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Stem biomass, C and N partitioning and growth efficiency of mature pedigreed black spruce on both a wet and a dry site

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ABSTRACT

Worldwide, efforts to manage atmospheric CO_2 are being explored both by reducing emissions and by sequestering more carbon (C). Stem biomass, C, and nitrogen (N) parameters were measured in plots of first-generation (F1), 32-year-old black spruce (*Picea mariana* (Mill.) B.S.P.) from four full-sib families studied previously for drought tolerance and differential productivity on both a dry and a wet site in central Ontario, Canada. The wet site had greater stem wood N and bark N concentrations than the dry site. Site differences in N were most likely driven by soil moisture stress impairing N uptake, as soil N was equal at both sites. Drought-tolerant (faster growing) families had lower wood density than drought-intolerant families on the wet site but there were no wood density differences between families on the dry site. Allometric analysis showed greater total stem dry mass per unit total belowground dry mass for drought-tolerant than intolerant families and for wet than dry sites, indicating a differential allocation of photosynthate dependent on both genotype and environment. Allometric analysis also showed greater total stem dry mass per unit total needle dry mass (growth efficiency) for drought-tolerant than intolerant families and for the wet than the dry site. This indicates greater productivity is a result of greater growth efficiency caused by greater net photosynthesis (shown previously) and greater partitioning of biomass to stem relative to total roots. The variation in physiological processes documented in our previous investigations and the biomass allocation variation shown here most probably underlie the increase in stem productivity from both black spruce tree improvement programs and increased water availability.

1. Introduction

Forestry, by tying up carbon (C) *in situ* (in biomass and soil) and *ex situ* (in products), may be an important avenue to increase biologically sequestered C (Johnsen et al., 2001a). Spruce (*Picea* spp.) is the major component in many boreal and temperate ecosystems and is by far the most important genus for the Canadian forest industry, accounting for 33–40% of the Canadian inventory (Canadian Council of Forest Ministers, 1999). In Canada, spruce accounts for 55%, and black spruce (*Picea mariana* (Mill.) B.S.P.) alone accounts for 35%, of the Canadian reforestation activities; most of this is from tree improvement programs (Morgenstern and Wang, 2001). Mature tree stems are the primary sink for C capture, which is a product of net photosynthetic rate (P_n) and total leaf area (or mass). Although traditional forest genetics research has clearly shown tree genotypes can vary in a number of traits, including aboveground volume growth, there are few if any studies—particularly for spruce—that examine allocation variation among site types and pedigreed families. There is also often significant genetic variation in wood quality traits, with wood density the most widely assessed due to its key relationship to quality of forest products. There are a number of reports of a negative relationship between growth rate and wood density (Zhang and Morgenstern, 1995; Corriveau et al., 1987, 1991; Cameron et al., 2005; Grans et al., 2009), and some show weak or non-significant relationships (Bouffier et al., 2009; Gaspar et al., 2009; Gort et al., 2009; Weng et al., 2011). Depending on the tree species, tree component, or chemical composition, C concentration can range from 47% to 59% (Laiho and Laine, 1997; Lamlom and Savidge, 2003). Thus, this implies the importance of not only quantifying stem dimensions, but also C concentrations and wood density (all contributing to long-term C storage) in the estimates of wood quantity and quality, and also its contribution to total C sequestration.

Water availability is a predominant factor in determining the geographic distribution of vegetation, and water stress has long been known to decrease plant growth and gas exchange and change water relations (Kramer, 1983). There have been a number

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of studies examining plant allocation variation under, and adaptations to, drought (Kramer, 1983; West et al., 1999; Litton et al., 2007). A standard quantitative genetic analysis of a first-generation (F1), 7 × 7 black spruce (*P. mariana* (Mill.) B.S.P.) diallel on three sites at the Petawawa Research Forest (PRF) indicated important genotype, environment, and genotype × environment (G × E) effects on growth characteristics (Boyle, 1987; Major and Johnsen, 1996). In practical terms, a statistically significant G × E effect means that the relative or absolute performance of genotypes does not remain constant under all test conditions (Baltunis et al., 2010). Four families (2 × 2) (Table 1) that exhibited this interaction in growth variation between two sites were selected for further examination (Fig. 1). One female parent (59) produced families that displayed relatively high productivity on both sites, whereas the other female parent (63) produced families that had high growth rates on one site but not on the other, less productive site. Multiple lines of evidence strongly support that site variation in productivity was largely driven by differences in soil moisture availability. The two sites are located within 5 km of each other and thus received approximately the same rainfall; the dry site had a sandy substrate, and the wet site had a hard pan layer about 30–40 cm below the surface that restricted drainage (S. Brown and R. Ponce-Hernandez, unpublished). On measurement days just after rainfall, physiological responses were the same at both sites. Collected on the same dates under drying conditions, predawn xylem water potential, daytime xylem water potential, P_n, and needle conductance were lower on the dry than on the wet site (Johnsen and Major, 1995; Major and Johnsen, 1996). Site differences in soil moisture were confirmed using foliar stable C isotope (^{13}C) discrimination analysis (Flanagan and Johnsen, 1995).

