Species and Spacing Effects of Northern Conifers on Forest Productivity and Soil Chemistry in a 50-Year-Old Common Garden Experiment

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This study examines the long-term effects of experimental conifer monocultures on stem volume and soil chemistry. Replicated plots of black spruce (Picea mariana), white spruce (Picea glauca), and red pine (Pinus resinosa) were planted in 1950 at three spacings (1.8, 2.7, and 3.6 m) on a briefly cultivated agricultural field on glaciolacustrine sandy loam soil near Thunder Bay, Ontario, Canada. Stem volumes per hectare and per tree were measured in 2002 (52 years after planting). Surface organic (i.e., forest floor) and mineral soil fertility in terms of pH, total N and P, and extractable NH4-N and P were measured in 2000 (50 years after planting). Of the three species red pine had the highest volume per hectare at all the three spacing followed by white spruce and black spruce; volume for all three species peaked at the 1.8-m spacing. The effects of conifer species on soil physical and chemical properties were more pronounced than spacing effects and the changes were mainly confined to forest floor layer. Few changes in mineral soil properties occurred because of the species and spacing treatments. Per hectare forest floor nutrient pools were higher under white spruce and red pine than black spruce, a pattern likely driven by higher litterfall and forest floor accumulation. It appears that toward the end of first rotation the higher productivity of red pine compared with the other conifers did not come at the cost of reduced soil pools of available NH4, PO4, or K, but it was associated with reduced Ca levels in the forest floor.

Keywords: conifer plantations, species and spacing trial, forest floor properties, soil nutrients, boreal forest

Many studies have attributed long-term changes in soil properties of plantation forests to differences in the characteristics of the tree species planted (Alban 1969, 1982, Miles 1985, Prescott et al. 2000a, Prescott 2005). For example, Perala and Alban (1982) found that tree species altered soil nutrients in 40-year-old plantations, particularly exchangeable Ca in the forest floor, which was much lower under trembling aspen (Populus tremuloides Michx.) and white spruce (Picea glauca [Moench] Voss) than under Jack pine (Pinus banksiana Lamb.). Fyles and Côté (1994) found higher concentrations of forest floor N, P, K, and Ca in a Norway spruce (Picea abies [L.]) plantation compared with a red pine (Pinus resinosa Sol. ex Aiton) plantation in northern Quebec. Concentrations of mineral soil exchangeable K and Ca were higher under spruce but exchangeable Mg, extractable P, and mineralizable N did not vary significantly between the two species. Fyles and Côté (1994) concluded that soil fertility can be altered significantly by tree species in a single rotation. Forest floor biomass was very high under white pine (Pinus strobus L.; 3,680 g/m2) compared with sugar maple (Acer saccharum Marshall; 240 g/m2) in a 27-year-old plantation in southern Ontario (France et al. 1989). Similarly, Prescott et al. (2000a) found strong effect of species on forest floor nutrient concentrations in

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24-year-old western redcedar (*Thuja plicata* Donn ex. D. Don), western hemlock (*Tsuga heterophylla* [Raf.] Sarg), Douglas-fir (*Pseudotsuga menziesii* Mirb), and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) plantations. They found that litter decomposition was most rapid under hemlock, intermediate under Douglas fir, and lowest under cedar, but forest floor nutrient concentrations were poorly correlated with litter chemistry. They also reported that differences in N mineralization among sites was more related to site factors such as density of ericaceous understory that appeared to override the effect of tree species on N mineralization rate.

Canopy species in plantations can affect both forest floor and mineral soil pH (Brand et al. 1986, France et al. 1989). For example, the forest floor pH under a white spruce plantation was 5.9 and that under sugar maple was 3.7, but there were no significant differences in mineral soil pH (France et al. 1989). Brand et al. (1986) reported increased mineral soil acidity over a 60-year period under experimental monocultures of white spruce, red pine, and Scots pine (*Pinus resinosa* Sol. ex Aiton), were planted in three different spacing regimes. Our objectives were to (i) compare the forest floor and mineral soil nutrient pools under the three species and (ii) relate the differences in productivity (periodic annual increment [PAI]) to species, spacing regime, and soil nutrient pools. We hypothesized that (i) because of their different autecological properties, the species effect on productivity and soil chemistry will dominate the spacing effect; (ii) there will be a strong positive relationship between productivity (PAI), forest floor mass, and nutrient capital; (iii) nutrient changes in the organic horizon will be more pronounced than that of mineral soil; and (iv) because of the sandy loam soil type of the experimental site red pine will outperform white and black spruce ingrowth.

