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Needle parameter variation of mature black spruce displaying genetic × soil moisture interaction in growth

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Abstract To examine soil moisture stress, light, and genetic effects on individual needle parameters and investigate total needle contribution to productivity, individual and total needle parameter variation were quantified in 32-year-old black spruce from five crown positions from four full-sib families studied previously for drought tolerance and differential productivity on a dry and a wet site. The wet site had greater average needle length (NL), specific needle area (SNA), and needle N concentration (NN) than the dry site. Site differences in NN were most likely driven by soil moisture stress impairing N uptake as soil N was equal at both sites. Drought-tolerant families had greater average needle area (NA), but also greater needle dry mass (NDM), than drought-intolerant families. From the top to bottom crown position, needle parameters showing a linear or near linear increase were NL, SNA, and NN; needle parameters showing a linear decrease were NW, NA, NDM and C:N ratio. For total tree needle area, the wet and dry sites had 18.7 and 16.0 m^2 $tree^{-1}$ (leaf area index (LAI) 5.6 and 4.8), respectively, whereas total needle C mass was not significantly different between sites. Drought-tolerant and intolerant families had a total NA of 18.8 and16.0 m^2 $tree^{-1}$, respectively. However, the greater total NA of drought-tolerant families was driven by one family. Thus, the role of total foliage area at these high LAI values in genetic differences in productivity is inconsistent and most likely low. Therefore, based on a previous 3-year campaign of gas exchange measurements and confirmed independently with carbon isotope analyses, the rate of net photosynthesis is a more important component of site and genetic growth differential in mature black spruce than total needle area.

Keywords Black spruce · Carbon · Crown position · Drought tolerance · Genetic variation · Needle size · Needle mass · Nitrogen · Soil moisture · Total needle area

Introduction

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 affect water relations and needle anatomy (Kramer 1983). In a closed canopy, crown position provides a vertical gradient of light exposure, which can also affect shoot and needle quantity and quality (Niinemets 1997; Niinemets et al. 2001; Richardson et al. 2000). Plant foliage is the primary pathway for carbon and energy capture, and both net photosynthetic rate and total foliage area are integral components of net primary productivity. Although traditional forest genetics research has clearly shown tree genotypes can vary in basic aboveground metrics (height,

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diameter, stem volume), there are few if any mature tree studies—particularly for spruce (*Picea* sp.)—that quantify the combined effects of moisture stress, crown position and genetics on individual and total needle quantity and quality and examine their contribution to productivity. Genetic studies planted on multiple sites allow biological variation to be more accurately partitioned, and thus, environmental effects as well as genetic and genetic × environmental effects can be accurately ascertained.

Spruce 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 % of reforestation activities, with black spruce [*Picea mariana* Mill. (B.S.P.)] alone accounting for 35 %; most of the planted trees result from tree improvement programs (Morgenstern and Wang 2001). To explore the variation among needle parameters, their distribution, and relation to the aboveground variation in productivity and drought tolerance, we used one of the oldest existing black spruce genetic studies planted on multiple sites (Morgenstern 1974). A standard quantitative genetic analysis of an (F1), 7 × 7 black spruce diallel planted in 1973 on three sites in the Petawawa Research Forest indicated an important effects of genotype, environment, and genotype × environment interaction in growth characteristics (Boyle 1987; Major and Johnsen 1996). Four families (2 × 2 breeding structure) that exhibited this interaction in growth between two sites were selected for further examination (Table 1). One female parent (59) produced progeny that displayed relatively high productivity on both sites, whereas the other female parent (63) produced progeny that had high growth rates on one site, but not on another, less productive site (Fig. 1). Multiple lines of evidence clearly show 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 (Brown and Ponce-Hernandez, unpublished). On measurement days just after rainfall, physiological measurements were the same at both sites. Collected on the same dates under drying conditions, predawn xylem water potential, daytime xylem water potential, net photosynthesis (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 carbon isotope (^{13}C) discrimination analysis (Flanagan and Johnsen 1995).

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

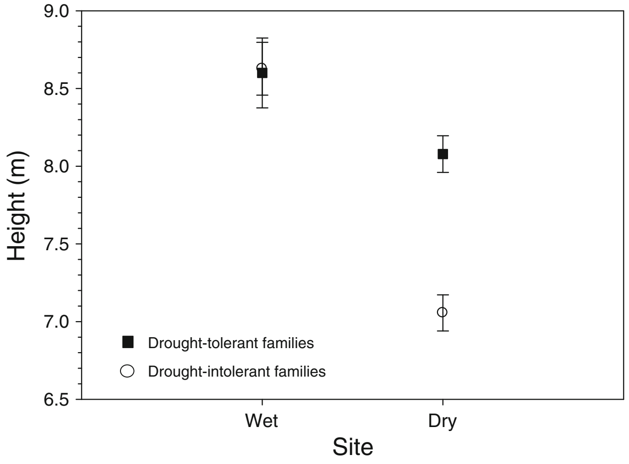

Fig. 1 Height of drought-tolerant and intolerant families (mean and SD) from two sites located at the Petawawa Research Forest, Ontario. Drought-tolerant families are progeny of female 59 (*filled symbols*), and drought-intolerant families are progeny from female 63 (*open symbols*). Dry and moist sites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

Also under drying conditions, it was found that drought-tolerant families generated lower osmotic potential, greater turgor, greater P_n, and lower ^{13}C discrimination than drought-intolerant families (Major and Johnsen 1996, 1999, 2001; Johnsen et al. 1999). Furthermore, half the diallel were measured for ^{13}C:^{12}C, which showed drought tolerance was under strong genetic control, 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). After an exhaustive literature search, we are not aware of any mature conifer species experiments quantifying individual and total needle attributes of drought-tolerant and intolerant families growing on dry and wet sites.

How do site (moisture), crown position (light) and drought tolerance (genetics) affect individual needle parameters? In addition, having shown that the P_n in these black spruce families on a dry and a wet site contributes to differences in productivity, how might total foliage area contribute to overall productivity? Our hypothesis was that drought-tolerant families would have greater total needle area, particularly on the dry site. We also hypothesized that there would be greater total needle area on the wet than on the dry site. Individual and total needle parameter variation were quantified in 32-year-old black spruce from five crown positions from the same four full-sib families studied previously for drought tolerance and differential productivity on a dry and a wet site.

Materials and methods

Plant material and location

A complete 7 × 7 diallel cross black spruce experiment was started at the Petawawa Research Forest (PRF, Latitude 46°N, Longitude 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 two female parent × two 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 spectrums within black spruce as a species.

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. Tree number 1 (corner tree) from each plot was sampled; if it was missing, then the tree in the adjacent corner was sampled. In addition, trees selected were surrounded by live trees on all sides. Trees were cut at the top of the root butt swell. Tree stems were first divided into two downward from the lowest live branch of the bole, which was approximately at half bole. The live crown was further divided into five equal lengths, designated crown position one (top) to position five (bottom). At the time of sampling, basal area was approximately 36 m^2 ha^{-1}, density of 2,900 trees ha^{-1}, and live crown length was approximately 50 %.

Two representative live crown sample branches were removed at the bole from each crown position, and the branch diameter at the bole was measured. All live branches were subsequently removed, and all branch diameters at the bole for each branch >0.5 cm were measured and documented. Two twigs with 1-year-old foliage were randomly sampled from each sample branch and stored in plastic bags at 4 °C. The remainder of each sample branch was put in a paper bag, and samples were dried to 65 °C for 48 h and weighed for needle and shoot dry weight.

All needles from each twig sample were used to determine average fresh needle length (NL), width (NW), and area (NA) using the WinSeedle® program (Régent Instruments, Quebec City, QC, Canada) and an Epson Perfection V700 Photo scanner (at 200 dpi). Needle dry mass (NDM) was measured after oven drying the needles at 65 °C for 48 h. Specific needle area (SNA) was calculated as needle area: needle dry weight (cm^2 g^{-1}). Needle C and N (NN) were determined for each sample using an elemental analyzer (CNS-2000, LECO Corporation, St. Joseph, MI, USA). Needle area: needle N mass (NA:NNM) was calculated as needle area: needle dry mass × N (%). Needle dry mass: needle N mass (NDM:NNM) was calculated as needle dry mass: needle dry mass × N (%).

