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Developmental quantitative genetics of growth in *Populus*

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Abstract Nursery growth and dry weight were analyzed for F_2 genotypes derived from *Populus trichocarpa* × *P. deltoides* that have been field tested with clonal replicates in three different environments. The correlations between nursery and plantation performance differed among the environments, with higher values at Boardman and Clatskanie (both planted with rooted cuttings) than Puyallup (planted with unrooted cuttings). At Puyallup, nursery height was more strongly associated with plantation growth than were nursery diameter and dry weight. Yet, this finding was not supported by QTL mapping. A single overdominant QTL on linkage group G affected the stem height of both seedlings and resprouts in the nursery but showed nonsignificant LOD scores for plantation height from ages 1 to 5 at Puyallup. A total of four QTLs were identified for nursery diameter, one of which on linkage group O also controlled plantation basal area at all ages. Two important nursery QTLs on linkage groups B and G were used to estimate the relative efficiency of marker-assisted selection for plantation productivity. Despite the fact that they were not detected in the plantation stage, these two QTLs could significantly increase the proportion of the phenotypic variance explained by plantation QTLs.

Key words Genetic correlation · Growth · *Populus* · Quantitative trait locus · Seedling

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Introduction

Early selection has an important place in forest tree genetic improvement (Namkoong et al. 1988). Indirect early selection for superior families or genotypes at mature ages can reduce progeny-testing costs and the time required to capture genetic gains. The efficiency of early selection for growth is affected by two variables: i.e. the ratio of the square root of heritability at early ages over that at mature ages and the genetic correlation between early and mature ages (Searle 1965; Falconer 1989). Thus, fundamental questions to be addressed for early selection are how the genetic differentiation of growth varies over age and how much genetic basis is shared between different ages.

The developmental changes of heritability for growth have been extensively observed in many tree species including conifers (Franklin 1979; Lambeth 1983; White and Hodge 1991) and hardwoods (Borralho et al. 1992; Wu et al. 1992). Based on the trends of changes in the genetic variance of height over age, Franklin (1979) classified stand development into three phases: (1) juvenile-genotypic, (2) mature-genotypic and (3) codominance-suppression. St. Clair and Admas (1991) found that patterns of age-dependent change of genetic variance were different between height and radial growth in Douglas-fir. During the juvenile phase, the heritability of height increases more strongly than diameter, whereas the inverse was true when the stand was developed into the second and third phase. Genetic correlations among different ages have also been examined: there were closer age-age associations within than between phases (Franklin 1979).

Early selection in trees has been further developed to use seedling traits as selective criteria for subsequent field growth (Wheeler 1979; Williams 1987; Carter et al. 1990). This method can typically reduce the size of the progeny test by culling poor genotypes at the nursery

stage. However, inconsistent conclusions have been made in these earlier studies about the effectiveness of predicting field growth based on the seedling traits (Squillace and Gansel 1974; Waxler and van Buijtenen 1981; Williams 1987; Li et al. 1991).

The effectiveness of early selection cannot be evaluated until the genetic mechanisms underlying the developmental changes of growth have been understood. The dynamics of the genetic control over growth may be examined via quantitative genetic approaches (Atchley 1984; Balocchi et al. 1993). Genetic mapping, pursued to study quantitative genetic variation, provides an excellent alternative to enhance our understanding of developmental genetics, especially for long-lived forest trees. By relating molecular markers to quantitative trait loci (QTLs), the number of genetic factors and the changes in their expression over ages can be identified throughout the genome.

Here we report quantitative and molecular genetic results on nursery traits that may have value as early selection criteria in an interspecific F_2 generation derived from *Populus trichocarpa* and *P. deltoides*. The relationships between the nursery growth and subsequent field performance were estimated for the plantations in three different environments. Finally, the efficiency of QTL mapping on plantation growth by incorporating nursery QTLs was analyzed. The implications of the results in poplar early selection are discussed.

Materials and methods

Pedigree and plantings

In 1981, a female *Populus trichocarpa* clone (93-968), native to western Washington, was crossed with a male *P. deltoides* clone (ILL-129) from central Illinois to generate F_1 family 53. Two F_1 hybrids, 53-246 and 53-242, were further crossed in 1988 to produce F_2 family 331, with 90 members. In 1990, the same cross was repeated to obtain additional 320 individuals of this F_2 family. All F_2 seedlings were raised in the greenhouse, then transplanted to a nursery site at Farm 5 of the Washington State University Research and Extension Center in Puyallup, Washington.

