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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).

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.

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

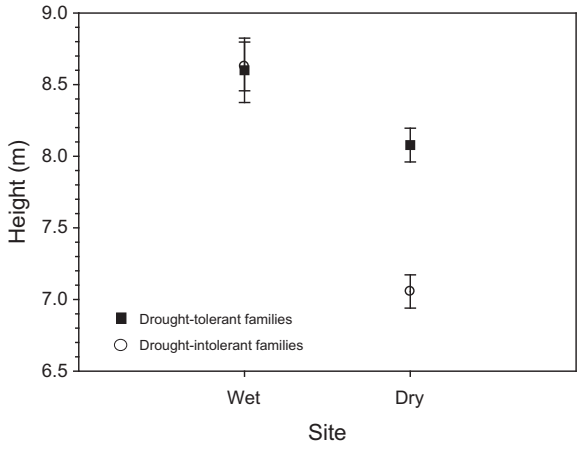

Fig. 1. Height of drought-tolerant and intolerant families (mean and SD) from two sites located at the Petawawa Research Forest, Ontario. Drought-tolerant families are progeny of female 59 (filled symbols), and drought-intolerant families are progeny from female 63 (open symbols). Dry and moist sites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

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

"drought-intolerant" families. We note that labels of "wet" and "dry" sites, as well as "tolerant" and "intolerant" families, are relative to this particular study and do not necessarily reflect where these sites, or families, fit along the larger-scale environmental and genetic variation spectra within black spruce as a species.

2.2. Methodology

The number of trees harvested on the dry site was 1 tree plot^{-1} × 4 families × 4 blocks or 16 trees. The number of trees harvested on the wet site was 1 tree plot^{-1} × 4 families × 3 blocks or 12 trees, for a grand total of 28 trees from both sites. Tree number 1 (corner tree) from each plot was sampled; if it was missing, then the tree in the adjacent corner was sampled. Also trees selected were surrounded by live trees on all sides. Trees were cut at the top of the root butt swell. Stems were first divided in two at the lowest live branch of the stem, which was approximately at half stem. The live crown and the mature stem (no live branches) were each further divided into five equal lengths, identified as stem section 1 (top) to 10 (bottom). At the time of sampling, trees were 32 years old, basal area was approximately 39.7 and 43.6 m^2 ha^{-1} for the dry and wet sites, respectively, tree density was 2900 trees ha^{-1} for both sites, and live crown length was 51.0% and 50.1% for the dry and wet sites, respectively.

Each stem section length was measured, and diameters at the top and bottom of each section were measured. A disk approximately 2.5 cm thick was cut from the bottom of each section. All disks were measured at four points for disk thickness. Diameter was measured with a tape. The bark radius was measured at four points around the disk. The disks were oven dried to 65 °C for 48 h, the bark was separated from the wood, and both were weighed. Stem wood and bark C and N were determined for each disk sample using an elemental analyzer (CNS-2000, LECO Corporation, St. Joseph, MI, USA). Densities were calculated for bark and wood for each disk using standard cylinder volume formulas and respective dry weights.

Stem sectional parameters were calculated by averaging the top and bottom disk for each section. For example, sectional volume was calculated by using the mean radius (r) of the top and bottom sectional disk to be used in πr^2 × sectional length. This was completed for all sections, except the top section where only the bottom disk is available. We did measure terminal diameter to calculate section 1 volume. Details of belowground soil and biomass and needle biomass methodology are found in Major et al. (2012a,b, 2013).

2.3. Analyses

The ANOVA model for overall volume and mass traits includes the following effects: site, female, and male, all considered fixed. The ANOVA model used is as follows:

$$Y_{ijkl} = \mu + S_i + F_j + M_k + SF_{ij} + SM_{ik} + FM_{jk} + SFM_{ijk} + e_{ijkl},$$

where Y_{ijkl} is the dependent tree trait of the ith site, of the jth female, of the kth male, μ is the overall mean, S_i is the effect of the ith site (i = 1, 2), F_j is the effect of the jth female (j = 59, 63), M_k is the effect of the kth male (k = 52, 62), SF_{ij} is the interaction effect of ith site and jth female, SM_{ij} is the interaction effect of ith site and kth male, MF_{jk} is the interaction effect of jth female and kth male, SMF_{ijk} is the interaction effect of ith site, jth female and kth male, and e_{ijkl} is the random error component.

The ANOVA model for testing concentration, density, and percent traits includes the following effects: site, stem section, female, and male, which were considered fixed. The ANOVA model used is as follows:

$$Y_{ijklm} = \mu + S_i + B_j + F_k + M_l + SB_{ij} + SF_{ik} + SM_{il} + BF_{jk} + BM_{jl} + FM_{kl} + SBF_{ijk} + SFM_{ijl} + BFM_{jkl} + SBFM_{ijkl} + e_{ijklm},$$

where Y_{ijklm} is the dependent tree trait of the ith site, of the jth stem section, of the kth female, of the lth male, of the mth tree. μ is the overall mean, S_i is the effect of the ith site (i = 1, 2), B_j is the effect of the jth stem section (j = 1, 2, . . . , 10), F_k is the effect of the kth female (k = 59, 63), M_l is the effect of the lth male (l = 52, 62) SB_{ij} is the interaction effect of ith site and jth stem section, SF_{ik} is the interaction effect of ith site and kth female, SM_{il} is the interaction effect of ith site and mth male, BF_{jk} is the interaction effect of jth stem section and kth female, BM_{jl} is the interaction effect of jth stem section and lth male, FM_{kl} is the interaction effect of kth female and lth male, SBF_{ijk} is the interaction effect of ith site, jth stem section, and kth female, SBM_{ijl} is the interaction effect of ith site, jth sole section, and lth male, BFM_{jkl} is the interaction effect of jth stem section, kth female, and lth male, $SBFM_{ijkl}$ is the interaction effect of ith site, jth stem section, kth female, and lth male, and e_{ijklm} is the random error component.

Two biomass partitioning allometric relationships, stem to needle mass, and stem to belowground mass, using data from Major et al. (2013), and Major et al. (2012b), were analyzed using analysis of covariance (ANCOVA). In these analyses, three sources of variation were studied: (1) covariate (i.e., needle biomass), (2) independent effect (site or female), and (3) independent effect x covariate. The analyses were done based on the following model (Major and Johnsen, 1996):

$$Y_{ij} = B_0 + B_{0i} + B_1 X_{ij} + B_{1i} X_{ij} + e_{ij}$$

where Y_{ij} is the dependent trait of the jth tree of the ith site or female, B_0 and B_1 are average regression coefficients, B_{0i} and B_{1i} are the site or female-specific coefficients, X_{ij} is the independent variable, and e_{ij} is the error term.

Due to the large samples and low replicates, and recognizing the work necessary to collect individual samples, mass and volume effects were considered statistically significant at the α = 0.10 level. For concentrations, densities, and percent traits that include data from ten stem sections from each tree and stem section interactions, results were considered statistically significant at the α = 0.05, although individual P values are provided for all traits so that readers can make their own interpretations. The data had satisfied normality and equality of variance assumptions. The general linear model from Systat (Chicago, Illinois) was used for analysis.

