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R.-L. Wu

Quantitative genetics of yield breeding for *Populus* short rotation culture. III. Efficiency of indirect selection on tree geometry

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Abstract Quantitative analysis of genetic covariances was used to identify the critical morphological components of wood productivity and to evaluate the efficiency of indirect selection for these components at the four levels of biological organization, (1) leaf, (2) branch, (3) main stem, and (4) whole-tree, in 4-year *Populus deltoides* × *P. simonii* and *P. deltoides* × *P. nigra* F_1 progeny. A total of 44 morphometric traits measured at the four organizational levels showed varying genetic associations with productivity, variations being dependent on traits, developmental processes (current terminal, sylleptics, and proleptics), and hybridization combinations. Most of the leaf and branch traits on the current terminal and/or sylleptic branches had higher genetic correlations with stem-wood volume than those on proleptics, which resulted in larger indirect selection responses in volume, especially in D×S progeny. Indirect clonal selection on leaf size and area, branching capacity, and branch angle at age 4 years was expected to generate 10–35% more genetic gain per year in 6-year volume than direct selection on 6-year volume in the D×S progeny. The efficiency of indirect selection on the numbers of different order branches and bifurcation ratio was greater than 1.0 relative to that for direct selection for stem-wood volume in the D×N progeny. Under the pressure of artificial selection for superior volume production, with the proportion selected=15%, the two F_1 progeny populations exhibited distinct evolutionary divergence in tree geometry. The high-yielding D×S clones displayed a decurrent-like crown with strong apical dominance, whereas the crown ideotype for the high-yielding D×N clones was found to be excurrent-like and surrounded by dense foliage and branches.

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R.-L. Wu (✉)
Department of Forestry, Nanjing Forestry University,
Nanjing, Jiangsu, 210037,
People's Republic of China

Present address:
College of Forest Resources, AR-10, University of Washington,
Seattle, Wash., USA

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Introduction

The major task of woody crop physiogenetics is to identify key components of productivity (Nelson et al. 1981; Ceulemans 1990; Ceulemans et al. 1990, 1992; Hinckley et al. 1989; Scarascia-Mugnozza 1991) and to incorporate them into genetic improvement programs (Greenwood and Volkaert; 1992; Wu 1994). The structural-functional relationships of yield components can be understood at different levels of biological organization: (1) leaf, (2) branch, (3) main stem, and (4) whole tree (Ceulemans 1990; Hinckley et al. 1992; Wu 1994). Branch and leaf architecture form the structural basis for photosynthesis and related metabolic processes at the whole tree level (Dixon 1990), and much of the variation in productivity can be explained by the geometry of branch and leaf placement (Horn 1971; Isebrands and Michael 1986). However, the influences of these morphological components on productivity have been phenotypically rather than genetically investigated in current studies (Ceulemans et al. 1990, 1992; Isebrands and Nelson 1982; Isebrands et al. 1988). Many of these studies also ignore the role of possible differences in physiological or physical properties, and thus, in the genetic effect on productivity, among leaf and branch traits on different developmental processes of a tree crown, i.e., current terminal, syllepsis, and prolepsis (see Wu 1994 for detailed discussion of this; Hallé et al. 1978; Tomlinson 1983). Indeed, an understanding of such differences from a quantitative genetic perspective could provide useful criteria for selecting high-yielding genotypes in forest crops.

As part of a broader study on the production physiological genetics in *Populus* short rotation intensive culture (SRIC), a previous study documented numerous morphometric traits at the four different organizational levels described above and their discrepancies in trait value, genetic control, and selection response across developmental processes and hybridization combinations (Wu 1994). How-

Table 1 Descriptions and abbreviations of the 44 morphometric traits at four different levels of biological organization underlying tree geometry in a 4-year SRIC poplar (*CT* current terminal, *SYL* sylleptic branch, *PRO* proleptic branch)

Trait	Abbreviation	Description
(1) Leaf level		
Single leaf area	SLA	Averaged over CT, SYL, and PRO
Petiole length	PL	Averaged over CT, SYL, and PRO
Cumulative leaf area	CLA	Summed over CT, SYL, and PRO
Midrib angle	MA	Averaged over CT, SYL, and PRO
Lamina angle	LA	Averaged over CT, SYL, and PRO
(2) Branch level		
Branch number	BN	Summed over SLY and PRO
Cumulative branch length	CBL	Summed over SLY and PRO
Single branch length	SBL	Averaged over SYL and PRO
Branch diameter	BD	Averaged over SYL and PRO
Branch angle	BA	Averaged over SYL and PRO
Internodal length	IL	Averaged over SYL and PRO
Second-order branch #	SBN	Summed over SYL and PRO
Third-order branch #	TBN	Summed over SYL and PRO
Bifurcation ratio	R_b	Averaged over SYL and PRO
(3) Main stem level		
Height	HT	4-year total height growth
Diameter at breast height	DBH	4-year total radial growth
Taper	TR	1 – ratio of diameter at 6 m height to DBH
Straightness	ST	Straight degree of the bole (0–10 scale)
Apical dominance	AD	Main stem height from the last SYL to tree tip
Branch zone	BZ	Main stem height from the first PRO to last SYL
Apical control	AC	Main stem height from the ground to first PRO
(4) Whole tree level		
Crown total volume	CTV	Estimated by the conic volume equation
Crown effective volume	CEV	CTV - inner crown volume without foliage
Crown effective surface area	CES	Estimated by the conic surface equation
Crown shape	CS	Ratio of HT to crown diameter