In spring 1991, a replicated plantation was established next to the nursery site at Farm 5 with 20-cm cuttings unrooted from the 1988 material. It contains six ramets of each of 55 genotypes of Family 331, both F_1 parents, and both original parents (93-968 and ILL-129). Two years later (1993), stecklings (rooted cuttings) of both the 1988 and 1990 material were planted in two other environments, one east of the Cascades in Boardman, Oregon, the other west of the Cascades in the lower Columbia River Valley near Clatskanie, Oregon. Both plantations contain a total of 375 genotypes of Family 331, as well as their F_1 parents and grandparents. All three plantations were laid out in a randomized complete block design with two-tree plots and surrounded by two border rows, with a spacing of 2×2 m at Puyallup and 1.5×3.0 m at Boardman and Clatskanie. Three replicates were used at Puyallup and Clatskanie, four at Boardman. To minimize competitive interactions among this highly varied material in the two plantations, we assigned each genotype to one of three size classes, based on its previous years' growth in the nursery. The three classes were laid out perpendicularly to the

blocks in ascending and descending order. At the end of the 3rd year of growth, the plantation at Puyallup was thinned to 50% by harvesting 1 tree of each genotype in each replicate. A triploid clone identified in the F_2 family (Bradshaw and Stettler 1993) was excluded from all genetic analyses.

Nursery and plantation assessment

Seedling height and basal diameter were measured for the 1988 material at the end of the 2nd year in the nursery. After the measurements, the seedlings were cut back, and 1 or more resprouts then appeared from each stump in the following spring. At the end of the 3rd year, the dominant shoot was chosen to measure resprout height, basal diameter, stem dry weight and branch dry weight. In addition, total dry weights of all shoots and their sylleptic branches were measured for each stool. The measurements of dry weight followed the procedures described by Heilman and Stettler (1990). For the 1990 material, seedling height and basal diameter were measured at the end of each of the first 2 years in the nursery. Stem proportion was estimated by the height:diameter ratio. Harvest index was described by two ratios, i.e. main stem over total main stem and branch dry weight, and main stem over total dry weight of all resprouts.

In the plantations, height and basal diameter were measured for each tree at the end of each of the first 5 (Puyallup), 3 (Clatskanie) and 2 years (Boardman) of growth. The 3rd-year measurement in the Boardman plantation had to be omitted due to serious damage inflicted by a hail storm in spring 1995. Stem basal area, volume index and proportion were calculated for each tree.

Data analysis

Quantitative genetic analysis was used to estimate broad-sense heritabilities and across-age genetic correlations among growth traits in the plantations. The genetic assumptions and methods to obtain these estimates from a single F_2 family have been described in Wu and Stettler (1997). These genetic parameters were estimated based on a single cell at Puyallup after age 3 due to the thinning. Thus, genotype \times replicate interactions cannot be ruled out in this case. The Pearson correlations between nursery traits and plantation growth were calculated using PROC CORR (SAS Institute 1988). Normality for trait distribution was tested by the Shapiro-Wilk statistic, calculated using PROC UNIVARIATE (SAS Institute 1988).

Molecular analysis was carried out based on genetic maps constructed by more than 350 restriction fragment length polymorphism (RFLP), sequence-tagged site (STS) and random amplified polymorphic DNA (RAPD) markers on the 1988 material (Bradshaw et al. 1994; Bradshaw and Stettler 1995). The maximum likelihood interval mapping method was employed to examine the magnitudes of the effects of individual QTLs and their locations on chromosomes (Lander and Botstein 1989). The threshold value of LOD score for declaring the existence of a QTL is 2.9, which corresponds to an approximate nominal significance level of $P = 0.05$ for the entire genome (Bradshaw and Stettler 1995). However, a small F_2 sample implies that only QTLs with large effects could reach statistical significance and, thus, QTLs with more moderate effects can be found only when a small LOD threshold is used. In this study, QTLs with a LOD threshold of 2.4–2.9 are suggestive (e.g. Stuber et al. 1992; Veldboom et al. 1994). The ratio of dominance (d) to additivity (a) was used to determine the mode of gene action based on the criteria of Stuber et al. (1987): $d/a = 0-0.20$, additive (A); $d/a = 0.21-0.80$, partial dominance (PD); $d/a = 0.81-1.20$, dominance (D); and $d/a > 1.20$, overdominance (OD). All these QTL analyses above were performed using MAPMAKER/QTL 1.1 (Lincoln et al. 1992).

Results

Phenotypic analysis

For the 1988 material, 2-year growth of F₂ seedlings averaged 100 cm in height and 8.9 mm in basal diameter. These values increased by 120–140% for the main shoots of resprouts from 3rd-year stools (Fig. 1),

Fig. 1A–F Frequency distributions for nursery traits in the 1988 material of F₂ Family 331. **A** Two-year seedling height, **B** 2-year seedling diameter, **C** main shoot height of 3rd-year resprouts, **D** main shoot diameter of 3rd-year resprouts, **E** stem dry weight of the main shoot of 3rd-year resprouts, **F** total dry weight including all 3rd-year resprouts of a stool

which were stouter in shape than 2-year seedlings. In both 2nd and 3rd years at the nursery stage, F₂ progenies showed considerable variation in growth, with larger coefficients of variation for dry weights (70–87%) than for height and diameter (33–48%). While the frequency distribution of phenotypes did not differ significantly from normality for nursery height and diameter (Fig. 1A–D), according to the Shapiro-Wilk statistic it was significantly skewed toward the low values for resprout dry weights (Fig. 1E, F), probably due to inbreeding depression (see Wu and Stettler 1994).