3. Results

3.1. Stem volume and mass

Total stem, wood, and bark volumes showed significant site and female effects (Table 2). Total stem volumes were 261.0 and 321.2 m^3 ha^{-1} for dry and wet sites and 337.7 and 244.5 m^3 ha^{-1} for drought-tolerant and intolerant families, respectively (Fig. 2a). There were no female x site effects, so the differences between drought-tolerant and intolerant families were similar for both sites. Stem wood volumes were 235.4 and 291.1 m^3 ha^{-1} for dry and wet sites, and 306.1 and 220.8 m^3 ha^{-1} for drought-tolerant and intolerant families, respectively. Both crosses with female 59 had nearly the same volume, with approximately 340 m^3 ha^{-1} (Fig. 2b). Males 52 and 62 crossed with female 63 resulted in 212 and 276 m^3 ha^{-1}, respectively. Proportion of bark by volume only showed a significant section effect, with a mean value of 11.7% (Table 3). Overall, there was a sharp decline in percent bark volume from section 1 (top) to 3, with 20.9%, 15.9%, and 12.4%, respectively. Then, there was a gradual decline from sections 4–9, with

Table 2
Wood, bark, and total stem volume and dry mass ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *P* values, and coefficient of determination (R^2). *P* values <0.10 are in bold print.

Source of variation	*df*	Wood volume (M^3 ha^{-1})		Bark volume (M^3 ha^{-1})		Total stem volume (M^3 ha^{-1})	
		MS	*P* value	MS	*P* value	MS	*P* value
Site (S)	1	21515.4	**0.036**	19.99	**0.027**	24848.8	**0.033**
Female (F)	1	49952.6	**0.003**	427.20	**<0.001**	59618.8	**0.002**
Male (M)	1	4923.9	0.294	25.09	0.288	5652.0	0.286
S * F	1	143.9	0.856	0.49	0.880	161.2	0.855
S * M	1	6861.7	0.218	28.13	0.261	7768.4	0.214
F * M	1	7247.3	0.206	38.85	0.189	8347.4	0.198
S * F * M	1	13.5	0.956	0.77	0.850	7.8	0.968
Error	20	4232.4		21.04		4711.2	
R^2			0.514		0.604		0.528
		Wood dry mass (Mg ha^{-1})		Bark mass (Mg ha^{-1})		Total stem mass (Mg ha^{-1})	
		MS	*P* value	MS	*P* value	MS	*P* value
Site (S)	1	2630.57	**0.031**	3.06	0.486	2813.16	**0.040**
Female (F)	1	4996.69	**0.004**	70.74	**0.003**	6256.50	**0.004**
Male (M)	1	834.67	0.205	16.98	0.110	1089.75	0.186
S * F	1	1.94	0.950	1.29	0.650	0.07	0.992
S * M	1	869.89	0.196	21.16	**0.077**	1162.37	0.172
F * M	1	769.56	0.223	2.95	0.494	867.84	0.236
S * F * M	1	20.37	0.840	0.93	0.700	12.59	0.884
Error	20	437.18		6.09		580.31	
R^2			0.507		0.478		0.509

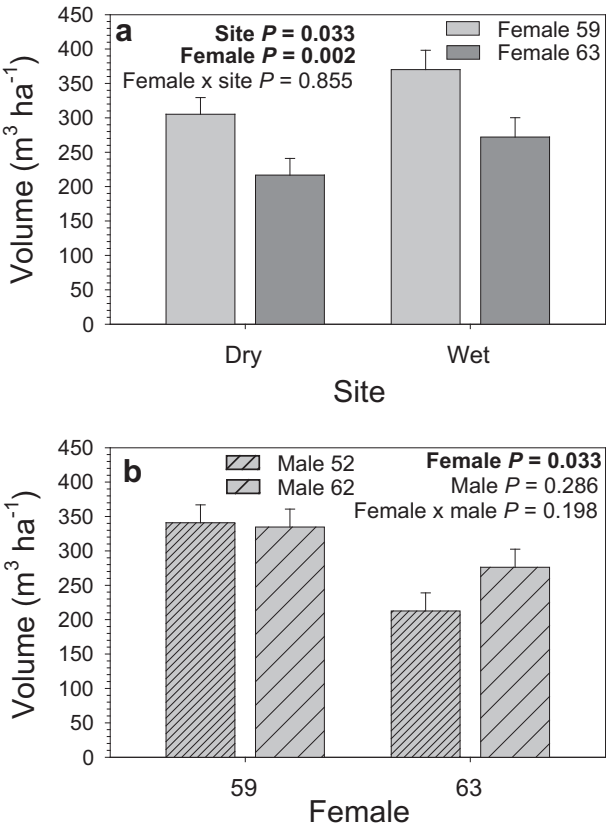

Fig. 2. Stem volume (a) by female × site, and (b) by female × male. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

10.9%, 10.4%, 9.8%, 9.2%, 8.8%, and 8.7%, respectively. Section 10 proportion of bark by volume then increased to 9.9%.

Total stem mass and wood mass had significant site and female effects (Table 2). Bark mass had a female and site × male effect. Total stem mass was 98.0 and 118.3 Mg ha^{-1} for dry and wet sites, and 123.3 and 93.1 Mg ha^{-1} for drought-tolerant and intolerant families, respectively. Wood mass was 84.0 and 103.6 Mg ha^{-1} for dry and wet sites, and 107.3 and 80.3 Mg ha^{-1} for drought-tolerant and intolerant families, respectively. The dry site had 16.7% bark by dry mass, significantly greater than the wet site at 15.0% (Table 3). Drought-tolerant families had significantly lower bark percentage by dry mass than drought-intolerant families with 15.6% and 16.2%, respectively. As with percent bark by volume, percent bark by mass showed a steep decline from sections 1–3, with values of 26.6%, 20.7%, and 17.0%, respectively. Then, there was a gradual decline from sections 4–9, with 15.2%, 14.0%, 13.6%, 12.9%, 12.4%, and 12.4% bark by mass, respectively. Section 10 proportion of bark by mass then increased to 14.0%. The female × site effect was due to a magnitude effect, not rank change. The female × male effect was due to one family (7122) having lower percent bark than the other three families.

3.2. Stem C and N concentrations

Stem wood C concentration had significant site, female, male, female × site, and male × site effects (Table 4). Stem wood from the dry and the wet sites had 54.3% and 53.5% C, respectively. Drought-tolerant families had greater wood C concentration than intolerant families on both sites (Fig. 3a). Progeny of male 52 had greater wood C concentration than progeny of male 62, and the male × site interaction was due to rank change: progeny of male 62 families had greater percentage C on the dry site—this ranking was reversed on the wet site. Interestingly, wood and bark C concentrations are the only traits that did not have a significant section effect. The female × site interaction was due to magnitude effects, not rank change. Although not significant, wood C showed a near-linear increase from the top (53.6%) to bottom (54.5%) section.

Bark C concentration had significant site, female, male, male × site, female × male, and female × male × site effects (Table 4). Dry and wet site bark had 52.6% and 53.3% C, respectively. Similar to wood C concentration, drought-intolerant families had greater bark C than drought-tolerant families on both sites (Fig. 3b). Similar to wood C concentration, progeny of male 52 had greater bark C than progeny of male 62. The male × site effect was due to rank

Table 3
Percent bark by volume, dry mass, wood and bark density ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *P* values, and coefficient of determination (R^2). *P* values <0.05 are in bold print.