**Materials and Methods**

**Study Site.** The spacing trial was established in 1950 by the Ontario Ministry of Natural Resources on an 8-ha site 20 km west of Thunder Bay, Ontario, Canada (48°8.22’N, 89°9.23’W). The area has a mean annual precipitation of 712 mm, including 559 mm of rain, and mean annual temperature is 2.5–10°C (Canadian Climate Normals 1971–2000). The plots were on a glacial lacustrine plain with deep (more than 160 cm to bedrock) moderately developed Dystric Brunisol (Soil Classification Working Group 1998) with fresh moisture regime (McClain et al. 1994) and moderate to weak soil structure (Anon 1985). The site has level to nearly level slopes (Towell and Siczkar 1988). Estimated site index (mean height at age 50 years) for black spruce and white spruce was 18 m and that for red pine was 21 m (Thrower 1986). The experimental plantations were established on a previously briefly (for 2 years) cultivated land and have since been maintained under the Provincial Forest Management Guidelines.

Monocultures of three conifer species: black spruce, white spruce, and red pine were planted in 41 × 32-m plots at three different spacing regimes: close (1.8 × 1.8 m, 2,900 trees ha⁻¹), medium (2.7 × 2.7 m, 1,300 trees ha⁻¹), and wide (3.6 × 3.6 m, 730 trees ha⁻¹). The species and spacing trial were established using completely randomized design with three replicates. The initial objective of the trial was to examine the effect of species and planting density on growth and yield (Ontario Ministry of Natural Resources 1989, McClain et al. 1994). The plantation has not been weeded, thinned, or pruned since establishment. With the exception of the 1.8-m black spruce, three replicates of each treatment were planted. Only one 1.8-m black spruce replicate was available because in that spacing one plot was planted with white spruce by mistake during the trial establishment and another plot was destroyed by a root rot infection in 1956.

**Growth and Yield.** All trees in each replicate plot except the outermost boundary rows were measured for outside bark dbh in 1998 and 2002. Total height was measured for 10% of the sample weighted according to diameter distribution. Total volume per hectare was estimated for each treatment using Zakrzewski’s (1999) taper model. PAI (centimeters cubed per hectare per year) for the 1998–2002 period was calculated from these data. Earlier volume measurements for this site are reported by McClain et al. (1994).

**Soil Sampling.** Soils were sampled in July 2000 at three random points in each replicate plot. Edge effects were avoided by restricting sample points to be at least two rows of trees from the plot edge. At each of the sampling points, first, 20 × 20 cm of the litter and forest floor were collected and then the mineral soil was sampled to a depth of 10 cm from a 10 × 10-cm subplot in the middle of the plot. Forest floor depth was measured at each sampling point and averaged to derive a mean thickness for each replicate plot. Separate composite samples of the forest floor organic horizon and mineral soil layers were created for each replicate plot and used for analysis. Separate samples of known volume of both mineral and forest floors were collected to determine bulk density. The remaining soil analyses were performed after the samples had been air-dried and sieved through a less than 2-mm sieve.

**Soil Analysis.** All the soil samples were analyzed for pH, organic matter content, total N and P, and extractable ammonium-N and phosphate-P. Soil pH was measured on fresh soil samples and distilled water using the paste method (Allen 1989). Soil organic carbon was determined by loss-on-ignition using approximately 1.5 g oven-dried (105°C) samples burning at 550°C.
stant weight (2 hours) in a Thermodyne 10,500 furnace (Allen 1989). Soil total N and P were determined by a semimicro Kjeldahl procedure using a Skalar Autoanalyzer, (SanPlus System, Breda, The Netherlands). Available P was determined colorimetrically as phosphomolybdenum blue on the Skalar autoanalyzer after extraction with ammonium fluoride, and available ammonia was extracted in 6% w/v KCl shaken for 30 min., allowed to settle for 30 min. and then determined by Skalar autoanalyzer (Allen 1989). Concentrations of extractable K$^+$ and Ca$^{2+}$ ($\text{NH}_4\text{Oac}$ extracts, pH 7.0) were determined by an Inductively Coupled Plasma Analyzer (Jarrell-Ash ICAP 9000, Varian, Palo Alto, CA). Soil total N, P, and extractable N, P, Ca, and K concentrations measured for the forest floor were converted to element pools (kilograms per hectare) using soil bulk density measurements and horizon thickness.