The correlations between nursery traits and subsequent plantation growth exhibited different patterns for the different plantations and traits. At Puyallup,

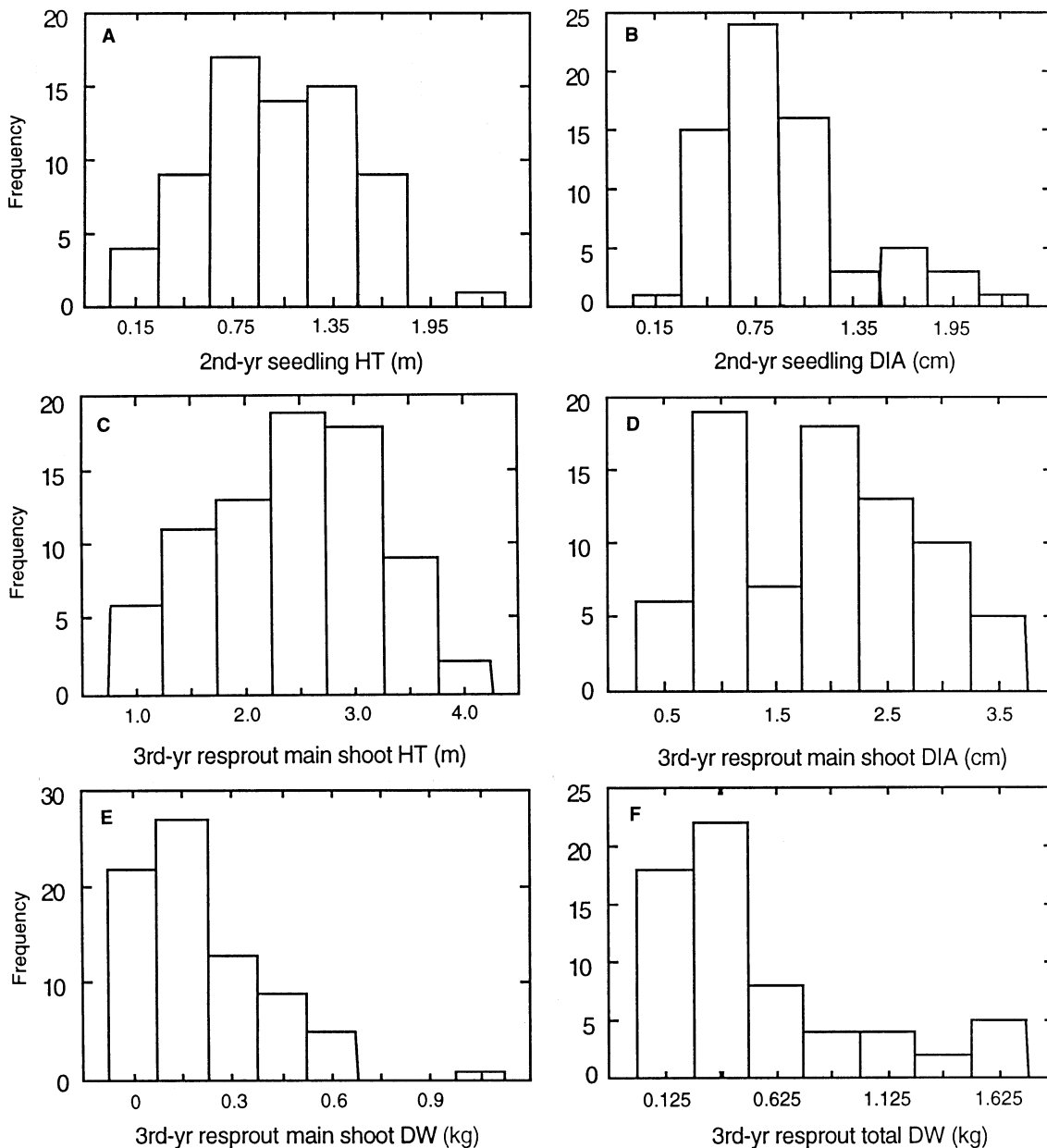


Table 1 Correlations between nursery traits and plantation performance at Puyallup (ages 1–5 years), Boardman (ages 1–2 years) and Clatskanie (ages 1–3 years) for the 1998 material of F₂ Family 331. Values greater than 0.27 are significant at $P < 0.05$

