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Genetic mapping of QTLs affecting tree growth and architecture in *Populus*: implication for ideotype breeding

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Abstract A segregated F_2 progeny derived from two highly divergent poplar species, *Populus trichocarpa* and *P. deltoides*, was used to evaluate the genetic basis of canopy structure and function in a clonally replicated plantation. The QTLs of large effect on growth, branch, and leaf traits were identified using the *Populus* linkage map constructed by 343 molecular markers. Stem height and harvest index appeared to be under the control of few QTLs with major effects, whereas variation in stem basal area, volume, and dry weight might be due to many more QTLs. Branch and leaf traits on sylleptics tended to include more QTLs with major effects than those on proleptics. In the environment where the pedigree was tested, sylleptics were very frequent in the *P. trichocarpa* parent but rare in the *P. deltoides* parent. For sylleptic traits for which two or more QTLs were identified, however, increases in the trait values were conditioned not only by the *P. trichocarpa* alleles, but also by the *P. deltoides* alleles. Similar findings were found for traits on proleptics that were differently expressed between the two parents. For both sylleptic and proleptic branch types, dominance (ranging from partial to over) was observed. The QTLs on specific linkage groups were found to be responsible for relationships between stem growth and its developmental components. Similar QTL clustering was also observed for morphological or developmental integration in poplar, i.e., traits with similar developmental origins are more strongly correlated with one another than traits with different developmental origins. The implications of these molecular genetic results for ideotype breeding of poplars are discussed.

Key words Growth · Ideotype breeding · *Populus* · QTL mapping · Quantitative variation

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Introduction

Under the pressure of natural selection, organisms tend to display a combination of form and function optimal for growth and reproduction in the environments in which they live (Rosen 1967). This principle of optimal design has been developed in crop physiology and led to the concept of ideotype breeding (Donald 1968). Crop breeders seek to create the ideotype through detailed studies on how various parts of a plant interact with each other to produce the best performance in a specific environment. In recent years tree physiologists have also developed a similar awareness of the need to correlate stem wood production with crown architecture, biomass partitioning, and leaf area duration (Dickmann 1985; Ford 1985; Kärki and Tigerstedt 1985; Cannell et al. 1988; Scarascia-Mugnozza 1991). Studies of tree structure have been carried out at the level of the individual leaf, the branch, and the canopy (Hinckley et al. 1992). Leaves are traditionally considered the most important components of canopy as a result of their role in carbon production. Branches determine stem wood productivity by influencing leaf display and transporting photosynthetic products and water among the organs. By intercepting more light, a larger canopy (and therefore larger leaf area) can produce more stem growth than a smaller canopy. However, a larger leaf area requires more than a linear increase in the support tissue of branches, which competes with the allocation of biomass to the stem (McMahon and Kronauer 1976; Chazdon 1986). Thus,

a way to balance maximum photosynthetic surface (leaf area) and minimum energy investment (branches) can potentially increase productivity (Leopold 1971; Farnsworth and Niklas 1995). Unfortunately, this functional relationship cannot be incorporated into tree genetic improvement programs because its underlying genetic mechanisms have not been fully understood.

Genetic mapping provides a robust means to shed light on the genetics of tree growth and structure. Genetic factors, i.e., quantitative trait loci (QTLs), affecting a trait can be identified on the chromosomes of the organisms with the aid of linked molecular markers. These factors can be further studied in terms of the magnitude of their effects on the phenotype, the mode of their gene action, the parental origins of the favorable QTL alleles, and the relationships between QTLs underlying different physiological processes. Molecular information on the inheritance and transmission of specific traits will permit the production of even better improved phenotypes through more effective breeding and parental selection.

Populus offers a good model system for the biological studies of forest trees. *P. trichocarpa* and *P. deltoides*, originating from different natural environments (Eckenwalder 1977), differ remarkably in morphology, anatomy, and physiology (Hinckley et al. 1989). F_1 hybrids between the two species display strong heterosis in stem-volume growth, whereas many developmental traits, especially with respect to syllepsis and prolepsis, segregate widely in the F_2 and backcrosses (Stettler et al. 1988). Based on a clonally replicated plantation of the three-generation *P. trichocarpa* × *P. deltoides* pedigree, the number of genes, broad-sense heritabilities, and genetic correlations among stem growth and morphological components have been systematically examined by a biometric approach (Wu 1995; Wu and Stettler 1994, 1996). Now, the genetic structure of this pedigree can be further understood at the individual QTL level using a DNA-based linkage map developed from the same material (Bradshaw et al. 1994). In this paper, we identify QTLs that affect tree growth and development by relating the *Populus* genome map to a number of phenotypic measurements on stem growth, branch architecture, and leaf display. The implications of molecular genetic results for the ideotype breeding of poplar are then discussed.

Materials and methods

The pedigree, genetic map, and clonal plantation

A female *Populus trichocarpa* clone, 93-968, from western Washington was crossed to the male *P. deltoides* clone, ILL-129, from central Illinois. In 1988, two siblings of the F_1 family, 53-242 and 53-246, were crossed to generate an F_2 family with 90 members. The seedlings for the F_2 were cultured in a nursery at Farm 5 of the Washington State University Research and Extension Center near Puyallup, Washington. A genetic linkage map consisting of 343 restriction fragment length polymorphism (RFLP), sequence-tagged site (STS), and random amplified polymorphic DNA (RAPD) markers was constructed based on the 90 F_2 progenies of the pedigree (Bradshaw et al. 1994; Bradshaw and Stettler 1995). The 19 largest linkage groups chosen, covering approximately two-thirds the length of the *Populus* genome, are roughly equivalent to 19 pairs of chromosomes in *Populus*. The linkage map was used for QTL identification in this study.

