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Effect of species composition on the production rate and efficiency of young *Picea glauca–Populus tremuloides* forests

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ABSTRACT

Stand stem volume growth, aboveground tree biomass growth, and site occupancy were measured in 20-year-old mixed stands dominated by white spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.) to examine the effects of species composition on the rate and efficiency of forest production. Measures of site occupancy derived from Plant Canopy Analyzer data indicated that sample plots were fully occupied, and that leaf area index and light interception increased with increasing softwood (SW) proportion. Relationships between site occupancy and SW proportion differed among occupancy metrics, suggesting that basal area, stand density index, and crown area index do not adequately represent use of the light resource. No significant effect of species proportion on the rate of volume or biomass production was detected, contradicting the hypothesis that competitive reduction and facilitation might increase the production of mixed stands. Production efficiency based on light interception for both stand components combined varied weakly with SW proportion. Efficiency metrics based on surrogates for light interception showed differing patterns with SW proportion, underscoring the need for caution in interpreting these metrics in relation to resource use.

1. Introduction

The possibility that the productivity of mixed species forest stands might differ from the productivity of pure stands has long intrigued growth and yield researchers (Pretzsch, 2005). Ecological theory suggests that when two or more species use resources differently, the resources may be exploited more completely by plants growing in mixture than by plants growing as single species, leading to higher productivity in mixed species stands (Kelty, 1992, 2006). The main mechanisms supporting greater productivity of mixtures are presumed to be competitive reduction and/or facilitation (Callaway and Walker, 1997; Kelty, 1992, 2006). Competition can be reduced when resource acquisition by the crowns and roots of different species is separated in space (e.g., different rooting patterns among species) or in time (e.g., different foliar phenology among species). The principal mode of facilitation in forests is improved nutrient availability through increased litter decomposition rates or nitrogen fixing.

Increased productivity in mixtures has not been consistently demonstrated by analyses of the effect of composition on stand growth (Pretzsch, 2005; Long and Shaw, 2009; Griess and Knoke, 2011). Vertically stratified mixtures of tree species, however, do appear to consistently yield greater volume than pure species stands (Kelty, 1992; Pretzsch, 2005).

White spruce (*Picea glauca* [Moench] Voss) and trembling aspen (*Populus tremuloides* Michx.) are among the mostly widely distributed tree species in North America, and frequently grow together in mixed stands (Rowe, 1972). Day and Bell (1988) reviewed yield models for white spruce-trembling aspen mixedwoods and observed that white spruce grew more slowly when overtopped by trembling aspen than in pure stand conditions, indicating that trembling aspen competes effectively with white spruce for resources. Man and Lieffers (1999) reviewed several mechanisms of interaction between these species and concluded that competition reduction could occur through differential shade tolerance, physical separation of canopies, phenological differences or differences in soil resource utilization. Furthermore, they suggested that aspen could facilitate the growth of white spruce through improved litter decomposition and nutrient cycling, amelioration of environmen-

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tal extremes, and control of shrubs, grasses, and pests. As a result, Man and Lieffers (1999) considered it likely that mixtures of these species could yield more than pure stands. This possibility has not been tested, however, and the effect of species composition on white spruce and aspen productivity remains uncertain.

The preferred approach to examine how species composition influences productivity is to obtain data from an experiment designed for the purpose, such as a replacement series (Man and Lieffers, 1999; Vanclay, 2006; Radosevich et al., 2007). Unfortunately, any formal white spruce—trembling aspen mixture experiments that have been established are not sufficiently mature to provide stand level productivity data (e.g., Bokalo et al., 2007). In this study, we took advantage of a silvicultural experiment (Lautenschlager et al., 1997) that created a range of species composition.

Ideally the sample units in which the mixtures occur should be at or near full site occupancy. Site occupancy can be quantified by measures such as stand basal area, stand density index (SDI), crown area index, leaf area index, and light interception. Stand basal area is the simplest to measure, but varies with stand age, stem density, and site quality. Its most useful application is in comparing sample units of the same age and site quality. SDI is a more robust measure of site occupancy since maximum SDI is not correlated with age or site quality (Long, 1985). An issue in assessing the site occupancy of mixed species stands is that species differ in the level at which full occupancy occurs. It might be possible to overcome this issue by examining production efficiency, which is the ratio of forest production to resource use. Because resource use can be difficult to measure, efficiency metrics employing site occupancy as a surrogate for resource use are common (Pretzsch and Schütze, 2005). In this study, we examined several efficiency metrics based on site occupancy as well as on light interception.