Nursery trait	Puyallup					Boardman		Clatskanie		
	1	2	3	4	5	1	2	1	2	3
With plantation height										
Seedling year 2										
Height	0.43	0.51	0.53	–	0.33	0.52	0.55	0.57	0.61	0.57
Diameter	0.35	0.40	0.48	–	0.29	0.43	0.43	0.51	0.61	0.51
Re-sprout year 3										
Main shoot (MS) height	0.54	0.63	0.59	–	0.48	0.62	0.66	0.70	0.69	0.66
Stem diameter of MS	0.35	0.39	0.30	–	0.27	0.58	0.57	0.64	0.65	0.60
Stem dry weight of MS	0.36	0.39	0.28	–	0.29	0.56	0.54	0.58	0.61	0.56
Total dry weight of MS	0.39	0.42	0.38	–	0.29	0.54	0.48	0.57	0.62	0.58
Total dry weight of resprouts	0.44	0.46	0.41	–	0.31	0.48	0.46	0.52	0.55	0.52
With plantation basal area										
Seedling year 2										
Height	0.28	0.21	0.22	0.04	0.07	0.44	0.44	0.51	0.50	0.45
Diameter	0.32	0.19	0.20	0.04	0.06	0.46	0.41	0.52	0.53	0.45
Re-sprout year 3										
Main shoot (MS) height	0.46	0.40	0.34	0.29	0.28	0.56	0.57	0.65	0.61	0.56
Stem diameter of MS	0.41	0.33	0.27	0.04	0.10	0.63	0.63	0.68	0.65	0.60
Stem dry weight of MS	0.45	0.37	0.32	0.12	0.13	0.63	0.63	0.64	0.59	0.58
Total dry weight of MS	0.44	0.34	0.30	0.08	0.07	0.57	0.54	0.60	0.54	0.55
Total dry weight of resprouts	0.49	0.28	0.26	0.08	0.10	0.52	0.48	0.53	0.43	0.46

seedling and resprout heights were more strongly associated with plantation growth than seedling and resprout diameters and resprout dry weight (Table 1). All nursery traits could predict plantation height better than basal area. The merit of seedling and resprout height over diameter as a predictor became more pronounced after the plantation was 2 years old. For example, the correlations of 3rd-year resprout height with 5-year plantation height and basal area were 0.48 ($P < 0.001$) and 0.28 ($P < 0.05$), respectively, whereas the corresponding values were only 0.27 ($P < 0.05$) and 0.10 ($P < 0.35$) for 3rd-year resprout diameter (Table 1).

Another interesting finding at Puyallup was that the relationship between nursery traits and plantation height increased slightly from year 1 to 2 and then decreased from years 3 to 5. For basal area, the correlations between nursery and plantation decreased consistently over stand development, especially from year 3 to 4.

At Boardman and Clatskanie, nursery performance displayed similar relationships with plantation growth, but the correlations were larger than their counterparts at Puyallup (Table 1). Unlike at Puyallup, the two plantations showed that: (1) nursery height and diameter did not differ much from one another in their correlations to plantation growth; (2) the growth of the main shoot was a better predictor of plantation growth than total dry weight of all resprouts per stool and (3) the correlations between nursery and plantation performance were quite stable over stand development (Table 1).

The correlations between seedling and plantation performance in the 1990 material were broadly in agreement with those in the 1988 material but provided additional information on a much larger scale (Table 2). In all cases, seedling performance at year 2 was a better indicator for plantation growth at Boardman and Clatskanie ($r = 0.51$ – 0.68) than that at year 1 ($r = 0.22$ – 0.51). However, even in year 2, there still was considerable variation in plantation growth given the same height or diameter of the corresponding seedling (data not shown).

Molecular dissection

QTL analysis was conducted for all nursery traits, with the results given in Table 3. The two original parents of the F₂ cross could not be compared for seedling and resprout performance in the nursery. However, it was known that *P. trichocarpa* had much more growth than *P. deltoides* in the clonally replicated plantation at the same site (Puyallup) (Wu and Stettler 1994, 1996). An overdominant QTL on linkage group G was detected to have a large effect on nursery height in both years, accounting for 42% (year 2) and 23% (year 3) of the phenotypic variance. At this QTL, the *P. trichocarpa* parent contributed a favorable allele to increased height. Four different QTLs affected nursery diameter, of which two, on linkage groups G and J, were effective in 2nd-year seedlings; the other two, on linkage groups B and O, were effective in 3rd-year resprouts. The mode of gene action at these QTLs

Table 2 Correlations between nursery traits and plantation performance at Boardman (ages 1–2 years), Clatskanie (ages 1–3 years) in the 1990 material of F₂ Family 331

Nursery trait	Boardman		Clatskanie		
	1	2	1	2	3
With plantation height					
Height 1	0.31	0.34	0.39	0.51	0.50
2	0.56	0.62	0.68	0.68	0.67
Diameter 1	0.35	0.36	0.33	0.39	0.41
2	0.47	0.54	0.57	0.58	0.60
With plantation basal area					
Height 1	0.31	0.22	0.42	0.44	0.41
2	0.52	0.51	0.64	0.58	0.58
Diameter 1	0.43	0.38	0.45	0.40	0.38
2	0.55	0.53	0.63	0.57	0.58

varied from overdominance in year 2 to dominance in year 3. Only the QTL on linkage group O showed a favorable allele from the *P. deltooides* parent. Two QTLs jointly explained over 61% of the phenotypic variance in each year.