Calculations

Total tree needle parameters were estimated by scaling up crown positional data. Total needle dry mass and branch diameter from two samples from crown positions 1–4 (total of eight data pairs) for each tree were used to produce a power regression equation $Y = aX^{\mathrm{b}}$ using branch diameter as the independent variable for needle mass (NM) calculation for each individual tree. A separate power regression equation was derived for position five (bottom) because the branch lacked a full complement of needles. Here we pooled across blocks and generated an equation for each family × site combinations. For crown positions 1–4 for the dry site, r^2 ranged from 0.56 to 0.95, and for the wet site from 0.74 to 0.94. For crown position 5, r^2 was much lower due to the high variability of needle retention; it ranged from 0.10 to 0.40. On an average, there were 140 $>$ 0.5 cm diameter branches per tree across families and sites. Estimates of total C, and N mass and area were determined by multiplying needle mass from each crown position with the corresponding average C and N concentration or specific needle area.

Statistical analyses

The ANOVA model for testing individual and total needle parameter includes the following effects: site, crown position, female, and male, which were considered fixed. The ANOVA model used is as follows:

$$Y_{ijklm} = \mu + S_i + C_j + F_k + M_l + \mathrm{SC}_{ij} + \mathrm{SF}_{ik} + \mathrm{SM}_{il} + \mathrm{CF}_{jk} + \mathrm{CM}_{jl} + \mathrm{FM}_{kl} + \mathrm{SCF}_{ijk} + \mathrm{SFM}_{ijl} + \mathrm{CFM}_{jkl} + \mathrm{SCFM}_{ijkl} + e_{ijklm},$$

where Y_{ijklm} is the dependent tree trait of the *i*th site, of the *j*th crown position, of the *k*th female, of the *l*th male, of the *m*th tree. μ is the overall mean, S_i is the effect of the *i*th site ($i = 1, 2$), C_j is the effect of the *j*th crown position ($j = 1, 2, 3, 4, 5$), F_k is the effect of the *k*th female ($k = 59, 63$), M_l is the effect of the *l*th male ($l = 52, 62$) SC_{ij} is the interaction effect of *i*th site and *j*th crown position, SF_{ik} is the interaction effect of *i*th site and *k*th female, SM_{il} is the interaction effect of *i*th site and *m*th male, CF_{jk} is the interaction effect of *j*th crown position and *k*th female, CM_{jl} is the interaction effect of *j*th crown position and *l*th male, FM_{kl} is the interaction effect of *k*th female and *l*th male, SCF_{ijk} is the interaction effect of *i*th site, *j*th crown position, and *k*th female, SCM_{ijl} is the interaction effect of *i*th site, *j*th crown position, and *l*th male, CFM_{jkl} is the interaction effect of *j*th crown position, *k*th female, and *l*th male, $SCFM_{ijkl}$ is the interaction effect of *i*th site, *j*th crown position, *k*th female, and *l*th male, and e_{ijklm} is the random error component.

Owing to the large sample size, low replicates, and recognizing the work necessary to collect individual samples, effects were considered statistically significant at the $\alpha = 0.10$ level, although individual *p* values are provided so that readers can make their own interpretations. A number of traits are measured on the same sample and thus are not completely independent. The general linear model from Systat (Chicago, IL) was used for analysis.

Results

Here, we present the significant and biologically meaningful effects in these sometimes complicated analyses, which include genetic (progeny of female and progeny of male), site, and crown position effects, as well as their interactions. A complete presentation of the four main effects and their interactions of the ANOVA model and the additional quantification documentation are available in the supplementary section of the online version.

Needle-level morphology traits

Average NL was significant for site ($p = 0.080$), crown position ($p < 0.001$), female × crown position ($p = 0.005$), male ($p = 0.017$), and male × site ($p < 0.001$) effects

Table 2 Needle-level morphology trait ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *p* values, and coefficient of determination (r^2)

Source of variation	*df*	Needle length (mm)		Needle width (mm)		Needle area (mm^2)		Needle dry mass (mg)		Specific needle area (cm^2 g^{-1})	
		MS	*p* value	MS	*p* value	MS	*p* value	MS	*p* value	MS	*p* value
Site (S)	1	2.255	**0.080**	0.002	0.597	2.638	0.134	0.259	0.194	83.558	**0.090**
Female (F)	1	0.934	0.257	0.467	**<0.001**	19.463	**<0.001**	3.117	**<0.001**	483.321	**<0.001**
Male (M)	1	4.213	**0.017**	0.063	**0.008**	0.005	0.948	0.414	0.102	123.771	**0.040**
Crown position (CP)	4	6.643	**<0.001**	0.311	**<0.001**	3.816	**0.014**	0.784	**<0.001**	111.811	**0.005**
Site × female	1	0.075	0.748	0.000	0.860	0.001	0.983	0.030	0.889	23.407	0.366
Site × male	1	10.031	**<0.001**	0.031	**0.057**	17.491	**<0.001**	1.288	**0.004**	164.395	**0.018**
Site × CP	4	0.065	0.985	0.004	0.742	0.399	0.846	0.049	0.862	18.690	0.623
Female × male	1	1.158	0.208	0.024	**0.096**	4.522	**0.051**	0.112	0.392	3.451	0.728
Female × CP	4	2.830	**0.005**	0.014	0.170	4.123	**0.009**	0.250	0.170	12.006	0.792
Male × CP	4	0.223	0.871	0.007	0.533	0.524	0.770	0.034	0.924	5.194	0.947
S × F × M	1	0.393	0.462	0.026	**0.080**	0.265	0.633	0.127	0.363	18.124	0.426
S × F × CP	4	0.293	0.803	0.003	0.806	0.565	0.744	0.057	0.825	4.740	0.955
S × M × CP	4	0.647	0.467	0.002	0.891	0.597	0.723	0.040	0.901	14.526	0.728
F × M × CP	4	0.435	0.661	0.009	0.374	1.339	0.333	0.153	0.407	18.221	0.635
S × F × M × CP	4	0.172	0.916	0.008	0.451	0.579	0.735	0.013	0.986	31.344	0.360
Error	100	0.720		0.008		1.155		0.152		28.432	
r^2			0.482		0.712		0.452		0.414		0.382

p values < 0.10 are in bold print

(Table 2). Needle length was 7.8 and 8.1 mm on the wet and dry sites, respectively (Fig. 2a). The difference was fairly consistent (site × crown position $p = 0.985$) over the five crown positions. The female effect was not significant ($p = 0.285$), but female × crown position was significant and it was not due to rank changes but magnitude effects as drought-intolerant female family needles were always longer than tolerant families (the average difference was 0.17 mm) (Fig. 2b). Needle length had a near linear increase from the top to the bottom position of the crown, with 7.4, 7.7, 7.8, 8.3, and 8.6 mm, respectively.

Average NW was significant for female ($p < 0.001$), crown position ($p < 0.001$), male ($p = 0.008$), site × male ($p = 0.057$), female × male (or family) ($p = 0.096$) and site × female × male effects (Table 2). Needle width was nearly identical at both sites at 0.94 mm ($p = 0.597$) (Fig. 2c). Female differences in NW were identical on both sites: 1.00 and 0.88 mm for tolerant and intolerant families, respectively. Drought-tolerant family needles were always wider than those of intolerant families throughout the crown (Fig. 2d). Average NW had a near linear decrease from the top to bottom position of the crown, with 1.08, 1.00, 0.95, 0.89 to 0.80 mm, respectively.

Average NA was significant for female ($p < 0.001$), crown position ($p = 0.014$), site × male ($p < 0.001$), female × crown position interaction ($p = 0.009$) and female × male ($p = 0.051$) effects (Table 2). Although not statistically significant, NA for dry and wet sites was 7.0 and 7.3 mm^2, respectively ($p = 0.134$) (Fig. 3a). Tolerant and intolerant families had 7.5 and 6.7 mm^2, respectively. Similar to NL, female × crown position interaction was the result of magnitude not rank change responses to the change in crown position. However, drought-intolerant families had an NA of 6.5 mm^2 at the top of the crown increased to maximum of 7.0 mm^2 and then declined to 6.5 mm^2 at the bottom position (Fig. 3b), whereas tolerant families had a high NA of 8.6 mm^2 at the top of the crown and there was near linear decline to the bottom of the crown with 6.5 mm^2. The overall NA had a near linear decrease from the top to bottom of the crown, with 7.6, 7.3, 7.1, 7.1 and 6.6 mm^2, respectively, with the wet site greater than the dry site at each crown position, but site was not significant.

