibi. For. Ecol. Manage. **49**: 247–266.

Béland, M., Bergeron, Y., and Longpré, M-H. 1992*b*. Évaluation de la productivité du pin gris (*Pinus banksiana* Lamb.) en Abitibi. Rapport d'étape présenté au ministère des Forêts du Québec, Unité de recherche et de développement forestier de l'Abitibi-Témiscamingue, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda.

Bergeron, Y., and Charron, D. 1994. Post-fire stand dynamics in Quebec's southern boreal forest: a dendroecological approach. EcoScience. In press.

Bergeron, Y., Camiré, C., Bouchard, A., and Gangloff, P. 1982. Analyse et classification des sols pour une étude écologique intégrée d'un secteur de l'Abitibi, Québec. Geogr. Phys. Quat. **36**: 291–305.

Binkley, D. 1983. Interaction of site fertility and red alder on ecosystem production in Douglas-fir plantations. For. Ecol. Manage. **5**: 215–227.

Binkley, D. 1984. Importance of size–density relationships in mixed stands of Douglas-fir and red alder. For. Ecol. Manage. **9**: 81–85.

Binkley, D. 1991. Mixtures nitrogen$_2$-fixing and non-nitrogen$_2$-fixing tree species. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford. Br. Ecol. Soc. Publ. 11.

Binkley, D., and Hart, S.C. 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. **10**: 57–112.

Binkley, D., and Valentine, D. 1991. Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. For. Ecol. Manage. **40**: 13–25.

Binkley, D., Dunkin, K.A., DeBell, D., and Ryan, M.G. 1992. Production and nutrient cycling in mixed plantations of *Eucalyptus* and *Albizia* in Hawaii. For. Sci. **38**: 393–408.

Biondi, F., Klemmedson, J.O., and Kuehl, R.O. 1992. Dendrochronological analysis of single-tree interactions in mixed pine–oak stands of central Arizona, USA. For. Ecol. Manage. **48**: 321–333.

Bockheim, J.G., Jepsen, E.A., and Heisey, D.M. 1991. Nutrient dynamics in decomposing leaf litter of four tree species on a sandy soil in northwestern Wisconsin. Can. J. For. Res. **21**: 803–812.

Boudoux, M. 1978. Tables de rendement empiriques pour l'épinette noire, le sapin baumier et le pin gris au Québec. Service d'Information, Gouvernement du Québec, ministère des Terres et Forêts, Québec.

Brisson, M.-C. 1992. Croissance en hauteur du pin gris (*Pinus banksiana* Lamb.) selon un gradient topographique, Abitibi, Québec. Mémoire de maîtrise en sciences de l'environnement, Université du Québec à Montréal, Montréal.

Brown, A.F.H. 1991. Functioning of mixed-species stands at Gisburn, N.W. England. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford. Br. Ecol. Soc. Publ. 11. pp. 125–150.

Brozek, S. 1990. Effect of soil changes caused by red alder (*Alnus rubra*) on biomass and nutrient status of Douglas-fir (*Pseudotsuga menziesii*) seedlings. Can. J. For. Res. **20**: 1320–1325.

Burkhart, H.E., and Tham, A. 1991. Predictions from growth and yield models of the performance of mixed-species stands. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford. Br. Ecol. Soc. Publ. 11. pp. 21–34.

Carmean, W.H. 1975. Forest site quality evaluation in the United States. Adv. Agron. **27**: 209–269.

Carmean, W.H., and Lenthall, D.J. 1989. Height-growth and site-index curves for jack pine in north central Ontario. Can. J. For. Res. **19**: 215–224.

Chrosciewicz, Z. 1963. The effects of site on jack pine growth in northern Ontario. Can. Dep. Fish. For. For. Branch Dep. Publ. 1015.

Dansereau, P.-R., and Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Day, R.W., and Quinn, G.P. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. **59**: 433–463.

Environnement Canada. 1982. Normales climatiques au Canada. Vol. 2. Températures. Vol. 3. Précipitations. Service de l'environnement atmosphérique, Environnement Canada, Ottawa, Ont.

Frivold, L.H., and Mielikäinen, K. 1990. The effects of hardwoods on softwood growth in mixed stands in Fennoscandia. *In* The Sylvics and Ecology of Boreal Spruces. IUFRO Working Party SI.05-12 Symposium Proceedings, 12–17 Aug. 1989, Newfoundland. For. Can. Nfld. For. Cent. Inf. Rep. N-X-271. pp. 75–82.