The objective of this study was to determine if the production rate of a young white spruce—trembling aspen forest was influenced by species proportion. The specific questions addressed were: does species proportion affect (i) Site occupancy? (ii) Rate of forest production?, or (iii) Production efficiency? The production efficiency estimates were also used to assess whether the vegetation control treatments influenced trembling aspen productivity.

These questions were examined by testing the following null hypotheses:

- Site occupancy is independent of species proportion (H1).
- Forest production rate is independent of species proportion (H2).
- Production rate of softwood (SW) and hardwood (HW) components varies linearly with species proportion and occupancy (H3).
- Production efficiency is independent of species proportion (H4).

2. Materials and methods

2.1. Site characteristics

The Fallingsnow Ecosystem Project (FEP; 89°49–53′W and 48°8–13′N at 380–550 m above sea level) was established approximately 60 km southwest of Thunder Bay, Ontario (Bell et al., 1997) in the transition between the Boreal and the Great Lakes-St. Lawrence forests (Rowe, 1972). Average daily temperatures in July and January, annual precipitation, and degree days above 5 °C, based on the 'Thunder Bay A' weather station,[1] were 17.6 °C, −14.8 °C, 711.6 mm, and 1434 degree days, respectively. The soils are predominantly imperfectly drained silt loam (Simpson et al., 1997).

Before harvesting, the area supported three different (i.e., *Populus* spp. 60%, *Abies balsamea* 20%, *Betula papyrifera* 10%, and *Picea glauca* 10%; *Populus* spp. 100%; and *Pinus banksiana* Lamb. 80%, *Populus* spp. 10%, and *Abies balsamea* 10%) 75- to 101-year-old stands (Bell et al., 1997). The original stands were clearcut between 1986 and 1988 and planted between 1987 and 1990 with 4-year-old (2 years as seedlings + 2 years as nursery transplants) bareroot white spruce stock, at 2- to 2.5-m spacing. Vigourous vegetative regeneration of trembling aspen occurred in the year following harvesting, as is typical on mesic mixedwood sites. A regeneration survey conducted on October 7, 1992 indicated that the spruce were on average 82-cm tall, and overtopped by trembling aspen.

The original objective of the FEP was to document the ecological consequences of conifer release treatments (Lautenschlager et al., 1997). The experimental design consists of three blocks[2] (28–52 ha) corresponding to the original three stands, in which a range of vegetation management treatments was applied in 1993–1994 in a randomized complete block design (Bell et al., 1997). Vegetation management improved white spruce establishment, and resprouting of trembling aspen following treatment created intimate species mixtures ranging from pure trembling aspen to pure white spruce, with a minor presence of other species (Pitt and Bell, 2005).

2.2. Plot establishment and data collection

The sampling design goal was to establish an equal number of plots that covered the range of species mixtures in each of the original three experimental blocks. Aerial photos captured during leaf-off conditions in early May 2003 at 1:5000 scale were used initially, followed by field surveys, to identify relatively uniform and fully occupied areas of white spruce—trembling aspen dominated mixtures; plots were then randomly established and prism sweeps were used to confirm species ratios. Fifteen circular plots were selected in each block for a total of 45 plots. The main plot size was 154 m^2 (7-m radius) with the selected mixture usually extending to at least 9 m from the plot centre to provide a buffer. For field measurement efficiency, all trees $\geqslant$6 cm in breast height diameter (DBH) were inventoried, tagged, and stem mapped to facilitate repeated measurements. Due to the age of the study (harvested in the late 1980s) and the previous stand composition (over mature trembling aspen), most plots had numerous small aspen stems. To account for their presence and effect on productivity, the DBH of all stems between 2 and 6 cm DBH within 3.5 m of the plot centre was measured and all stems between 3.5 and 7 m were counted. Measurements from the inner (3.5 m radius) plot were used to estimate basal area for small stems in the outer plot. The number of stems $\geqslant$6 cm DBH averaged 41 per plot, meeting the minimum tree number per plot requirement for growth and yield research suggested by Pretzsch (2009). All site occupancy and production variables were estimated using measurements from all stems $\geqslant$2 cm DBH.

To estimate production, DBH was measured at the end of the 2008, 2009, and 2010 growing seasons in all plots. Height, crown widths, and heights to the base of the live crown were measured for trees sampled randomly from a range of 2 cm DBH size classes for both white spruce and aspen in all three blocks during summer 2008. Heights were measured with Suunto clinometers and/or height poles. Crown widths were measured across the widest points along north–south (N–S) and east–west (E–W) directions. Heights, crown widths, and heights of the base of live crowns of

[1] Source: http://climate.weatheroffice.gc.ca/climate_normals (accessed June 16, 2011).

[2] Four blocks were included in the original study design (as per Bell et al., 1997) but operational issues resulted in Block 1 being discarded.