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Factors influencing overyielding in young boreal mixedwood stands in western Canada

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ABSTRACT

Mixtures of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are a prominent component of the boreal forests of western Canada. Overyielding, indicating higher productivity in mixtures than in monocultures, has been observed in mature stands but has not been examined in young stands (< 30 years old) in this region. We used data collected between 2006 and 2015 at 7 locations in Alberta and Saskatchewan for the Western Boreal Growth and Yield Association (WESBOGY) Long Term Study to examine whether overyielding occurs in young mixtures of these species and to identify factors (species composition, stand density, tree size, species proportion, site quality, and climate) that influence overyielding. Our results show that overyielding is occurring in these young boreal mixedwood stands in western Canada. Relative productivity total (RPT), indicating mixing effect (RPT > 1 indicates overyielding), varies from 0.921 to 1.537 among mixedwood treatments, and thinned aspen stands show higher production than unthinned aspen stands. Initial stand density (basal area) and initial aspen size (QMD at the start of the measurement interval) positively influence mixing effect while initial spruce size (QMD) negatively influences mixing effect. The magnitude of overyielding declines with increasing growing season length (DD5) and the relative productivity of aspen decreases with increasing site quality. Species mixtures support higher stocking than pure stands due to differences in growth rate and shade tolerance of the two species. Tree size is also important since productivity will decline when two species compete with each other for space and resources. Consequently, a mixed species stand that has space partitioning and size inequality between species, which reduces competition and favours expression of the functional traits (e.g., shade tolerance) of each species, tends to have better productivity.

1. Introduction

Several studies have demonstrated the benefits of tree species diversity on forest productivity, resilience, wildlife habitat, and aesthetics (Macdonald, 1995; Hoffman and Palmer, 1996; Macdonald et al., 2010; Cavard et al., 2011b; Zhang et al., 2012; Pretzsch et al., 2013b; Liang et al., 2016; Ma and Chen, 2017). Increases in productivity are of interest since this is closely associated with carbon capture and economic values (Ruiz-Benito et al., 2014; Liang et al., 2016). When productivity is higher in mixtures than in associated monocultures, it is termed overyielding (Hector, 1998; Beckage and Gross, 2006; Pretzsch and Schutze, 2009). Overyielding may result from competitive reduction, facilitation or other factors and is often also termed the "mixing effect". In such cases an increase in production results from the mixed environment encouraging species traits to surpass their behaviors in pure stands (Kelty, 2006; Forrester, 2014; Pretzsch, 2014).

Niche partitioning between species can lead to reductions in competition (Man and Lieffers, 1999; Hooper et al., 2005; Kelty, 2006; Pretzsch and Schutze, 2009). For example, shade tolerant species in the understory have a capacity for carbon fixation at low light levels (Givnish, 1988) with shade intolerant species in the overstory needing full light, and with mixtures of understory tolerant and overstory intolerant species resulting in a stand structure that more fully utilizes light over the growing season leading to higher net primary production. In the case of mixtures of coniferous and deciduous species, they can also differ in utilization of light during the growing season due to differences in phenology of leaf development (Constabel and Lieffers, 1996; Man and Lieffers, 1997, 1999). Understory spruce can utilize higher light when overstory aspen does not have leaves in the spring and autumn. For example, young aspen stands (< 20 years old) allowed about 60% of full light at 1.3 m in the spring and autumn but allowed about 20% of full light in the summer (Constabel and Lieffers, 1996). Consequently, spruce can photosynthesize with higher light and accumulate carbon during the spring and autumn (Man and Lieffers, 1997).

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Overyielding in mixtures also results from them supporting potentially higher stocking and canopy stratification (Garber and Maguire, 2004; Condés et al., 2013; Pretzsch and Schütze, 2016). Functional differences (e.g., shade tolerance) and traits (e.g. crown shapes of species) may allow stands to stock more trees in mixtures compared to monocultures (Pretzsch, 2014; Peer et al., 2018; Toïgo et al., 2018). When species occupy different crown layers, there can also be an increase in leaf area index which may contribute to higher productivity of the mixed stand (Man and Lieffers, 1999; Kelty, 2006; Forrester and Albrecht, 2014; Forrester et al., 2018).

Facilitation, which involves certain species improving the environment for other species (Hooper et al., 2005), may also contribute to overyielding (Pretzsch and Schutze, 2009; Forrester, 2014; Mason and Connolly, 2014). Increases in productivity could result from higher humidity in the understory, reductions in frost, insect attacks, and wind exposure (Taylor et al., 1996; Groot and Carlson, 1996; Man and Lieffers, 1999), and/or increases in nutrient availability.

Stand developmental stages can influence the mixing effect because growth rates of each species may differ with age (del Río et al., 2016). Early successional species, such as trembling aspen (*Populus tremuloides* Michx.), typically have rapid initial growth that reaches a maximum over a short period while late successional species, such as white spruce (*Picea glauca* (Moench) Voss), often have slow early growth rates (Cavard et al., 2011a). As a result, the contribution of each species to total production may vary with stand age and influence the magnitude and occurrence of overyielding.

Site quality and climate influence the productivity of mixtures through effects on growth of the component species, nature and intensity of interactions, and potential stocking (Pretzsch et al., 2010; Paquette and Messier, 2011; Prior and Bowman, 2014; Potter and Woodall, 2014; Toïgo et al., 2015; Jucker et al., 2016; Peer et al., 2018; Mina et al., 2018). The stress gradient hypothesis, suggests that interactions among species will tend to be more positive (i.e., interactions leading to increased growth) under poor or stressful conditions whereas under rich or moderate conditions weak positive or negative outcomes are more common (Callaway and Walker, 1997; Paquette and Messier, 2011; Toïgo et al., 2015).