Gower, S.T., and Son, Y. 1992. Differences in soil and leaf litterfall nitrogen dynamics for five forest plantations. Soil Sci. Soc. Am. J. **56**: 1959–1966.

Hamilton, W.N., and Krause, H.H. 1985. Relationship between jack pine growth and site variables in New Brunswick plantations. Can. J. For. Res. **15**: 922–926.

Heilman, P., and Stettler, R.F. 1985. Mixed, short-rotation culture of red alder and black cottonwood: growth, coppicing, nitrogen fixation and allelopathy. For. Sci. **31**: 607–616.

Hendrickson, O.Q., and Burgess, D. 1989. Nitrogen-fixing plants in a cut-over lodgepole pine stand of Southern British Columbia. Can. J. For. Res. **19**: 936–939.

Jensen, A.M. 1983. Aedelgranens (*Abies alba* Mill.) vekst sammenlignet medrodgranens (*Picea abies* (L.) Karst.) i henholdsvis rene og blandede bevoksninger pa sandede jorder i Midt-og Vestjylland. (Growth of silver fir (*Abies alba* Mill.) compared with the growth of Norway spruce (*Picea abies* (L.) Karst.) in pure and mixed stands on sandy soils in the western parts of Denmark.) Medd. Skovbruksinst. 2(14).

Jonsson, B. 1962. Om barrblandskogens volymproduktion. (Yield of mixed coniferous forest.) Medd. Statens Skogsforskningsinst. **50**: 1–143.

Kelty, M.J. 1989. Productivity of New England hemlock/hardwood stands as affected by species composition and canopy structure. For. Ecol. Manage. **28**: 237–257.

Kelty, M.J. 1992. Comparative productivity of monocultures and mixed-species stands. *In* The ecology and silviculture of mixed-species stands. *Edited by* M.J. Kelty, B.C. Larson, and C.D. Oliver. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 125–141.

Klinka, K., and Carter, R.E. 1990. Relationships between site-index and synoptic environmental factors in immature coastal Douglas-fir stands. For. Sci. **36**: 815–830.

Lafond, A. 1966. Notes sur l'écologie de quatre conifères du Québec. Nat. Can. **93**: 823–842.

Lanier, L. 1992. La forêt doit-elle être mélangée? Rev. For. Fr. **2**: 105–127.

Leary, R.A., and Smith, W.B. 1990. Test of the TRIM inventory projection methods on Wisconsin jack pine. Can. J. For. Res. **20**: 774–780.

McKay, H.M., and Malcolm, D.C. 1988. A comparison of the fine root component of a pure and mixed coniferous stand. Can. J. For. Res. **18**: 1416–1426.

McKeague, J.A. 1978. Manual on soil sampling and methods of analysis. 2nd ed. Canadian Society of Soil Sciences, Ottawa, Ont.

Mielikäinen, K. 1985. Koivousekoituksen vaikutus kuusikon rakenteeseen ja kehitykseen. (Effect of an admixture of birch on the structure and development of Norway spruce stands.) Commun. Inst. For. Fenn. 133. pp. 1–79.

Monserud, R.A., Moody, U., and Breuer, D.W. 1990. A soil-site study for inland Douglas-fir. Can. J. For. Res. **20**: 686–695.

Morgan, J.L., Campbell, J.M., and Malcolm, D.C. 1991. Nitrogen relations of mixed-species stands on oligotrophic soils. *In* The ecology of mixed-species stands of trees. *Edited by* M.G.R. Cannell, D.C. Malcolm, and P.A. Robertson. Blackwell Scientific Publications, Oxford. Br. Ecol. Soc. Publ. 11. pp. 65–85.

Paré, D., Bergeron, Y., and Camiré, C. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. **4**: 811–818.

Pawluk, S., and Arneman, H.F. 1961. Some forest soil characteristics and their relationship of jack pine growth. For. Sci. **7**: 160–173.

Perala, D.A. 1990. Quaking aspen (*Populus tremuloides* Michx.). *In* Silvics of North America. Vol. 2. Hardwoods. *Technical coordinators*: R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 555–569.

Perron, J.-Y. 1979. Tarif de cubage général, volume marchand brut. Service de l'inventaire forestier, ministère de l'Énergie et des Ressources du Québec, Québec. Doc.ERF-3209-11.