In spring 1991, the three-generation poplar pedigree, including 55 progenies from the F_2, both F_1 parents, and the two original parents, was field planted at the same farm using unrooted cuttings. The experimental plantation was laid out in a randomized complete block design with three clonal replicates and two-tree plots at a spacing of 2×2 m, surrounded by two border rows. A triploid F_2 clone was omitted from the genetic analysis.

Morphometric measurements

P. trichocarpa and *P. deltoides* have strikingly different morphological architecture, especially with respect to prolepsis and syllepsis (Hinckley et al. 1989). The morphological development of their F_2 hybrids during the first 3 years of growth in the plantation has been described elsewhere (Wu and Stettler 1996). Quantitative traits used for QTL mapping were those which reflect the most important components of tree canopy in poplar and best discriminate between the two original parents. They were measured for each tree at the level of the stem, the branch, and the leaf, with procedures described in detail by Wu and Stettler (1996). In year 2, the branch traits measured included number, average length, angle of origin, and curvature (described as the difference between angles of origin and of terminal), each separately for sylleptics (SYL) and proleptics (PRO) formed in different years (1 or 2), whereas the leaf traits measured included total number and total area separately for the current terminal (CT), SYL2, PRO1, and SYL1.

At the end of the third year, the plantation was thinned to 50% by harvesting 1 tree for each genotype in each replicate. Three-year total height growth, basal-area growth, and stem volume, and third-year stem-height increment and basal-area increment were analyzed on all trees, whereas third-year stem dry weight and harvest index were analyzed on the 3 harvested trees per genotype. Branch measurements of the harvested trees were taken separately for sylleptics and proleptics formed in 3 different years and included number, third-year terminal increment, and dry weight. Single-leaf traits (size and shape) were measured in all trees on PRO2, PRO1, and SYL1, whereas cumulative leaf traits (leaf area and number) were estimated only on harvested trees for CT, SYL3, PRO2, SYL2, PRO1, and SYL1.

Quantitative trait locus analysis

In this QTL mapping experiment, the accuracy and power for detecting a QTL may be limited due to the small progeny size used. However, this can be largely overcome by use of clonal replicates that have two advantages for QTL mapping. First, as derived by Knapp and Bridges (1990), an additional clonal replicate of a progeny can increase statistical power, analogous to adding another progeny genotype if all the additive genetic variance is explained by markers. Second, clonal replicates provide a possibility to exclude the contamination of the block and QTL × block interaction effects from the QTL effect and, thereby, increase the accuracy of QTL identification. Because interval mapping based on maximum likelihood has not incorporated clonal replicates in the current program package, a single-factor regression analysis model was used to test for significant associations between each of the molecular markers and phenotypic traits in the F_2 poplar progeny. By assuming that the effects due to QTLs, genotypes within QTLs and

Table 1 Single-factor analysis of variance model used to identify QTLs associated with a molecular marker

Source of variance	*df*	MS	*F* value	EMS[a]
Replicate	$r-1$	MS1	MS1/MS3	$V_e + nV_{cr} + rtV_r$
Clone	$t-1$	MS2	MS2/MS3	$V_e + nV_{cr} + rnV_c$
Between QTL genotypes	2	MS21	(MS21 + MS32)/(MS22 + MS31)	$V_e + nV_{wr} + nt'V_{qr} + rnV_w + rnt'V_q$
Within QTL genotypes	$t-3$	MS22	MS22/MS32	$V_e + nV_{wr} + rnV_w$
Clone × replicate[b]	$(t-1)(r-1)$	MS3	MS3/MS4	$V_e + nV_{cr}$
Between QTL × replicate	$2(r-1)$	MS31	MS31/MS32	$V_e + nV_{wr} + nt'V_{qr}$
Within QTL × replicate	$(t-3)(r-1)$	MS32	MS32/MS4	$V_e + nV_{wr}$
Error	$tr(n-1)$	MS4		V_e

Note: The linear regression model used in this molecular experiment is $y_{ijk} = \mu + c_i + r_j + (cr)_{ij} + e_{ijk}$ where y_{ijk} is the phenotypic value of the kth tree of the ith clone in the jth replicate, μ is the overall mean, c_i is the effect due to the ith clone, r_j is the effect due to the jth replicate, $(cr)_{ij}$ is the effect due to interaction between the ith clone and jth replicate, and e_{ijk} is the random error. c_i is further partitioned into two effects due to the ξth genotype and the ζth genotype within the ξth QTL genotype, i.e., $c_i = q_\xi + (w/q)_{\zeta/\xi}$

[a] t' is the harmonic mean averaged over the numbers of genotypes within three different QTL genotypes

[b] For traits measured based on a single tree in a plot, clone × replicate interaction effects cannot be estimated, but QTL genotype × replicate interaction effects are estimatable

replicates are all random, the *F*-values were calculated based on the structure of the expected mean squares as shown in Table 1. The significance level of $P < 0.001$ was chosen to declare the existence of a putative QTL in the marker region. The component of quantitative genetic variance explained by a significant QTL was estimated by equating the mean squares with the expected mean squares derived from Type III sums of squares, PROC GLM (SAS Institute 1988). The percentage of the total phenotypic variance accounted for by the QTL, i.e., broad-sense heritability at the single genetic locus level (H_Q^2), was estimated following the procedure for estimating broad-sense heritability on the clonal mean basis (see Table 1; Wu and Stettler 1994, 1996).