Source of variation	*df*	Percent bark by stem volume		Percent bark by stem dry mass		Wood density (g cm^{-3})		Bark density (g cm^{-3})	
		MS	*P*-value	MS	*P*-value	MS × 10^{-3}	*P*-value	MS	*P*-value
Site (S)	1	0.002	0.983	193.073	**<0.001**	0.026	0.837	0.283	**<0.001**
Section (Sec)	9	411.581	**<0.001**	564.537	**<0.001**	6.279	**<0.001**	0.026	**<0.001**
Female (F)	1	5.303	0.304	28.940	**0.022**	1.510	0.118	0.024	**0.038**
Male (M)	1	2.150	0.513	2.769	0.478	3.271	**0.022**	0.010	0.172
S * Sec	9	5.889	0.312	2.540	0.898	0.124	0.994	0.003	0.887
S * F	1	0.245	0.825	43.280	**0.005**	2.513	**0.044**	0.027	**0.028**
S * M	1	7.551	0.221	3.055	0.456	0.024	0.842	0.046	**0.004**
Sec * F	9	1.127	0.991	2.803	0.865	0.841	0.203	0.010	0.074
Sec * M	9	3.721	0.669	2.614	0.889	0.147	0.988	0.002	0.938
F * M	1	3.642	0.395	37.189	**0.010**	0.000	0.994	0.013	0.135
S * Sec * F	9	0.710	0.998	0.610	0.999	0.134	0.992	0.002	0.968
S * Sec * M	9	0.577	0.999	2.344	0.919	0.273	0.910	0.002	0.920
S * F * M	1	1.932	0.535	1.751	0.572	0.522	0.357	0.002	0.548
Sec * F * M	9	2.076	0.926	2.352	0.918	1.051	0.088	0.002	0.980
S * Sec * F * M	9	1.332	0.983	1.704	0.971	0.387	0.769	0.002	0.972
Error	200	5.005		5.480		0.613		0.006	
R^2			0.793		0.836		0.432		0.432

Table 4
Stem wood and bark C and N concentration ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *P* values, and coefficient of determination (R^2). *P* values <0.05 are in bold print.

Source of variation	*df*	Wood carbon (%)		Bark carbon (%)		Wood nitrogen (%)		Bark nitrogen (%)	
		MS	*P*-value	MS	*P*-value	MS × 10^{-3}	*P*-value	MS × 10^{5}	*P*-value
Site (S)	1	41.394	**0.001**	39.990	**<0.001**	5.161	**<0.001**	0.083	**<0.001**
Section (Sec)	9	1.801	0.892	3.381	0.513	3.157	**<0.001**	0.545	**<0.001**
Female (F)	1	246.375	**<0.001**	21.424	**0.017**	0.704	**0.020**	0.002	0.556
Male (M)	1	24.014	**0.013**	206.771	**<0.001**	0.213	0.200	0.409	**<0.001**
S * Sec	9	0.144	0.999	3.116	0.577	0.051	0.937	0.006	0.372
S * F	1	20.986	**0.020**	0.073	0.888	0.279	0.143	0.016	0.094
S * M	1	57.033	**<0.001**	304.064	**<0.001**	0.019	0.701	0.017	0.088
Sec * F	9	0.253	0.999	3.588	0.465	0.250	**0.049**	0.002	0.943
Sec * M	9	1.538	0.932	1.789	0.884	0.089	0.719	0.002	0.906
F * M	1	5.000	0.254	152.000	**<0.001**	0.339	0.106	0.010	0.185
S * Sec * F	9	0.570	0.998	1.113	0.974	0.048	0.947	0.007	0.324
S * Sec * M	9	1.553	0.930	1.901	0.863	0.189	0.164	0.011	**0.057**
S * F * M	1	0.553	0.704	21.797	**0.016**	1.487	**<0.001**	0.071	**<0.001**
Sec * F * M	9	0.824	0.992	1.158	0.970	0.158	0.283	0.002	0.942
S * Sec * F * M	9	1.516	0.935	0.764	0.993	0.152	0.308	0.003	0.894
Error	200	3.817		3.694		0.129		0.006	
R^2			0.389		0.569		0.638		0.841

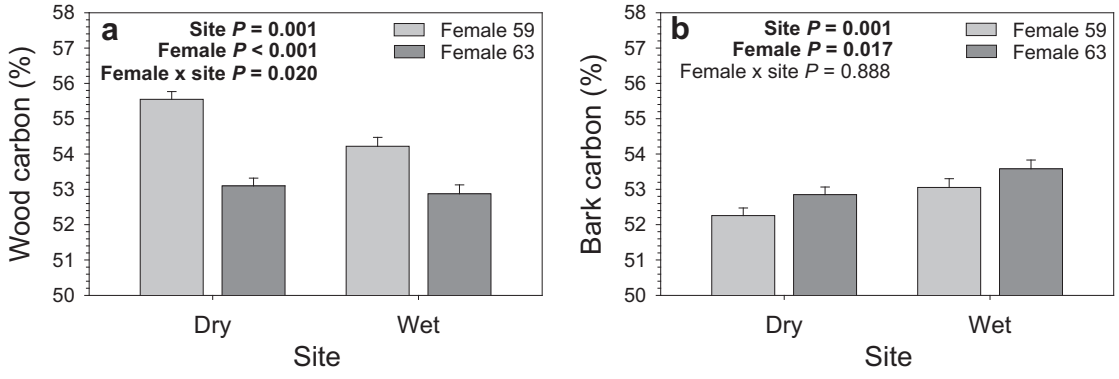

Fig. 3. Carbon concentration by female × site for (a) stem wood and (b) stem bark. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

change between sites: progeny of male 52 families had a greater bark C percentage than progeny of male 62 families on the dry site; this was reversed on the wet site. The female × male × site was the same as described in the last sentence with minor female magnitude effects.

Wood N concentration had a significant site, section, female, female × section, and female × male × site effects (Table 4). The dry site had consistently lower wood N concentration than the wet site, with an average of 0.026% and 0.035%, respectively (Fig. 4a and b). Overall, drought-tolerant families had greater wood N concentration