ever, further information about genetic correlations is crucial in order to determine the possibility of indirect selection on tree geometry for improving desired traits such as stem-wood productivity (Falconer 1989). Moreover, such information would be useful when exploring the physiological mechanisms that underlie productivity and trait evolution and the methods by which the materials can be manipulated genetically and environmentally (Hinckley et al. 1989; Hodge and White 1992). For example, Ceulemans et al. (1990) and Dunlap (1991) asserted that sylleptic branches might play a more critical role in superior volume growth than proleptic branches. The fast-growing *Populus trichocarpa* clones from a mesic drainage in Washington (USA) allocated a higher proportion of leaf area to sylleptic branches than did slow-growing clones from a xeric drainage (Dunlap 1991). If the relative advantage of sylleptics over proleptics is genetically confirmed, one can expect enhanced genetic gain for stem-wood volume by selecting for sylleptic traits (see Namkoong 1979; Zobel and Talbert 1984).

The objectives of the study presented here were to (1) elucidate the genetic associations of 4-year tree morphological traits at the leaf, branch, main stem, and whole tree level, as described in Wu (1994), with stem-wood volume growth at the same and subsequent ages in *Populus deltoides*×*P. simonii* and *P. deltoides*×*P. nigra* F_1 hybrid progeny; (2) estimate indirect responses to selection on tree geometry and the relative efficiency of indirect selection over direct selection on stem-wood volume itself; and (3) explore the physiological basis of juvenile selection for mature volume. Of equal interest is the comparison of genetic correlation with volume and efficiency of indirect selection across traits, developmental processes, and hybridization combinations.

Materials and methods

The interspecific hybridizations were developed to exploit hybrid vigor or heterosis between *Populus deltoides* (D) and *P. simonii* (S) as well as *P. deltoides* and *P. nigra* (N) (Wang et al. 1991). The origins of the parents for the two cross combinations have been described in Wu et al. (1992). Throughout two successive seedling and clonal selection on superior growth and paternal characteristics, 20 D×S and 14 D×N hybrid clones were used to conduct physiogenetic studies on yield breeding for *Populus* short rotation culture. In spring 1984, a replicated plantation of these selected clones, as well as of the common female parent clone *P. deltoides* I-69 and a standard Euroamerican poplar clone I-214, was established with 1-year rooted stocks in a temperate region of China. The experimental plantation used a randomized complete block design with three replicates and a four-tree square plot at a spacing of 6.0×6.0 m and was surrounded by two border rows.

In 1987 intensive morphometric measurements were done on a tree chosen from each plot at random for all clones. For a 4-year hybrid poplar, two types of branches, sylleptic and proleptic, are alternately distributed on the main stem, by means of a morphological development process described in Wu (1994). Sylleptic and proleptic branches result from the continuous or discontinuous development of a lateral from a terminal meristem without or with an evident rest period, respectively (Hinckley et al. 1992). In total, we recorded 44 tree architectural traits at the four organizational levels:

Table 2 Genetic correlation [$r_g \pm s(r_g)$] between leaf traits[a] on three different developmental processes of a 4-year tree crown and stem-wood volume[b] at the same or subsequent ages, and expected indirect response to selection (EIRS, in percentage)[c] and relative efficiency (RE) for indirect selection on the 15 leaf morphological traits in *Populus deltoides* (D)×*P. simonii* (S) and *P. deltoides* (D)×*P. nigra* (N) F_1 hybrid progeny. Calculations were based on improving stem-wood productivity (*VOL4* and *VOL6* stem wood volume at 4 or 6 years, respectively, Q_{rotation} and Q_{year} the relative efficiency for indirect selection over direct selection for wood volume productivity expressed on a per rotation or year basis, respectively)

