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Branchlet nutrient concentration in hoop pine (*Araucaria cunninghamii*) relative to family, stable carbon and oxygen isotope ratios and growth rate in contrasting environments

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Summary Genetic variation in branchlet nutrient (N, P, K, Na, Ca, Mg, Mn and Fe) concentrations and mineral concentration (sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations) of 8–9-year-old hoop pine (*Araucaria cunninghamii* Ait. ex D. Don) half-sib families was assessed for four canopy positions at a wet site (23 families) and two canopy positions at an N- and water-limiting dry site (22 families) in relation to tree growth and associated branchlet carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope composition in southeast Queensland, Australia. Branchlet nutrient and mineral concentrations varied significantly among families and with canopy position and site. Depending on the canopy position sampled, the hoop pine family effect accounted for 0 to 13.8% of the total variation in branchlet N concentration, and for 0 to 30.3% of the total variation in branchlet mineral concentration at the wet site. The corresponding values for the family effect at the dry site were 0–13.3% for branchlet N concentration and 0–25.7% for branchlet mineral concentration. There were significant variations in branchlet P, K, Ca and Mg concentrations at both sites, and these variations differed with canopy position. Relationships between family means of branchlet N concentration and tree growth or $\delta^{13}C$ or $\delta^{18}O$ varied with canopy position at both sites. At the wet site, there were significant positive correlations between branchlet mineral concentration in the upper-outer or upper-inner canopy and tree height ($r = 0.26$ and 0.37, $P < 0.01$) and between branchlet mineral concentration and $\delta^{13}C$ ($r = 0.24$, $P < 0.01$) in the upper-inner canopy, and a significant negative correlation between branchlet mineral concentration and $\delta^{13}C$ ($r = -0.21$, $P < 0.05$) in the upper-outer canopy. At the dry site, branchlet mineral concentrations in the upper-inner and upper-outer canopy were significantly correlated with branchlet $\delta^{13}C$ ($r = -0.28$ and -0.51, $P < 0.01$), and branchlet N concentration in the upper-inner canopy was significantly correlated with tree growth ($r = 0.29$, $P < 0.01$). A significant correlation between branchlet $\delta^{18}O$ (an index of stomatal conductance) and branchlet mineral concentration at the dry site ($r = 0.39$, $P = 0.020$) indicated that stomatal conductance might be a factor regulating the variation in branchlet mineral concentration of the hoop pine families. Both branchlet N concentration and mineral concentration at particular canopy positions assist in selecting hoop pine families with improved tree growth and N- and water-use efficiency in environments where both N deficiency and a limited water supply are major factors affecting plantation productivity.

Keywords: carbon isotope composition, oxygen isotope composition, stomatal conductance, water-use efficiency.

Introduction

Improved understanding of the relationships among foliar nutrient concentrations, water-use efficiency and growth of tree species and genotypes under contrasting environmental conditions is necessary to assess the potential use of physiological indices in tree breeding programs. Significant relationships between tissue concentrations of a range of nutrients and tree growth have been demonstrated for several species in the field (Pereira et al. 1989, Snowdon and Benson 1992, Nilsson and Wiklund 1994, 1995, Paques 1994, Wang and Klinka 1997), for particular soil types (Bergmann et al. 1994, Dreshel and Zech 1994, Stuhrmann et al. 1994, Turvey and Smethurst 1994), under fertilization (Goddard et al. 1976, Schonau 1981, Judd et al. 1996) and other site management conditions (Kennedy 1993, Smith et al. 1994), and under laboratory conditions (Ericsson 1981, Ericsson and Ingestad 1988, Goransson 1993). Genotypic differences in nutrient accumulation and nutrient requirements have also been considered (Jones and Curlin 1968, Li et al. 1991, Hawkins 1992, Bal and Toky 1995, Schmidtling 1995, Cornelius and Mesen 1997, Gonzalez and Fisher 1997, Karim and Hawkins 1999). The significant genetic variations observed in these studies indicate that forest productivity on infertile soils could be improved not

only by application of fertilizers, but also by employing genotypes with certain physiological characteristics such as efficient uptake and utilization of mineral nutrients (Goddard and Hollis 1984, Evans 1999).

Foliar nutrient concentration is a good indicator of nutrient stress in many tree species; however, there can be large differences in nutrient concentration within a tree canopy (Helmisaari 1992, Kennedy 1993, Amir et al. 1996, Saur et al. 2000). An important consideration is the selection of a suitable canopy position for determination of foliar nutrient concentrations, particularly for studies of genetic variation in canopy nutrient concentration. The need to standardize methods of foliar nutrient analyses with respect to leaf position has been noted (Kennedy 1993, Amir et al. 1996, Zhang and Allen 1996). Most studies, however, have examined only one canopy position, usually the upper crown (Xu et al. 1995, 2000*b*, Cornelius and Mesen 1997, Gonzalez and Fisher 1997), or a composite sample of foliage from the whole crown (Wisniewski et al. 1997). Several studies have identified positions other than the upper crown as being suitable for foliar nutrient analyses (Zhang and Allen 1996, Jayamadhavan et al. 2000, Xu et al. 2000*b*, Huett et al. 2001). Genetic effects of tree species on foliar nutrient concentrations may vary widely and be a function of canopy position and growth environment, but there is little published information about such effects.