Stem dry weight of the main shoot and its total stem and branch dry weight in 3rd-year resprouts were controlled by a QTL on linkage group B and O, respectively (Table 3). However, four different QTLs on linkage group D, G, J, and L were identified for total resprout dry weight, three of which individually explained very high percentage (>66%) of the phenotypic variance. Again, only one QTL had a favorable allele contributed by the *P. deltooides* parent. Harvest indices were affected by two QTLs on linkage group B and E for the main stem (HI1) and by other two QTLs on linkage group J and M for all resprouts (HI2). At the two HI1 QTLs, the *P. trichocarpa* parent contributed alleles to increased stem allocation, whereas the inverse was true at the two HI2 QTLs. All overdominant, the HI2 QTLs jointly explained a much higher percentage of the phenotypic variance (84%) than the HI1 QTLs (39%).

Table 4 summarizes QTL analysis of plantation growth and productivity in the three environments. At Puyallup, one to two QTLs were detected to influence height in both years, but none of them was associated with the nursery height QTL on linkage group G (see above). Except for year 1, a common QTL on linkage group D consistently affected plantation height in each

Table 3 The chromosomal locations, effects and modes of gene action of individual QTLs for growth traits in the nursery in the 1988 material of F₂ Family 331

Nursery trait	Chromosome location ^a		LOD	Effect ^b			Gene action		
	LG	Dist.		R ²	a	d	d/a	Mode ^c	Direction ^d
Stem height 2	G	10	4.21	41.8	-0.12	0.57	-4.75	OD	trich
3	G	6	2.33	22.9	-0.11	0.75	-6.82	OD	trich
Stem diameter 2	G	14	3.02	31.5	-0.12	0.17	-1.42	OD	trich
	J	26	2.84	42.2	-0.14	0.18	-1.29	OD	trich
	Total		7.69	61.5					
3	B	4	3.20	53.3	-0.56	-0.65	1.16	D	trich
	O	0	3.02	39.5	0.54	-0.50	0.93	D	delt
	Total		5.18	68.9					
Stem dry weight of MS	B	0	2.38	34.7	-0.193	-0.196	1.02	D	trich
Total dry weight of MS	O	0	2.39	27.6	0.142	-0.089	-0.63	PD	delt
Total dry weight of resprouts	D	68	5.12	73.6	-0.512	-0.463	0.90	D	trich
	G	10	2.33	31.2	-0.051	0.521	-10.22	OD	trich
	J	59	3.84	67.6	0.496	-0.539	-1.09	D	delt
	L	13	4.29	66.6	-0.541	-0.447	0.83	D	trich
	Total		7.16	76.0					
Harvest index on MS	B	58	2.06	14.3	-0.063	-0.080	1.27	OD	trich
	E	0	2.38	26.2	-0.060	0.073	-1.22	OD	trich
	Total		4.67	38.7					
Harvest index on all resprouts	J	24	3.17	35.1	0.113	-0.230	-2.04	OD	delt
	M	123	2.90	63.0	0.023	-0.266	-11.56	OD	delt
	Total		6.14	83.5					

^a LG, Linkage group referring to the map in Bradshaw et al. (1994); Dist., QTL position described by the distance (cM) from the “top” of the linkage group

^b R², The percentage of the total phenotypic variance explained by the QTL; a, the additive effect expressed as the effect of substituting a *P. deltooides* (D) allele for a *P. trichocarpa* (T) allele; d, the dominant effect of a *P. deltooides* allele to a *P. trichocarpa* allele

^c Mode, The mode of gene action regarded as additive (Add), partial dominance (PD), dominance (D) and overdominance (OD) when the dominant: additive effect ratio = 0–0.20, 0.21–0.80, 0.81–1.20 and > 1.20, respectively

^d Direction, The direction of additive effect on the phenotype

Table 4 The number and position of QTLs (with LOD > 2) for growth traits at different sites in the 1988 material of F₂ Family 331. The LOD and R² values, explained by all these QTLs, are given, with a comparison between combining and not combining two important nursery QTLs on linkage groups B and G