Average NDM was significant for female ($p < 0.001$), crown position ($p < 0.001$), and site × male ($p = 0.004$) effects (Table 2). Although not statistically significant but

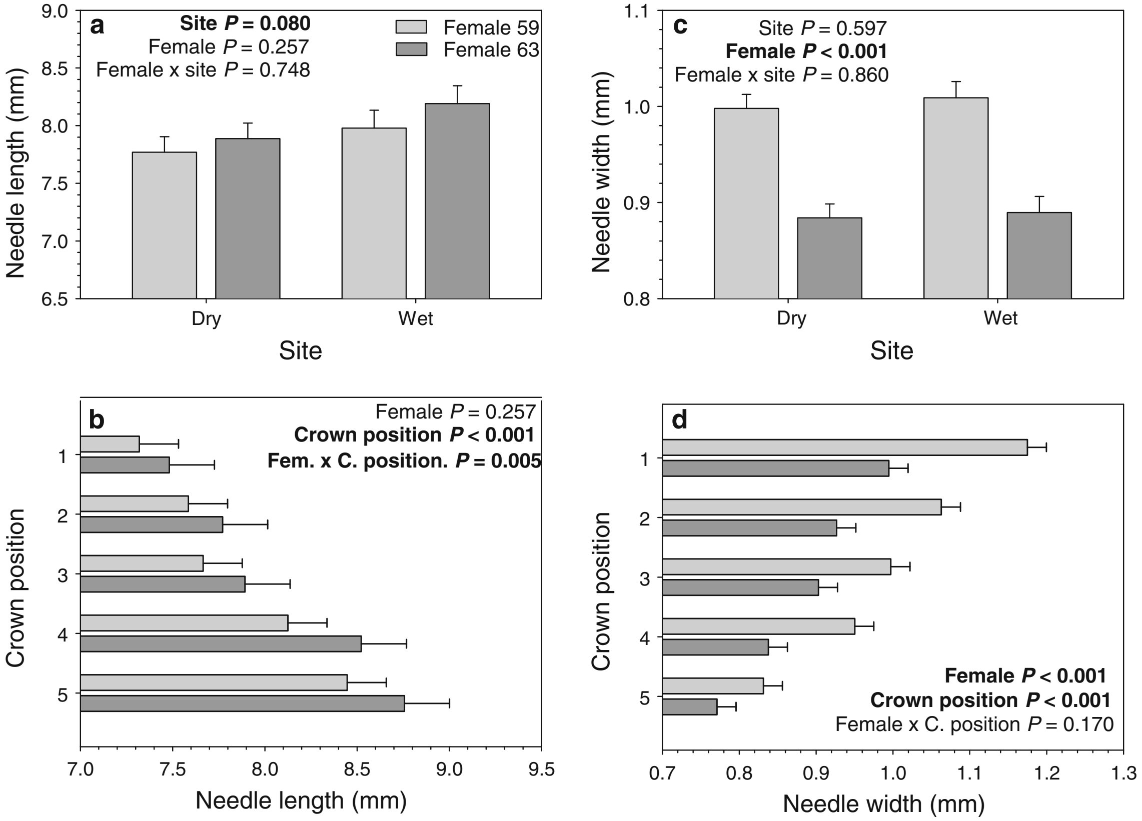

Fig. 2 Average needle length by **a** female × site, and **b** female × crown position. Average needle width by **c** female × site, and **d** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

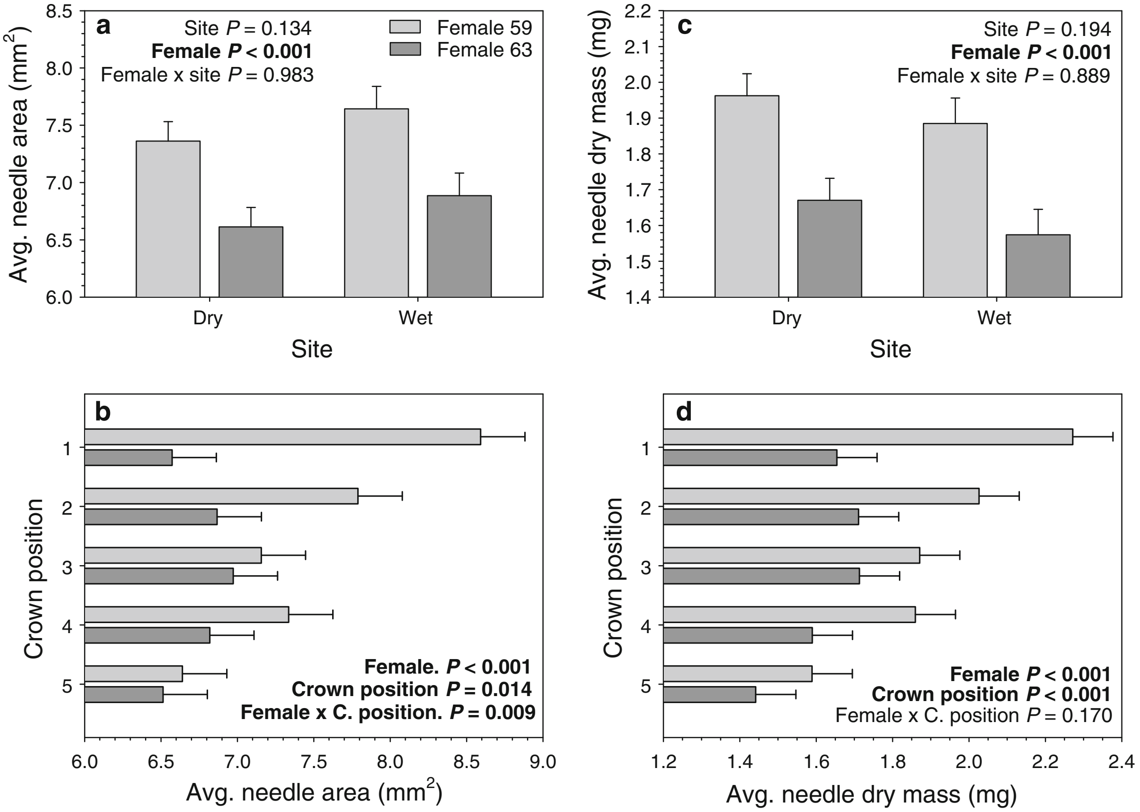

Fig. 3 Average needle area by **a** female × site, and **b** female × crown position. Average needle dry mass by **c** female × site, and **d** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

contrary to average NA results, the dry site had greater NM than the wet site, with 1.82 and 1.73 mg, respectively ($p = 0.194$ (Fig. 3c). Similar to NA results, drought-tolerant and intolerant families NDM were 1.92 and 1.62 mg, respectively. Overall NDM had a near linear decrease from the top to bottom position of the crown, with 1.96, 1.87, 1.79, 1.72, and 1.52 mg, respectively (Fig. 3d).

Specific needle area was significant for site ($p = 0.090$), female ($p < 0.001$), male ($p = 0.040$), crown position ($p = 0.001$), and site × male ($p = 0.018$) (Table 2). The dry and wet sites had 41.7 and 43.3 cm^2 g^{-1}, respectively (Fig. 4a). Tolerant and intolerant families had SNA of 40.6 and 44.4 cm^2 g^{-1}, respectively. Drought-intolerant families consistently had greater SNA than tolerant families across all crown positions (Fig. 4b). Overall SNA increased from the top to bottom of the crown, with 41.0, 41.3, 41.2, 43.4, and 45.7 cm^2 g^{-1}, respectively.

Needle level C and N

Needle C (%) was significant only for site × male ($p = 0.078$) (Table 3). The site × male effect was due to male rank change between sites. Needle C of progeny of male 52 was slightly greater than that of progeny of male 62 on the dry site, with 54.0 and 53.3 %, respectively, and was slightly lower than progeny of male 62 on the wet site, with 53.6 and 54.2 %, respectively. For the record, needle C was 53.7 and 53.9 % for dry and wet sites, respectively ($p = 0.647$).

Needle N (%) was significant for site ($p = 0.008$), male ($p = 0.004$), crown position ($p = 0.077$), site × male ($p = 0.048$), and site × female × male ($p = 0.073$) (Table 3). Overall, the wet and dry sites had 1.70 and 1.57 % NN, respectively (Fig. 5a). Drought-tolerant and intolerant families had on average 1.61 % and 1.65 % NN, respectively, but it was statistically non-significant. From the top crown position, the average needle N was the same for the first two top positions at 1.56 % and then increased to 1.60 % for the middle position and was 1.72 % for the fourth and fifth lower positions (Fig. 5b). The wet site had greater or equal NN than the dry site for each crown position.