Additive and dominant effects were calculated from the mean trait values for the F_2 trees having homozygous *P. trichocarpa*, homozygous *P. deltoides*, and the heterozygous genotype at each of the significant QTLs, and the mode of gene action was determined from the ratio of dominance over additivity (Wu 1995). The contribution of multiple QTLs to the total phenotypic variance was estimated with the multi-factor analysis of variance method (SAS Institute 1988).

For the traits which were not normally distributed, data transformation was used to produce approximately normal distributions before QTL analysis was conducted.

Results

The two original parents differed remarkably in all traits studied, with *P. trichocarpa* having larger growth and stronger branching (especially syllepsis) than *P. deltoides* (Figs. 1–3). The F_2 derived from the two parents exhibited continuous variation and an approximately normal distribution in growth traits (Fig. 1A,B) and harvest index (Fig. 1C). In both year 2 and 3, sylleptic and proleptic traits segregated widely in the F_2 families, with sylleptics tending to display non-normal distribution (Figs. 2,3). The distribution for leaf traits on the current terminal was approximately normal (e.g., Fig. 3A).

The QTLs with large effects on the third-year stem growth and production traits were located on the *Populus* linkage map. A QTL was detected for height

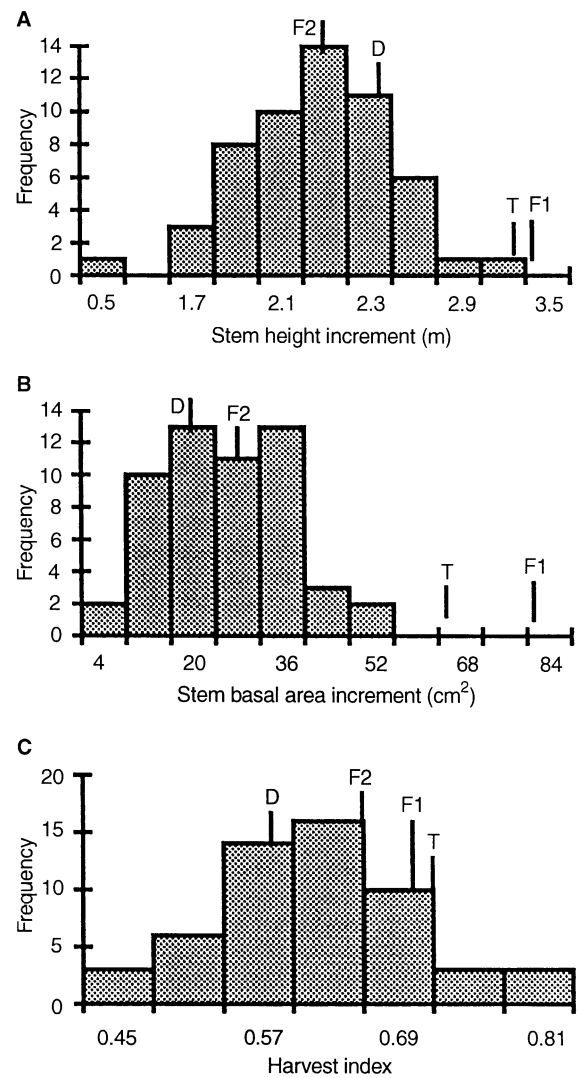

Fig. 1A–C Distribution of phenotypes for third-year stem height increment (**A**), basal-area increment (**B**), and harvest index (**C**) in the F_2 progeny. Means for the two original parentals (*P. trichocarpa*, *T* and *P. deltoides*, *D*), the F_1 parents, and the F_2 are indicated