There is evidence of a significant decline in soil nitrogen (N) fertility on second rotation sites in hoop pine (*Araucaria cunninghamii* Ait. ex D. Don) plantations of southeast Queensland, Australia (Bubb 1996, Xu et al. 2002). The deployment of genetic material with enhanced growth potential and high nutrient demand has exacerbated the problem. Inadequate water is another factor limiting the productivity of second-rotation hoop pine plantations (Bubb et al. 1998, Xu et al. 2002). Because hoop pine plantations are grown on a range of soil types, a better understanding of genetic effects on the demand for and uptake of nutrients by trees could be of economic benefit.

There have been several studies on the interactions between tree nutrition, water-use efficiency (WUE), gas exchange and tree growth (Brix 1972, Linder et al. 1987, Hogberg et al. 1993, Guehl et al. 1995). In related work on hoop pine, Prasolova et al. (2000*a*, 2001) examined environmental and family relationships among canopy carbon isotope composition ($\delta^{13}C$) as an indicator of WUE, oxygen isotope composition ($\delta^{18}O$) as an index of stomatal conductance (Farquhar et al. 1998), and tree growth. In this study, we evaluated family relationships between mean branchlet nutrient concentrations and mean branchlet $\delta^{13}C$ and $\delta^{18}O$, and tree growth at dry and wet sites differing in soil fertility. Our objectives were to (1) quantify the genetic variation in foliar nutrient concentration at different canopy positions of 8–9-year-old, open-pollinated hoop pine families in a progeny test; (2) analyze branchlet nutrient concentration–growth relationships for different canopy positions at a wet and a dry site; and (3) assess the relationships between canopy nutrient concentrations and branchlet $\delta^{13}C$ and $\delta^{18}O$. We also discuss canopy nutrient concentration as a basis for selecting hoop pine families with high nutrient-use efficiency and WUE. We speculate that planting such families in nutrient- and water-limiting environments of subtropical Australia will enhance plantation productivity.

Materials and methods

Experimental sites

We used two hoop pine (*Araucaria cunninghamii*) progeny trials located in southeast Queensland, Australia. The climate at the sites is subtropical, with hot moist summers (mean temperatures of 25–27 °C in January) and mild, relatively dry winters (mean temperatures of 13–15 °C in July). The wet site is located in the Imbil State Forest (26°28′ S, 152°37′ E) with annual rainfall between 495 and 1964 mm (mean of 1188 mm). The dry site is located in the Yarraman State Forest (26°50′ S, 151°59′ E) with annual rainfall between 386 and 1418 mm (mean 814 mm). The annual rainfall recorded for the experimental period 1986–1997 at both sites is shown in Figure 1. Both sites are on a red-brown clay loam, with a 10 to 20° slope. Soil chemical properties (0–10 cm) at the wet site are: pH (1:5 H_2O) = 6.49, total N = 0.285%, organic C = 4.20%, cation exchange capacity (CEC) = 38.4 cmol kg^{-1} and available P = 20 mg kg^{-1}; and at the dry site are: pH (1:5 H_2O) = 6.16, total N = 0.190%, organic C = 2.96%, CEC = 26.5 cmol kg^{-1} and available P = 25 mg kg^{-1} (see Prasolova et al. 2000*b*).

Experimental design

The progeny trials were established in November 1987 and consisted of 42 families. In November 1987, approximately 2-year-old container-grown seedlings of the 42 hoop pine families were transplanted from the nursery to the field at both sites. Site preparation and establishment management (including weed control) were in accordance with operational forestry practices in southeast Queensland (cf. Xu et al. 2002).

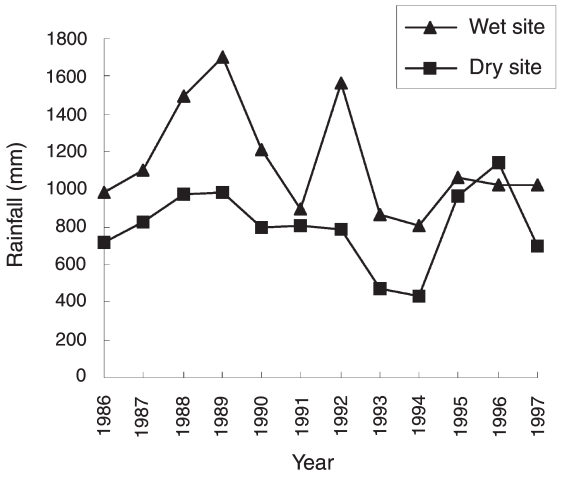

Figure 1. Annual rainfall recorded for both wet (Imbil State Forest) and dry (Yarraman State Forest) sites during the experimental period 1986–1997.

The open-pollinated (half-sib) families selected were a subset of the southern population of hoop pine (provenances collected from Noosa, Imbil and Gympie areas) of Breeding Population No. 1, Queensland Forestry Research Institute. A randomized complete block design was used. Six blocks were sampled at the wet site and five at the dry site. There was one replication per family per block, and single tree plots. Block area was 0.0378 ha.

A subset of 23 half-sib families at the wet site and a subset of 22 half-sib families at the dry site were selected for measurement of branchlet nutrient concentrations, $\delta^{13}C$ and tree growth. A subset of the trees (14 open-pollinated families in three blocks) was selected from both trials for measurement of branchlet $\delta^{18}O$. Detailed sampling procedures, analyses and results for the branchlet $\delta^{13}C$ and $\delta^{18}O$ have been reported elsewhere (Prasolova et al. 2000*a*, 2001). When sampled, mean tree height for the blocks varied from 9.5 to 12.2 m at the wet site and from 7.7 to 9.5 m at the dry site.

Branchlet sampling

The branchlet samples were collected at age 8 years (September 1996) at the wet site, and at age 9 years (April 1997) at the dry site. Branchlets (7–23 cm in length) with mature leaves from four positions (P) at the wet site and two positions (P2 and P3) at the dry site were selected: P1 = uppermost whorl of the tree (top canopy position); P2 = tip of the branch situated about 6 m above ground pointing due north (upper-outer canopy position); P3 = the same branch as for P2, but collected as close to the trunk as possible (the upper-inner canopy position); and P6 = tip of the branch situated about 3 m above ground pointing due north (lower-outer canopy position). All samples were analyzed for branchlet nutrients and $\delta^{13}C$. Only selected samples at P2 for both sites were analyzed for branchlet $\delta^{18}O$. For most trees, the canopies were not closed at the time of sampling. Foliage from branchlets of P3 contained a large proportion of older (darker colored) leaves. On average, branch length was about 2 m at the wet site and 1.5 m at the dry site (but up to 3.5 m). The distance between the sampled trees was 3 m.

Tree height and stem diameter measurements

Total tree height (H) and diameter (D) at 1.3 m above ground were determined at age 8 years.

Branchlet nutrient analysis

Branchlet samples were oven-dried at 65 °C to constant mass and ground to a fine powder with a ring grinder before nutrient analysis. Branchlet N concentration was determined by the Kjeldahl method. Other nutrient concentrations (P, K, Ca, Mg, Mn, Fe, Cu and Zn) were determined as reported by Xu et al. (1995). Mineral concentration (expressed as % of branchlet dry mass) was calculated as the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site, and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

Data analysis

Statistical analyses of the data were performed with STATISTICA (StatSoft, Tulsa, OK). Site, block and family variations in branchlet nutrient concentration were subjected to analysis of variance (ANOVA). Block and family effects were considered random. Relationships between the variables were analyzed by Pearson's correlation. Heritability (h^2) of branchlet nutrient concentration is defined as:

$$h^2 = \sigma_A^2/\sigma_P^2 \quad (1)$$

where σ_A^2 is additive genetic variance in the parameter measured and σ_P^2 is total phenotypic variance. Genetic variance of open-pollinated families (half-sib families) is estimated to be 1/4 of the additive genetic variance of the parent genotype population (van Buijtenen 1992). However, we note that the heritability estimates calculated by Equation 1 are biased upward because the parents of the selected open-pollinated families originated from different breeding populations.

Results

Genetic variation in branchlet nutrient concentration at different canopy positions

Branchlet nutrient concentration differed significantly between hoop pine families at most of the canopy positions sampled (Tables 1 and 2). At the wet site, family variance accounted for 12.6–13.8% of the total variation in branchlet N concentration for the top and upper-inner canopy, 12.6–25.8% of the total variation in branchlet P concentration for the top and upper-outer canopy, and 10.0–30.3% of the total variation in branchlet mineral concentration for the top, upper-outer and upper-inner canopy. At the dry site, family variance accounted for 12.3% of the total variation in branchlet N concentration, 19.2% of the total variation in branchlet K concentration, and 25.7% of the total variation in branchlet mineral concentration for the upper-inner canopy. There was no family effect on branchlet Mn and Fe concentrations for any canopy position at the wet site or on branchlet P, Na, Mn and Fe concentrations for any canopy position at the dry site.

Variation in branchlet nutrient concentrations as a function of height, position on branch, block and site

There were considerable variations in branchlet nutrient concentrations between canopy positions, between blocks and between sites. Branchlet nutrient concentrations showed significant differences between the four sampling positions at the wet site and between two sampling positions at the dry site (Table 3). Branchlets from the top and the upper-outer crown had significantly higher ($P < 0.001$) N concentrations than branchlets from the inner or lower crown (Prasolova et al. 2000*a*, 2001). The upper-inner canopy had the highest branchlet P concentration. No difference in branchlet P concentration was observed between the upper-outer canopy and the lower-outer canopy. Among canopy positions, branchlet K

Table 1. An *F*-test and variance component (VC) of block and family effects for branchlet nutrient concentrations at different canopy positions for 8–9-year-old half-sib hoop pine families at a wet ($n = 23$) and a dry site ($n = 22$). Abbreviations: P1 = uppermost whorl of tree crown; P2 = tip of the branch situated about 6 m above ground pointing due north; P3 = the same branch as for P2, but collected as close to the trunk as possible; P6 = tip of the branch situated about 3 m above ground pointing due north; ns = not significant ($P > 0.10$); and nc = not calculated because the *F*-value was not significant ($P > 0.05$).

Canopy position	Statistics[1]	N (%)		P (%)		K (%)		Mineral (%)[2]	
		Block	Family	Block	Family	Block	Family	Block	Family
Wet site									
P1	*F*-value	4.24	2.05	1.68	1.85	2.06	0.37	2.98	1.64
	P-value	0.001	0.008	ns	0.021	ns	ns	0.015	0.050
	VC (%)	11.2	13.8	nc	12.6	nc	nc	8.1	10.0
P2	*F*-value	10.30	1.60	2.03	3.08	0.60	1.15	8.53	4.36
	P-value	< 0.001	ns	ns	< 0.001	ns	ns	< 0.001	< 0.001
	VC (%)	27.8	nc	nc	25.8	nc	nc	18.1	30.3
P3	*F*-value	8.38	2.09	3.92	0.64	1.66	1.57	12.75	3.13
	P-value	< 0.001	0.007	0.003	ns	ns	ns	< 0.001	< 0.001
	VC (%)	22.6	12.6	11.9	nc	nc	nc	29.6	19.9
P6	*F*-value	5.18	1.16	0.33	1.17	4.73	1.41	11.88	1.12
	P-value	< 0.001	ns	ns	ns	< 0.001	ns	< 0.001	ns
	VC (%)	22.0	nc	nc	nc	19.9	nc	43.3	nc
Dry site									
P2	*F*-value	19.62	0.74	5.50	0.58	3.84	0.81	5.76	1.24
	P-value	< 0.001	ns	< 0.001	ns	0.007	ns	< 0.001	ns
	VC (%)	51.6	nc	20.4	nc	14.0	nc	20.8	nc
P3	*F*-value	13.38	1.95	14.43	1.45	3.96	2.10	1.88	2.42
	P-value	< 0.001	0.022	< 0.001	ns	0.006	0.013	ns	0.004
	VC (%)	37.6	12.3	41.6	nc	12.3	19.2	nc	25.7

[1] Degrees of freedom for block and family are 5 and 22 at the wet site, and 4 and 21 at the dry site.

[2] Mineral concentration (%) is the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

Table 2. An *F*-test and variance component (VC) of site, block and family effects for branchlet N, P and K concentrations, and mineral concentration (Mineral) at two canopy positions (P2 and P3) for 8–9-year-old half-sib hoop pine families ($n = 22$) at a wet and a dry site. Abbreviations: P2 = tip of the branch situated about 6 m above ground pointing due north; P3 = the same branch as for P2, but collected as close to the trunk as possible; ns = not significant ($P > 0.10$); and nc = not calculated because the *F*-value was not significant ($P > 0.05$).

Statistics[1]	N (%)			P (%)			K (%)			Mineral (%)[2]		
	Site	Block	Family	Site	Block	Family	Site	Block	Family	Site	Block	Family
P2												
F-value	67.87	11.93	0.99	168.45	3.39	1.24	148.56	2.97	1.07	366.10	3.63	1.45
P-value	< 0.001	< 0.001	ns	< 0.001	0.037	ns	< 0.001	0.048	ns	< 0.001	ns	ns
VC (%)	35.4	15.7	nc	61.9	2.8	nc	59.8	2.5	nc	76.7	nc	nc
P3												
F-value	50.23	4.85	1.61	63.34	9.63	1.18	98.27	4.29	2.02	78.89	3.29	3.32
P-value	< 0.001	0.003	ns	< 0.001	< 0.001	ns	< 0.001	0.011	0.020	< 0.001	0.024	< 0.001
VC (%)	31.2	6.8	nc	34.6	13.8	nc	46.3	4.9	5.8	38.5	3.4	13.4

[1] Degrees of freedom are 1, 4 and 21 for site, block and family, respectively.

[2] Mineral concentration (%) is the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

concentration was highest in the top and upper-outer canopy. Branchlet Ca, Mg, Mn and Fe concentrations and mineral concentration tended to be highest in the upper-inner and lower-outer canopy, with the exception of Mg for which the highest concentration was observed in branchlets from the top canopy. Strong positive family correlations were observed be-

Table 3. Descriptive statistics for branchlet nutrient concentrations at different canopy positions for 8–9-year-old half-sib hoop pine families at a wet (n = 23) and a dry site (n = 22). Abbreviations: P1 = uppermost whorl of tree crown; P2 = tip of the branch situated about 6 m above ground pointing due north; P3 = the same branch as for P2, but collected as close to the trunk as possible; P6 = tip of the branch situated about 3 m above ground pointing due north; and SD = standard deviation.

Canopy position	Statistics[1]	N (%)	P (%)	K (%)	Mineral (%)[2]
Wet site					
P1	Mean	0.83 a[3]	0.133 b	0.83 b	2.67 c
	Minimum	0.55	0.085	0.33	1.87
	Maximum	1.10	0.232	1.85	3.88
	SD	0.11	0.027	0.24	0.34
P2	Mean	0.78 b	0.122 c	0.89 a	2.70 c
	Minimum	0.53	0.083	0.45	1.71
	Maximum	1.07	0.193	1.32	3.45
	SD	0.10	0.021	0.17	0.32
P3	Mean	0.64 d	0.157 a	0.61c	2.92 b
	Minimum	0.44	0.055	0.20	1.81
	Maximum	0.95	0.366	1.13	4.51
	SD	0.09	0.053	0.17	0.52
P6	Mean	0.67 c	0.116 c	0.59 c	3.08 a
	Minimum	0.49	0.063	0.27	2.15
	Maximum	0.87	0.166	1.16	4.34
	SD	0.10	0.024	0.22	0.48
Dry site					
P2	Mean	0.66 a	0.182 b	1.36 a	3.65 a
	Minimum	0.44	0.090	0.78	2.53
	Maximum	1.09	0.335	2.65	4.83
	SD	0.12	0.045	0.35	0.44
P3	Mean	0.56 b	0.245 a	0.88 b	3.55 a
	Minimum	0.41	0.050	0.33	2.66
	Maximum	0.82	0.570	1.75	5.12
	SD	0.08	0.112	0.24	0.50

[1] Number of data for mean mineral nutrient concentration of branchlets sampled at the wet site for P1, P2 and P3 ranged from 122 to 132, and from 85 to 87 for P6; and number of data for mean mineral nutrient concentration of branchlets sampled at the dry site for P2 and P3 ranged from 87 to 101.

[2] Mineral concentration (%) is the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site, and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

[3] Means followed by the same letter within a column at each site are not significantly different ($P > 0.05$) according to the t-test.

tween mean branchlet nutrient concentrations at the different canopy positions (Table 4).

There were also significant differences in branchlet nutrient concentrations among blocks for most nutrients and canopy positions at the wet and dry sites and when ANOVA was performed for both sites (Tables 1 and 2). There were no variations in branchlet Ca and Fe concentrations for the upper-outer and upper-inner canopy positions (data not shown), or for mineral concentration for the upper-inner position at the dry site (Table 1).

There were statistically significant differences in branchlet nutrient concentrations between sites (Table 2). Branchlets from the upper-outer canopy had significantly higher N and Mg concentrations at the wet site, but higher P, K, Na, Ca, Mn and Fe concentrations and mineral concentration at the dry site (data for Na, Ca, Mg, Mn and Fe are not shown). Branchlets from the upper-inner canopy had higher N, Na and Mg concentrations at the wet site, but higher P, K, Ca, Mn and Fe concentrations and mineral concentration at the dry site (data not shown). Branchlet Ca concentrations accounted for 46–62% of the variation in branchlet mineral concentration, depending on canopy position.

Relationships between branchlet nutrient concentrations and $\delta^{13}C$, $\delta^{18}O$ and tree growth

There were significant positive correlations between family means of branchlet nutrient concentrations at four canopy positions at the wet site, and between family means of branchlet N, P, K, Mg and Mn concentrations at two canopy positions at the dry site (Table 4).

There were positive correlations between family means of branchlet Ca and Mg concentrations in the upper-outer canopy at both the wet and dry sites, and between family means of branchlet Ca, Mg and Fe in the upper-inner canopy at both the

Table 4. Correlations between hoop pine family means of branchlet nutrient concentrations (%) at different canopy positions for the wet site (P1, P2, P3 and P6) (n = 23) and for the dry site (P2 and P3) (n = 22). Abbreviations: P1 = uppermost whorl of tree crown; P2 = tip of the branch situated about 6 m above ground pointing due north; P3 = the same branch as for P2, but collected as close to the trunk as possible; and P6 = tip of the branch situated about 3 m above ground pointing due north. Symbols: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; and ns = $P > 0.05$.

Canopy position	P1	P2		P3
	Wet site	Wet site	Dry site	Wet site
N (%)				
P2	0.799***			
P3	0.567**	0.605**	0.572**	
P6	0.429*	ns		0.500*
P (%)				
P2	0.854***			
P3	0.516*	0.642**	0.470*	
P6	0.444*	0.627**		0.622**
K (%)				
P2	ns			
P3	ns	ns	0.518*	
P6	ns	ns		0.567**
Mineral (%)[1]				
P2	0.822***			
P3	0.719***	0.657**	ns	
P6	0.734***	0.509*		0.404*

[1] Mineral concentration (%) is the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

wet and dry sites (data not shown). There was a positive correlation between family means of mineral concentration in the upper-inner canopy at both the wet and dry sites (Figure 2). Branchlet mineral concentration was negatively correlated with branchlet $\delta^{18}O$ in the upper-outer canopy at the dry site (Figure 3).

There were significant positive correlations between branchlet mineral concentration in the upper-outer or upper-inner canopy and H, and between branchlet mineral concentration and $\delta^{13}C$ in the upper-inner canopy, and a significant negative correlation between branchlet mineral concentration and $\delta^{13}C$ in the upper-outer canopy at the wet site (Table 5). Significant negative correlations were found between branchlet mineral concentration in the upper-outer canopy and H or stem diameter at 1.3 m above ground, and between branchlet mineral concentration and $\delta^{13}C$ in the upper-outer and upper-inner canopy positions at the dry site (Table 5). No consistent correlations were found between other branchlet nutrient concentrations at different canopy positions and tree growth or $\delta^{13}C$ or $\delta^{18}O$ (data not shown).

Discussion

Genetic variation in branchlet nutrient concentration

Branchlet nutrient concentrations differed significantly between the hoop pine families for most of the canopy positions sampled at both sites. The genetic effects on branchlet nutrient concentrations were dependent on canopy position at a particular site, and varied between sites for a particular canopy position. Variation in branchlet nutrient concentration in the upper-outer canopy attributable to families was comparable with that reported for the upper crown of other forest species (Knight 1978, Kleinschmit 1982, Gonzalez and Fisher 1996). To our knowledge, our study represents the first attempt to estimate the genetic variation of tree foliar nutrient concentrations at canopy positions other than the upper crown. Significant positive correlations existed between family means of branchlet Ca and Mg concentrations in the upper-outer canopy for both sites, and between family means of branchlet Ca, Mg and Fe concentrations and mineral concentration in the upper-inner canopy, indicating that the ranking of the hoop pine fam-

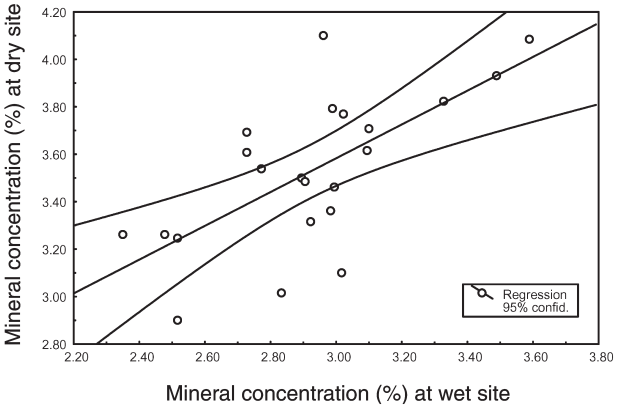

Figure 2. Relationships between family means of branchlet mineral concentration in the upper-inner canopy position (P3) of 8-year-old hoop pine trees at the wet site and those of 9-year-old hoop pine trees at the dry site with correlation coefficient r = 0.672 (n = 22, P = 0.001).

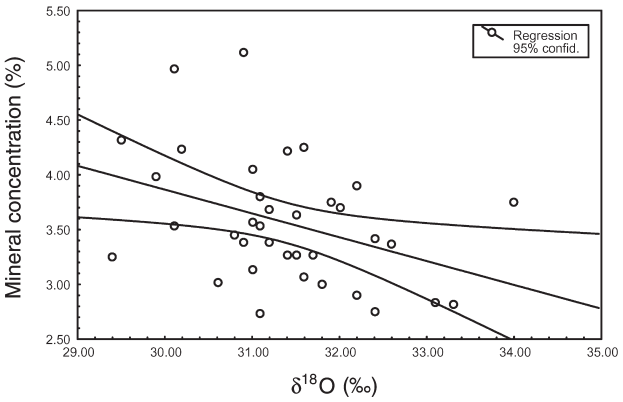

Figure 3. Relationships between branchlet mineral concentration and oxygen isotope composition ($\delta^{18}O$) in the upper-outer canopy position (P2) of 9-year-old hoop pine families at the dry site with correlation coefficient r = –0.385 (n = 36, P = 0.020).

Table 5. Correlations between branchlet mineral concentration (Mineral) at two canopy positions (P2 and P3) and hoop pine tree height (*H*; m), stem diameter at 1.30 m above ground (SD; mm) and carbon isotope composition ($\delta^{13}C$; ‰) at age 8 years for the wet site and at age 9 years for the dry site. Abbreviations: P2 = tip of the branch situated about 6 m above ground pointing due north; P3 = the same branch as for P2, but collected as close to the trunk as possible; and ns = not significant ($P > 0.05$).

Canopy position	Mineral (%)[1]					
	Wet site ($n = 132$)			Dry site ($n = 87$)		
	H	SD	$\delta^{13}C$	*H*	SD	$\delta^{13}C$
P2	0.256 $P = 0.003$	ns	–0.211 $P = 0.015$	–0.264 $P = 0.013$	–0.219 $P = 0.042$	–0.514 $P < 0.001$
P3	0.371 $P < 0.001$	0.335 $P < 0.001$	0.238 $P = 0.007$	ns	ns	–0.281 $P = 0.008$

[1] Mineral concentration (%) is the sum of branchlet P, K, Na, Ca, Mg, Mn and Fe concentrations for the wet site and the sum of branchlet P, K, Na, Ca, Mg, Mn, Fe, Cu and Zn concentrations for the dry site.

ilies for these nutrients was similar between sites. The significant correlations between family means of branchlet nutrient concentrations (with the exception of branchlet K concentration at the wet site) at different canopy positions at both sites provide further evidence of genetic variation in branchlet nutrient concentration in hoop pine families.

The observed differences in branchlet nutrient concentrations between hoop pine families may reflect genetic differences in nutrient uptake, transport and utilization within individual trees among the families. The family effect on branchlet N concentrations at the tree top could be indicative of selective allocation of N to strong sinks at growing points. Developing lateral branches were also strong sinks for C and N, as has been reported for other tree species (Dickson 1989). Nambiar and Fife (1987) found that up to 54% of N in mature *Pinus radiata* D. Don needles was translocated to the developing flush of needles. Thus the observed family effect on branchlet N concentration in the upper-inner canopy, which has a higher proportion of mature foliage, may reflect retranslocation of N at the wet site. Sampling at the wet site was carried out at the beginning of active growth (spring). The negative correlation between *H* and branchlet N concentration might be related to tissue dilution (Xu et al. 1995) or more active retranslocation of N from mature foliage in fast-growing trees than in slower growing trees. At the dry site, correlations between *H* and branchlet N concentration in both the upper-outer and upper-inner canopy were positive, indicating that N was limiting growth. Faster-growing trees may store larger amounts of N than slower-growing trees, and this may have been partially reflected in the family effects on branchlet N concentration in the upper-inner canopy at the dry site.

Higher availability of soil N at the wet site than at the dry site (Prasolova et al. 2000*b*) was associated with increased tree growth and branchlet N concentration, and decreased branchlet P concentration. Because plant nutrient uptake is regulated by the nutrient requirement to support a given growth rate (Clarkson and Hanson 1980), an N-induced increase in tree growth rate might result in the dilution of P (Valentine and Allen 1990).

There were significant between-family differences in branchlet mineral concentration in the upper canopy at the wet site, but only in the upper-inner canopy at the dry site. Masle et al. (1992) reported a positive linear relationship between total mineral concentration of vegetative tissues and transpiration ratio. This suggests that genetic effects on branchlet mineral concentration may be related to transpiration efficiency, and that they should be more apparent in branchlets containing a larger proportion of older tissues because of continuous absorption of nutrients by mature foliage from the transpiration stream (Masle et al. 1992). At the dry site, family differences in branchlet mineral concentration were found only in the upper-inner canopy, which has a larger proportion of older needles. Branchlet N concentration and mineral concentration at the upper-inner canopy were under strong genetic control, with heritabilities of 0.49 and about 1.00, respectively.

Environmental variation in branchlet nutrient concentration

There have been many studies on environmental control of variation in foliar nutrient concentration (Snowdon and Benson 1992, Kennedy 1993, Bergmann et al. 1994, Dreshsel and Zech 1994, Nilsson and Wiklund 1994, Judd et al. 1996, Wang and Klinka 1997). We found that the effects of canopy position on branchlet nutrient concentrations were nutrient dependent at both sites. Branchlet concentrations of the mobile nutrients, N and K, were higher in the upper-outer canopy, whereas branchlet concentrations of Ca, Mn and Fe and mineral concentration were higher in the lower and inner canopy positions. These trends correspond to those in other tree species (Kennedy 1993, Zhang and Allen 1996). Among canopy positions, highest branchlet N concentrations were in the upper canopy. This may be attributed to the mobility of N and its translocation to meristematic areas where new tissues are being formed. Generally, plants reallocate N so that leaves most exposed to light have the highest N concentrations (Mooney and Gulman 1979). The higher branchlet P and K concentrations in the upper-outer canopy compared with the lower-outer canopy may be related to the higher proportion of younger tissues in the upper-outer canopy. Developing leaves are strong nutrient sinks, and both N and P are translocated to meet leaf demand for these nutrients (Dickson 1989). Branchlet P con-

centrations were lower in the upper-outer canopy than in the upper-inner canopy at both sites, probably because of the dilution effect associated with the larger needle size of younger tissues in the outer canopy than in the inner canopy.

The immobility and low translocation rates of branchlet Ca, Mn and Fe may result in their accumulation in old tissue. Dilution due to larger needle size in the upper canopy compared with the lower canopy may also contribute to the lower Ca, Mn and Fe concentrations in the upper canopy. One exception was branchlet Mg concentration, for which similar concentrations were found in the top, upper-outer and lower-outer canopy, possibly because an interaction between tissue age and canopy position appears to determine branchlet Mg concentration (Zhang and Allen 1996). Zhang and Allen (1996) reported that foliar Mg concentration was lower in 1-year-old foliage than in current-year foliage in the upper canopy of loblolly pine, but higher in 1-year-old foliage than in current-year foliage in the lower canopy. In our study, the proportion of current-year tissue was higher in the upper canopy than in the lower canopy, and if a similar interaction occurred in our trees, branchlet Mg concentration could be uniform throughout the canopy.