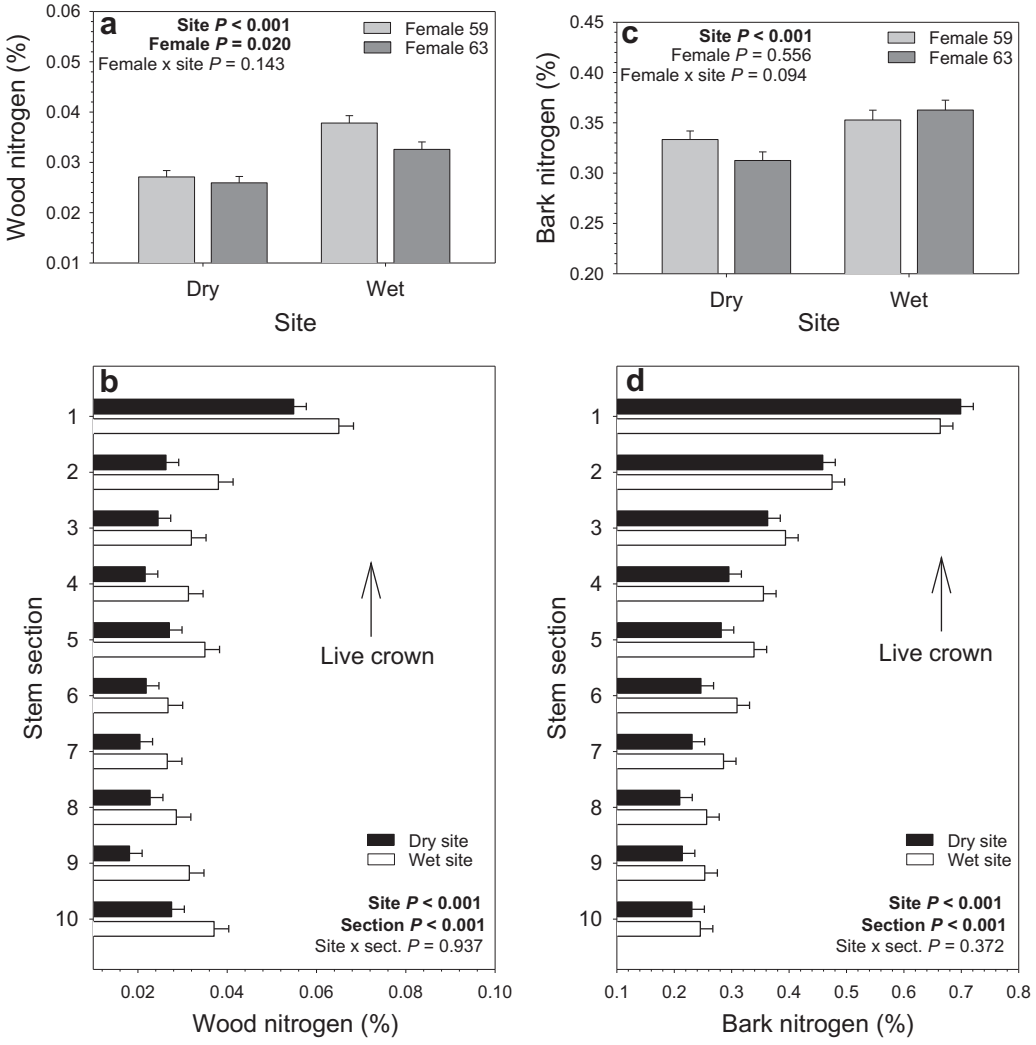

Fig. 4. Nitrogen concentration for (a) stem wood, female × site, (b) stem wood, site × stem section, (c) stem bark, female × site, and (d) stem bark, site × stem section. Crown positions range from top (1) to bottom (10) of the stem. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

than intolerant families (Fig. 4a). The female × section effect was due to minor female rank change with section. Female × male × site effect was due to a magnitude effect; all families had greater wood N concentration on the wet than the dry site.

Bark N concentration had significant site, section, male and female × male × site effects (Table 4). Dry and wet site bark had 0.32% and 0.36% bark N, respectively (Fig. 4c). The section effect was curvilinear from a high at the top section with 0.68% N and dropping to 0.46%, 0.38%, 0.33% N in sections 2–4, respectively (Fig. 4d). There was a linear decline from sections 5–10 of 0.31% N to 0.24% N. Female × male × site effect was also due to a magnitude effect; all families had greater bark N on the wet than the dry site.

3.3. Wood and bark density

Wood density had significant male, section, female × site effects (Table 3). Overall, the two sites had the same wood density of 0.35 g cm^{-3}. The female × site effect was the result of both drought-tolerant and intolerant families having similar values on the dry site, whereas drought-intolerant families had greater density than tolerant families on the wet site (Fig. 5a). Sections 1–5 (live crown) had a near-linear increase in density with 0.31, 0.33, 0.35, 0.36, and 0.37 g cm^{-3}, respectively (Fig. 5b). From sections 6–10 the average density was fairly constant around 0.36 g cm^{-3}.

Bark density had significant site, section, female, site × female and site × male effects (Table 3). The dry and the wet site had 0.55 and 0.48 g cm^{-3} bark density, and drought-intolerant and tolerant families had 0.52 and 0.50 g cm^{-3}, respectively. The female × site interaction was the result of no female differences on the wet site and drought-intolerant families with greater density than drought-tolerant families on the dry site (Fig. 5c). The site × male effect was due to male rank change by site: progeny of male 52 had greater bark density than progeny of male 62 on the dry site, and this was reversed on the wet site. Bark density by section was similar to wood density. Sections 1–5 had a near-linear increase in density from 0.44, 0.47, 0.51, 0.53, and 0.52 g cm^{-3}, respectively (Fig. 5d). From sections 6–10, the average density was fairly constant around 0.53 g cm^{-3}.

3.4. Stem C and N mass

Total stem and wood C mass had significant site and female effects (Table 5). Total stem C mass was 53.4 and 63.4 Mg ha^{-1} for the dry and the wet site, and 67.4 and 49.4 Mg ha^{-1} for drought-tolerant and intolerant families, respectively (Fig. 6a). Wood C mass was 46.0 and 55.6 Mg ha^{-1} for the dry and the wet site, and 58.9 and 42.6 Mg ha^{-1} for drought-tolerant and intolerant families, respectively. Bark C mass had a significant female and

Table 5
Wood, bark and total stem C and N mass ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *P* values, and coefficient of determination (R^2). *P* values <0.10 are in bold print.

Source of Variation	*df*	Wood C mass (Mg ha^{-1})		Bark C mass (Mg ha^{-1})		Total stem C mass (Mg ha^{-1})	
		MS	*P* value	MS	*P* value	MS	*P* value
Site (S)	1	630.29	**0.053**	1.253	0.393	687.75	**0.060**
Female (F)	1	1,833.0	**0.002**	17.32	**0.004**	2206.6	**0.002**
Male (M)	1	169.81	0.298	2.287	0.252	211.51	0.283
S * F	1	5.164	0.854	0.402	0.626	2.683	0.902
S * M	1	170.27	0.298	11.44	**0.016**	269.95	0.227
F * M	1	198.12	0.263	0.126	0.785	208.23	0.286
S * F * M	1	6.133	0.841	0.682	0.527	2.726	0.902
Error	20	149.07		1.645		173.63	
R^2			0.504		0.493		0.509
		Wood N mass (Kg ha^{-1})		Bark N mass (Kg ha^{-1})		Total stem N mass (Kg ha^{-1})	
		MS	*P* value	MS	*P* value	MS	*P* value
Site (S)	1	1362.1	**0.001**	310.54	0.073	2973.4	**0.006**
Female (F)	1	552.65	**0.020**	634.66	**0.014**	2371.8	**0.012**
Male (M)	1	247.34	0.107	234.76	0.115	0.1644	0.982
S * F	1	130.36	0.234	35.084	0.532	300.70	0.339
S * M	1	73.184	0.369	92.400	0.314	330.05	0.317
F * M	1	22.237	0.618	53.870	0.440	145.33	0.504
S * F * M	1	230.21	0.119	29.542	0.566	94.815	0.589
Error	20	86.737		86.618		313.71	
R^2			0.595		0.447		0.492

male × site effect. Similar to wood C mass, drought-tolerant families had greater bark C mass than drought-intolerant families. The male × site effect was a change in rank with site; progeny of male 52 had greater bark C mass than progeny 62 on the dry site, and this was reversed on the wet site. Overall, bark and wood represented 13.1% and 86.9% of stem C mass.