	Number	Linkage group	Not combining		Combining		
			LOD	R ²	LOD	R ²	
Puyallup							
Height 1	1	E	2.38	38.1	3.54	48.7	
2	2	D, M	6.87	56.1	9.69	82.2	
3	2	D, M	6.72	55.9	7.85	60.0	
5	1	D	2.17	17.2	3.30	27.0	
Basal area 1	3	E, I, O	9.06	75.6	12.08	89.5	
2	2	E, O	4.97	39.7	6.24	6.17	
3	1	O	2.36	22.2	4.79	41.7	
4	1	O	2.14	20.6	4.39	40.1	
5	1	O	2.15	24.0	4.48	45.3	
Volume 5 ^a	0	–	2.46	23.6	3.85	43.1	
Boardman							
Height 1	2	M, O	6.47	60.7	7.75	75.1	
2	3	E, M, M	7.63	45.0	9.06	55.6	
Basal area 1	2	C, E	4.53	36.3	5.21	44.6	
2	2	C, E	6.15	42.9	6.49	45.4	
Clatskanie							
Height 1	2	G, M	5.22	30.9	6.90	41.1	
2	1	G	2.14	16.3	3.68	29.8	
3	4	D, E, G, J	9.17	71.6	12.55	89.6	
Basal area 1	1	E	2.09	16.1	3.53	37.7	
2	1	J	2.53	15.5	3.63	24.9	
3	4	E, G, J, Q	9.61	50.8	11.39	56.3	

^a No QTL was detected for VOL5 at Puyallup, but this trait was mapped using two respective QTLs for HT5 (on linkage group D) and BA5 (on linkage group O). It was further mapped by combining two seedling QTLs

year. More QTLs (2–3) were identified for basal area at younger ages than older ages (1); a QTL on linkage group O was common for that trait in each year. The pleiotropic effect of common QTLs might partially explain moderate to high across-age genetic correlations for plantation height and basal area, as described in Table 5. As expected, some QTLs were conserved across all three environments: e.g. a QTL on linkage group M governing height growth and a QTL on linkage group E governing basal area. Other QTLs seemed to be effective only in one or two environments. At Boardman, both height and basal area appeared to have more common QTLs among different years, whereas growth QTLs varied more considerably over years at Clatskanie.

As mentioned above, two QTLs on linkage groups G and B might be important for nursery height and diameter growth, respectively. These two QTLs, although not identified at the plantation stage, were further used to simulate the relative efficiency of QTL mapping on plantation growth (Table 4). At Puyallup, the combination of the two nursery QTLs with the plantation QTLs significantly increased LOD scores and percentages of the phenotypic variance explained, as compared to the plantation QTLs alone (Table 4). For example, no QTL above the threshold of the LOD score was detected for 5-year volume index, whereas by combining the two nursery QTLs and those for 5-year

Table 5 Genetic correlations of growth traits at different ages in the clonally replicated plantation of the 1988 material of F₂ Family 331 at Puyallup

	Age (years)				Volume 5
	2	3	4	5	
1 Height	0.85	0.77	–	0.71	0.60
Basal area	0.75	0.58	0.51	0.49	0.41
Basal area increment	0.63	0.49	0.37	0.39	0.41
2 Height		0.92	–	0.84	0.69
Basal area		0.84	0.79	0.77	0.60
Basal area increment		0.70	0.59	0.61	0.55
3 Height			–	0.87	0.72
Basal area			0.95	0.93	0.90
Basal area increment			0.74	0.72	0.81
4 Height				–	–
Basal area				0.97	0.95
Basal area increment				0.81	0.84

height and basal area, one could obtain a high LOD score (3.85) and explain over 40% of the phenotypic variance in volume by QTLs. Given the broad-sense heritability of 0.80, these combined QTLs explained half of the genetic variance in this trait. Increased QTL mapping efficiency through the combined approach

was also found at Boardman and Clatskanie, although it was not as pronounced as at Puyallup.

Discussion

Information about seedlings, resprouts and clonal plantation for interspecific poplar F_2 progenies permits us to study the developmental genetics of growth in trees over phase changes at the phenotype level. The *Populus* linkage map constructed by DNA-based markers further allows for the genetic dissection of developmental changes at the molecular level. We found that pronounced differences existed in growth, correlation to plantation performance and genetic control between seedlings and resprouts. Owing to the proximity of roots to shoots and a large root system, resprouts displayed greater growth than seedlings (Sennerby-Forsse et al. 1992). Although the same QTL on linkage group G was identified for stem height in both seedlings and resprouts, stem diameter at the two stages was affected by different QTLs with a changed mode of gene action. It seemed that QTLs on linkage groups B and O were specific to resprouts and affected the diameter and dry weight of their main shoot.