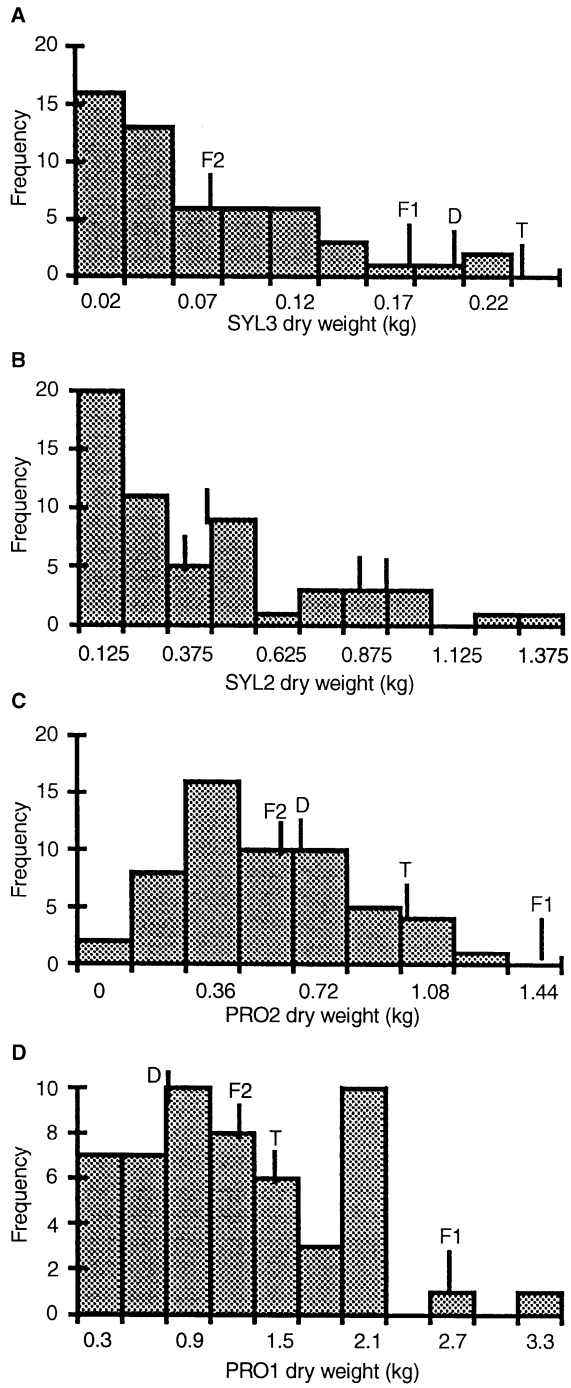

Fig. 2A–D Distribution of phenotypes for branch dry weights on SYL3 (**A**), SYL2 (**B**), PRO2 (**C**), and PRO1 (**D**) in 3-year-old trees of the F_2 progeny. Means for the two original parentals (*P. trichocarpa*, *T* and *P. deltoides*, *D*), the F_1 parents, and the F_2 are indicated

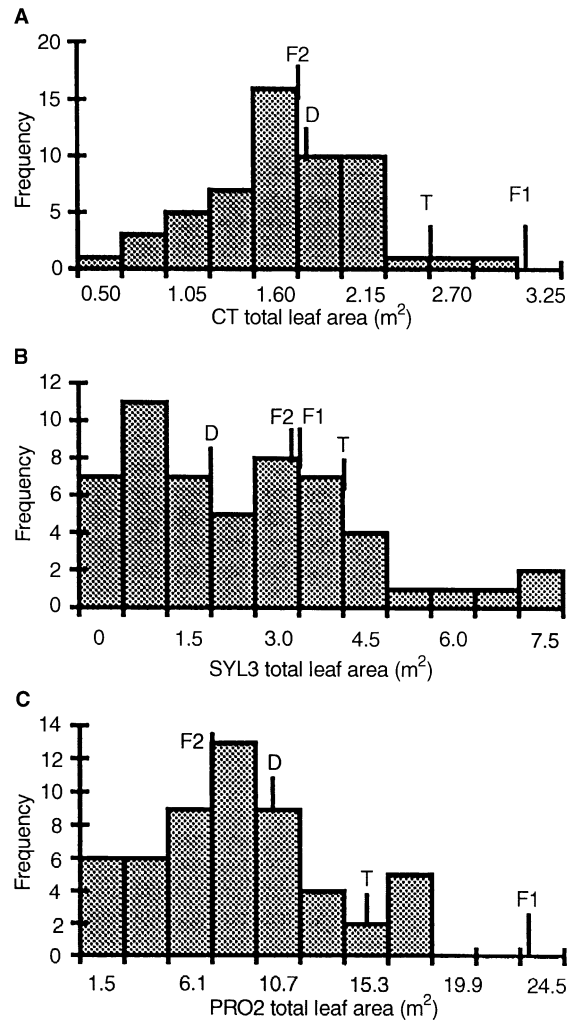

Fig. 3A–C Distribution of phenotypes for total leaf areas on CT (**A**), SYL3 (**B**), and PRO2 (**C**) in 3-year-old trees of the F_2. Means for the two original parentals (*P. trichocarpa*, *T* and *P. deltoides*, *D*), the F_1 parents, and the F_2 are indicated

increment on linkage group M that explained 14.2% of the phenotypic variance in this trait. This QTL, along with that on linkage group D, also affected total height, both jointly explaining 27.3% of the phenotypic variance (Table 2). As expected (see Fig. 1A), the *P. trichocarpa* parent contributed all additive alleles to height growth with partially or overdominant effects to the *P. deltoides* allele. No QTL for basal-area increment and volume was identified, but there was a QTL for total basal area on linkage group O that explained 15% of the phenotypic variance. Unexpectedly (Fig. 1B), increased radial growth was contributed by the *P. deltoides* allele in an overdominant fashion. Two QTLs of large effect were found to jointly account for 24.1% of the phenotypic variance in stem dry weight on linkage groups E (the *P. trichocarpa* allele has a positive recessive effect) and O (the *P. deltoides* allele was dominant with a positive effect). About 50% of the phenotypic variance in harvest index was jointly explained by QTLs on linkage group J and O, at each of which low harvest index was dominant to high harvest index regardless of the origin of the allele.

Table 2 Summary of significant QTL effects for stemwood growth and production in year 3

Trait	Chromosome location		H_Q^{2b}	Effect[c]		Gene action[d]	
	LG[a]	marker		*a*	*d*	Mode	Direction
Height increment	M	P1012	14.2	− 11	35	OD	*trich*
Basal-area increment	–						
Total height	D	I20_05	12.9	− 55	32	PD	*trich*
	M	P1012	13.7	− 23	85	OD	*trich*
	Total		**27.3**				
Total basal area	O	A18_05	15.0	5.92	15.43	OD	*delt*
Volume	–						
Dry weight	E	B11_10	13.9	− 1.02	− 0.25	PD	*trich*
	O	P1202	11.7	0.27	1.38	OD	*delt*
	Total		**24.1**				
Harvest index	J	I17_04	26.5	0.086	− 0.051	PD	*delt*
	O	chiD	21.4	− 0.067	− 0.041	PD	*trich*
	Total		**48.6**				

[a] LG = linkage group with reference to the map shown in Bradshaw et al. (1994)
[b] H_Q^2 = the percentage of the phenotypic variance explained by the QTL (the multi-QTL model is shown in boldface)
[c] a = the additive effect expressed as the effect of substituting a *P. deltoides* allele for a *P. trichocarpa* allele; d = the dominant effect of a *P. deltoides* allele to a *P. trichocarpa* allele
[d] PD, Partial dominance; OD, Overdominance. Direction, The direction of additive effect on the phenotype

Each branch and leaf trait was also subject to QTL mapping using the *Populus* linkage map. A total of 113 significant QTLs ($P < 0.001$) were detected for all traits in both year 2 and 3 with a range of 0 to 5 QTLs per trait in a crown position (Tables 3 and 4). The percentage of the phenotypic variance explained by each QTL ranged from 10% to 48.6%. For many traits, the identified QTLs jointly explained at least half of the genetic variance (see Wu and Stettler 1996, for broad-sense heritability estimates). The majority of the QTLs (103/113) had additive-dominant effects, half of which (52/103) were overdominant.