Cross combination traits/developmental process		$r_g \pm s(r_g)$		EIRS (%)		RE		
		VOL4	VOL6	VOL4	VOL6	Q_{rotation} VOL4	VOL6	Q_{year} VOL6
D×S								
SLA	CT	0.91±0.01	0.89±0.01	44	43	0.91	0.88	1.32
	SYL	0.92±0.01	0.87±0.01	42	40	0.87	0.82	1.23
	PRO	0.67±0.02	0.62±0.02	32	30	0.68	0.62	0.93
PL	CT	0.70±0.02	0.76±0.01	33	36	0.70	0.75	1.13
	SYL	0.91±0.01	0.87±0.01	40	39	0.85	0.80	1.20
	PRO	0.60±0.03	0.58±0.02	29	28	0.60	0.57	0.86
CLA	CT	0.94±0.01	0.90±0.01	45	43	0.94	0.90	1.35
	SYL	0.88±0.02	0.91±0.01	40	41	0.83	0.85	1.28
	PRO	0.61±0.02	0.42±0.02	29	20	0.61	0.41	0.62
MA	CT	0.77±0.02	0.59±0.03	36	27	0.75	0.56	0.84
	SYL	–0.65±0.04	–0.41±0.04	–30	–19	–0.62	–0.38	–0.57
	PRO	0.42±0.05	0.35±0.04	20	16	0.41	0.34	0.51
LA	CT	–0.88±0.01	–0.69±0.02	–40	–32	–0.85	–0.66	–0.99
	SYL	–0.41±0.06	–0.59±0.03	–18	–26	–0.38	–0.55	–0.83
	PRO	0.39±0.04	0.37±0.03	18	17	0.38	0.36	0.54
D×N								
SLA	CT	0.57±0.05	0.45±0.06	25	18	0.57	0.45	0.68
	SYL	0.69±0.05	0.60±0.06	29	23	0.67	0.58	0.87
	PRO	0.39±0.06	0.34±0.06	17	14	0.39	0.34	0.51
PL	CT	0.72±0.03	0.67±0.04	31	27	0.72	0.67	1.01
	SYL	0.84±0.03	0.81±0.03	35	31	0.81	0.78	1.17
	PRO	0.57±0.04	0.55±0.05	25	22	0.58	0.56	0.84
CLA	CT	0.93±0.01	0.90±0.01	40	36	0.94	0.90	1.35
	SYL	0.71±0.05	0.77±0.04	28	28	0.66	0.71	1.07
	PRO	0.45±0.05	0.41±0.06	20	17	0.46	0.42	0.63
MA	CT	0.58±0.04	0.61±0.04	25	24	0.58	0.61	0.92
	SYL	–0.32±0.08	–0.30±0.08	–13	–11	–0.31	–0.29	–0.44
	PRO	0.38±0.06	0.34±0.06	17	14	0.38	0.34	0.51
LA	CT	–0.88±0.01	–0.61±0.04	–38	–25	–0.89	–0.62	–0.93
	SYL	–0.43±0.06	–0.30±0.07	–18	–12	–0.43	–0.30	–0.45
	PRO	0.39±0.06	0.24±0.06	17	10	0.40	0.24	0.36

[a] See Table 1 for the definitions of leaf traits and developmental processes

[b] Mean stem wood volume was VOL4=0.12599 m^3 and VOL6=0.33067 m^3, with phenotypic standard deviations of 0.04243 m^3 and 0.11091 m^3, respectively, in the D×S progeny; the corresponding values were 0.11829 m^3 and 0.30882 m^3, and 0.03742 m^3 and 0.08944 m^3 in the D×N progeny. The broad–sense heritability based on clonal mean was H^2 (VOL4)=0.95 and H^2 (VOL6)=0.96 in the D×S progeny; the corresponding values were 0.91 and 0.92 in the D×N progeny (see Wu et al. 1989, 1992)

[c] Expected indirect response to selection was estimated when assuming 15% top clones to be selected from the D×S and D×N F_1 hybrids. The corresponding intensity of selection is i=1.469 and 1.456 for the D×S with 20 clones and the D×N with 14 clones, respectively (Falconer 1989)

(1) leaf, (2) branch, (3) main stem, and (4) whole tree (see Table 1 for details). Leaf traits were sampled on the basis of the current terminal, sylleptics, and proleptics, and branch traits on sylleptics and proleptics (see Wu 1994). Stem-wood volume (VOL) was estimated at ages 4 (1987) and 6 (1989) years using the volume equation derived for the temperate poplars given in Wu et al. (1989).

Clone-replicate Analysis of Covariance (ANCOVA) was used to evaluate the associations of tree geometry with productivity. In this study, clone effect was assumed to be random, and replicate effect was assumed to be fixed. No clone×replicate interaction effect was detected because of a single tree per cell (see Wu 1994). Coefficient of genetic correlation (r_g) was estimated according to Wu et al. (1992), with a sampling error as shown in Falconer (1989). Expected indirect response of 4- or 6-year stem-wood volume Y to selection for the 4-year tree geometric trait X was calculated using a general genetic gain model (Falconer 1989). The relative efficiency of early indirect selection on trait X to improve rotation trait Y, compared with direct selection on trait Y, was determined as:

$$Q_{\text{rotation}} = i_X H_X H_Y r_{g_{XY}} \sigma_{pY} / (i_Y H_Y^2 \sigma_{pY}) \tag{1}$$

on a per rotation basis and as

$$Q_{\text{year}} = (t_Y / t_X)\, Q_{\text{rotation}} \tag{2}$$

on a per year basis, where i_X and i_Y represent the standardized selection differentials for indirect or direct clonal selection, with $i_X = i_Y$ in this study; r_{gXY}, the genetic correlation between traits X and Y; H_X and H_Y, the square roots of the broad-sense heritabilities based on the clonal mean for the two traits; σ_{pY}, the phenotypic standard deviations based on the clonal mean for trait Y; and t_X and t_Y, the 'generation' intervals (in years) of indirect and direct selection. The 'generation' intervals in clonal forestry may be considered to be ages of selection assuming that vegetative propagules are maintained in the clo-