Since resprouts have developed root systems, their growth can be more fully expressed in the nursery than the growth of seedlings. For this reason, resprouts were found to be better predictors of subsequent plantation growth than seedlings (Table 1). However, the correlations between nursery performance and field clonal growth differed between plantations, with larger values at Boardman and Clatskanie than at Puyallup. The lower correlations at Puyallup were not unexpected, although the plantation was at the same site as the nursery. This plantation was established with unrooted cuttings, so its early growth was largely affected by the rooting ability of the cuttings. Given a remarkable discrepancy in rooting ability between the two parents, *P. trichocarpa* and *P. deltoides* (Heilman et al. 1994), the F_2 generation was expected to display much variation in this trait. Thus, genotypes that perform well in the establishment year are those with a strong rooting capacity from cuttings, although these genotypes do not necessarily display an intrinsically higher growth rate than poorly rooting genotypes. It is certain that better root systems positively influence the early growth of cuttings (Ying and Bagley 1974; Struve et al. 1984; Heilman et al. 1994), but the favorable effect of rooting rate on the early growth of trees disappears shortly after a stable root system is formed (Foster et al. 1985). For these reasons, considerable changes in the ranking order of growth from the nursery to plantation stages are unavoidable at Puyallup (Fig. 2). On the contrary, genotypic growth at Boardman and Clatskanie can be fully expressed early because of the development of root systems. In these two plantations,

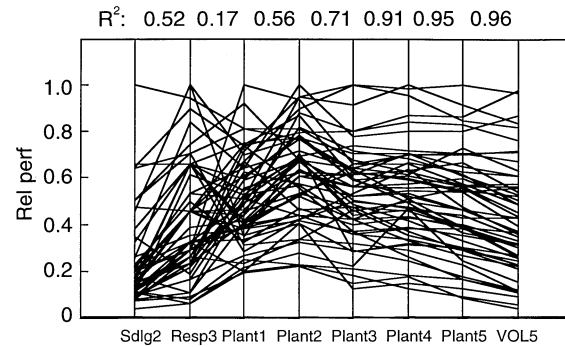


Fig. 2 Rank changes of radial growth for genotypes from the 1988 material of F_2 Family 331 during nursery and plantation stages at Puyallup. Relative performance was relative to the best genotype at each age. The squared Spearman correlations are given at the top

genotypes with pronounced seedling or resprout growth tend to exhibit more clonal growth, and such a trend does not change with stand development. The findings at Boardman and Clatskanie were further confirmed on a larger scale by the 1990 material (Table 2).

The relationship between the nursery and plantation growth may also be affected by inter-tree competition in the plantation. At Puyallup, the plantation has smaller spacing in which trees tended to invest more carbon to height growth in the early stage in order to first capture spatial advantages or prevent themselves from suppression. Thus, genotypes displaying vigorous height growth tend to be dominant in this plantation, which leads to closer relationships between nursery and plantation for height than diameter or dry weight (Table 1). This discrepancy becomes more pronounced when interactive competition totally sets in the stand (at age 3 years at Puyallup).

Competition also affects the age-age genetic correlations of growth during the plantation stage. To obtain larger growing space, tree height displays stronger age-age correlations in the early ages than basal area. However, in order to better respond to the competition among trees, dominant genotypes tend to invest more carbon into radial growth, whereas suppressed genotypes put more energy into height growth at the cost of radial thickening (Wu and Stettler 1996). Basal area then becomes a better predictor of late volume growth than height at the time when competition emerges in the stand (Table 5, Fig. 2). At Puyallup, owing to a deep influence by competition, the advantage of radial growth as a predictor was maintained even after the plantation was thinned to 50% at year 3.

At Boardman and Clatskanie, since wider spacing was used, there was virtually no competition in the first 3 years. Therefore, for each genotype, the potential of both height and radial growth can be equally expressed in the two plantations. Before crown closure, nursery height and diameter should have similar effectiveness to predict plantation growth.

In this study, we used a QTL mapping experiment to explore the genetic control of nursery traits and their correlation to plantation growth. Nursery traits were found to be under the control of a few genomic regions with large effects. In most cases, a single QTL identified explained 20–70% of the total phenotypic variance. There appeared to be different patterns of genetic control over nursery height and radial growth. We only found an overdominant QTL on linkage group G for nursery height. At the QTL, a positive allele for that trait was derived from the *P. trichocarpa* parent, consistent with the better growth of this parent in the plantation at the same site (Wu and Stettler 1994, 1996). However, more underlying QTLs were detected for nursery diameter which changed from seedlings to resprouts in their chromosomal positions and gene action. For resprout diameter, the two parents respectively contributed a favorable allele to their F₂ progenies at QTLs on linkage groups B and O.