In general, mapped QTLs jointly explained higher percentages of the phenotypic variance in branch and leaf traits on sylleptics than on proleptics or the current terminal, or in lower than upper positions for the same sylleptics (Table 5). However, by year 3, SYL1 traits tended to display decreased control by QTLs of large effects. On average, the phenotypic variance was more strongly contributed by QTLs identified for third-year morphological traits than for second-year ones. For the same traits, increased numbers of QTLs with large effects were detected from year 2 to 3, but some QTLs seemed to be involved in both years. For example, 2 QTLs on linkage groups G and J affected total leaf area on sylleptics developing from the current terminal in both years 2 and 3. A QTL on linkage group L affected total leaf area on proleptics formed in each of these 2 years. Similar QTLs were also observed for leaf number. In both years, almost no common QTLs were detected for different but allometrically related traits, such as total leaf number *vs.* total leaf area, on proleptics or the current terminal. However, these morphometrical traits on sylleptics had quite a few shared QTLs, e.g., those on linkage groups E and O for the lower sylleptics (SYL1) in year 2. The 2 above SYL1 QTLs were significantly associated with, or tightly linked with those for, second-year basal area (Bradshaw and Stettler, 1995) and third-year basal area, stem dry weight, and harvest index (Table 2). In year 2, few common QTLs were found for the same traits across different branch types or positions. Yet, by year 3, there were increased QTLs to be shared between the same trait expressed in the neighboring positions or on the same branch types, either sylleptics or proleptics (Table 4).

Although syllepsis is characterized by *P. trichocarpa* and prolepsis is prevalent in *P. deltoides*, positive alleles for these two branching processes were virtually contributed by both parents. For example, of 64 QTLs identified for branch and canopy traits associated with sylleptics, the *P. deltoides* parent contributed 44 (69%) positive alleles to increased trait values. Of the positive alleles 46% were contributed by the *P. trichocarpa* parent to increase the values of those traits on proleptics.

Two single leaf traits, leaf size and shape, appeared to display different developmental patterns from branch and canopy traits. Both tended to have a similar genetic basis among different positions, as evidenced by common QTLs (linkage groups I and L for leaf size and I and O for leaf shape). Whereas a larger leaf size was due to the dominant *P. trichocarpa* allele, increased leaf width was, as expected (see Wu 1995), contributed by the allele from the *P. deltoides* parent with wide leaves (Table 4).

Table 3 Summary of significant QTL effects for branch and leaf traits in year 2 (*A* addivity · *D* dominance)

Trait		Chromosome location		H_Q^2	Effect		Gene action	
		LG	Marker		*a*	*d*	Mode	Direction
Branch								
Number	SYL2	–						
	PRO1	C	P12962	30.2	− 5	− 7	OD	*trich*
	SYL1	C	P755	14.0	5	0.01	A	*delt*
		D	P201	13.3	1	− 7	OD	*delt*
		E	P12242	20.1	− 5	− 3	PD	*trich*
Average length	SYL2	–						
	PRO1	–						
	SYL1	J	G02_11	14.2	− 8	− 22	OD	*trich*
		O	P805	16.5	19	14	PD	*delt*
Origin of angle	SYL2	D	P1298	26.2	− 10	− 13	OD	*trich*
		G	P1273	23.1	2	14	OD	*delt*
		N	P1139	24.0	13	− 7	PD	*delt*
	PRO1	G	P1273	15.9	5	7	OD	*delt*
	SYL1	E	F15_10	28.2	− 16	16	D	*trich*
		I	G04_20	15.5	− 12	2	A	*trich*
		M	P13292	20.1	9	17	OD	*delt*
Curvature	SYL2	Y	P792	21.0	1	8	OD	*delt*
	PRO1	G	P912	19.1	4	3	PD	*delt*
		N	P1139	15.0	− 5	1	A	*trich*
	SYL1	B	I07_06	11.3	6	− 0.09	A	*delt*
		I	P856	13.7	− 1	− 10	OD	*trich*
Leaf								
Total number	CT	G	C06_18	14.8	− 5	− 4	PD	*trich*
	SYL2	G	C06_18	15.3	− 93	− 71	PD	*trich*
		I	P1317	17.9	117	− 92	PD	*delt*
		X	F15_18	37.6	− 173	− 230	OD	*trich*
	PRO1	C	P1049	24.3	− 160	− 263	OD	*trich*
		J	G02_11	20.1	242	− 336	OD	*delt*
	SYL1	A	C04_04	37.8	− 1438	− 1129	PD	*trich*
		C	E11_07	40.0	1188	− 665	PD	*delt*
		E	P1018	19.9	− 692	− 549	D	*trich*
		O	G12_09	13.1	502	446	PD	*delt*
Total area	CT	D	I20_05	11.3	− 0.201	0.099	PD	*trich*
	SYL2	G	C06_18	23.7	− 0.95	− 0.83	D	*trich*
		J	I17_04	42.6	1.54	− 1.95	OD	*delt*
		X	F15_18	48.6	− 1.51	− 2.05	OD	*trich*
	PRO1	L	P1291	19.2	− 1.04	3.00	OD	*trich*
	SYL1	C	E11_07	11.0	4.42	0.39	A	*delt*
		M	C01_16	39.0	5.55	− 7.12	OD	*delt*
		O	G12_09	17.2	3.52	4.33	OD	*delt*
Density	CT	F	F03_04	21.1	0.002	− 0.162	OD	*delt*
		I	D03_09	11.8	− 0.107	0.035	PD	*trich*
	SYL2	C	P755	17.6	0.021	− 0.030	OD	*delt*
	PRO1	I	D03_09	14.9	− 0.058	0.010	A	*trich*
		N	P1150	12.0	0.047	0.017	PD	*delt*
	SYL1	E	F15_10	36.7	0.178	− 0.201	OD	*delt*
		O	A18_05	16.4	0.096	0.101	D	*delt*