Table 3 Genetic correlations [$r_g \pm s(r_g)$] between branch traits on two different developmental processes of a 4-year tree crown and stem-wood volume at the same or subsequent ages, and expected indirect response to selection (EIRS, in percentage) and relative efficiency (RE) for indirect selection on the 18 branch traits in *Populus deltoides*×*P. simonii* (S) and *P. deltoides* (D)×*P. nigra* (N) F_1 hybrid progeny. Calculations were based on improving stem-wood productivity[a]

Cross combination trait/developmental process		$r_g \pm s(r_g)$		EIRS (%)		RE		
						Q_{rotation}		Q_{year}
		VOL4	VOL6	VOL4	VOL6	VOL4	VOL6	VOL6
D×S								
BN	SYL	0.40±0.06	0.31±0.05	18	14	0.37	0.29	0.44
	PRO	0.30±0.05	0.52±0.03	14	24	0.29	0.49	0.74
CBL	SYL	0.97±0.00	0.80±0.02	45	38	0.95	0.79	1.19
	PRO	0.39±0.03	0.65±0.02	19	31	0.39	0.65	0.98
SBL	SYL	0.31±0.06	0.55±0.03	14	26	0.30	0.53	0.80
	PRO	0.75±0.02	0.60±0.02	36	29	0.75	0.60	0.90
BD	SYL	0.88±0.01	0.85±0.01	41	40	0.87	0.83	1.25
	PRO	0.52±0.03	0.71±0.01	25	34	0.53	0.71	1.07
BA	SYL	0.82±0.02	0.80±0.02	36	36	0.76	0.74	1.11
	PRO	0.35±0.03	0.52±0.02	17	24	0.35	0.39	0.59
IL	SYL	0.77±0.04	0.71±0.05	32	29	0.67	0.60	0.90
	PRO	0.47±0.03	0.41±0.02	22	19	0.47	0.40	0.60
SBN	SYL	0.80±0.02	0.53±0.03	37	25	0.78	0.51	0.77
	PRO	0.42±0.02	0.42±0.02	20	20	0.43	0.42	0.63
TBN	SYL	0.87±0.02	0.71±0.02	39	33	0.84	0.68	1.02
	PRO	0.31±0.02	0.29±0.02	15	14	0.32	0.29	0.44
R_b	SYL	0.91±0.01	0.84±0.02	38	35	0.79	0.72	1.08
	PRO	0.71±0.03	0.63±0.03	33	29	0.69	0.61	0.92
D×N								
BN	SYL	0.99±0.00	0.91±0.01	43	36	1.08	0.91	1.37
	PRO	0.49±0.06	0.48±0.06	21	19	0.52	0.47	0.71
CBL	SYL	0.59±0.05	0.40±0.07	25	16	0.63	0.40	0.60
	PRO	0.38±0.07	0.41±0.06	16	16	0.41	0.40	0.60
SBL	SYL	0.33±0.08	0.53±0.06	14	21	0.35	0.52	0.78
	PRO	0.52±0.05	0.50±0.05	23	20	0.57	0.51	0.77
BD	SYL	0.59±0.05	0.52±0.06	25	21	0.63	0.51	0.77
	PRO	0.49±0.05	0.53±0.04	22	21	0.54	0.53	0.80
BA	SYL	0.58±0.06	0.59±0.06	24	23	0.61	0.58	0.87
	PRO	0.21±0.05	0.22±0.05	9	9	0.23	0.22	0.33
IL	SYL	0.32±0.09	0.21±0.10	13	8	0.33	0.20	0.30
	PRO	−0.40±0.06	−0.34±0.06	−17	−14	−0.43	−0.34	−0.51
SBN	SYL	0.91±0.02	0.88±0.02	38	34	0.96	0.86	1.29
	PRO	0.83±0.01	0.74±0.01	37	31	0.93	0.77	1.16
TBN	SYL	0.92±0.01	0.93±0.01	39	36	0.98	0.90	1.35
	PRO	0.84±0.01	0.85±0.01	38	35	0.95	0.88	1.32
R_b	SYL	0.89±0.03	0.85±0.04	33	29	0.83	0.73	1.10
	PRO	0.70±0.04	0.71±0.04	30	28	0.76	0.71	1.07

[a] See Table 1 for the definitions of branch traits and of developmental processes and Table 2 for the explanations about indirect selection

nal stoolbed for various uses, namely t_X=4 and t_Y=6 in this study. If Q_{year} is greater than 1.0, then early clonal selection on tree geometry can be expected to generate more gain per year in terms of subsequent stem-wood volume than later direct selection on the volume.