Needle C:N ratio was significant for site ($p = 0.026$), male ($p = 0.010$), and crown position ($p = 0.020$) (Table 3). The average needle C:N ratios for the wet and dry sites were 32.8 and 34.8 (Fig. 5c), respectively. From

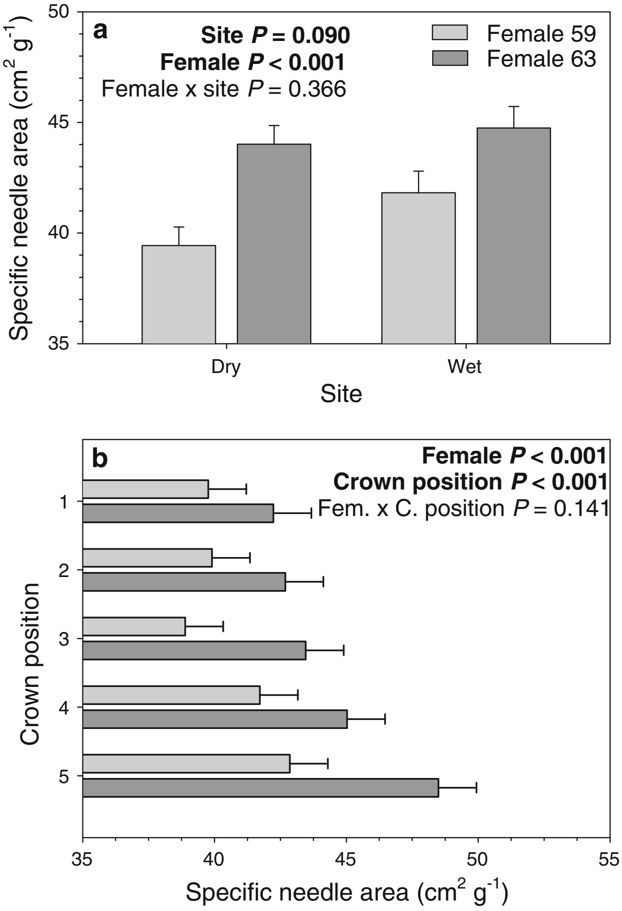

Fig. 4 Specific needle area by **a** female × site, and **b** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

the top crown position, average needle C:N ratios were 35.2, 35.3, 34.5, 32.1, and 31.7 (Fig. 5d).

Per unit needle N mass

Needle area: needle N mass had non-significant site ($p = 0.282$) and crown position effects ($p = 0.677$) but significant female ($p = 0.087$), male ($p < 0.001$) and site × male interaction ($p = 0.027$) and site × female × male ($p = 0.001$) effects (Table 3). Drought-tolerant families had less NA: NNM than intolerant families, with 0.25 and 0.26 m^2 g^{-1} N, respectively (Fig. 6a). This was the only needle variable that did not have a crown position effect (Fig. 6b).

Needle mass: needle N mass was significant for site ($p = 0.014$) and crown position effects ($p = 0.015$), male ($p = 0.006$), and site × male interaction ($p = 0.029$) and site × female × male ($p = 0.018$) effects (Table 3). The dry and wet sites had an NM:NNM of on average 64.7 and 60.9 g mg^{-1} NN, respectively. The top crown position had 65.7 g mg^{-1} NN and ranged to 59.4 g mg^{-1} NN for the bottom position.

Total needle area

Total needle area per tree by crown position was significant for site ($p = 0.081$), female ($p = 0.063$), crown position ($p < 0.001$), and female × male interaction ($p = 0.027$) effects (Table 4). The wet and dry sites had an average needle area of 18.7 and 16.0 m^2 $tree^{-1}$, respectively (Fig. 7a). Drought-tolerant families had greater total needle area than intolerant families, with 18.8 and 16.0 m^2 $tree^{-1}$, respectively. The significant female × male interaction was a result of one particular family (7143), which had 21.4 m^2 $tree^{-1}$, whereas the other three families were similar with approximately 16.0 m^2 $tree^{-1}$ (Fig. 7b). From the top crown position, total needle area increased from positions 1 to 4, with on an average 0.83, 3.43, 4.82, 6.50 m^2 $tree^{-1}$, respectively, and then declined to 1.80 m^2 $tree^{-1}$ for the fifth (bottom) position (Fig. 7c).

Total needle C and N mass

Total needle C mass was significant for female ($p = 0.003$), male ($p = 0.067$), male × site interaction ($p = 0.052$), female × male interaction ($p = 0.028$), and crown position ($p < 0.001$) effects (Table 4). Although not significant, wet and dry sites had 7.1 and 6.3 Mg C ha^{-1}, respectively ($p = 0.148$). Tolerant and intolerant families had 7.6 and 5.8 Mg C ha^{-1}, respectively (Fig. 8a). The female × male interaction was a result of family 7143 (59 × 62) having greater total needle C mass than the other families (Fig. 8b). Total needle C mass increased from crown positions 1 to 4, with 0.33, 1.37, 1.91 and 2.44 Mg C ha^{-1} on average, then declining to 0.6 Mg C ha^{-1} in position 5 (Fig. 8c).

Total NN mass was significant for site ($p = 0.027$) female ($p = 0.008$), male ($p = 0.007$), male × site interaction ($p = 0.010$), female × male interaction ($p = 0.031$), and crown position ($p < 0.001$) effects (Table 4). Wet and dry sites had 227.2 and 184.4 kg N ha^{-1}, respectively (Fig. 9a). Drought-tolerant and intolerant families had 231.7 and 180.0 kg NN ha^{-1}, respectively. Similarly to the total needle C mass, the significant female × male interaction was a result of family 7143 having greater total NN mass than the other three families (Fig. 9b). Total NN mass increased from crown positions 1 to 4, with 9.9, 40.1, 57.5 and 77.5 kg NN ha^{-1} on average, then declined to 20.8 kg NN ha^{-1} in position 5 (Fig. 9c).

Discussion

Site effect

As previously reported (Johnsen and Major 1995, 1999; Major and Johnsen 1996) and discussed above, the primary

Table 3 Average needle elemental property ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *p* values, and coefficient of determination (r^2)

Source of variation	*df*	Needle carbon (%)		Needle nitrogen (%)		Needle C:N ratio		Needle area: needle N^{-1}		Needle mass: needle N^{-1}	
		MS	*p* value	MS	*p* value	MS	*p* value	MS	*p* value	MS	*p* value
Site (S)	1	1.215	0.647	0.544	**0.008**	135.379	**0.026**	2.23×10^{-3}	0.282	477.642	**0.014**
Female (F)	1	4.866	0.361	0.058	0.377	4.962	0.666	5.68×10^{-3}	**0.087**	5.947	0.782
Male (M)	1	0.041	0.933	0.637	**0.004**	181.551	**0.010**	46.21×10^{-3}	**<0.001**	613.057	**0.006**
Crown position (CP)	4	3.206	0.695	0.161	**0.077**	81.262	**0.020**	1.11×10^{-3}	0.677	251.042	**0.015**
Site × female	1	0.580	0.752	0.130	0.188	22.993	0.354	0.79×10^{-3}	0.520	87.709	0.289
Site × male	1	18.246	**0.078**	0.296	**0.048**	64.844	0.121	9.53×10^{-3}	**0.027**	377.909	**0.029**
Site × CP	4	0.215	0.997	0.027	0.832	6.171	0.920	1.50×10^{-3}	0.536	20.905	0.896
Female × male	1	4.299	0.390	0.000	0.946	4.222	0.691	0.23×10^{-3}	0.728	30.787	0.529
Female × CP	4	2.191	0.822	0.006	0.988	0.253	1.000	0.27×10^{-3}	0.967	2.65	0.998
Male × CP	4	2.532	0.780	0.103	0.241	41.125	0.194	2.32×10^{-3}	0.308	117.391	0.201
S × F × M	1	16.917	0.090	0.243	**0.073**	71.716	0.104	22.96×10^{-3}	**0.001**	444.064	**0.018**
S × F × CP	4	2.649	0.765	0.019	0.905	2.773	0.981	0.52×10^{-3}	0.893	15.558	0.937
S × M × CP	4	1.811	0.868	0.052	0.592	10.712	0.806	0.66×10^{-3}	0.844	50.508	0.624
F × M × CP	4	1.906	0.857	0.034	0.768	10.995	0.798	0.69×10^{-3}	0.834	40.788	0.714
S × F × M × CP	4	2.169	0.825	0.034	0.765	7.756	0.883	1.02×10^{-3}	0.708	15.511	0.937
Error	100	5.767		0.074		26.562		1.90×10^{-3}		77.063	
r^2			0.164		0.319		0.292		0.381		0.337

p values < 0.10 are in bold print

difference between sites is water availability. Our results seem to suggest another possible factor, N, influencing site productivity differences, as NN was greater on the wet than on the dry site. This occurred despite the fact that soil N (%) profile analysis of the two sites showed no significant site or site × depth interaction effects (Major et al. 2012b). In fact, the overall mean N (soil depth 0–50 cm) was slightly greater on the dry site (0.18 %) than on the wet site (0.16 %) (Major et al. 2012b). As with the foliage, fine (<2 mm) and small (>2 mm) root analysis from both sites found that roots from the wet site had greater N (%) than those from the dry site (Major et al. 2012a). However, perhaps compensating for this was greater fine and small root dry mass for the dry site compared with the wet site, respectively; resulting in no site difference in total fine and small root N mass, with 43.5 and 43.3 kg ha^{-1}, respectively (Major et al. 2012a). Helmisaari et al. (2007), working with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) over a number of sites, found that a greater C:N ratio of the organic matter (less site N) often results in greater fine root mass.