For explanation of terms, see Table 2

Discussion

QTLs for stemwood growth

The traditional polygenic model assumes that a quantitative trait is controlled by many genes each with minor effect on the phenotype. This assumption has governed forest tree breeding for several decades because tree growth and production are quantitatively inherited. However, results from the present molecular experiment indicate that these multigenic traits are virtually controlled by a limited number of QTLs explaining a fairly large proportion of the genetic variance individually or jointly. Similar results have been obtained in a number of other organisms such as tomato, maize, rice, pine, and eucalyptus (Paterson et al. 1991; Stuber et al. 1992; Doebley and Stec 1993; Groover et al. 1994; Grattagalia et al. 1995; Xiao et al. 1996a).

Table 4 Summary of significant QTL effects for branch and leaf traits in year 3

Trait		Chromosome location		H_Q^2	Effect		Gene action	
		LG	Marker		*a*	*d*	Mode	Direction
Branch								
Number	SYL3	H	E18_07	44.8	− 3	11	OD	*trich*
		I	A18_06	14.1	5	1	A	*delt*
		N	P1139	19.0	6	2	PD	*delt*
	PRO2	C	P755	13.4	− 3	3	PD	*trich*
		H	G06_08	21.8	3	− 6	OD	*delt*
		Q	E18_07	16.1	2	− 6	OD	*delt*
	SYL2	E	F15_10	28.2	− 3	− 8	OD	*trich*
		I	P856	19.3	5	− 0.22	A	*delt*
	PRO1	–						
	SYL1	D	P991	15.5	3	− 8	OD	*delt*
		O	P1202	14.2	5	4	PD	*delt*
Terminal increment	SYL3	O	P1202	28.3	10	21	OD	*delt*
		I	A18_06	18.2	11	8	PD	*delt*
	PRO2	O	chiD	33.9	− 2	43	OD	*trich*
		Y	P792	21.9	14	23	OD	*delt*
	SYL2	–						
	PRO1	A	H12_14	19.0	− 17	− 4	PD	*trich*
		J	G02_11	18.3	− 5	− 19	OD	*trich*
		L	P1093	21.2	− 3	23	OD	*trich*
	SYL1	M	B10_18	15.6	8	3	PD	*delt*
Dry weight	SYL3	E	F15_10	34.1	− 0.050	− 0.051	D	*trich*
		M	P13292	20.5	0.032	− 0.036	D	*delt*
	PRO2	L	P986	16.4	− 0.052	0.277	OD	*trich*
		R	E14_08	11.2	0.087	0.179	OD	*delt*
	SYL2	C	P12182	30.5	0.253	− 0.163	PD	*delt*
		J	G02_11	34.3	0.410	− 0.380	D	*delt*
	PRO1	D	A18_04	18.7	− 0.123	− 0.789	OD	*trich*
		J	P1203	14.6	− 0.447	− 0.242	PD	*trich*
	SYL1	A	H12_14	13.9	− 0.063	0.267	OD	*trich*
		J	I17_04	12.2	− 0.182	− 0.070	PD	*trich*
		M	C01_16	20.8	0.136	− 0.225	OD	*delt*
Leaf								
Single leaf area	PRO2	E	P761	13.3	− 36	28	PD	*trich*
		I	D03_09	12.4	− 49	12	PD	*trich*
		L	P1291	18.5	− 37	51	OD	*trich*
	PRO1	I	D03_09	10.0	− 18	4	PD	*trich*
		L	P1291	12.4	− 8	21	OD	*trich*
	SYL1	I	D03_09	14.9	− 11	− 4	PD	*trich*
		L	P1291	20.3	− 0.3	14	OD	*trich*
Width : length	PRO2	I	A18_06	29.1	0.071	− 0.013	A	*delt*
		O	A18_05	12.8	0.034	− 0.052	OD	*delt*
		N	P789	26.5	0.027	− 0.091	OD	*delt*
	PRO1	I	A18_06	14.6	0.061	− 0.031	PD	*delt*
	SYL1	O	D07_09	25.0	0.051	− 0.079	OD	*delt*
Total number	CT	J	P1203	15.3	7	− 8	OD	*delt*
		M	P1308	11.9	− 2	7	OD	*trich*
	SYL3	G	P993	10.1	− 73	− 5	PD	*trich*
		H	P1059	17.5	13	156	OD	*delt*
		I	A18_06	28.4	129	57	PD	*delt*
	PRO2	C	P755	13.8	− 87	61	PD	*trich*
		D	P1253	14.7	− 111	− 124	D	*trich*
		H	P1077	22.3	117	− 88	PD	*delt*
		J	P1203	13.7	117	− 193	OD	*delt*
	SYL2	B	P911	17.6	426	− 390	D	*delt*
		C	E11_07	41.6	959	− 808	D	*delt*
		I	P1317	24.0	560	− 593	D	*delt*
	PRO1	H	P1077	16.8	531	− 382	PD	*delt*
		J	91203	12.0	− 288	− 560	OD	*trich*
	SYL1	A	C04_04	32.1	− 1112	− 1181	D	*trich*
		C	E14_15	30.9	1097	− 1154	D	*delt*
		D	A18_04	15.3	210	− 1059	OD	*delt*
		M	C01_16	25.7	1168	− 1002	D	*delt*