Results

Genetic associations of tree architecture with productivity

Leaves at different developmental positions of a 4-year tree crown showed varying influences on stem-wood volume, the degree of influence being dependent on leaf traits (Table 2). Cumulative leaf area on the current terminal was more strongly associated with the current year's total volume than that on sylleptic branches, whereas sylleptics were more important to the volume than the current terminal for single leaf area and petiole length. The leaf size and area traits on the current terminal and sylleptics had much greater contributions to the volume growth than those on proleptics. Both midrib and lamina angle on sylleptic or proleptic branches were expected to display moderate magnitudes and adverse signs of genetic correlations with the volume variable. Midrib angle and lamina angle on the current terminal was positively or negatively genetically correlated with the volume, respectively. Leaf traits on sylleptics generally showed greater effects on the volume growth in the D×S hybrid progeny than in the D×N hybrid progeny. The D×S progeny clearly had a tighter ge-

Table 4 Genetic correlations $[r_g \pm s(r_g)]$ between the traits at the 4-year main stem level and stem-wood volume at the same or subsequent ages, and expected indirect response to selection (EIRS, in percentage) and relative efficiency for indirect selection on the seven main stem component traits in *Populus deltoides* (D)×*P. simonii* (S) and *P. deltoides* (D)×*P. nigra* (N) F_1 hybrid progeny. Calculations were based on improving stem-wood productivity[a]

Cross combination/ trait	$r_g \pm s(r_g)$		EIRS (%)		RE		
	VOL4	VOL6	VOL4	VOL6	Q_{rotation} VOL4	VOL6	Q_{year} VOL6
D×S							
HT	0.90±0.01	0.83±0.01	41	38	0.86	0.79	1.19
DBH	0.91±0.01	0.85±0.01	43	41	0.91	0.84	1.26
TR	–0.84±0.02	-0.75±0.02	–37	–34	–0.79	–0.70	1.05
ST	–0.44±0.01	–0.05±0.01	–22	–2	–0.45	–0.05	–0.08
AD	0.85±0.01	0.72±0.01	40	35	0.85	0.71	1.07
BZ	0.52±0.04	0.62±0.02	24	29	0.51	0.60	0.90
AC	0.60±0.06	0.52±0.05	24	22	0.52	0.45	0.68
D×N							
HT	0.94±0.01	0.91±0.02	40	35	0.99	0.88	1.32
DBH	0.95±0.01	0.92±0.01	41	37	1.03	0.92	1.38
TR	–0.71±0.04	–0.72±0.03	–31	–29	–0.77	–0.72	–1.08
ST	0.40±0.02	0.59±0.08	18	24	0.46	0.61	0.92
AD	0.50±0.07	0.32±0.06	21	13	0.53	0.31	0.47
BZ	0.41±0.07	0.44±0.06	17	17	0.44	0.43	0.65
AC	0.39±0.14	0.41±0.14	14	14	0.36	0.35	0.53

[a] See Table 1 for the definitions of main stem component traits and Table 2 for the explanations about indirect selection

netic relationship between single leaf area on all three crown processes and the wood volume than the D × N progeny. The correlation of 4-year leaf traits with the subsequent 6-year total volume was nonsignificantly different from that with the current year's total volume.

Branch characteristics also showed different genetic correlations with the current year's or subsequent total volume growth, varying over traits, developmental positions, and hybridization combinations (Table 3). All branch traits, with the exception for single branch length, on sylleptic branches were more closely related to volume growth than those on proleptic branches. Branch size (length and diameter), branch cumulative length, branch angle, and internodal length were more strongly associated with wood productivity in the D×S progeny than in the D×N progeny, while branch number on the main stem and second- and third-order branch number showed closer correlations with productivity in the D×N progeny than in the D×S progeny. Bifurcation ratio affected volume of the two progenies in a similar way. Overall, the difference between sylleptic and proleptic branches and their influence on volume growth was more evident in the D×S progeny than in the D×N progeny.

At the main stem level, 4-year height and diameter at breast height were highly associated to the current year's total stem volume (r_g=0.90–0.95, Table 4). These two growth traits contributed more significantly to wood productivity than did stem form and apical dominance and control in both D×S and D×N progeny. Main stem taper showed a closer genetic relationship with volume than straightness, and the latter was negatively correlated with volume in the D×S hybrid progeny. Apical dominance was more important for volume growth than apical control, but both had higher genetic correlations with wood volume in the D×S progeny than in the D×N progeny. A similar trend was found to occur in genetic associations of the seven main stem components with the 6-year volume, with increased differentiations between the two F_1 progenies.

Crown effective volume and surface were more strongly correlated with wood productivity than crown total volume, especially in the D×N progeny (Table 5). Narrow crown (high ratio of main stem height to crown width) favored stem volume growth in the D×S progeny, more than in the D×N progeny, having potentially a greater effect on the subsequent year's total volume in both hybrid populations.

Expected indirect response to selection

Wood productivity gain from indirect selection for single and cumulative leaf area and petiole length was expected to be similar on the current terminal and sylleptic branches in both D×S and D×N hybrid progeny (Table 2). Selection for the leaf size and area traits had higher indirect responses for volume than selection for leaf orientations. Much larger indirect responses in volume stemmed from selecting for leaf size and area on the current terminal and sylleptic branches than on proleptic branches. Leaf orientations appeared to generate greater genetic gain in volume on the current terminal than on both sylleptics and proleptics. Indirect selection for single leaf area on all developmental processes yielded consistently larger improvement for volume in the D×S progeny than in the D×N progeny, despite small differences in the volume response by selecting other traits on at least a process between these two progenies. Different directional selection for leaf orientations on the two alternate sylleptics and proleptics on the main stem would benefit volume improvement.