In a controlled light × soil moisture experiment under equal fertilization, 5-year-old black spruce *average needle N* concentration (traits bolded for discussion clarity) under full sun for irrigated and sustained drought treatments were 1.68 and 1.19 %, respectively (Barsi et al. 2009). Our field experiment did not have sustained drought, but showed the same effect and trend with 1.70 and 1.57 % NN for wet and dry sites, respectively, again despite the soil N levels being equal. So why the difference in NN from different soil moisture levels but equal soil or applied N for both experiments? It has been found that N assimilation is often impaired under drought stress due to 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 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 NN and often total needle area (Chmura et al. 2007). As approximately 75 % of the N in a plant leaf is invested in the chloroplasts (Evans 1989; Chapin et al. 1987), this can reduce P_n (Proietti 2003; Ripullone et al. 2003; Yoo et al. 2003) and thus growth (Gratani and Ghia 2002; Guo et al. 2005). This modest difference at these N levels did not have a detectable impact on P_n at high soil moisture (Johnsen and Major 1995; Major and Johnsen 1996) and is discussed in more detail below in the total tree needle section. The *needle C:N ratios* of the controlled experiment for black spruce under full sun for irrigated and drought stress conditions were 30.6 and 38.1, respectively (Barsi et al. 2009), consistent with our results.

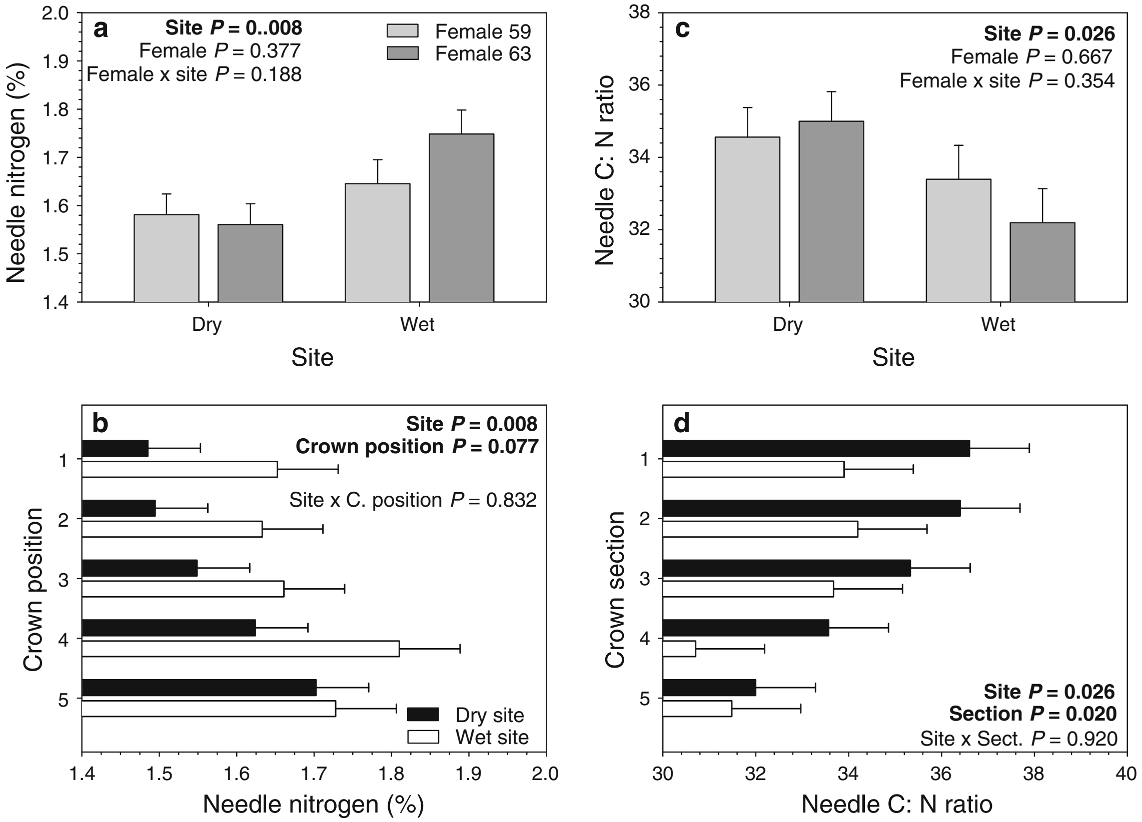

Fig. 5 Average needle nitrogen by **a** female × site, and **b** site × crown position. Average needle C:N ratio by **c** female × site, and **d** site × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

The wet site had a significantly greater *needle length*, no difference in *needle width* and thus slightly larger individual mean *needle area* (not significant) than the dry site. In the controlled drought experiment, black spruce NL under full sun in irrigated and sustained drought treatments was 8.4 and 7.6 mm, respectively (Barsi et al. 2009), consistent with our results. *Picea jezoensis* had lower NL on a dry site than on a well-developed, moister soil (Ishii et al. 2007). Scots pine grown on a fertile site had longer NL than low fertile sites (Niinemets et al. 2001) and Norway spruce grown in elevated CO_2 had longer NL than ambient CO_2 (Pokorny et al. 2011), thus showing a similar response of NL in relation to resource availability. Needle widths under a controlled drought experiment for black spruce were 0.74 and 0.67 mm for irrigated and drought treatments, respectively (Barsi et al. 2009), differing with our results. *Picea jezoensis* on a dry site had lower NW than on a well-developed, moister soil (Ishii et al. 2007). The average NA for black spruce was 5.9 and 5.6 mm^2 ($p = 0.357$) for the irrigated and sustained drought treatments, respectively (Barsi et al. 2009) showing a similar trend with our wet and dry sites, respectively. The lower NA in response to drought has been observed in other conifers (Olivas-Garcia et al. 2000; Ishii et al. 2007) and in relation to reduced fertility (Niinemets et al. 2001).

Black spruce average *needle dry mass* under full sun in controlled irrigated and sustained drought treatments was 1.44 and 1.38 mg, respectively (Barsi et al. 2009). The present study showed an opposite but not significant trend. However, in the controlled drought experiment, NDM increased for red spruce, with 1.25 and 1.31 mg for irrigated and sustained drought treatments, respectively (Barsi et al. 2009). Despite the inconsistent trends for needle dry mass for spruce, it was found that *specific needle area* was significantly greater for irrigated than for sustained drought treatments, with 41.7 and 40.9 $cm^2\ g^{-1}$ in full sun (Barsi et al. 2009), consistent with our field experiment. Mean SNA for black spruce in northern Saskatchewan and Manitoba was somewhat higher, at 58.2 $cm^2\ g^{-1}$ (Bond-Lamberty et al. 2002). They found that well-drained sites compared with poorly drained bogs had higher SNA, but in another well-drained and poorly drained group comparison there was no difference. For *Picea jezoensis*, SNA was lower on a dryer than on a well-developed, moister soil, consistent with our results (Ishii et al. 2007).