**Data Analysis.** Two-way analysis of variances (ANOVA) with species and spacing as fixed factors were used to compare stand and tree volume and soil properties between species and spacing treatments. Post hoc tests were not done because the treatments responsible for any significant ANOVA results were obvious from the figures. These tests were done using SPSS 9.0 (SPSS 1999).

**Results**

For all three species, total volume per hectare was highest at the 1.8-m spacing with a decline in volume with increasing spacing (Figure 1). Red pine had the highest volumes per hectare at all three spacings, and the significant species by spacing interaction indicated that the effects of spacing on red pine volume was much stronger than for the spruce species. PAI for 1998–2002 was much higher for red pine than the spruce species (Figure 1). PAI was not influenced by spacing, indicating that the effects of spacing on total volume occurred earlier in the rotation.

There were significant species and spacing effects on total N pool of the forest floor with the highest value for white spruce and black spruce at the 2.7-m spacing (Figure 2). On the other hand, there was only significant species effect on forest floor total P with the lowest value for black spruce and no significant difference between white spruce and red pine (Figure 2). There were no significant differences between species and spacings effects on mineral soil N, P, K, and Ca pools although mineral soil K was higher in red pine than white spruce (Figures 2 and 3). Forest floor total N was lowest under red pine at wide spacing compared with the other two conifers. Forest floor pH was highest under white spruce at all spacing. Among the three species mineral soil pH was highest under red pine. Wide spacing (3.6 m) of all the three conifers had higher mineral soil pH than their other spacing (Figure 3). Forest floor exchangeable Ca pool was lowest under red pine having minimum value at the 2.7-m spacing (Figure 3). Similarly, forest floor exchangeable K pool peaked at the 2.7-m spacing of red pine. The higher productivity of red pine did not come at the cost of reduced soil pools of available NH$_4$, PO$_4$, or K, but it was associated with reduced Ca levels on the forest floor (Figure 4).

**Discussion**

The evidence suggesting that the dominant species can drive changes in soil chemistry has been circumstantial because few replicated common garden experiments have directly tested this question (Binkley 1995, Binkley and Menyailo 2005). This long-term study of three conifer monocultures clearly indicates that the choice of species in plantation forestry can have profound effects on soil properties, particularly base cations. From a management perspective, this study shows that the benefits of high volume production do not
Figure 2. Forest floor and mineral soil total and available N and P concentrations (milligrams per kilogram) under black spruce, white spruce, and red pine stands at 1.8-, 2.7-, and 3.6-m spacings. Error bars are 1 SD. No error bars are shown for the 1.8-m black spruce treatment because only one replicate was available for sampling. *P < 0.05; **P < 0.01; ***P < 0.001.
necessarily come at a cost of reductions in most soil nutrient pools, at least in the first rotation.

Growth and Yield. The freely drained sandy loam soil at the site, clearly, is most suitable for red pine because that species had much higher yield than the other two species. These results are consistent with several other studies in similar soil types in Ontario and elsewhere (Schaege 1975, Alban et al. 1978, Alban 1985, Carmean and Thower 1995, Carmean 1996). The highest per hectare total volumes were achieved by all three species at the 1.8-m spacing followed by the 2.7- and 3.6-m spacings, a result consistent with Sobachkin et al. (2005) who found the largest volume per hectare at the highest planting density from an 18-year-old garden experiment conducted with three conifer species, Scots pine, Siberian larch (Larix sibirica L.), and Norway spruce. Even at 128,000 trees ha\(^{-1}\) (between tree spacing of 0.28 m) they did not find any sign of yield “stagnation” after 18 years. However, the PAI data on our study site show that there are few differences in current productivity between spacings. Clearly, the greatest total volume per hectare in the smaller spacings was achieved by higher productivity earlier in the rotation.

Species and Spacing Effects on Soil Characteristics. We observed significant species effects on forest floor mass and nutrient concentrations. Overall, forest floor nutrient levels were highest under white spruce and red pine and lowest under black spruce. These results support our hypothesis...
that species effects play a predominant role in changing forest floor biomass and chemistry compared with spacing effects. There were few concurrent changes in the mineral soils chemistry, indicating that the soil changes are likely driven primarily by litter fall rather than nutrient uptake.