Most branch traits produced substantial correlated selection response for volume in the D×S progeny (Table 3). The volume variable responded more strongly to indirect

Table 5 Genetic correlations [$r_g \pm s(r_g)$] between the traits at the 4-year whole tree level and stem-wood volume at the same or subsequent ages, expected indirect response to selection (EIRS, in percentage) and relative efficiency (RE) for indirect selection on the four traits in *Populus deltoides* (D)×*P. simonii* (S) and *P. deltoides* (D)×*P. nigra* (N) F_1 hybrid progeny. Calculations were based on improving stem-wood productivity[a]

Cross combination/trait	$r_g \pm s(r_g)$		ERIS (%)		RE		
	VOL4	VOL6	VOL4	VOL6	Q_{rotation} VOL4	VOL6	Q_{year} VOL6
D×S							
CTV	0.81±0.02	0.51±0.02	38	24	0.80	0.50	0.75
CEV	0.93±0.01	0.88±0.01	44	42	0.92	0.86	1.29
CES	0.96±0.00	0.92±0.01	45	44	0.95	0.90	1.35
CS	0.65±0.03	0.90±0.01	30	42	0.64	0.87	1.31
D×N							
CTV	0.45±0.06	0.41±0.06	19	18	0.16	0.46	0.69
CEV	0.95±0.01	0.91±0.01	40	35	1.00	0.89	1.34
CES	0.92±0.01	0.88±0.02	39	35	0.99	0.88	1.32
CS	0.41±0.07	0.65±0.05	18	26	0.26	0.65	0.98

[a] See Table 1 for the definitions of traits and Table 2 for the explanations of indirect selection

selection for branch count traits and bifurcation ratio than for branch vigor and angle traits in the D×N progeny. Discrepancies in indirect selection response for volume between sylleptics and proleptics were significantly larger in the D×S progeny than in the D×N progeny for many branch traits. Single proleptic branch length was detected to generate a much higher correlated response for the current year's total volume than single sylleptic branch length, typically in the D×S progeny. Relative to sylleptic branches, proleptic branches showed increased indirect genetic gain for the subsequent volume in both hybrid progenies.

Selection for main stem height, diameter at breast height, and taper led to considerable increases in volume at ages 4 and 6 years in the two progenies (Table 4). Selection for apical dominance and control was expected to produce higher indirect genetic gains for volume in the D×S progeny than in the D×N progeny. An unfavorable response for 4-year volume was due to selection on main stem straightness in the D×S progeny, but it dramatically declined for 6-year volume.

Selection for crown effective volume and surface area produced higher indirect responses for 4- and 6-year volume than crown total volume and crown shape in the D×S and D×N progeny (Table 5). However, crown shape showed increased selection response for late volume growth.

Efficiency of indirect selection

The efficiency of indirect selection for leaf traits to direct selection for the current year's or subsequent total stem volume differed among developmental processes, traits, and progeny populations. Leaf size and area traits on the current terminal and sylleptics were expected to generate siginificantly higher efficiency of indirect response in volume than those on proleptics (Table 2). Although total genetic gain of rotation volume from indirect selection for single leaf area, petiole length, and cumulative leaf area did not exceed that from direct selection for volume, indirect selection for these leaf traits on the current terminal and sylleptics produced 13–35% more gain per year in 6-year volume than did direct selection on volume in the D×S progeny. However, for the D×N progeny, petiole length and cumulative leaf area, rather than single leaf area, offered $Q_{\text{year}}>1.0$ of relative efficiency for indirect selection for 6-year volume. Indirect selection for leaf orientations proved much more efficient on the current terminal than on both sylleptics and proleptics in the two progenies.

Branch size (length and diameter) and angle traits on sylleptic branches showed 11–25% higher selection response per year in 6-year volume than did direct selection on the 6-year volume in the D×S progeny (Table 3). Furthermore, indirect selection for these branch traits on proleptic branches led to increased efficiency for subsequent volume. Expected genetic gains per year in 6-year volume from indirect selection for branch count traits and bifurcation ratio on sylleptic and/or proleptic branches were expected to be greater than those from direct selection for the 6-year volume in the D×N progeny. Despite the greater advantage of sylleptics over proleptics in improving stem volume for most of the branch traits, single proleptic branch length consistently showed higher efficiency for indirect selection in the volume than single sylleptic branch length in both D×S and D×N progeny.

Compared to direct selection on volume at the same age, indirect selection on 4-year main stem height and diameter at breast height gave relative efficiency on a per rotation basis of 0.86–0.96 in the two progenies (Table 4). Indirect phenotypic selection on the 2 growth traits produced more genetic gain per year (19–38%) in 6-year volume than direct selection on the volume itself. Main stem taper had a comparable efficiency of indirect selection between the D×S and D×N progeny, but indirect selection on apical dominance and control were expected to yield a larger response in volume in the former than in the latter progeny.