Total stem and wood N mass had significant site and female effects (Table 5). Total stem N mass was 54.7 and 75.5 kg ha^{-1} for the dry and the wet sites and 74.4 and 55.8 kg ha^{-1} for drought-tolerant and intolerant families, respectively (Fig. 6b). Wood N mass was 19.7 and 33.8 kg ha^{-1} for the dry and the wet site and 31.2 and 22.2 kg ha^{-1} for drought-tolerant and intolerant families, respectively. Bark N mass had a significant female effect. Similar to wood N mass, drought-tolerant families had greater bark N mass than drought-intolerant families. Overall, bark and wood represented 59% and 41% of stem N mass.

3.5. Stem relationship to total needle and belowground mass

Allometric analysis of total stem dry mass, using total belowground dry mass as covariate and testing for site effect, showed no significant site × belowground dry mass interaction ($P = 0.251$). Further analysis showed a consistent site effect ($P = 0.016$) and needle dry mass effect ($P < 0.001$) (Fig. 7a). Covariate analysis of total stem dry mass, using total belowground dry mass as covariate and testing for female effect had no significant female × needle dry mass interaction ($P = 0.331$). Further analysis showed a consistent female effect ($P = 0.098$) and needle dry mass effect ($P = 0.003$) (Fig. 7b).

Allometric analysis of total stem dry mass, using total needle dry mass as covariate and testing for site effect, likewise indicated no significant site × needle dry mass interaction (slopes were the same, $P = 0.441$). Further analysis showed a consistent site effect ($P = 0.090$) and needle dry mass effect ($P < 0.001$) (Fig. 8a). Covariate analysis of total stem dry mass, using total needle dry mass as covariate and testing for female effect had no significant female × needle dry mass interaction ($P = 0.287$). Further analysis showed a consistent female effect ($P = 0.026$) and needle dry mass effect ($P < 0.001$) (Fig. 8b).

4. Discussion

Although there were some statistically significant results for male and male × site interactions for C and N concentrations, we focus the discussion on examining the hypotheses and results regarding biomass, C and N mass, volume, density, biomass partitioning, and growth efficiency.

4.1. Stem mass and volume

Stem volume was 23% greater on the wet than the dry site, which is directly linked to site differences in water availability (see more below and Major et al. (2012b)). Overall stem volume was 38% greater for drought-tolerant than intolerant families. We found significant female and site effects for most stem volume and mass traits; however, female × site interaction effects seen in earlier studies were not significant for stem volume or mass. There was evidence of a female × site interaction trend, for example with wood mass, which showed 39.2% and 29.3% differences between drought-tolerant and intolerant families on the dry and the wet site, respectively. The lack of a significant female × site interaction effect in productivity in this study is probably due to the smaller sample size necessitated by the effort to complete a total above and belowground quantification of these mature trees. We sampled the first tree in each plot of each block, resulting in a robust but limited selection that represents 15% of the total 182 individuals from the two sites used in this experiment, unlike Boyle (1987) who used all the trees and Johnsen et al. (1999) where 50% of the trees were measured.

Our overall estimate for our black spruce total wood C concentration across stem sections averaged 53.93%, very close to values found by Bert and Danjon (2006) in a detailed study of *Pinus pinaster*, but we found bark C was lower than wood C at 52.93%, compared with their value of 55.18% C. For Sitka spruce (*Picea sitchensis* (Bong.) Carr.), no differences were found between wood and bark components, with an average of 52.0% C (Green et al., 2007). Carbon concentration is driven, in part, by chemical composition. Softwood lignin is a phenolic polymer that has a C concentration of 66.0% and can make up between 18% and 35% of biomass

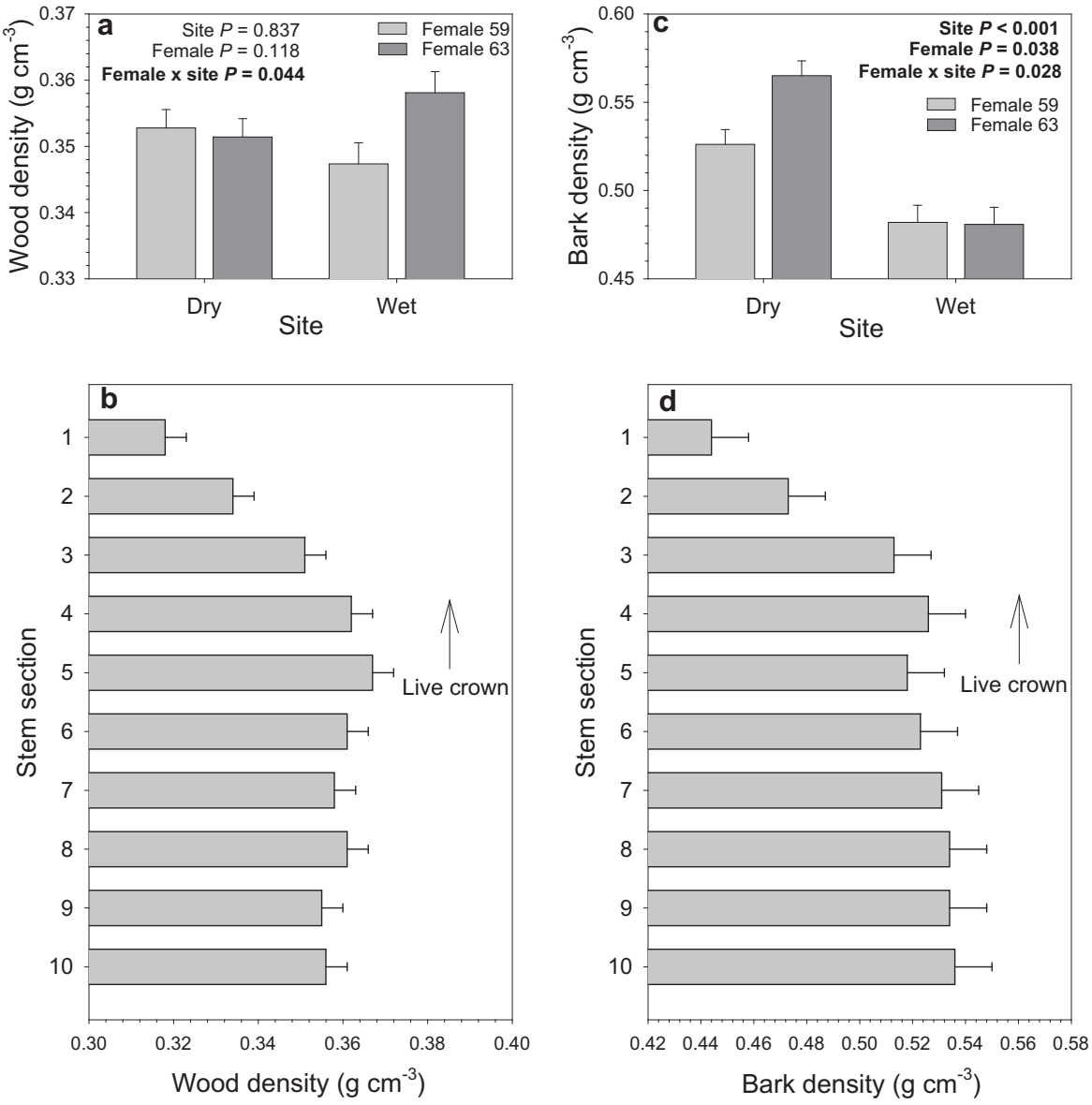

Fig. 5. Density for (a) stem wood, female × site, (b) stem wood, by stem section, (c) stem bark, female × site, and (d) stem bark, by stem section. Crown positions range from top (1) to bottom (10) of the stem. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

(Bert and Danjon, 2006). The other dominant components of biomass are the holocelluloses (α-cellulose and hemicelluloses), which can make up between 65% and 75% of biomass. α-cellulose is a glucan polymer and has a C concentration of 44.4% (Bert and Danjon, 2006). The principle hemicelluloses found in softwoods contain 42–46% C. Faster growing trees generally have greater early wood, which in turn, has greater lignin, consistent with what we found (Rozenberg and Cahalan, 1997).