Table 4 Continued

Trait		Chromosome location		H_Q^2	Effect		Gene action	
		LG	Marker		*a*	*d*	Mode	Direction
Total area	CT	N	P1150	13.8	0.329	0.071	PD	*delt*
	SYL3	G	C06_18	16.3	− 1.06	− 0.82	PD	*trich*
		H	P1059	24.9	− 0.03	2.33	OD	*trich*
		I	G04_20	35.1	2.11	− 1.24	PD	*delt*
		J	I17_04	26.5	2.01	− 2.69	D	*delt*
		N	P1150	14.3	1.39	− 0.20	A	*delt*
	PRO2	B	D08_07	12.8	− 2.35	1.50	PD	*trich*
		C	P755	16.4	− 2.35	2.43	D	*trich*
		L	P1291	14.2	− 2.12	3.28	OD	*trich*
	SYL2	C	P12182	20.3	2.49	− 1.43	PD	*delt*
		D	G02_09	26.1	1.45	− 4.20	OD	*delt*
		E	F15_10	46.3	− 2.98	− 4.45	OD	*trich*
		M	C01_16	46.1	3.51	− 3.39	D	*delt*
	PRO1	O	P1202	10.2	0.20	5.12	OD	*delt*
	SYL1	–						

For explanation of terms see Tables 2 and 3

Table 5 The chromosomal locations of mapped QTLs and their contributions to the genotypic variance in branch and leaf traits of year 2 and 3

	CT	SYL3	PRO2	SYL2	PRO1	SYL1
Year 2						
Branch number	–[a]	–	–	None	47.1 C	65.2 CDE
Avg. branch length	–	–	–	None	None	40.0 JO
Angle of origin	–	–	–	60.7 DGN	25.1 G	84.5 EIM
Branch curvature	–	–	–	37.0 Y	27.6 GN	34.4 BI
Leaf number	22.8 G	–	–	84.1 GIX	55.1 CJ	76.5 ACEO
Total leaf area	14.9 D	–	–	62.8 GJX	34.9 L	84.7 CMO
Leaf density	36.5 FI	–	–	25.5 C	33.8 IN	87.8 EO
Year 3						
Branch number	–	72.5 HI	60.1 CHQ	57.0 EI	None	70.3 DO
Branch terminal increments	–	59.0 OI	55.7 OY	None	59.6 AJL	73.2 M
Branch dry weight	–	69.2 EM	35.8 LR	86.0 CJ	45.7 DJ	98.1 AJM
Single-leaf area	×	×	40.7 EIL	×	31.6 IL	59.4 IL
Leaf width : length	×	×	73.9 ION	×	26.0 I	None
Leaf number	26.7 JM	51.7 GHI	70.5 CDHJ	93.8 BCI	59.1 HJ	99.0 ACDM
Total leaf area	17.9 N	74.7 GHIJN	40.8 BCL	87.6 CDEM	55.6 O	None

[a] No traits in the crown positions; None, no QTL was identified; ×, no data were measured

In this study, height was found to have more QTLs of large effect than basal area, whereas no QTLs were identified for volume. When very few or no QTLs at all can be identified for a quantitative trait, this trait is likely affected by many genes with relatively small effects whose observation requires a dense linkage map and a large sample size of mapping pedigree. That more minor genes are involved in basal area than height is not surprising in view of the complex nature of secondary growth (Zimmermann and Brown 1971). For the same reason, more genes can be expected for stem volume, as it is also the function of stem taper and form. Although any explanation for the difference in the stem form of trees is controversial, it has been widely recognized that stem-form development involves a number of physiological processes, such as nutritional, hydrological, mechanistic, and hormonal ones (Larson 1963), all of which are potentially governed by genetic factors.

The two poplar parents contributed favorable alleles differently to height and basal area, with the *P. trichocarpa* alleles beneficial for height and the *P. deltoides* alleles beneficial for basal area (Table 2). This finding validates second-year results reported in Bradshaw and Stettler (1995) by including older plantation growth. The present study was also expanded to observe genetic variation for productivity traits. Two QTLs of large effect were identified for both stem biomass and harvest index, with a QTL on linkage group O common to these two traits. At the QTLs for harvest index, "branch denseness" was partially dominant to "branch sparseness".

QTLs for branch and leaf development

In the second-year plantation growth, more QTLs of large effect were found for traits on sylleptics than on proleptics and more were found in lower than in upper positions (Table 5). More likely major gene control over sylleptics was in agreement with the non-normal distribution of sylleptic-related traits (Figs. 2A,B; 3B).