Indirect selection on crown effective volume and surface area produced an approximately same response ($Q_{\text{year}} \approx 1.0$) to direct selection on 4-year volume in the D×S and D×N progeny (Table 5). These 2 traits at the whole-tree level had obviously larger genetic gain per year in 6-year volume relative to direct selection on late volume.

Tree crown shape could be used as a selected trait for improving productivity in the D×S progeny.

Discussion

The coefficient of genetic correlation reflects the degree to which two traits of biological organization are controlled by the same set of genes (Falconer 1989), and thus it has advantages over the coefficient of phenotypic correlation which is contaminated by genetic effects and environmental noises, when exploring actual genetic relationships between biological traits (see Hodge and White 1992). The study presented here documents genetic associations of morphometric characteristics at the four different organizational levels with productivity in the *Populus deltoides*× *P. simonii* and *P. deltoides* × *P. nigra* hybrid clones grown under short rotation culture. While leaf and branch traits on proleptic branches show low impacts on volume growth, current terminal leaves and sylleptic branches and their leaves confer a potential productivity advantage to the vegetative growth of hybrid clones (Scarascia-Mugnozza 1991; Dunlap 1991; Hinckley et al. 1992; Ceulemans 1990; Ceulemans et al. 1990). However, in many cases, proleptic branches, in comparison to sylleptic branches, display many obvious characteristics that favor volume growth, such as greater leaf size and cumulative leaf area, stronger branching capacity, and more acute orientation from the stem (Larson and Isebrands 1972; Ridge et al. 1986; Dunlap 1991; Rogers et al. 1989; Hinckley et al. 1989, 1992; Ceulemans et al. 1990; Wu 1994). Scarascia-Mugnozza (1991) attributed the more dominant role in productivity of sylleptic branches over their proleptic counterparts to higher number and greater carbon export to the main stem. The better balance between photosynthetic surface production and energy investment in sylleptic branches (reflected by bifurcation ratio, Leopold 1971) is also a possible factor causing their more pronounced role (Wu 1994).

Leaf orientation within a crown affects light penetration and interception and its repartitioning between different levels or layers of leaves at different depths (Hinckley et al. 1992; Sprugel 1989; Delucia et al. 1991). The present study indicates the different genetic effects of leaf orientation on three different processes of a crown on volume production. Vertically-oriented leaves (low lamina angle) on the current terminal and sylleptic branches tend to display identical photosynthetic rates on either the adaxial or abaxial surface in a high light intensity environment. The photosynthetic symmetry of these leaves may lead to maximum daily integrated carbon gain and water use efficiency (Sprugel 1989; Delucia et al. 1991) and thus to a more significant contribution to vegetative productivity as compared to the asymmetric horizontally-oriented leaves (high lamina angle) on proleptic branches. While leaf orientations on sylleptics and proleptics alternately distributed on the main stem have opposite signs in their genetic correlation with volume, further examinations appear to be necessary for identifying the anatomical and biochemical differentiations (e.g., Knapp et al. 1988; Vogelmann 1989; Vogelmann et al. 1989) and optimal display structure maximizing whole tree photosynthesis between proleptic and sylleptic leaves (Honda and Fisher 1978; Wu 1993).

The genetic variation of a quantitative trait might decline in response to various successive directional selections made on it (Bulmer 1980; Namkoong 1979). Selection will reach a plateau when variation approaches zero. Main stem height and radial growth traits tend to display a decreased genetic basis and, thus, decreased selection response relative to other morphometric traits in the two interspecific hybridization combinations in this study because their maternal parent is a highly selected clone in growth rather than in tree geometry (Wu et al. 1992; Wu 1993). The present study demonstrates that some leaf and branch traits associated with sylleptic process have a higher preponderance for the improvement of stem-wood volume than these 2 growth traits.

The expected indirect genetic gain, which reflects a collective effect of the heritability level of selected traits and their genetic correlations with desired traits, is used to evaluate the efficacy of indirect selection (Falconer 1989). Volume growth strongly responds to indirect selection on leaf traits on the current terminal, resulting from their high heritabilities (Wu 1994) and high genetic correlations. Although many leaf and branch traits on sylleptic branches are less strongly inheritable than those on proleptic branches (Wu 1994), they produce a higher indirect selection response in volume than their proleptics-associated counterparts due to tighter relationships with volume. Such a result shows a nonsignificant correlation between heritability and genetic correlation for the morphometric traits of 4-year hybrid poplars (see also Huang et al. 1990).