Mixtures of trembling aspen and white spruce are a prominent natural component of the boreal plains and a common forest type in Canada (Man and Lieffers, 1999). As the economic and ecological values of mixed-species stands is recognized, the management of mixedwood stands is being emphasized in contrast to the management of separate pure stands of white spruce and aspen (Macdonald, 1995; Man and Lieffers, 1999; Chen and Popadiouk, 2002; Macdonald et al., 2010). Trembling aspen grows on a broad range of sites with a wide range in soil conditions (Perala, 1990). Aspen regenerates rapidly after stand replacing disturbances such as fire or harvesting and occupies the stand for several decades as a shade intolerant species. White spruce establishes on exposed mineral soil following stand destroying disturbances, and also regenerates on decomposing logs, organic layers, and moss beds under established stands (Nienstaedt and Zasada, 1990; DeLong et al., 1997). In contrast to aspen, white spruce is moderately shade tolerant and can grow under aspen canopies (albeit at slower rate than in the open) until aspen starts declining at age 50–70. At this time it begins to grow into the aspen canopy. In aspen-spruce mixed stands, aspen plays an important role as a nurse tree in protecting young spruce trees from frost damage and winter injury (Filipescu and Comeau, 2011). At the same time, however, shade from aspen does reduce the growth of white spruce (Filipescu and Comeau, 2007).

Higher productivity of these aspen-spruce mixtures has been identified in mature natural forests (Man and Lieffers, 1999; MacPherson et al., 2001) and modelling studies (Comeau et al., 2005; Comeau, 2014) in western Canada, but overyielding has not been examined in young stands in this region. Groot et al. (2014) found no significant effect on production of mixtures in young aspen-spruce stands in eastern Canada, contrary to predictions derived from previous research.

The objectives of the study presented in this paper were to investigate (1) whether or not overyielding occurs in young (< 30 years old) mixed stands, and to examine: (2) effects of species composition, stand density, proportion (i.e., the proportion of basal area of each species), and tree size on overyielding if it occurs; and (3) effects of climate and site quality (Site index) on the magnitude of overyielding in these stands if it occurs.

2. Material and methods

2.1. WESBOGY long-term study and data selection

Data from the Western Boreal Growth and Yield Association (WESBOGY) Long-Term Study (LTS) collected between 2006 and 2015 were used for these analyses. The WESBOGY LTS uses a randomized block design with 11 agencies and companies, and each agency or company involves one or two installations which differ in site quality (Superior and Median) and contain two replicates of 15 treatment plots. The 15 treatments include five monospecific stands of aspen (1500, 4000 trees/ha, and natural) and white spruce (500 and 1000 trees/ha), as well as mixtures with spruce densities of 500 and 1000 trees per hectare and five aspen densities (200, 500, 1500, 4000 trees/ha, and natural). Spruce was planted at uniform spacing for the two spruce densities and aspen was also fairly uniformly distributed in these stands. At year 5 after planting of spruce and natural regeneration of aspen after harvest, spruce and aspen were thinned to these treatment densities. Each plot is square with 20 m × 20 m (0.04 ha). Diameter at breast height (DBH), tree height (HT), crown width, species age, and tree condition (e.g., dead or alive) for all tagged trees in thinned plots have been measured over time. However, because unthinned aspen plots are so dense, all tagged trees in subplots (e.g., age 1–4: 1 m × 1 m, age 5–19: 2 m × 2 m, and after age 20: 5 m × 5 m) have been measured instead. All tagged trees in each plot were measured at 2 (age 10 through 18) or 3 (age 20 or above) year intervals. Four mixtures (spruce 500 trees/ha with aspen 200 and 500 trees/ha and spruce 1000 trees/ha with aspen 200 and 500 trees/ha) were excluded from this study because of the lack of reference pure aspen stands with these densities (200 and 500 trees/ha).

All study installations are located in the Boreal Plains ecozone (Fig. 1) where mixed stands of trembling aspen and white spruce are naturally common. The Boreal plains ecozone has a mean annual temperature of 0.2 °C and annual precipitation of 472 mm (Price et al., 2013), and it has moderately warm summers with most precipitation occurring during the growing season. Gray Luvisolic soils are prevalent in forested areas in this region (Wiken, 1986; Lavkulich and Arocena, 2011).

This study utilized data from 7 agencies with trees taller than breast height (1.3 m). Alberta-Pacific Forest Industries Inc. (ALP), Daishowa-Marubeni International Ltd. (DMI), Government of Alberta (ESRD), Alberta Plywood (WFR), and Weyerhaeuser Company Ltd. (WGR) are located in Alberta, and Canadian Forest Service (CFS) and Saskatchewan Ministry of Environment (SPA) are from the province of Saskatchewan. In total, 11 installations, 20 replicates, and 220 plots (20 replicates × 11 treatments) were used for the study (Table 1). The number of measurements ranges from 2 to 4 at each location, and years between successive measurements are 2–3 years. In this study, the data from ages (Sw_age and Aw_age) indicated in Table 1 were used for the analysis.

2.2. Mixing effect and potential variables

2.2.1. Calculation of relative productivity total for mixing effect

The dry mass of stems in each stand was calculated based on Canadian national biomass equations (Ung et al., 2008) using diameter at breast height (DBH) and tree height (HT), and the equation is given as: