First-year growth response of four *Populus* trichocarpa × Populus deltoides clones to fertilizer placement and level

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Abstract: Fertilizer (18:40:0, N:P:K) was applied by two methods, each at different levels, following establishment of a hybrid poplar (*Populus trichocarpa* Torr. & Gray × *Populus deltoides* Bartr. ex Marsh.) plantation, containing four clones, on central Vancouver Island. Nitrogen and P were supplied at 0, 100, and 200 kg·ha⁻¹ by banding, and at 0, 25 and 50 kg·ha⁻¹ by placing in holes adjacent to cuttings. After one season, response to placed treatments (mean height 182 cm) was greater than to banded treatments (mean height 149 cm). The 50 kg·ha⁻¹ placed treatment increased stem volume 4.3-fold above control, and the 200 kg·ha⁻¹ banded treatment increased stem volume 2.4-fold above control. Uptake of N and P was about 10-fold greater per kilogram of fertilizer nutrient for placed than banded treatments. Fertilizer increased leaf N concentration, but concentrations of most other nutrients declined despite increased uptake. Significant increases in stem volume occurred when leaf N concentration was about 29 g·kg⁻¹ in clone 1, but 23–25 g·kg⁻¹ in the other clones. Clone 2 tolerated foliage P concentrations below 1.4 g·kg⁻¹ at the greatest growth rates. Stem volume was positively correlated with soil total N% and organic C% in the 16–30 cm horizon.

Résumé: Un fertilisant (18–40–0, N : P : K) a été appliqué selon deux méthodes, chacune à différents niveaux, suite à l'établissement d'une plantation de peuplier hybride (*Populus trichocarpa* Torr. & Gray × *P. deltoides* Bartr. ex Marsh.), constituée de quatre clones, au centre de l'île de Vancouver. L'azote et P ont été appliqués aux taux de 0, 100 et 200 kg·ha⁻¹ en bandes et aux taux de 0, 25 et 50 kg·ha⁻¹ (traitement localisé) dans des trous adjacents aux boutures. Après une saison, la réponse au traitement localisé (hauteur moyenne de 182 cm) était plus grande que celle aux traitements en bandes (hauteur moyenne de 149 cm). Le traitement localisé de 50 kg·ha⁻¹ a augmenté le volume de la tige de 4,3 fois par rapport au témoin et le traitement en bandes de 200 kg·ha⁻¹ a augmenté le volume de 2,4 fois par rapport au témoin. Le prélèvement de N et P par kilogramme de nutriments ajoutés a été environ 10 fois plus élevé pour le traitement localisé comparativement au traitement en bandes. La fertilisation a augmenté la concentration de N foliaire, mais la concentration de la majorité des autres nutriments a diminué en dépit d'un accroissement du prélèvement. Des augmentations significatives du volume de la tige sont survenues quand la concentration de N était d'environ 29 g·kg⁻¹ dans le clone 1, et de 23–25 g·kg⁻¹ dans les autres clones. Le clone 2 a toléré des concentrations de P foliaire inférieures à 1,4 g·kg⁻¹ aux plus forts taux de croissance. Le volume de la tige était positivement corrélé avec les pourcentages de N et C organique totaux du sol dans l'horizon de 16–30 cm de profondeur.

[Traduit par la rédaction]

Introduction

Plantations of *Populus trichocarpa* Torr. & Gray × *Populus deltoides* Bartr. ex Marsh. hybrids (T × D hybrids) are being established on central Vancouver Island sites that originally supported Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), although some sites were used agriculturally prior to establishment of poplars. Phosphorus deficiencies have been detected in several plantations, and it is recognised by plantation managers that fertilization leads to improved growth on most of these sites.

Hybrid poplars are responsive to additions of N fertilizer. Response of a P. deltoides var. $angulata \times P$. trichocarpa clone to N fertilizer occurred only on weedy sites in the sec-

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ond and third years, but there was no response on weed-free sites (Hansen et al. 1988). Response of several T \times D hybrids to 500 kg N·ha $^{-1}$, applied in equal dressings during the second, third, and fourth years after planting resulted in significant response in the third year (Heilman and Xie 1993). Nitrogen is said to be the major nutrient limiting poplar productivity, although P, Zn and lime can be beneficial (Heilman et al. 1996). In practice, T \times D hybrid plantations that are fertilized usually receive 200 kg N·ha $^{-1}$ in the third year of growth.

On Vancouver Island, fertilization with N in year 3 significantly increased height (19%), and addition of N, P, and K further increased height (39%) over controls (Zabek 1995). Responses to both N and P supplied separately at planting have also been obtained (van den Driessche and Brown 1996), and it seemed likely that fertilization with N and P at planting could prove advantageous. Current practice is to band the fertilizer along the row to be planted. The ability of plants to exploit nutrient patches (Caldwell 1994) suggested that local placement of fertilizer might be an improvement.

Table 1. Analysis of covariance for stem height (cm) and volume (cm³) and analysis of variance for leaf area (cm²).

		Height		Volume		Leaf area	1
Source	df	MS	P	$\overline{{ m MS}^a}$	P	$\overline{{ m MS}^a}$	P
Block (B)	7	59 038	< 0.001	5 108	0.002	451	< 0.001
Treatment (T)	5	129 654	< 0.001	16 411	< 0.001	563	< 0.001
Contrasts							
$Method^b$	1	151 236	< 0.001	18 838	< 0.001	417	0.017
Control vs. high fertilization	1	402 126	< 0.001	50 064	< 0.001	1930	< 0.001
Error 1	35	8 062		1 224		66	
Clone (C)	3	4 975	0.215	1 318	0.050	220	< 0.001
$T \times C$	3	6 912	0.014	962	0.024	46	
Error 2	126	3 292		493		27	
Covariate ^c	1	48 028	< 0.001	3 940	< 0.001		
Error 3	375	1 765		269			

^aSums of squares are multiplied by 10⁻³.

Table 2. Stem heights and volumes, adjusted for cutting diameter at planting, and leaf masses and areas by treatments and levels.

	Treatment			
Treatment	1	2	3	means
Height (cm)				
Banding	124	150	174	149
Placement	130	203	213	182
Volume (cm ³))			
Banding	328	490	786	535
Placement	308	1084	1322	904
Leaf dry mas	ss (g)			
Banding	0.81	1.28	1.56	1.22
Placement	0.90	1.83	1.87	1.53
Leaf area (cn	n^2)			
Banding	109	155	179	148
Placement	118	207	218	181

^{*}Banding levels are 0, 100, and 200 kg·ha $^{\!-1}$ N, and placement levels are 0, 25, and 50 kg·ha $^{\!-1}$ N.

The present work was undertaken to determine the response of selected clones to fertilizer applied in different amounts, either by banding along the row, or by placement adjacent to the cutting.

Methods

Site and clones

An experimental plantation was established on a site near Parksville on eastern Vancouver Island, that was previously Douglas-fir forest. It had been cleared, stumped and the debris windrowed the previous year. Hybrid poplar (P. $trichocarpa \times P$. deltoides) cuttings 45 cm long, were planted at 3×3 m spacing. The clones were numbered 1-4 as their exact pedigree is proprietary.

Design

Two fertilizer application methods, each supplying three different levels resulted in six treatments. Banding supplied (i) 0, (ii) 100, and (iii) 200 kg of N and P per hectare, and placed fertilizer supplied (iv) 0, (v) 25, and (vi) 50 kg·ha⁻¹ of N and P. The

banding treatment therefore supplied four times as much fertilizer per hectare as the placement treatment. The treatments were split to accommodate four clones, and randomized in eight blocks. Treatment plots consisted of 12 cuttings in a row, arranged as groups of three cuttings per clone. The order of the four clones was randomized in the split plots. To prevent treatments interfering with one another, treated plots were 9 m apart, separated by two rows of untreated cuttings. The number of treated cuttings was 576, and the experiment occupied 1.73 ha.

Fertilizer

Cuttings were planted on 9 April 1997, and fertilizer was applied on 27 May 1997. The fertilizer was a mixture of urea, ammonium phosphate, and copper and zinc sulphates with an analysis of 18:40:0 plus 0.5% Cu, 0.5% Zn, and 1.5% S and, therefore, supplied equal masses of N and P. Fertilizer was either (*i*) placed in a band about 20 cm wide and about 25 cm away from the row and then incorporated into the soil by cultivation or (*ii*) placed into two or four holes, 12 cm deep, made with a planting dibble at 15 cm from the cutting. The placement treatments supplied either 0, 22.5, or 45 g per cutting of N and P. Mechanical weed control was carried out between the rows three times during the summer.

Measurements

The soil was a duric dystric brunisol (Jungen et al. 1989). It was sampled from the 0- to 15-cm and 16- to 30-cm horizons at three points along each block, and a single composite sample representing each horizon was prepared for each block on 23 April 1997. Samples were air-dried, crushed, and sieved through a 2-mm screen, and a portion was ground to 0.25 mm for analysis of total N with a continuous flow analyser (Alpkem RFA 300; Lavkulich 1981). Available P was extracted with dilute acid fluoride and determined colourimetrically (Bray 1, Olsen and Dean 1965), and organic matter determined by oxidation with chromic acid according to the method of Walkley and Black (Lavkulich 1981). Exchangeable cations were displaced with neutral ammonium acetate and determined by absorption spectrophotometry (Varian Spectra AA 400; Lavkulich 1981; Chapman 1965), and pH was measured in a 1:1 soil:water mixture.

Diameter of cuttings was measured near the top, twice at right angles, to reduce effects of stem eccentricity, on 27 April. This measurement was used to adjust final height and diameter measurements in covariance analysis. Leaf samples were removed from all trees on 17 August. The number harvested from the three trees per clone varied from three to nine according to leaf size, and expanded leaves were taken from the top of the shoot at about the

^bBanding vs. placement.

^cThe covariate is cutting diameter at planting.

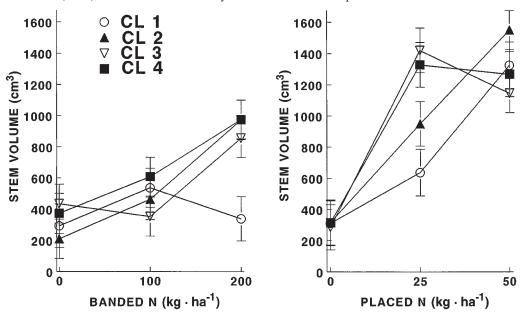


Fig. 1. Stem volume means (± SE) for four clones shown by amounts of banded or placed N fertilizer

fifth to eightth position according to tree size. Their areas were determined on a leaf area meter (LI-COR, Lincoln, Neb.), and after drying for 48 h at 80°C, they were weighed, milled, and analysed to determine nutrient concentrations.

Milled leaf samples were digested in a mixture of sulphuric and perchloric acids (Parkinson and Allen 1975). Colourimetric analysis of the dissolved N and P was carried out on an Alphem RFA 300 autoanalyser, and cations were determined by atomic absorption spectrophotometry (Varian Spectra AA 400). Sulphur was determined on a sulphur analyser (Fisher Model 475), and sulphate was extracted with 0.1 M HCl and determined colourimetrically (Johnson and Nishita 1952).

Heights and two basal diameters, at right angles, of new shoots were measured on 11–12 October.

Statistical analysis

Measurements were treated by analysis of variance for a randomized block design with six treatments, and contrast tests were used to compare groups of treatments (Steel and Torrie 1980). Clones were regarded as random factors, and the "random" statement of SAS (SAS Institute Inc., Cary, NC) was applied to this source of variance. Covariance analysis was used to adjust height and diameter measurements for size of cuttings at planting. Relationships between stem volume and mean leaf dry mass and area and between mean stem volume and mean soil analysis values for blocks were examined by regression. Interpretation of response to fertilization was partly based on vector analysis (Timmer 1991; Swift and Brockley 1994).

Results

Growth

There was significantly greater response to placed than to banded fertilizer treatment (Tables 1 and 2). Mean stem heights for banded and placed treatments were, respectively, 149 and 182 cm, and comparable stem volumes were 535 and 904 cm³. The 200 kg·ha⁻¹ banded treatment (level 3) increased stem volume 2.4-fold above control (level 1), and the 50 kg·ha⁻¹ placed treatment increased stem volume 4.3-fold above control (Table 2).

For the whole experiment, mean volumes of clones were significantly different (Table 1), and were : 575, 743, 750, and 811 cm³ for clones 1–4, respectively. However, height and volume measurements showed that clones interacted with treatments (Table 1). Clone 1 showed no significant volume response to fertilizer level in the banded treatment but a relatively strong response to level in the placed treatment (Fig 1). Clones 1 and 2 showed volume responses between 25 and 50 kg·ha⁻¹ in the placed treatment, but clones 3 and 4 did not.

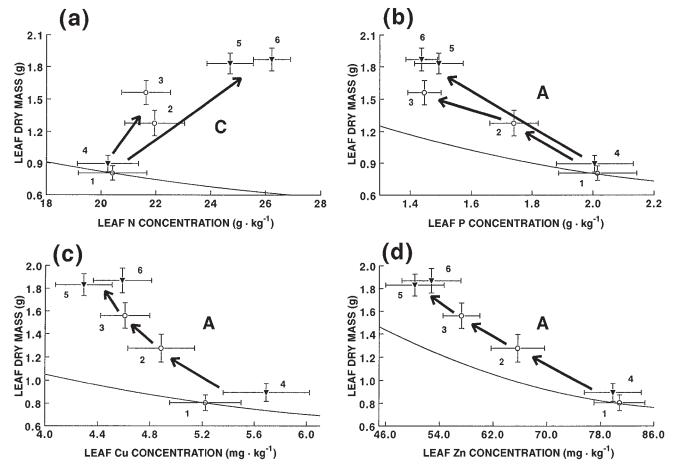
Increases in leaf mass and area with increase in fertilizer level were respectively about 2-fold and 1.7-fold, and placed treatment resulted in significantly greater increases than banded treatment (Tables 1 and 2). Specific leaf area was significantly (p = 0.001) less in fertilized treatments (118 cm²·g⁻¹) than in controls (129 cm²·g⁻¹).

Stem volume showed a significant linear correlation ($r^2 = 0.67$, $p \le 0.001$) with mean leaf dry mass for all data, but showed a better correlation ($r^2 = 0.76$, $p \le 0.001$) with the square of mean leaf area and no linear term. The coefficients of determination (r^2) for the quadratic correlations between stem volume and the square of mean leaf area were 0.86, 0.71, 0.85, and 0.70 for clones 1–4, respectively.

Nutrition

Graphs of treatment means for leaf dry mass plotted over leaf nutrient concentration showed that placed fertilizer (treatments 5 and 6) increased leaf N uptake and concentration more strongly than banding (treatments 2 and 3, Fig. 2a). The graphs for P, Cu and Zn showed decreases in leaf concentration that were more or less proportional to increase in leaf mass (Figs 2b-2d). However, the trends, indicated by the dark arrows, were steeper than the line representing constant content, so that there appeared to be some uptake of each of these nutrients. Nutrient uptake was confirmed by analysis of variance of leaf nutrient content calculated from individual observations. Positive differences in content between control and treated leaves were regarded

Fig. 2. Relationships between mean leaf dry masses and nutrient concentrations shown by treatments for (a) N, (b) P, (c) Cu, and (d) Zn. Treatments (per hectare) were as follows: (1) banded, 0 kg; (2) banded, 100 kg; (3) banded, 200 kg; (4) placed, 0 kg; (5) placed, 25 kg; and (6) placed, 50 kg. Standard errors are shown for dry masses and concentrations, and the curved line running through treatment 1 represents the isoline for constant nutrient content. Arrows (vectors; Timmer 1991) indicate how treatments affected mass and concentration in relation to control. Uppercase letters indicate diagnosis: A, nutrient is sufficient, with decreasing concentration and increasing content; C, nutrient is growth limiting, with increasing concentration and content. Details of the diagnostic scheme appear in Swift and Brockley (1994).



as uptake resulting from treatment. Leaf content of all elements, including those not supplied by the fertilizer, were seen to increase significantly in fertilized trees (Table 3). Mean nutrient content per leaf at the high level of placed fertilization was increased, compared with control, as follows: N, 153%; P, 42%; K, 33%; Ca, 88%; Mg, 126%; S, 104%; Fe, 52%; Mn, 65%; Cu, 61%; and Zn, 31%.

When leaf nutrient contents (Table 3) for control treatments were subtracted from fertilizer treatments and expressed per unit of fertilizer nutrient applied (Table 4), it was seen that placed fertilization was more efficient than banded fertilization. For example, the 25 kg·ha⁻¹ placed treatment resulted in about nine times the amount of N uptake per leaf than the 100 kg·ha⁻¹ banded treatment. Corresponding uptake values for P, Cu, and Zn were, respectively, 13, 8, and 4 times greater.

Clones

Plotting treatment and level means of stem volume over corresponding mean leaf N concentrations showed that growth of clone 1 only increased when leaf N concentration was high (Fig 3). In contrast, stem volume growth of clone 2

increased sharply with small increases in leaf N concentration. Clones 3 and 4 had relatively high control N concentrations (20–23 $g \cdot kg^{-1}$), and volume increased sharply to a maximum with slight increase in leaf N concentration (Fig 3). No significant increases in volume occurred when mean leaf N concentration increased from 23 to 26 $g \cdot kg^{-1}$ in clone 3, and from 25 to 27 $g \cdot kg^{-1}$ in clone 4.

There were differences between clones in their nutrient concentrations, and these differences often varied according to whether they were unfertilized or fertilized (Table 5). Clone 2 had the lowest concentrations of N and P after fertilization, but it had among the highest K and Ca concentrations. There were clonal differences in S, Fe, Cu, and Zn concentrations in unfertilized trees, but not in fertilized trees.

Soil

The planting site soil was a sandy loam with a pH averaging 5.2, and nutrient concentrations varied quite widely (Table 6). Maximum between block variation for P was from 5 to 84 mg·kg⁻¹ at the surface, and from 2 to 59 mg·kg⁻¹ in the 16- to 30-cm horizon. Mean stem volumes of all trees

Table 3. Content per leaf of nutrients shown by fertilizer treatments and levels, with significance levels for treatments (1–6), method (banding vs. placement for fertilized treatments), and controls vs. fertilized treatments.

	Treatmen	t levels*			Contrasts	
Foliar nutrient and method	1	2	3	Treatments	Method	Control vs. fertilized
N (mg/leaf)						
Banded	18	30	34	<0.001**	< 0.001	< 0.001
Placed	19	44	48			
P (mg/leaf)						
Banded	1.8	2.3	2.3	0.038	0.090	0.003
Placed	1.9	2.7	2.7			
K (mg/leaf)						
Banded	13	19	17	0.025	0.123	0.002
Placed	15	20	20			
Ca (mg/leaf)						
Banded	7	10	12	< 0.001	< 0.001	< 0.001
Placed	8	15	15			
Mg (mg/leaf)						
Banded	2.3	3.8	5.0	< 0.001	< 0.001	< 0.001
Placed	2.7	5.8	6.1			
S (mg/leaf)						
Banded	2.2	3.5	4.0	< 0.001	0.003	< 0.001
Placed	2.6	4.5	5.3			
Fe (μg/leaf)						
Banded	132	177	237	0.003	0.811	< 0.001
Placed	132	204	201			
Mn (μg/leaf)						
Banded	156	300	314	< 0.001	0.118	< 0.001
Placed	213	361	352			
Cu (µg/leaf)						
Banded	4.6	6.5	7.3	< 0.001	0.035	< 0.001
Placed	5.4	7.9	8.7			
Zn (µg/leaf)						
Banded	66	89	88	0.408	0.660	0.041
Placed	74	91	97			

^{*}Banding levels are 0, 100, and 200 kg·ha⁻¹ N, and placement levels are 0, 25, and 50 kg·ha⁻¹ N.

Table 4. Difference in leaf uptake of N, P, Cu, and Zn between the four fertilizer treatments and control expressed per unit of nutrient applied per hectare in fertilizer.

	Placed treatment		Banded treatmen	nts
Nutrient	25 kg·ha ⁻¹	50 kg·ha ⁻¹	100 kg·ha ⁻¹	200 kg·ha ⁻¹
N (mg·kg ⁻¹)	1.020	0.590	0.115	0.078
$P (mg \cdot kg^{-1})$	0.058	0.029	0.005	0.002
Cu $(mg \cdot kg^{-1})$	23.2	14.8	3.0	2.3
Zn (mg·kg ⁻¹)	168	108	38	18

(unfertilized and fertilized) for the eight blocks were significantly correlated with soil organic carbon (p = 0.01, $r^2 = 0.69$) and with soil total N (p = 0.03, $r^2 = 0.56$) in the 16- to 30-cm horizon.

Discussion

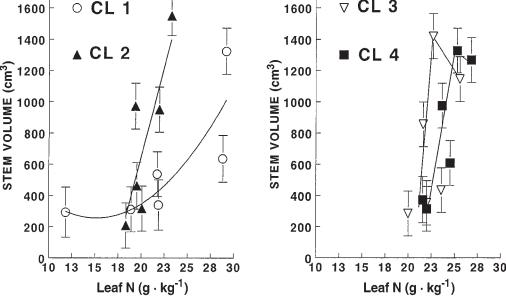
Growth

Application of fertilizer to cuttings shortly after planting caused large increases in all measures of growth, with placement of fertilizer being about twice as effective as banding in increasing stem volume. This was remarkable because the amount of fertilizer placed was a quarter of that banded per hectare. The reason for the greater effectiveness of placement could be localization of the fertilizer close to the cutting that initially had no roots, and to absence of weed stimulation between cuttings. Although unmeasured, weed growth appeared greater in banded than placed treatments.

The good correlations obtained for the four clones between mean fully expanded leaf mass, or mean leaf area and

^{**}Values are significance levels.

Fig. 3. Stem volume means (\pm SE) for four clones plotted over corresponding leaf N concentration means for the six treatments.



stem volume are useful because relationships between nutrition and leaf size that are observed can largely be interpreted as relationships between nutrition and stem volume. Linear correlation between stem volume and leaf area has been shown previously for *P. trichocarpa*, *P. deltoides*, and their hybrids (Ridge et al. 1986). Terminal shoot leaf area and dry mass were found to be significantly linearly correlated with biomass, height and diameter of 2-year-old *Populus* clones (Harrington et al. 1997), but the correlations were lower than those reported here.

Greater effectiveness of placement, in increasing leaf uptake of nutrient, can probably be extended to the whole plant in view of the relationship between leaf size and total plant size. Even if the efficiencies of fertilizer use for the whole plant are somewhat less than for leaves, they are still likely to be important since the N and P efficiencies determined for leaves were about 10-fold different between the two methods. This could be valuable for fertilizing plantations where large nutrient inputs would be environmentally undesirable, as well as for economising the use of fertilizer.

Nutrition

Growth response appeared mainly due to the addition of N because only N concentration increased, whereas concentrations of P, Cu, and Zn decreased, although these nutrients were applied in the fertilizer. However, response seemed limited when leaf N concentrations were above about $24~{\rm g\cdot kg^{-1}}$, as indicated by the much reduced response between the $25~{\rm kg\cdot ha^{-1}}$ and the $50~{\rm kg\cdot ha^{-1}}$ levels of the placed method.

Unfertilized trees had mean leaf P concentrations of only about 2.0 g·kg⁻¹, and results for *P. trichocarpa*, *P. deltoides* (van den Burg 1985), and clone 1 (van den Driessche 1998¹) indicate 2.5 g·kg⁻¹ as adequate. The mean P concentration dropped from about 2.0 g·kg⁻¹ for unfertilized trees to about

1.4 g·kg⁻¹ for fertilized trees. This latter value is regarded as critical for *P. deltoides* and *P. trichocarpa* (van den Burg 1985), and the critical value for clone 1 was found to be 1.6 g·kg⁻¹ P (van den Driessche 1998; see footnote 1). However, besides the decreased concentration of P caused by fertilization, there was a small but significant uptake of P attributable to fertilization. Thus addition of P in the fertilizer may have avoided more severe deficiency developing in fertilized treatments.

The decrease in P concentrations to near-critical levels, despite substantial supplies of P fertilizer, and the lack of any detectable effect of large block differences in available P on volume growth, suggest that these trees had difficulty taking up P. This may have been because root systems were not sufficiently developed to exploit the relatively immobile P resources during this first year of growth. However, mycorrhizae are associated with poplars, although little is known of their function (Pregitzer and Friend 1996). Assuming that mycorrhizae would play a part in P uptake in these poplar clones, it could be that suitable fungi to form mycorrhizae were not abundant on this previous conifer site.

Potassium, Ca, S, Cu, and B leaf contents were also significantly increased as a result of fertilization. Of these elements, K, Ca, and B were not present in the fertilizer, so that their increased uptake must have resulted from increased growth. It is not possible to say whether uptake of P, S, and Cu was a result of only increased growth, or because they were present in the fertilizer.

Soil

The positive relationship between block means for stem volume and total N in soil suggests that this may be a useful measurement of soil N for assessing site potential. The reason for the positive relationship between stem volume and organic carbon could be because of nutrient release from

¹ van den Driessche, R. 1998. Phosphorus, copper and zinc supplies influence growth and nutrition of a *Populus trichocarpa* × *P. deltoides* hybrid. Unpublished manuscript.

Table 5. Clonal nutrient	concentrations for	r unfertilized	(treatments	1 and 4)	, and fertilized	(treatments	3
and 6) trees.							

Nutrient	Treatment	Clone 1	Clone 2	Clone 3	Clone 4
N	Control	18.5 <i>b</i>	19.2 <i>b</i>	21.8 <i>a</i>	21.8 <i>a</i>
	Fertilized	25.5 <i>a</i>	21.3b	23.6 <i>a</i>	25.3 <i>a</i>
P	Control	1.8b	1.9 <i>ab</i>	2.2a	2.2a
	Fertilized	1.6 <i>a</i>	1.3b	1.5 <i>a</i>	1.5 <i>a</i>
K	Control	14.1b	17.2 <i>a</i>	12.8b	17.0 <i>a</i>
	Fertilized	11.6 <i>a</i>	10.7ab	9.7 <i>b</i>	10.2ab
Ca	Control	8.1 <i>b</i>	9.2a	9.9b	8.0b
	Fertilized	7.6b	8.7 <i>a</i>	8.3 <i>ab</i>	7.2b
Mg	Control	3.0b	2.9b	3.7 <i>a</i>	3.1b
	Fertilized	3.3a	3.1 <i>a</i>	3.5 <i>a</i>	3.3 <i>a</i>
S	Control	2.3c	2.5bc	2.9a	2.7 <i>ab</i>
	Fertilized	2.7a	2.5a	2.8a	2.6 <i>a</i>
Fe	Control	160 <i>a</i>	152 <i>a</i>	186 <i>a</i>	144 <i>a</i>
	Fertilized	144 <i>a</i>	139 <i>a</i>	113 <i>a</i>	129 <i>a</i>
Mn	Control	197 <i>a</i>	228a	238 <i>a</i>	210 <i>a</i>
	Fertilized	235 <i>a</i>	205ab	160b	192 <i>ab</i>
Cu	Control	4.4c	5.3b	5.9 <i>ab</i>	6.3 <i>a</i>
	Fertilized	4.7 <i>a</i>	4.2a	4.6 <i>a</i>	4.9 <i>a</i>
Zn	Control	77 <i>b</i>	73 <i>b</i>	82 <i>ab</i>	90 <i>a</i>
	Fertilized	59a	52 <i>a</i>	54 <i>a</i>	55a

Note: Values for N, P, K, Ca, mg and S are grams per kilogram, and values for Fe, Mn, Cu, and Zn are milligrams per kilogram. Values within a row not followed by the same letter are significantly different at $p \le 0.05$ by Duncan's multiple range test.

Table 6. Means and ranges of soil analysis variables based on samples from three points in every block at each of two depths.

Variable	Mean	Minimum	Maximum
рН	5.24	5.00	5.50
Sand (%)	63.8	37	84
Silt (%)	23.7	8	45
Clay (%)	12.6	7	22
Organic carbon (%)	4.43	1.53	6.92
N (%)	0.14	0.08	0.27
$P (mg \cdot kg^{-1})$	31.7	1.8	83.9
$K (cmol_{(+)} \cdot kg^{-1})$	0.18	0.10	0.28
Ca (cmol ₍₊₎ ·kg ⁻¹)	6.1	2.8	10.5
$Mg (cmol_{(+)} \cdot kg^{-1})$	1.90	0.53	4.40
Na (cmol ₍₊₎ ·kg ⁻¹)	0.09	0.06	0.18
$CEC (cmol_{(+)} \cdot kg^{-1})$	21.6	10.9	33.3

decomposing organic matter, and this relationship also makes organic carbon content a possible indicator of site potential. The aboveground volume response was probably matched by root response to total soil N and organic matter, because the length of fine root per unit soil volume was found to be positively correlated with these two soil parameters for several T \times D hybrids (Heilman et al. 1994). This also emphasises that the relationship is more general, and therefore probably more useful for predicting site quality.

The negative relationship between growth and soil pH observed by McLennan (1996) for *Populus trichocarpa* was not seen here. The range of soil pH among blocks was only

0.5 units, and the mean of 5.24 corresponds to the pH of *P. trichocarpa* sites where P availability was maximum. It is therefore surprising that, with a favourable pH and added fertilizer P, leaf P concentrations were reduced to such low levels. However, the presence of urea in the fertilizer may have raised pH locally rendering P less available, since urea is know to raise pH in forest soils (Otchere-Boateng and Ballard 1978).

Clones

Optimal leaf N concentrations may vary between the four clones. Clone 1 apparently only responded to high levels of N, clone 2 responded over the whole range of N, and clones 3 and 4 did not respond to the highest level of N provided. Response only occurred in clone 1 when mean leaf N concentration was 29 g·kg⁻¹. This is close to the optimal value of 30 g·kg⁻¹ N proposed by Heilman and Xie (1993). Clone 2 showed a linear response to increase in fertilizer level and to increasing concentrations of leaf N. However, the maximum concentration of N achieved was only 23 g·kg⁻¹ N. Clone 3 achieved a foliage N concentration of 22 g·kg⁻¹, with placement at 25 kg·ha⁻¹, and additional fertilizer raised N to 23 g·kg⁻¹ without further growth response. Maximum stem volume of clone 4 also occurred with placement of 25 kg·ha⁻¹ with a leaf concentration of 25 g·kg⁻¹ N, and there was no further increase in volume with additional fertilizer, although leaf concentration increased to 27 g·kg⁻¹ N.

The concentrations of nutrients, other than N, were all lower in fertilized trees than in unfertilized trees, but this did not prevent substantial growth response to fertilization. The ability of clone 2 to utilize N for increasing growth may have been partly because it could tolerate low leaf P concentrations. The mean concentration of clone 2 was below the

usually accepted critical value of 1.4 g·kg⁻¹ (van den Burg 1985) in the fertilized treatments. Means for the other three clones were above this value. Clone 2 also maintained higher leaf Ca and K concentration after fertilization than clones 3 and 4. The significance of this is not clear since the concentrations of these elements in clones 3 and 4 did not decrease to critical values.

From this work it seems likely that the optimal N concentration is lower than 30 g·kg⁻¹ for clones 2, 3, and 4, although this value may be approximately correct for clone 1. With reduction in concentration of other nutrients, especially P, as N concentration increased, the situation is not clear. It might have been possible to achieve continued response to N up 30 g·kg⁻¹ concentration in clones 2, 3, and 4 if concentration of other nutrients had been maintained. If so, the potential is enormous, but it seems unlikely, and the optimal value for these three clones may be closer to 23–25 g·kg⁻¹ N. This range of concentrations is also much closer to those shown for several poplar species and hybrids (van den Burg 1985) and to the value of 24.5 g·kg⁻¹ for *P. trichocarpa* (McLennan 1996).

Concentrations of nutrients reported for fertilized clones here should support rapid growth provided they can be maintained by continued uptake, which was shown to be occurring. Differences in nutrient concentrations among clones tended to be consistent between unfertilized and fertilized trees and, therefore, can be expected to occur under a range of nutrient supply conditions.

Conclusions

Both growth response and the efficiency of nutrient uptake were greater in placed fertilizer treatments than in banded fertilizer treatments. By reducing the requirement for fertilizer, placement would be useful where large quantities of fertilizer are environmentally or economically undesirable. During the first season of growth, N was taken up more readily than P from a fertilizer that supplied equal masses of both elements. Investigation of both tree mycorrhizal status and N source used in the fertilizer might offer explanations of the low P uptake.

Clones differed in their responses to nutrients, as shown by relationships between maximum growth and leaf N and P concentrations and changes in other nutrients associated with fertilization. Thus matching fertility levels to specific clones may be necessary to achieve maximum productivity. Measurements of mineral soil total N and organic carbon might be valuable for predicting site suitability for hybrid poplar.

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