Perry, D.A., Choquette, C., and Shroeder, P. 1987. Nitrogen dynamics in conifer-dominated forests with and without hardwoods. Can. J. For. Res. **17**: 1434–1441.

Plonski, W.L. 1974. Normal yield tables (metric) for major forest species of Ontario. Division of Forests, Ontario Ministry of Natural Resources, Toronto, Ont.

Rowe, J.S. 1972. Les régions forestères du Canada. Can. For. Serv. Publ. 1300F.

Rudolph, T.D., and Laidly, P.R. 1990. Jack pine (*Pinus banksiana* Lamb.). *In* Silics of North America. Vol. 1. Conifers. *Technical coordinators*: R.M. Burns and B.H. Honkala. U.S. Agric. Dep. Agric. Handb. 654. pp. 290–293.

SAS Institute Inc. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, N.C.

Schmidt, M.G., and Carmean, W.H. 1988. Jack pine site quality in relation to soil and topography in north central Ontario. Can. J. For. Res. **18**: 297–305.

Shetron, S.G. 1972. A study concerning the soil–growth relationships of native jack pine and pine plantation on Mosinee Paper Company lands. Michigan Technical University, Houghton.

Spurr, S.H., and Barnes, B.V. 1980. Forest ecology. 3rd ed. John Wiley & Sons, New York.

Stuanes, A.O., Ogner, G., and Opem, M. 1984. Ammonium nitrate as extractant for soil exchangeable cations, exchangeable acidity and aluminium. Commun. Soil Sci. Plant Anal. **15**: 773–778.

Tarrant, R.F. 1961. Stand development and soil fertility in a Douglas-fir/red alder plantation. For. Sci. **7**: 238–246.

Tarrant, R.F., and Trappe, J.M. 1971. The role of *Alnus* in improving the forest environment. Plant Soil (special volume), 1971: 335–348.

Tham, A. 1988. Produktionsförutsägelser vid kraftiga gallringar av björk i blandbestand av gran (*Picea abies* (L.) Karst.) och björk (*Betula pendula* Roth and *Betula pubescens* Ehrh. (Yield prediction after heavy thinning of birch in mixed stands of Norway spruce (*Picea abies* (L.) Karst.) and birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.)). Department of Forestry Yield Research, Swedish University of Agricultural Sciences, Research, Garpenberg. Rep. 23.

Thibault, M., and Hotte, D. 1985. Les régions écologiques du Québec méridional. Deuxième approximation, Service de la Cartographie, ministère de l'Énergie et des Ressources du Québec, Québec.

Valsta, L. 1988. Optimizing species composition in mixed, even-aged stands. *In* Forest growth modelling and prediction. Proceedings of the IUFRO Conference, 23–27 Aug. 1987, Minneapolis, Minn. pp. 913–920.

Valsta, L., and Mielikäinen, K. 1987. Blandskogens ekonomi: tall med inblandand vartbjörk. (The economy of mixed stands of Scots pine and silver birch.) Sver. Skogsvärdsförb. Tidsk. **85**: 21–25.

Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Objiway en territoire québécois. Geogr. Phys. Quat. **31**: 357–372.

Vitousek, P.M., and Denslow, J.S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. J. Ecol. **74**: 1167–1178.

Wierman, C.A., and Oliver, C.D. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir – western hemlock. Can. J. For. Res. **9**: 1–9.

Wilde, S.A., Iyer, J.G., Tanzer, C.H., Trautmann, W.L., and Watterston, K.G. 1964. Growth of jack pine (*Pinus banksiana* Lamb.) plantations in relation to fertility of non-phreatic sandy soils. Soil Sci. **98**: 162–169.

Wilson, C.V. 1973. Le climat du Québec. Partie 1: Atlas climatologique du Québec. Partie 2: Mise en application des renseignements climatologiques. Service de l'environnement atmosphérique, Environnement Canada, Ottawa, Ont. Publ. 551.582.3(714).

Zarnovican, R. 1979. Fonction de la croissance de Korf. For. Chron. **55**: 194–197.

Zarnovican, R. 1985. analyses de tiges: une méthode à redécouvrir. Nat. Can. **112**: 253–260.

Zarnovican, R., Ouellet, D., and Gendron, S. 1988. Saisie informatisée de la croissance radiale. Can. For. Serv. Cent. For. Laurentides Inf. Rep. LAU-X-80E.