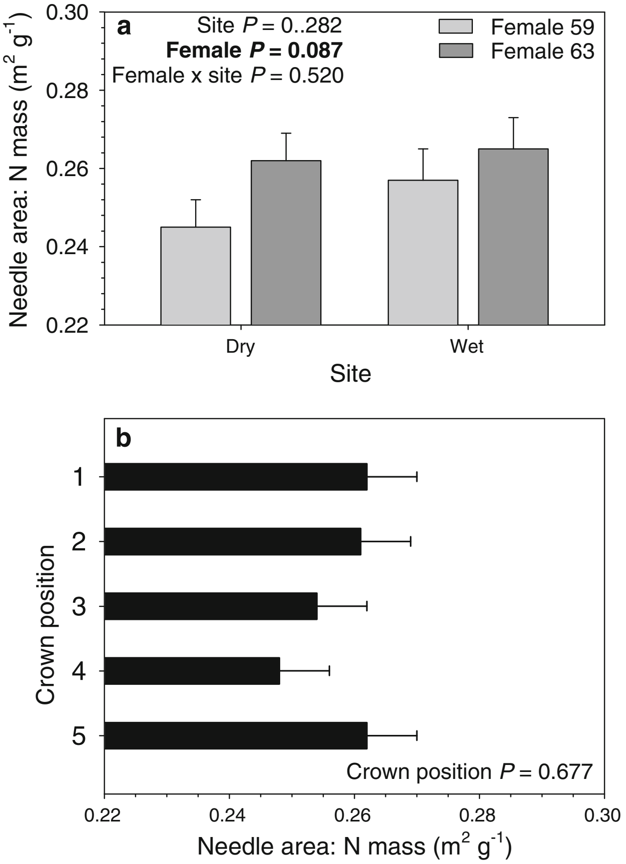

Fig. 6 Average needle area: N g^{-1} by **a** female × site, and **b** crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

Crown position

In the seedling controlled light experiment under equal fertilization, black spruce *needle N* under full sun and shaded (20 % light transmittance) treatments was 1.45 and 2.01 %, respectively (Barsi et al. 2009). Our study showed a near linear NN increase from top to bottom crown position. Often shade-grown seedlings have a greater NN (%) than sun-grown seedlings (Meziane and Shipley 2001; Leal and Thomas 2003; Richardson 2004; Duan et al. 2005). In addition, sun-grown seedlings had a higher C:N ratio, a trait closely related to N use efficiency (NUE), and this is most likely due to higher efficiencies with a limited resource (N) in the context of the greater availability of another resource, light, for sun-grown seedlings. The *C:N ratio* for black spruce in the controlled light experiment were 34.2 and 26.1 for the sun and shade treatments, respectively (Barsi et al. 2009), and our field results showed the same trend across crown positions. Old-growth white pine (*Pinus strobus*) foliage showed a similar trend, with 33.2, 31.0, and 30.5 C:N ratio for top, middle, and lower canopy, respectively (Leal and Thomas 2003).

Needle length and *width* increased and decreased, respectively, from top to bottom crown position. Scots pine grown on a fertile site had a slight but significant reduction in NL from the top to bottom of the crown, but had no crown position difference in the low fertile site (Niinemets et al. 2001). In the controlled light experiment, NL under full sun and shade treatments was 8.0 and 8.1 mm, respectively, showing a small but non-significant trend (Barsi et al. 2009). In the controlled light experiment NW was 0.70 and 0.57 mm for black spruce with sun and shade treatments, respectively (Barsi et al. 2009), showing the same significant trend as our field study. Scots pine grown on fertile and low fertile sites showed a reduction in NW from the top to bottom of the crown (Niinemets et al. 2001). As our NL increased from the top to the bottom, NW decreased proportionally faster, resulting in an overall reduction in NA. *Needle area* also declined in the controlled sun and shaded treatments, with 5.42 and 4.64 mm^2 for black spruce (light $p < 0.001$; Barsi et al. 2009), respectively. Norway spruce NA also declined with canopy position under both elevated and ambient CO_2 treatments (Pokorny et al. 2011). This change in needle NA in response to shade is seen with other conifers (Stenberg et al. 1998, 2001; Robakowski et al. 2003).

In the controlled light experiment, black spruce *needle dry mass* under full sun and shaded treatments was 1.40 and 0.79 mg, respectively (Barsi et al. 2009), consistent with our study from top and bottom crown position. *Specific needle area* increased for Douglas-fir (*Pseudotsuga menziesii*) from the top to the bottom of the crown with 50 to 70 cm^2 g^{-1}, respectively (Ishii et al. 2002), consistent with our study. In the light controlled experiment, SNA under full sun and shaded treatments for black spruce was 41.1 and 58.5 cm^2 g^{-1}, respectively (Barsi et al. 2009). Although calculated inversely, SNA was also greatest at the bottom compared with the top of the crown for all four age classes from 13- to 82-year-old Norway spruce (Merilo et al. 2009). Thus, not only was there more NN and by extension more chlorophyll *a*, chlorophyll *b*, and carotenoids per unit mass (Barsi et al. 2009) in shade-grown seedlings, but also more area per unit weight and total chlorophyll per unit NN, which makes for a more efficient trapping of light energy in a low light environment (Niinemets et al. 2001).

Needle area: needle N mass was one of the few traits that did not show a crown position effect. Thus, there appears to be some economy for this ratio in relation to light levels, although there is genetic variation in this trait. However, NDM:NNM showed a decline with crown position. Thicker needles at the top require more supporting structural carbon due to increased lignification and thickening of needle cell walls (Niinemets 1997).

Table 4 Total needle area and mass ANOVAs, including source of variation, degrees of freedom (*df*), mean square values (MS), *p* values, and coefficient of determination (r^2)

Source of variation	*df*	Total needle area m^2 $tree^{-1}$		Total needle C mass (Mg ha^{-1})		Total needle N mass (kg ha^{-1})	
		MS	*p* value	MS	*p* value	MS	*p* value
Site (S)	1	9.521	**0.081**	0.961	0.148	2512.331	**0.027**
Female (F)	1	10.792	**0.063**	4.251	**0.003**	3659.410	**0.008**
Male (M)	1	4.771	0.214	1.550	**0.067**	3786.862	**0.007**
Crown position (CP)	4	143.037	**<0.001**	20.823	**<0.001**	20417.304	**<0.001**
Site × female	1	0.016	0.943	0.029	0.800	37.245	0.785
Site × male	1	7.522	0.120	1.740	**0.052**	3439.733	**0.010**
Site × CP	4	1.802	0.671	0.214	0.755	316.532	0.640
Female × male	1	15.406	**0.027**	2.236	**0.028**	2379.593	**0.031**
Female × CP	4	0.824	0.897	0.120	0.900	148.421	0.879
Male × CP	4	1.022	0.854	0.293	0.630	489.798	0.422
S × F × M	1	0.026	0.927	0.060	0.717	267.219	0.466
S × F × CP	4	1.370	0.774	0.185	0.802	264.602	0.714
S × M × CP	4	2.287	0.562	0.298	0.622	256.052	0.727
F × M × CP	4	2.207	0.579	0.296	0.625	304.415	0.657
S × F × M × CP	4	3.976	0.275	0.374	0.510	344.694	0.601
Error	100	3.057		0.452		499.682	
r^2			0.690		0.693		0.678

p values < 0.10 are in bold print

Genetic effects

Drought-tolerant families had greater average NW, NA, and NDM than the drought-intolerant families. Drought-tolerant families had greater P_n (per unit area) than intolerant families under drying conditions (Johnsen and Major 1995; Major and Johnsen 1996). Average NA and NDM moved in the same direction, thus not likely affecting gas exchange results. Furthermore, examining the correlation between NA and NDM results showed that there was a very strong relationship between NA and NDM ($r = 0.852$, $p < 0.001$). A P_n analysis comparing black, red, and hybrid spruce, using both NA and NDM, showed the same results (Johnsen et al. 1998).

Does greater NN give drought-tolerant families an advantage over drought-intolerant families? It has been shown that NN can be strongly and positively correlated to total chlorophyll and P_n (Proietti 2003; Ripullone et al. 2003; Yoo et al. 2003; Kayama et al. 2007; Major et al. 2007), and productivity (Gratani and Ghia 2002; Guo et al. 2005; Major et al. 2007). However, drought-tolerant and intolerant families had almost the same NN with 1.61 and 1.65 %, respectively, confirming that there was no N (%) (genetic) relationship to productivity (Johnsen et al. 1999).