In addition, under drying conditions it was found that drought-tolerant families generated lower osmotic potential, greater turgor, greater photosynthesis, and lower ^{13}C discrimination than drought-intolerant families (Major and Johnsen, 1996, 1999, 2001; Johnsen et al., 1999). Also trees from half the diallel were measured for ^{13}C discrimination, which showed drought tolerance was under strong genetic control, was highly heritable (heritability coefficient, 0.54, highest of all traits measured), and had a strong genetic correlation ($r = -0.97$) to growth (Johnsen et al., 1999). The physiological mechanism affecting C_i (internal CO_2) was one controlled by the rate of P_n (demand) and not by stomatal conductance (supply) (Johnsen and Major, 1995; Major and Johnsen, 1996; Johnsen et al., 1999).

Table 1
Parentage of the four full-sib families (7122, 7125, 7143, and 7146) of black spruce.

Male	Female 59	Female 63
52	7122	7125
62	7143	7146

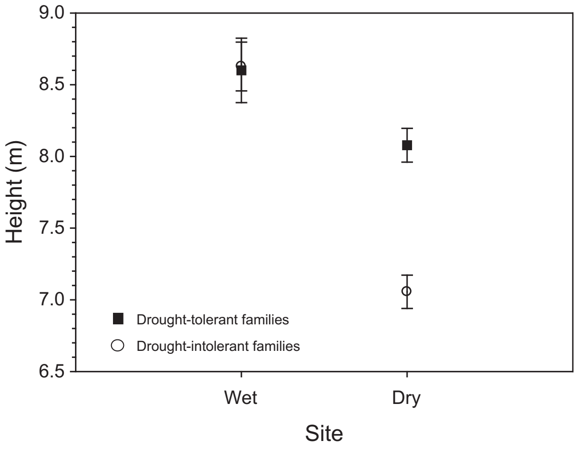

Fig. 1. Height of drought-tolerant and intolerant families (mean and SD) from two sites located at the Petawawa Research Forest, Ontario. Drought-tolerant families are progeny of female 59 (filled symbols), and drought-intolerant families are progeny from female 63 (open symbols). Dry and moist sites refer to sites 2 and 3, respectively.

How do site (soil moisture) and genetics (drought tolerance) affect stem biomass, C, and N mass properties? How might growth differences due to site moisture and family drought tolerance affect the relationship of total stem mass to total belowground mass (data from Major et al., 2012b) and to total needle mass (data from Major et al., 2013)? Our hypothesis is that drought-tolerant families and the dry site will have lower biomass allocation to the stem relative to belowground, for greater drought tolerance. Another hypothesis is that drought-tolerant families will have greater growth efficiency (total stem dry mass per unit total needle dry mass) due to their greater net photosynthesis compared with drought-intolerant families. It is also hypothesized that there would be greater stem wood density on the dry than the wet site and in drought-intolerant (slower growing) than tolerant families. Another goal was to quantify stem wood and bark component parameters from mature black spruce plantations to contribute to our complete and detailed assessment of the total above and belowground biomass, C, and N mass pools. Thus, our objectives for this study were to (1) quantify stem wood and bark C and N (%) from wet and dry sites of drought-tolerant and intolerant families from 10 stem positions to accurately calculate stem dry, C, and N mass ha^{-1} and stem density, (2) examine genetic and environmental effects on stem mass and volume parameters, and with stem section for C and N concentrations, wood and bark densities, and percentage bark parameters, (3) examine genetic and environmental effects on stem mass partitioning in relation to belowground mass, and (4) examine genetic and environmental effects on growth efficiency.

2. Materials and methods

2.1. Plant material and location

A complete 7 × 7 diallel cross black spruce experiment was initiated at the Petawawa Research Forest (PRF, Lat. 46°N, Long. 77°30′W) in 1970 (Morgenstern, 1974; Boyle, 1987). The seven parental trees used for the diallel cross were from a plantation at PRF, but the exact origin of the trees is unknown, except that they were grown from seed collected in the Lake Simcoe-Rideau region in Ontario (Morgenstern, 1974). The seeds were germinated in March 1971, and seedlings were grown for 2 years in a greenhouse before being planted at three field sites at PRF in 1973. At each site, trees from a full-sib family were planted in either nine-tree (site 3) or 16-tree (site 2) square (1.83 × 1.83 m) spacing (site 1 was not used for this study). At site 3, there were three replicate blocks, and at site 2, there were four replicate blocks. Family plots were randomized within each block at each site.

As previously reported (Major and Johnsen, 1996, 1999, 2001; Johnsen and Major, 1999), and discussed above, the primary difference between study sites was water availability. Site 2 will be referred to as the "dry" site and site 3 as the "wet" site. A subset of four full-sib families that displayed differences in drought tolerance were used and comprised a 2 female parent × 2 male parent breeding structure (Table 1). Progeny of female 59 (families 7122 and 7143) are referred as "drought-tolerant" families and progeny of female 63 (families 7125 and 7146) are referred to as