In general, the wet site has higher soil fertility than the dry site (Prasolova et al. 2000*b*), with higher total N, organic C, and exchangeable Ca, Mg, Mn and Na. Because soil nutrients other than N have probably not restricted tree growth at either site, differences in branchlet N concentrations are related to differences in soil N fertility between sites. In loblolly pine, increased N availability leads to an increase in fascicle mass and foliar N concentration, and a decrease in foliar P and Mg concentrations (Zhang and Allen 1996). Dilution probably contributed to higher concentrations of K, Ca, Mn and Fe, and mineral concentration at the dry site than at the wet site. The significantly lower concentration of soil exchangeable Mg at the dry site than at the wet site (Prasolova et al. 2000*b*) may have contributed to the lower branchlet Mg concentrations at the dry site.

Relationships between branchlet nutrient concentrations and $\delta^{13}C$, $\delta^{18}O$ and tree growth

No consistent correlations were found between branchlet nutrient concentrations at different canopy positions and tree growth or $\delta^{13}C$ or $\delta^{18}O$, except for branchlet N concentration and mineral concentration at the dry site. This was expected, because nutrients other than N were not growth-limiting at either site (Prasolova et al. 2000*a*) and the differences in the variation of these nutrient concentrations with canopy position, tissue age and site condition may disrupt the consistency of these relationships. Branchlet N concentration and mineral concentration at the upper-inner canopy were highly heritable, branchlet N concentration was significantly related to tree growth, and mineral concentration was significantly correlated with branchlet $\delta^{13}C$ at the dry site. Mineral concentration has shown promise as a breeding tool for selecting genotypes with contrasting transpiration efficiencies (Masle et al.1992, Mayland et al. 1993, Araus et al. 1998), and has been proposed as a surrogate for carbon isotope discrimination owing to its analytical simplicity (Masle et al. 1992, Mayland et al. 1993). Masle et al. (1992) reported a positive linear relationship between total mineral concentration of vegetative tissues and either transpiration ratio or carbon isotope discrimination, and a negative relationship between mineral concentration and $\delta^{13}C$. In our study and the study of Masle et al. (1992), branchlet mineral concentration was a better surrogate for carbon isotope discrimination than any mineral nutrient alone. However, our observation that the relationship between branchlet mineral concentration and $\delta^{13}C$ was better for more drought-exposed and N-limited trees differs from the findings of Masle (1992) and Pitman (1988) for herbaceous plants. The physiological causes of the linear relationship between foliar mineral concentration and $\delta^{13}C$ are not well understood. It may be partly related to the passive accumulation of minerals in the vegetative parts of the plant through the transpiration stream. It is commonly assumed that stomata provide the main short-term control of transpiration (Jones 1998). Thus, it is possible that this causes covariation between branchlet mineral concentration and stomatal conductance (as indicated by $\delta^{18}O$) in the upper-outer canopy at the dry site.

Branchlet $\delta^{13}C$ was better correlated with *H* at the dry site than at the wet site, but branchlet mineral concentration was better correlated with growth at the wet site than at the dry site. At the dry site, branchlet $\delta^{13}C$ would have incorporated signatures of both water and N limitations to tree growth. As discussed by Prasolova et al. (2001), high-WUE genotypes are probably the faster-growing individuals at the dry site. The negative correlation between branchlet mineral concentration, and therefore transpiration efficiency, and *H* further supports this hypothesis. At the wet site, faster-growing trees might have higher water losses through branchlets in the upper-outer canopy (Prasolova et al. 2000*a*). Thus, branchlet mineral concentration has potential as a tool for selecting genotypes with contrasting WUE (Masle et al. 1992).

In conclusion, branchlet nutrient concentration differed significantly between hoop pine families, but the differences varied with nutrient, canopy position and site. This has important implications for the use of branchlet nutrient concentrations as a breeding tool for selecting tree genotypes with improved nutritional traits. The significant correlations between branchlet $\delta^{18}O$ (an index of stomatal conductance) and mineral concentration at the dry site indicate that stomatal conductance might be a factor regulating the variation in branchlet mineral concentration of hoop pine families. At the N- and water-limiting dry site, branchlet N and mineral concentrations in the upper-inner canopy were highly heritable. In addition, branchlet N concentration correlated significantly with tree growth. Because well-adapted families are expected to use soil N reserves efficiently, it may be possible, through genetic programs, to develop breeding procedures for the identification, selection, and improvement of genotypes that are adapted to an N-limiting growth environment. Mineral concentration significantly correlated with branchlet $\delta^{13}C$ (an index of WUE), indicating that branchlet mineral concentration might be used to screen for tree genotypes with improved WUE for use on water-limiting sites.

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