The ability to resprout from stools varies widely within and among poplar species (Heilman and Stettler 1990; Tuskan and Rensema, 1992). In this study, a total of four QTLs were identified for total dry weight of resprouts per stool, each with very large effect on the phenotype. Three of the QTLs showed dominant gene action, and the fourth was overdominant. We also found that the *P. trichocarpa* parent was responsible for increased resprout biomass at most QTLs. This is not unexpected given the strong capacity of *P. trichocarpa* to form shoots by stump sprouting (Heilman and Stettler 1990; Han et al. 1994). Using the same poplar pedigree and linkage maps, Han et al. (1994) identified a QTL on linkage group C accounting for 24% of the phenotypic variance for shoot regeneration in vitro, with a positive allele contributed by the *P. trichocarpa* parent. In *Eucalyptus*, six QTLs from different chromosomes jointly explained 67.1% of the genetic variance for the number of resprouts per stump, with the better-resprouting parent contributing more alleles to increase the value in this trait than the other parent (Grattapaglia et al. 1995).

Harvest indices at the main stem and stump levels are influenced by different QTLs. There was significant genetic variation in the harvest index estimated as the ratio of stem dry weight over total stem and branch dry weight, with a broad-sense heritability of approximately 0.85 in the plantation at Puyallup (Wu and Stettler 1996). In many species, harvest index has been found to have high additive variance (Kärki and Tigerstedt 1985). However, our QTL mapping showed strong overdominance control over the two measures for harvest index. The *P. trichocarpa* allele was associated with increases in harvest index at the main stem level, which was expected since that parent has the higher allocation of carbon to the stem (Wu and Stettler 1996). Harvest index measured on the basis of all resprouts inversely describes the intensity to produce multiple shoots from a stool. The *P. deltoides*

parent with low resprouting ability contributed alleles to increase this ratio.

During the plantation stage, height and basal area were also controlled by different QTLs, but each trait had a common QTL through different ages of the plantation. Owing to the pleiotropic effect of the QTLs on growth at different ages, high age-age genetic correlations were detected (Table 4). Those QTLs that are effective in the plantation stage generally differ from those for the nursery stage. This can be immediately seen from the Puyallup plantation in which only two linkage groups, D and O, may have shared QTLs for resprout and plantation growth. Even so, no QTLs were identified to explain a relatively tight relationship for height between nursery and plantation. However, the nursery QTLs, despite they could not be identified in the plantation, may have potential impacts on plantation growth. For example, two nursery QTLs on linkage groups B and G significantly increased LOD scores (by 40–110%) and QTL-contributed broad-sense heritabilities (by 30–100%) at the plantation stage when they were combined with the plantation QTLs.

For the other two plantations, large correlations between nursery and plantation growth seem to have different genetic bases. At Clatskanie, a QTL on linkage group G may be responsible for these correlations during the first 3 years of plantation growth, whereas such a QTL cannot be detected at Boardman. Failure to identify QTLs underlying close relationships between nursery and plantation performance may be due to limits of the assumption and sample size used. The current QTL mapping experiment was based on the assumption that QTLs were fixed for alternative alleles in either parent. Thus, we cannot find QTLs that are heterozygous between the two parents (see Andersson et al. 1994). Also, QTLs with modest effects cannot be detected with a small sample size. By incorporating the two nursery QTLs, we can also increase the mapping efficiency of plantation growth at Boardman and Clatskanie, but to a less extent than at Puyallup. Different genetic mechanisms underlying the relationship between nursery and plantation growth at Boardman and Clatskanie were obviously due to significant genotype × environment interactions. Variation in clonal response to the two environments was observed at the phenotype level (Wu and Stettler 1997) and can be further explained by specific QTLs (Table 4).

The important nursery QTLs might contribute to the variation of growth in the plantation via their cumulative effects with the plantation QTLs. Nonlinear interactions between the nursery and plantation QTLs may also play an important role in controlling the development of poplar, although the QTL mapping package employed in this study ignores epistasis. However, this question can be addressed only when a robust statistical program to deal with epistasis is developed (Tanksley 1993).

The increased mapping power using the nursery QTLs may mean a possibility to use a “molecular breeding” technique to improve the efficiency of early selection in *Populus*, a model system for forest trees. Although marker-assisted selection may be limited in forest trees due to linkage equilibrium (Strauss et al. 1992), the use of this kind of technique can be expected to produce considerable efficiency if trait correlations are low (Lande and Thompson 1990), as observed at Puyallup.

Moderate relationships between nursery traits and plantation growth, along with potential marker-assisted selection using the nursery QTLs, permit breeders to carry out preliminary nursery selection for growth. However, the accuracy of the nursery selection is contingent upon what planting systems (rooted or unrooted) are used in the field trial. Also, selection intensity at the nursery stage should be strictly controlled because in many cases genotypes with the same nursery growth show very different growth at the plantation stage (data not shown). Depending on planting spacing used in the plantation, breeders should determine an optimal criterion (height or diameter) for the nursery selection from which maximum genetic gain for plantation growth can be expected.

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