The genetic basis for the morphological variation of canopy may change with stand development. The numbers of QTLs with large effects increased in leaf number and total leaf area from year 2 to year 3 (Table 5). Some linkage groups that are stable for these two traits across ages suggest that the pleiotropic or linkage effect of genes on these linkage groups maintains the continuity of organ development over years. A similar genetic basis may also control the developmental integration of a poplar canopy, but dependent on different physiological processes. For example, morphological traits, such as total leaf number and area, on sylleptic (SYL) branches tend to have QTLs on the same linkage group, whereas independent QTLs were observed for different traits, even those allometrically related, on proleptics (PRO). In year 3, the same traits were more strongly correlated on the same branch types than on different ones. The current terminal (CT) showed a higher similarity to proleptics than to sylleptics due to the same origin of its bud as proleptics (Wu and Stettler 1996). The hypothesis of developmental integration that traits from the same origins are more strongly associated with each other than with those of different origins (Berg 1960; Waitt and Levin 1993) seems to have its underlying genetic mechanism. For example, QTL(s) associated with linkage group I affects leaf number on both SYL3 and SYL2, whereas those on linkage groups H and/or J affect leaf number on CT, PRO2, and PRO1.

In the environment where the F_2 progenies were tested, *P. trichocarpa* exhibits an inherently high capacity to produce sylleptic branches from lateral meristems without the rest period (Wu and Stettler 1996), whereas *P. deltoides* is strongly branched from dominant buds (proleptics). The direction of this branching habit between the two parents could not be predicted from QTL mapping. At the sylleptics QTLs, the *P. deltoides* parent contributed over half of the positive alleles to increased sylleptic branching. Near half of the positive alleles were contributed by the *P. trichocarpa* parent to generate proleptics. The opposite direction of allelic effect relative to the parental difference has also been observed in the wide cross of tomato (deVicente and Tanksley 1993) and the intraspecific cross of rice (Xiao et al. 1996a, b).

Ideotype breeding

In an earlier study, we observed that branch/leaf traits in upper crown positions were more strongly correlated with stem height whereas those in lower positions were more correlated with basal area (Wu and Stettler 1996). It was found that tight correlations between leaf number or total leaf area on the current terminal and height increment might be due to QTL(s) on linkage group D in year 2 and to QTL(s) on linkage group M in year 3. In year 2, sylleptic traits in a lower crown position had a considerable impact on basal area increment; this impact is apparently controlled by common QTLs on linkage groups E and O (Bradshaw and Stettler 1995). Yet, by year 3, vigorous proleptic development replaced sylleptics to play a critical role in basal-area growth (Wu and Stettler 1996). The two basal area (and therefore stem dry weight) QTLs then showed significant effects on upper proleptics. QTLs affecting stem height and basal area (linkage groups D, E, M, and O) were also associated with those for SYL1 traits in year 3 (Table 3). However, suppressed by upper branches, SYL1 virtually lost its close relationship with stem growth by that time (Wu and Stettler 1996), which may thus result from a mutual canceling of effects between the common QTLs and other QTLs.

Of the two QTLs identified for harvest index, one on linkage group O was associated with stem dry weight and the other on linkage group J associated with branch dry weights in three lower crown positions, SYL1, PRO1, and SYL2, and with total leaf number or total leaf area in three upper positions, CT, SYL3, and PRO2 (Table 4). Harvest index was found to have negative correlations with SYL1, PRO1, and SYL2 traits but positive or nonsignificant correlations with CT, SYL3, and PRO2 traits (Wu and Stettler 1996). Thus, opposite (pleiotropic) effects of linkage group J on harvest index and branches in the lower positions, as demonstrated by different directions of additive effect (Tables 2 and 4), may be the cause of negative correlations between these two kinds of traits. However, linkage group J positively affects harvest index by developing more physiologically active leaves in the upper positions.

The identification of important QTLs for the relationship of growth and architecture promises the utility of ideotype concept in forest crop breeding. Theoretical models suggest that forest trees can generally display optimal architecture for growth in a specific environment that they inhabit (Wu 1993; Chen et al. 1994; Farnsworth and Niklas 1995). The ideotype of a tree is the application of such structural optimality to intensive forestry that is designed to produce more stem wood than conventional cultivars or types under the same environmental conditions (Dickmann 1985; Dickmann et al. 1990, 1994). Advantageous over conventional material, an ideotype is the gathering of many favorable characteristics, such as maximum stem-wood growth, reasonable morphological structure, and efficient physiological metabolism. The breeding of ideotypes attempts to combine favorable QTLs that determine various ideotype traits in specific genotypes.

By marker-aided selection or gene manipulation for QTLs on linkage group O (see Gasser and Fraley 1989; Xiao et al. 1996b), for example, one can obtain increased gain in third-year stem biomass and harvest index from indirect selection for second-year sylleptic leaf area. The QTLs for these ideotype traits can be perpetually fixed in poplar commercial populations through clonal propagation (Dickmann and Keathley 1996).

It should be noted that ideotype breeding may be seriously frustrated by unfavorable correlations due to negative pleiotropic effects of the genes involved, as shown by QTLs for harvest index and branch dimension in lower crown positions. Marker-aided selection for these QTLs may be favorable for single-stem height and perimeter growth, but seriously limits community productivity since these QTLs simultaneously induce expanded tree crowns. Maximum productivity per unit land area requires a balance between the largest single-tree growth and the lowest branch/leaf investment, which may be controlled by specific QTLs. Unfortunately, such QTLs cannot be identified in the present study, because patterns of stem growth and canopy development in multi-tree plots were not explored. In addition, the efficiency of ideotype breeding through molecular markers cannot be well justified until data are accumulated on multiple mapping pedigrees, finer genetic maps, and QTL × environment interactions.

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