The effects of spacing on forest floor properties were much less pronounced than the effects of species. Sangari (1993) determined annual litter fall, litter mass loss, and litter quality of red pine and white spruce in this plantation. She reported that annual red pine litter fall was significantly higher than white spruce (981, 866, and 724 g/m² per year in close [1.8 m], medium [2.7 m], and wide [3.8 m] spacing of red pine as opposed to 639, 527, and 387 g/m² per year in white spruce, respectively) but there was no significant difference in the rate of annual litter mass loss between the two species. Spacing however, had a significant effect on litter mass loss with higher loss in close spacing than wide spacing (23, 21, and 19% dry matter loss in close, medium, and wide spacing of red pine as opposed to 23, 22, and 20% loss in similar spacing in white spruce). The effect of species and spacing on time to 95% litter decay was not significant (15.8–13.6 years from wide to close spacing for red pine compared with 15.0–13.0 years for white spruce). Therefore, the rate of litter accumulation under a species and spacing

Figure 4. Relationships between PAI (meters cubed per hectare) and total and available N and phosphate (kilograms per hectare) under black spruce, white spruce, and red pine at the 1.8-, 2.7-, and 3.6-m spacings. Error bars are 1 SD. No error bars are shown for the 1.8-m black spruce treatment because only one replicate was available for sampling.
seems to be determining forest floor mass (Sangari 1993).

Many other studies have shown that species differences in litter chemistry drive changes in forest floor chemistry (e.g., Gower and Son 1992, Fyles and Coté 1994, Prescott et al. 2000a, 2000b, Prescott 2002). Drawing from common garden experiments Prescott (2005) found that common British Columbia tree species exert consistent effects on forest floor pH and nutrient concentrations. For example, western redcedar forest floors have high pH and Ca but western hemlock and lodgepole pine (Pinus contorta Dougl.) forest floors have low pH and Ca concentrations where as Douglas-fir forests have intermediate pH, Ca, and P concentrations but high N concentrations. She concluded that forest floor nutrient concentrations are related to foliar litter nutrients but are not related to the rate of litter decay. Finally, the high nutrient concentrations found under red pine treatments relative to white and black spruce is interesting because pine litter, with the exception of white pine, is thought to be poorer in quality than spruce litter (Binkley and Giardina 1998, Prescott 2002).

Species-driven changes in mineral soil chemistry also have been found in other studies. For example Brand et al. (1986) attributed the increasing mineral soil acidity in a white pine plantation to immobilization and uptake of exchangeable cations in the forest floor humus and acidic litter under spruce and pine. In our study the predominating changes in soil chemistry under the different conifer species were in the organic horizon and changes in the mineral soil nutrient concentrations were minor by comparison.

Following a regional study of 50 conifer and hardwood stands distributed across the Lakes States Riech et al. (1997) found a linear relationship between aboveground net primary productivity and soil N availability. They suggested this positive relationship to be a fundamental feature of temperate ecosystem, which they assumed, stems from the effect of N availability on productivity. They also suggested potential feedback effects of vegetation on N availability. Our data agree with this suggestion in the sense that higher productivity (PAL) of red pine and white spruce was consistent with higher forest floor mass, total N, NH₄N, and P than that of black spruce (Figures 1 and 4). However, when compared between red pine and white spruce the generality did not hold. The higher stem volume of red pine was associated with substantially lower total N, NH₄N, and Ca of forest floor than white spruce. We suggest that the aboveground productivity of red pine, white spruce, and black spruce and their associated forest floor biomass and humus chemistry is a product of the ecophysiological response of species to this particular soil and the physical chemical feedback effects of their litter. This study used a 50-year-old replicated common garden experiment established on an old agricultural field, exactly the kind of evidence required to resolve the debate that the dominant tree species can have long-term effects on soil properties (Binkley 1995, Binkley and Menyailo 2005).

**Conclusion**

Several conclusions can be drawn from this half-a-century-long study: (i) species effects are much more important than spacing effects on forest soil properties, (ii) forest floor biomass accumulation under the three species is mainly driven by their litter fall rates, and (iii) most of the soil nutrient changes were confined to forest floor with few changes occurring in the mineral soil. The randomized planting of these three species on a small site on previously tilled soils indicates that the ecophysiological characteristics of the species, particularly rates of litter fall, can have strong effects on soil properties. The higher productivity of red pine may be a consequence of higher nutrient acquisition and use efficiencies contributing relative to the other two species (Alban 1985, Carmean 1996); however, this remains to be tested.

**Literature Cited**


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