Bark biomass percentages for Norway spruce (*Picea abies*) have been shown to decline in a curvilinear to linear fashion with increasing diameter at breast height (DBH), from a high of 20% at 5 cm to just over 10% at 40 cm DBH (Lestander et al., 2012). These numbers are slightly lower than our results. Also in the same study, Scots pine (*Pinus sylvestris* L.) had 11% at 5 cm DBH to approximately 4% at 40 cm DBH, approximately half that found for spruces. Estimates of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) bark ratio by diameter, a measure correlated to volume, also showed a curvilinear to flat response, with 13% at 10 cm DBH to 8% at 50 cm DBH (Kohnle et al., 2012). Overall, our stem bark was 11–12% by volume. Stem mass by bark averaged approximately 10% under a number of fertilizer treatments for 59-year-old Norway spruce (Ingerslev and Hallbacken, 1999). The overall percentage of stem mass made up of bark was greater, at 12–20%, in our experiment. Sitka spruce measuring 15 cm DBH had approximately 15% bark mass but varied from 20% to 10% for 12 and 29 cm, respectively (Green et al., 2007).

Black spruce sapwood and heartwood N percentages averaged through the stem were 0.08% and 0.07%, respectively, for a slow-growing ⩾100-year-old forest (Gower et al., 2000). In a study of 59-year-old Norway spruce, stem wood at DBH and in the middle of the canopy had 0.09% and 0.10% N, respectively (Ingerslev and Hallbacken, 1999). Both studies had values greater than ours, which averaged 0.03% N. In one of the few published studies to quantify bark N (Ingerslev and Hallbacken, 1999), values were more than an order of magnitude greater than wood N, with 0.44% and 0.55% N for DBH and middle of the canopy, which were

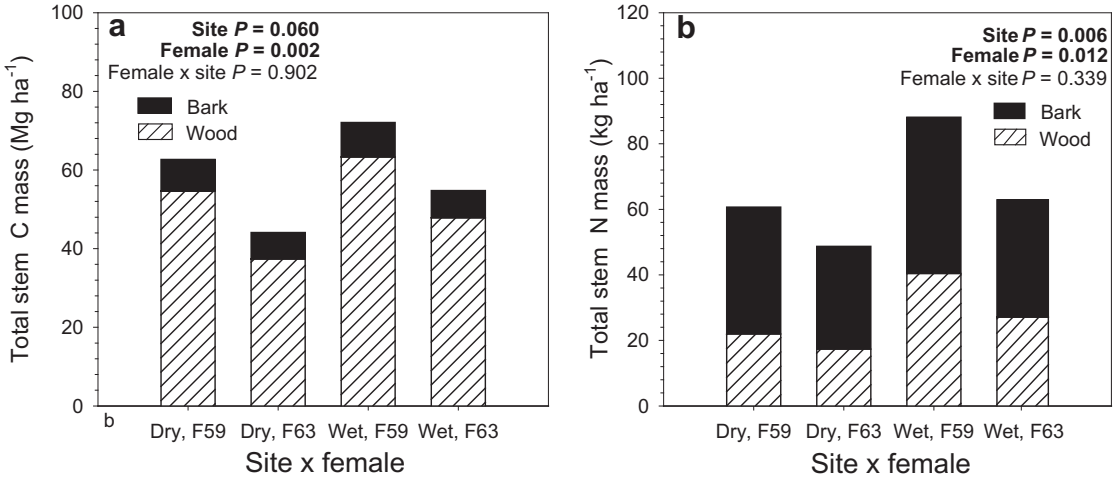

Fig. 6. (a) Total stem C mass, female × site, and (b) total stem N mass, female × site. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

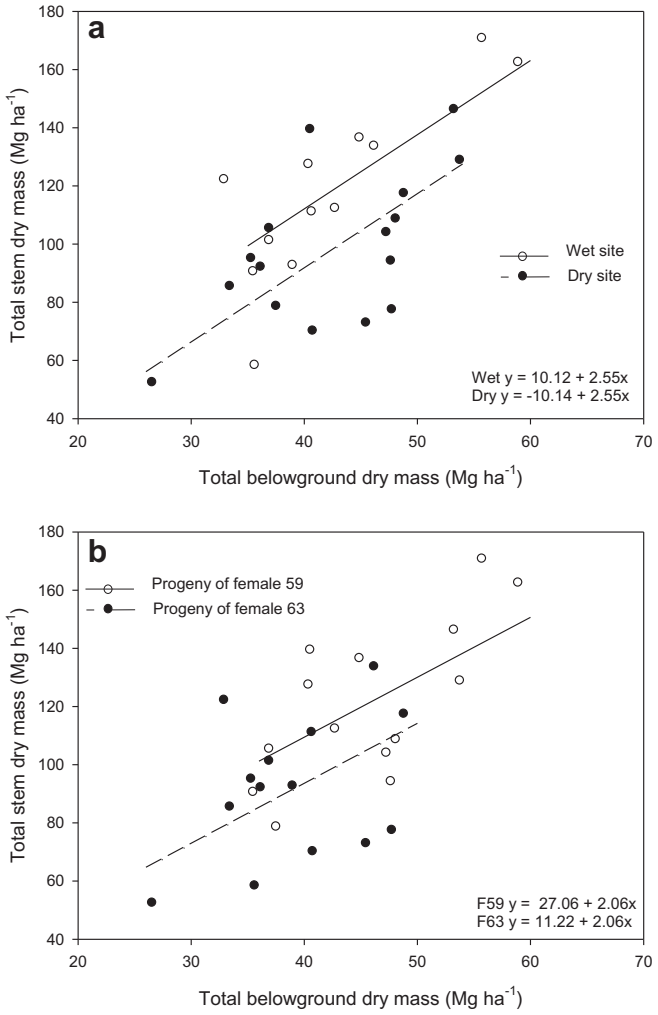

Fig. 7. Covariate analysis of total stem dry mass versus total belowground dry mass by (a) site and (b) female. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

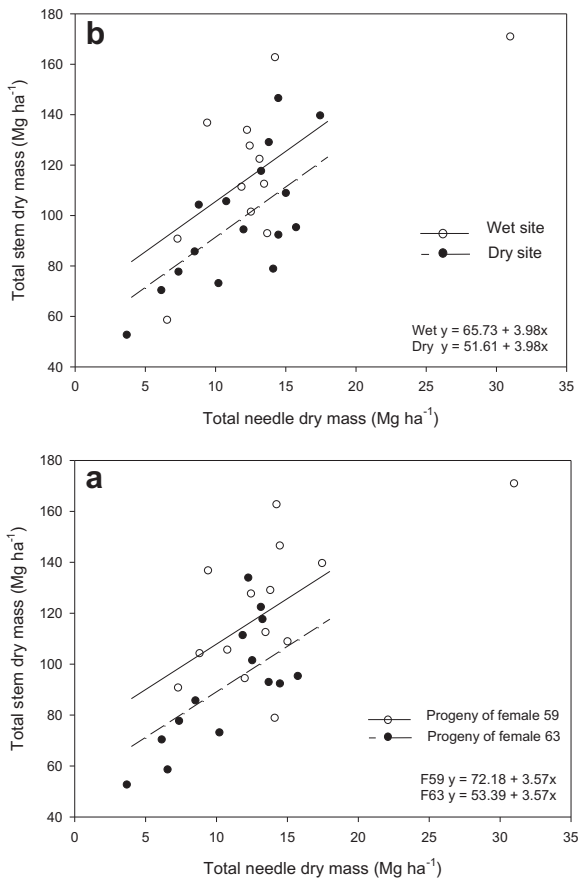

Fig. 8. Covariate analysis of total stem dry mass versus total needle dry mass by (a) site and (b) female. Progeny of female 59 are drought-tolerant families, and progeny of female 63 are drought-intolerant families.

again slightly greater than our values at these respective positions. Clearly, stem bark is not only a greater N pool than stem wood but a significant tree N pool.

4.2. Site effect

There was significantly greater percent N in both bark and wood on the wet site than on the dry site, despite the soil N concentration profile analysis, which showed no significant site or site × depth effects (Major et al., 2012b). In fact, the overall mean N concentration (soil depth 0–50 cm) was slightly greater on the

dry site (0.18%) than on the wet site (0.16%). Interestingly, foliage and roots (fine and small) from the wet site had a greater N percentage than those from the dry site (Major et al., 2012a, 2013), consistent with our bark and wood results. So why the difference in N from different soil moisture levels despite equal soil N for both experiments? It has been found that N assimilation is often impaired under drought stress because of the decrease in ion mobility and, in turn, the diffusion rate via the roots (Chapin, 1991). Thus, drought appears to have a dual negative feedback on growth. First, the direct effect, which is the reduction of cell turgor, which reduces cell expansion and thus growth (Johnsen and Major, 1999; Major and Johnsen, 1999, 2001). Second, the indirect effect of reduced N absorption lowers plant and often total needle area (Chmura et al., 2007; Major et al., 2013). This can reduce net photosynthesis, but our needle N differences were modest, with 1.70% and 1.57% for the wet and the dry site, respectively (Major et al., 2013). There was no difference in needle N between drought-tolerant and intolerant families, and this confirms that family growth and P_n differences were not driven by needle N (Major et al., 2013).

4.3. Density

We found overall mean wood and bark densities were 0.35 and 0.51 g cm^{-3}, respectively, very similar to previously published values for spruce. Englemann spruce (*Picea engelmannii* Parry ex Englelm.) wood and bark densities were 0.35 and 0.49 g cm^{-3}, respectively, according to Brown et al. (1977). Bark's greater density compared with wood held for a number of other species in the report, including lodgepole (*Pinus contorta* Dougl. ex Loud.) and western white pine (*Pinus monticola* Dougl. ex D. Don), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn ex D. Don), but was reversed for Ponderosa pine (*Pinus ponderosa* P. Laws ex C. Laws), Douglas-fir, and western larch (*Larix occidentalis* Nutt.) (Brown et al., 1977). In another species comparative study, wood and bark density were, respectively, 0.37and 0.47 g cm^{-3} for white spruce (Bowyer et al., 2007). From that same study, white pine and western hemlock had greater bark than wood densities; however, for western larch, ponderosa pine, jack pine (*Pinus banksiana* Lamb.), and red pine (*Pinus resinosa* Ait.), bark density measurements were lower than wood density.

A number of studies have shown a modest to substantial negative genetic correlation between wood density and tree diameter growth (*P. mariana*, Zhang and Morgenstern, 1995; *Picea glauca*, Corriveau et al., 1987, 1991; *P. sitchensis*, Cameron et al., 2005; *P. abies*, Grans et al., 2009; *P. sylvestris*, Fries, 2012; *P. radiata*, Baltunis et al., 2010). However, other studies have found slightly negative or non-significant genetic correlation between tree diameter growth and wood density (*P. pinaster*, Bouffier et al., 2009; Gaspar et al., 2009; *P. sylvestris*, Gort et al., 2009; some black spruce tests, Weng et al., 2011). What is interesting in our results is that, on the wet site, the faster growing families had lower wood density than slower growing families, as might be expected; however, on the dry site, faster growing drought-tolerant families had the same wood density as the slower growing drought-intolerant families. Generally, growth traits (diameter and branch size) tend to have stronger G × E than other traits (density and branch angles) (Baltunis et al., 2010; Gapare et al., 2010, 2012). On the wet site, compared with the drought-intolerant families, the reduction in wood density (−3.2%) by the faster growing drought-tolerant families is more than offset by the increase in volume (+36.5%), resulting in 29.3% greater stem wood mass. However, the volume gain of the faster growing families on the dry site (41.4%) is largely captured in terms of mass (39.2% more), as the wood density was almost the same for both faster and slower growing families. These studies indicate that G × E in both growth and wood density need to be considered in order to optimize deployment. As might be expected, bark volume was greater (+35.1%) for the faster growing, drought-tolerant families than the slower growing, drought-intolerant families on the dry site, and the bark density was lower (−7.4%) for the faster growing families than the slower growing families, resulting in an overall greater bark mass (+21.9%) for the faster growing families. Bark volume was greater (+31.8%) for the faster growing families than the slower growing families on the wet site, but there were no differences in bark densities, thus approximately the same bark mass difference was found between families.

4.4. Total stem mass in relation to belowground biomass

Root mass makes up between 20% and 40% of total tree mass (Brunner and Godbold, 2007). Above- and belowground development are linked in a biophysical model of resource transport (West et al., 1999). Few studies have completely excavated mature tree roots of northern conifers. Haynes and Gower (1995) uprooted seven red pine trees, Ostonen et al. (2005) uprooted seven 40-year-old Norway spruce trees, and Steele et al. (1997) empirically estimated fine roots of jack pine and black spruce, but had to estimate coarse root biomass using allometric equations from another species. Albaugh et al. (2006) found some loblolly genetic (provenance) variation where a coastal family on a coastal site produced less root mass per unit stem mass in agreement with Bongarten and Teskey's (1987) observations with seedlings. Interestingly, our drought-tolerant families partitioned 16 Mg ha^{-1} more mass to stem per Mg of total root mass than did the drought-intolerant families. This is surprising, and suggests that these families tolerate drought better despite less root mass. It should be noted that drought-tolerant families also had a greater foliage to fine root (<2 mm) ratio than intolerant families, which were 3.8 and 2.6, respectively (Major et al., 2012a). The ability of drought-tolerant families to maintain greater stem mass to belowground mass and foliage to fine root mass ratios is associated with earlier findings that these families generate lower osmotic potential and greater turgor and display greater photosynthesis and lower ^{13}C discrimination than drought-intolerant families (Major and Johnsen, 1996, 1999, 2001; Johnsen et al., 1999).