This confirms that family growth and P_n differences were not driven by NN. It was found that family photosynthetic differences were driven by water relations; however, not through stomatal-regulated P_n (Johnsen and Major 1995; Major and Johnsen 1996). It was found that drought-tolerant and intolerant families had no differences in P_n under moist conditions on both the dry and wet sites. Moisture stress conditions generated both atmospherically (by vapor pressure deficit stress) and by soil moisture stressors acting together resulted in greater P_n for the drought-tolerant compared with the intolerant families. This was confirmed by measuring needle ^{13}C discrimination. Drought-tolerant families' greater P_n compared with that of intolerant families resulted in greater demand for CO_2, but equal supply (stomatal conductance) of CO_2, resulting in lower internal CO_2 concentration (C_i). This resulted in lower discrimination against the naturally occurring ^{13}C and thus a greater content of ^{13}C in drought-tolerant than intolerant families. ^{13}C discrimination was further tested on half the diallel (21 outcrossed families), which showed families to be under strong genetic control, highly heritable (heritability coefficient = 0.54, highest of all traits measured) for drought tolerance and aboveground productivity (Johnsen et al. 1999). Genetic correlations were very strong: −0.97 between height growth and ^{13}C discrimination.

Does greater P_n drive growth or is it a consequence of the more productive families? The link between P_n (source) and carbon sink (demand) is thought now to be

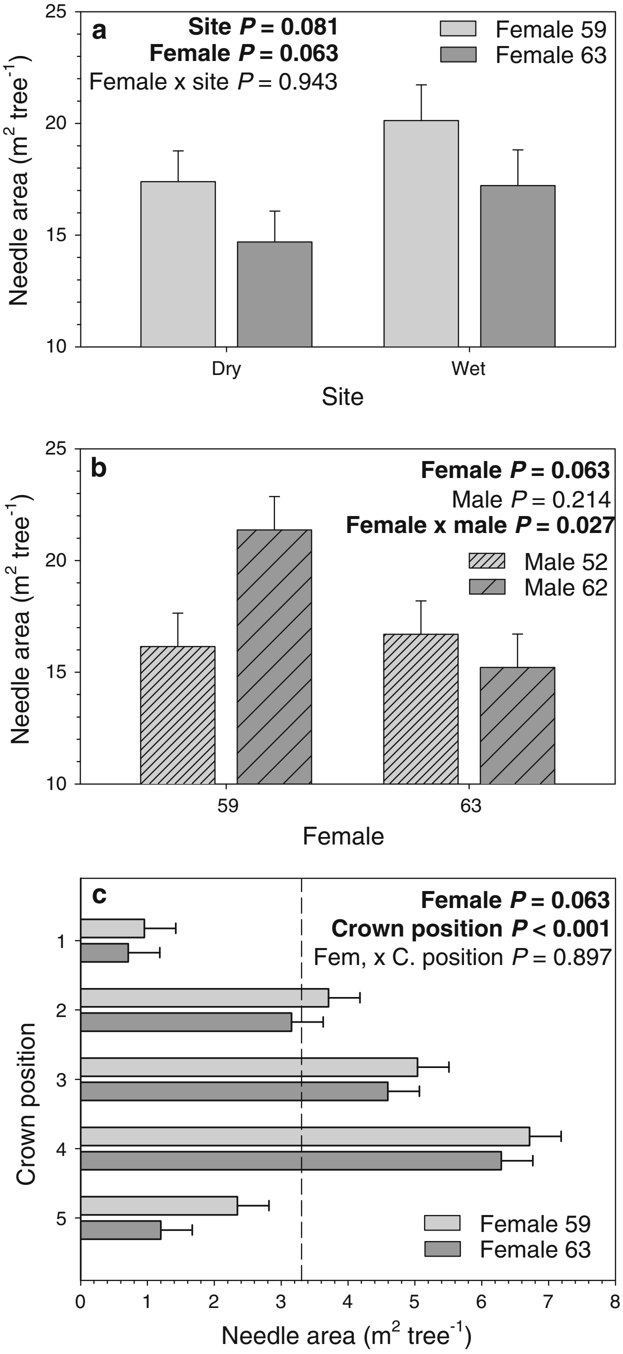

Fig. 7 Total needle area tree^{-1} by **a** female × site, **b** female × male, and **c** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

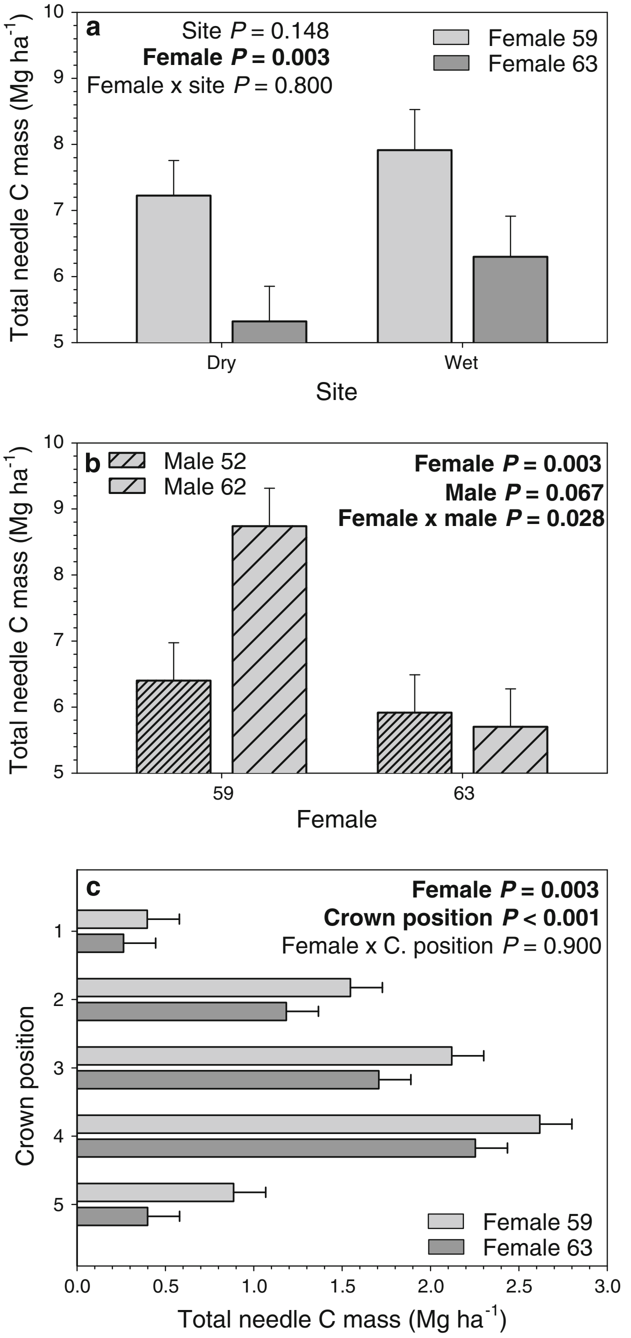

Fig. 8 Total needle C mass by **a** female × site, **b** female × male, and **c** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

largely driven by growth sink and has been empirically supported (Myers et al. 1999; Paul and Foyer 2001; Equiza et al. 2006). In previous work with these families, shoot turgor pressure was correlated to growth in varying degrees. Mean daytime shoot turgor had the weakest ($r = 0.750$), and predawn shoot turgor pressure displayed the strongest ($r = 0.904$) relationship to growth (Johnsen and Major 1999). Lockhart (1965) describes a minimum turgor necessary for cell expansion, also known as cell wall yield threshold, as the pressure level where the cell wall begins to irreversibly expand. These conditions are best found in the predawn and early dawn hours, when turgor is highest and most expected to exceed the cell wall threshold (Randell and Sinclair 1987). Often, daytime turgor is below