For a number of studies with loblolly pine, which exhibited family and site differences in aboveground components, the stem to root partitioning ratio was fairly consistent across families, sites, and spacing (Retzlaff et al., 2001; Albaugh et al., 2006; Samuelson et al., 2008). However, we found black spruce trees on the wet site had partitioned approximately 20 Mg ha^{-1} more stem mass per Mg of root mass than trees on the dry site. Our stem to root mass slope was 2.6 across both sites; in Albaugh et al. (2006), loblolly pine stem to root mass ratio was 2.0 across three sites, a number of families, tree sizes, and measurement years (R^2 = 0.91). The lower stem to root mass ratio for pine than spruce is probably a reflection of pine's adaptations to generally drier conditions than those inhabited by black spruce. In a long-term 39-year-old Norway spruce experiment, control and nutrient optimization treatments had no significant difference in stem to root mass ratio, with an average value of 2.7 (Iivonen et al., 2006), similar to our ratio. Increased nutrient resource availability has been shown to increase partitioning to aboveground net primary productivity and decrease partitioning to total belowground net primary productivity in a number of controlled irrigation × fertilization studies. In their review, Litton et al. (2007) found that water availability changed partitioning similarly, but not as consistently or with nearly the same magnitude as for nutrient availability changes. For water + fertilization treatment, average C partitioning to belowground decreased on average by 60% (mean of two Eucalyptus and two

pine species), mostly by reducing fine roots (Litton et al., 2007), whereas C partitioning increased by 22% to wood and by 11% to foliage.

4.5. Growth efficiency – environmental effect

The ratio of stem mass to foliage mass or area is considered a measure of growth efficiency (Jokela and Martin, 2000; Albaugh et al., 2004; Aspinwall et al., 2013). Although a site or seed source could be considered "efficient", but have low productivity, this productivity measure is in relation to total stem mass, making it an effective measure of efficiency. In our study, allometric analysis showed greater growth efficiency for the wet than the dry site; due to both the effects of differential biomass allocation and greater net photosynthesis (Johnsen and Major, 1995; Major and Johnsen, 1996; Johnsen et al., 1999). The result of the above effects was an average gain of 14 Mg ha^{-1} stem mass for the wet compared with the dry site. The slope of stem mass per unit needle mass was 4.0. Long-term fertilization of 39-year-old Norway spruce did not change the proportion of needle mass (19.5%) or stem mass (44%) (Iivonen et al., 2006). The ratio of stem mass to needle mass for these Norway spruce was 2.3 for both control and long-term nutrient optimization treatments. In 16-year-old loblolly pine after 9 years of treatment, it was found that control, irrigation, fertilization, and irrigation + fertilization had an effect, with stem mass reflecting differences in slope with 1.9, 2.4, 2.7, and 2.9 Mg ha^{-1} per year per unit LAI, respectively (Albaugh et al., 2004). However, it does not appear that they were statistically tested for significant differences nor was an intercept (constant) tested.

Hard pines are sparsely foliated trees compared with densely foliated black spruce, which can retain foliage up to 10 years (Greenway et al., 1992). Albaugh et al. (1998) showed that, in 15-year-old loblolly pine on an extremely well-drained sandy site, LAI crested at approximately two for the control and irrigation-only treatments and plateaued at an average of three for the fertilization and irrigation + fertilization treatments (Albaugh et al., 2004). Productivity for loblolly pine appears strongly linked to an increase in foliage area related to irrigation, fertilization, and genetics (Albaugh et al., 1998; Jokela and Martin, 2000; Chmura et al., 2007; Chmura and Tjoelker, 2008). Thus, for hard pines, it appears that a number of strong positive relationships between aboveground growth and total needle area (or LAI) have been found independent of management intensity or genetics (Albaugh et al., 1998; Samuelson et al., 2004; Will et al., 2005; Chmura et al., 2007).

4.6. Growth efficiency – genetic effects

Growth efficiency was similar for average and superior loblolly families and for slash pine (Chmura et al., 2007). And although Aspinwall et al. (2013) conducted a detailed study using genotypes that varied in stem mass productivity, this variation was not related to growth efficiency, nor was variation in productivity associated with variation in biomass partitioning. Allometric analysis showed our drought-tolerant families had greater growth efficiency than drought-intolerant families. Greater growth efficiency can occur via two main avenues: altered biomass partitioning (seen here) and greater net photosynthesis, which we observed over a previous 3-year period (Johnsen and Major, 1995; Major and Johnsen, 1996) and confirmed independently with ^{13}C analysis (Flanagan and Johnsen, 1995; Johnsen et al., 1999). Thus, in our case, genetic variation in growth efficiency appears to come from both causes and is positively related to productivity. The result was an average of 19 Mg ha^{-1} additional stem dry mass for drought-tolerant families compared with intolerant families after 32 years.

Besides having greater growth efficiency, do our more productive spruce families have more foliage than the less productive families? In this study, where the average LAI was 5.2 and the live crown ratio was approximately 50%—well beyond initial crown closure (Major et al., 2013)—drought-tolerant and intolerant families had total foliage area tree^{-1} of 18.7 versus 16.0 m^2, respectively ($P = 0.063$). However, the greater total needle area of the tolerant families was driven solely by one family, which had 21.4 m^2 tree^{-1} (Major et al., 2013). The other drought-tolerant family had 16.0 m^2 tree^{-1} total needle area, which was the same as both intolerant families. So, our more productive families do not necessarily carry more total foliage. Thus, the role of total foliage area or marginally greater foliage in genetic differences in productivity is inconsistent at best at these high LAI values.

Do more productive individual spruce trees have proportionally more foliage? The stem mass per unit needle mass slope was 3.6 for both drought-tolerant and intolerant families. There were no changes in efficiency with size (no difference in slope). Thus, for black spruce individual trees, the total foliage mass to total stem mass relationship has a significant effect but must be taken with some caveats. Again, marginal gains in total foliage area at these high LAI values may be limited. We do know that mature spruces produce a great deal of foliage compared with other species (see below), which may imply that perhaps spruces produce and retain more foliage than necessary to meet C sink demands. Defoliation experiments with spruce show that productivity can remain the same despite significant loss of foliage due to compensatory effects (Piene, 1991, 1998).

How do these results fit with respect to overall black spruce genetic variation? The area that the parent trees (seed) came from is large (Lake Simcoe-Rideau region in Ontario), and the trees selected were at least 50–100 m from each other to avoid inbreeding effects (Johnsen et al., 2003; Major et al., 2012a). In most cases with northern softwoods, there is much more genetic variation within a population than among populations (Morgenstern, 1996). From this 7 $\times$ 7 diallel, genetic variation was very large, evidenced by the large differences in stem volume and mass of just these four families, which fall within the upper-fifth percentile for family height and ^{13}C discrimination tolerance (Johnsen et al., 1999).

Thus, the sum of our previous investigations on these field experiments, as well as this allometric analysis of mature spruce trees show that 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 due to both genetics and environment. Carbon isotope and tree growth measurements clearly showed productivity was under strong genetic control and highly heritable, and ^{13}C discrimination was highly correlated ($r = -0.97$) to growth for half the diallel, not only the four families studied here. This physiological and biomass allocation variation probably underlies the increases in productivity captured by current tree improvement programs. In addition, growth efficiency appears to provide another effective measure of productivity potential. For our determination of growth efficiency, destructive harvests were labor intensive but, of course, genetic plot-level LAI can alternatively be measured indirectly. Furthermore, it is possible that early assessments of ^{13}C discrimination, a series of gas exchange measurements under varied environmental conditions, and/or the quantification of growth efficiency of seedlings could prove effective for the early selection of stem biomass productivity in black spruce tree improvement programs.

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