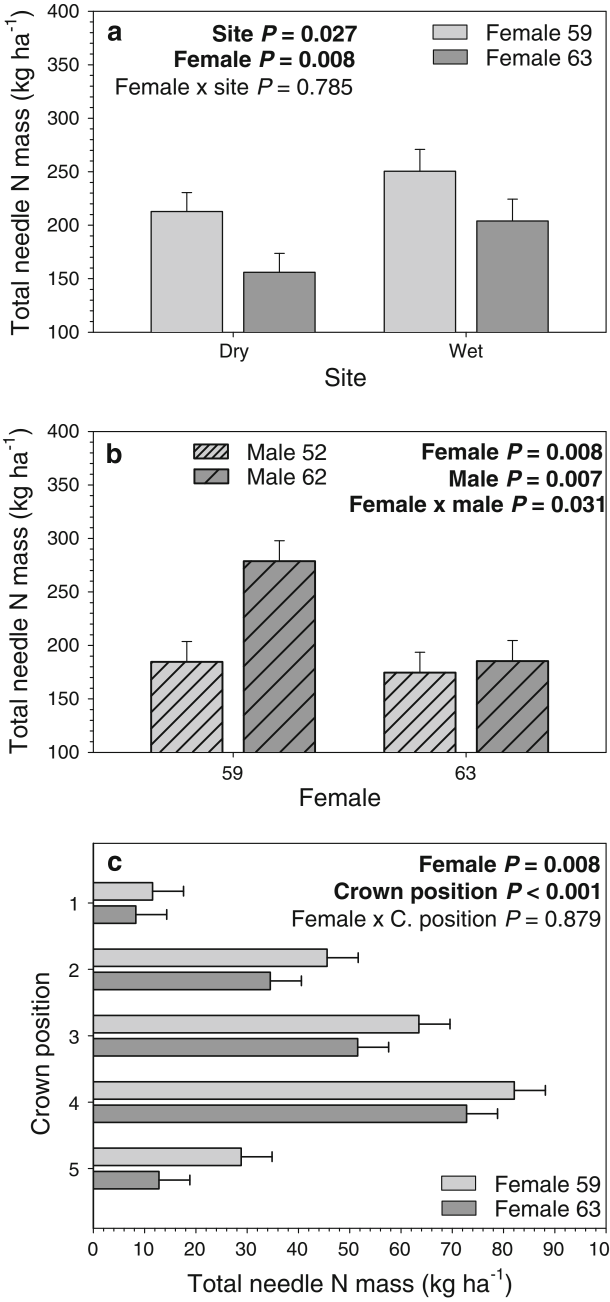

Fig. 9 Total needle N mass by **a** female × site, **b** female × male, and **c** female × crown position. Crown positions range from *top* (*1*) to *bottom* (*5*). Progeny of female 59 are drought-tolerant families and progeny of female 63 are drought-intolerant families

the minimum for growth, but enough to maintain stomatal opening and other physiological processes other than growth. We know that the P_n for black spruce in particular, and perhaps other spruces, directly contributes to differences in productivity, but does the total amount of needle area or mass also contribute to environmental and/or genetic variation in productivity?

Total needle parameters and their relationship to growth performance

A common conceptual equation describes growth as a product of average P_n and total foliage area. The average total NA per tree was 17.3 m^2 and each tree occupied an area of 3.34 m^2, which is equivalent to an average LAI of 5.2. The wet site had a significantly greater total NA per tree than the dry site, with total 18.7 and 16.0 m^2 tree^{-1} ($p = 0.081$), respectively (equivalent to an LAI of 5.6 and 4.8). However, total needle dry mass and total needle C mass did not have statistically significant site differences but had similar trends as total NA with 11.7 and 13.2 Mg ha^{-1} for total needle dry mass and 6.3 and 7.1 C Mg ha^{-1} for total needle C mass, for the dry and wet sites, respectively. In some of the only comparable North American spruce studies, black spruce stands from a northern stand and southern stands in northern Saskatchewan and Manitoba—which were far older (155 and 115 years), had half the DBH (8.5 and 7.1 cm), twice the stand density (5,450 and 5,900 stems ha^{-1}), but similar basal area (BA) (35.6 and 27.2 m^2 ha^{-1})—had estimated average foliage of 4.0 and 5.0 Mg C ha^{-1}, respectively (Gower et al. 1997). Direct estimates of LAI were 4.2 and 5.6 for the northern and southern sites, respectively (Gower et al. 1997). In a chronosequence study, the estimated black spruce LAI from approximately 70-year-old stands in northern Saskatchewan and Manitoba was 6.8 and 3.0 for well- and poorly drained stands, respectively (Bond-Lamberty et al. 2002). From a 59-year-old Norway spruce C budget experiment, control (non-fertilized) total needle dry mass was 4.0 and 7.7 Mg ha^{-1} for current-year and older needles, respectively, for a total of 11.7 Mg ha^{-1} (Ingerslev and Halbacken 1999). Interestingly, the fertilizer treatments of CaMgPS, CaMgPS + NPK, and CaMgP + NPK resulted in 12, 13, and 14 Mg ha^{-1} total dry needle mass, respectively.

There was a compensatory trade-off for fine (<2 mm) and small (>2 mm) root N (%) with fine and small root mass, which resulted in equal total fine and small root N mass for both sites (Major et al. 2012a, b), but this phenomenon does not appear to hold with foliage. Total foliage dry mass was statistically equal for the dry and wet sites, respectively, but NN (%) was lower on the dry than wet site, resulting in statistically lower total NN mass for the dry than the wet site, with 184.4 and 227.2 kg ha^{-1} ($p = 0.027$), respectively. This was comparable to a 59-year-old Norway spruce budget experiment: control (non-fertilized) needles had 48 and 100 kg ha^{-1} total NN mass for current and older needles, respectively, for a total of 148 kg ha^{-1} NN (Ingerslev and Halbacken 1999). In addition, the fertilizer treatments of CaMgPS, CaMgPS + NPK, and CaMgP + NPK resulted in 150, 180, and 200 kg ha^{-1} total NN mass, respectively.

Do more productive spruce families allocate more mass to foliage? On the surface, it appears that way, as drought-tolerant families had greater total NA than intolerant families with 18.8 vs. 16.0 m^2 total foliage area $tree^{-1}$, respectively ($p = 0.063$). However, the greater total NA of the tolerant families was driven solely by one family (7143 = 59 × 62), which had 21.4 m^2 $tree^{-1}$. The other drought-tolerant family, 7122 (59 × 52), had total NA 16.0 m^2 $tree^{-1}$, which was the same as both intolerant families (Fig. 7b). Thus, it is inconclusive whether leaf allocation contributes to differences in productivity, particularly at these high LAI values. We do know that 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 sink demands. Defoliation experiments with spruce show that the productivity can remain the same despite significant loss of foliage due to compensatory effects (Piene 1991, 1998). Thus, for black spruce, the total foliage area relationship to total carbon gain is inconclusive, and marginal gain in total foliage area at these high LAI values and its contribution to total productivity are probably minor or nonexistent.

Hard pines typically have much lower LAI values or needle dry mass than spruces. Direct estimates of LAI for overmature (age) jack pine (*Pinus banksiana*) from the same north and south areas of black spruce in northern Saskatchewan and Manitoba were 2.4 and 2.2 for northern and southern sites, respectively (Gower et al. 1997). A 70- to 80-year-old lodgepole pine (*Pinus contorta*) study on a dry and wet site found 4.9 and 7.5 Mg ha^{-1}, respectively, in foliage dry mass (Comeau and Kimmins 1989). After 4 years of irrigation and fertilization treatments of 8-year-old loblolly pine (*Pinus taeda*) planted (2.5 × 3 m spacing) on a sandy site, it was found that irrigation increased LAI by 16 %, but fertilization increased LAI by 101 % (Albaugh et al. 1998). The foliage dry mass was 3.0, 3.5, 5.7 and 6.9 Mg ha^{-1} for control, irrigation, fertilization, and irrigation with fertilization, respectively with concurrent increase in productivity. A follow-up to Albaugh et al. (1998) showed that, in 15-year-old loblolly pine, LAI crested at two for the control and irrigation-only treatments and plateaued at an average of three for the fertilizer and irrigation-and-fertilization treatments (Albaugh et al. 2004). Therefore, productivity for loblolly pine appears strongly linked to an increase in foliage area related to irrigation, fertilization, and genetics (Albaugh et al. 1998, Chmura et al. 2007, Chmura and Tjoelker 2008).

It would appear that, in mature spruces, in contrast to pine, photosynthetic rates have a stronger contribution to overall productivity than does total foliage area. As discussed above, loblolly pine and most hard pines are sparsely foliated trees compared with the densely foliated black spruces, which can retain foliage up to 10 years (Greenway et al. 1992; Kayama et al. 2007). Differences in leaf-level P_n between slash pine (*Pinus elliottii*) and loblolly pine are mixed. Some have found no significant differences in P_n (Will et al. 2001; Chmura and Tjoelker 2008). However, McGarvey et al. (2004) found 14 % greater P_n for slash than loblolly pine, but when corrected for total foliage area, total canopy P_n was slightly greater for loblolly pine. Thus, for hard pines, it appears that a number of positive relationships between aboveground growth and total NA (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). In contrast, it appears that differences in the rate of P_n for black spruce, in particular, and perhaps other spruces, directly contributes to differences in productivity, and total needle area is a minor influence on productivity, particularly at high LAI.

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