Correlated responses of volume to selection on tree morphology were found to be different between the D×S and D×N F_1 progeny. The possibility with which main stem volume and straightness are simultaneously improved is much higher in the D×N progeny than in the D×S progeny. However, apical dominance shows the greater potential as an indirect selection trait of volume in the D×S progeny than in the D×N progeny. In the D×S progeny, there is a greater genetic gain on a per year basis for 6-year volume by indirect selection on leaf size and area as well as branch vigor and angle at 4 years than by direct selection on the late volume. In addition, while most of the traits have higher advantage for the improvement of volume on sylleptics than on proleptics, single proleptic branch length, which reflects the capacity for apical control of the main stem over its lateral branches (Ford 1985), has been found to show a distinctive larger response in volume than single sylleptic branch length owing to a much stronger correlation with volume in this progeny. Thus, it can be found that the high-volume D×S poplars tend to exhibit vigorous and decurrent-like crown geometry. On the other hand, few differences were found between sylleptic and proleptic branches in correlated responses of volume to selection on the traits reflecting photosynthetic surface production (second-, and third-order branch numbers) and its energy balance (R_b) in the D×N progeny. Furthermore, effective crown volume and surface area with foliage have a much higher correlated response than total crown volume in this progeny. In conjunction with high genetic association between the number of sylleptic branches and volume growth (Table 3), these facts would suggest that the high-volume D×N poplars possess an excurrent-like crown architecture that optimizes the balance between photosynthetic organ production and energy cost. The present study on the efficiency of indirect selection verifies the possible evolutionary differentiations in tree geometry, which reflects the competitive ability of a species in space (Horn 1971), between the D×S and D×N progeny, as found in Wu (1994).

It is of interest to note that proleptic branches show increasing importance for volume growth with stand development despite their weaker impact on growth than sylleptic branches in the current year. Proleptic branches are likely to have a potentially high carbon accumulation, which supports the initial energy investment for early leaf flush on sylleptic branches (Scarascia-Mugnozza 1991). Further cooperative studies of geneticists and physiologists on a larger scale will be essential for gaining an understanding of the physiological mechanisms of these phenomena (Greenwood and Volkaert 1992).

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References

Bulmer MG (1985) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Ceulemans R (1990) Genetic variation in functional and structural productivity determinants in poplar. Thesis Publishers, Amsterdam, The Netherlands

Ceulemans R, Stettler RF, Hinckley TM, Isebrands JG, Heilman PE (1990) Crown architecture of *Populus* clones as determined by branch orientation and branch characteristics. Tree Physiol 7:157–167

Ceulemans R, Scarascia-Mugnozza G, Wiard BM, Braatne JH, Hinckley TM, Stettler RF, Isebrands JG, Heilman PE (1992) Production physiology and morphology of *Populus* species and their hybrids grown under short rotation. I. Clonal comparisons of 4-year growth and phenology. Can J For Res 22:1937–1948

Delucia EH, Shenoi HD, Naidu SL, Day TA (1991) Photosynthetic symmetry of sun and shade leaves of different orientations. Oecologia 87:51–57

Dixon RK (1990) Physiological processes and tree growth. In:Dixon RK, Meldal RS, Ruark GA, Warren WG (eds) Process modelling of forest growth responses to environmental stress. Timber Press, Portland, Ore., pp 21–32

Dunlap JM (1991) Genetic variation in natural populations of *Populus trichocarpa* T. & G. from four river valleys in Washington. PhD thesis, University of Washington, Seattle, Wash.

Falconer DS (1989) Introduction to quantitative genetics, 4th edn. Longham, New York

Ford ED (1985) Branching, crown structure and the control of timber production. In: Cannell MGR, Jackson JE (eds) Attributes of trees as crop plants. Titus Wilson & Son Ltd, Kendal, Cumbria, UK, pp 228–252

Greenwood MS, Volkaert HA (1992) Morphophysiological trait as markers for the early selection of conifer gentic families. Can J For Res 22:1001–1008

Hallé F, Oldman RAA, Tomlinson PB (1978) Tropical trees and forests:An architectural analysis. Springer-Verlag, Berlin

Hinckley TM, Ceulemans R, Dunlap JM, Figliola A, Heilman PE, Isebrands JG, Scarascia-Mugnozza G, Schulte PJ, Smit B, Stettler RF, van Volkenburgh E, Wiard BM (1989) Physiological, morphological and anatomical components of hybrid vigor in *Populus*. In:Kreeb KH, Richter H, Hinckley TM (eds) Structural and functional responses to environmental stresses. SPB Academic Publ., The Hague, the Netherlands, pp 199–217

Hinckley TM, Braatne JH, Ceulemans R, Clum P, Dunlap J, Newman D, Smit B, Scarascia-Mugnozza G, van Volkenburgh E (1992) Growth dynamics and canopy structure. In: Mitchell CP, Ford-Robertson JB, Hinckley T, Sennerby-Forsse L (eds) Ecophysiology of short rotation forest crops. Elsevier Publ, Amsterdam New York, pp 1–34

Hodge GR, White TC (1992) Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genet 41:252–262

Honda H, Fisher JB (1978) Tree branch angle:maximizing effective leaf area. Science 199:888–890

Horn H (1971) The adaptive geometry of trees. Princeton University Press, Princeton

Huang H, Harding J, Byrne T, Huang N (1990) Quantitative analysis of correlations among flower traits in *Gerbera hybrida*, Compositae. Theor Appl Genet 80:559–563

Isebrands JG, Michael DA (1986) Effects of leaf morphology and orientation on solar radiation interception and photosynthesis in *Populus*. In:Fujimori T, Whitehead D (eds) Crown and canopy structure in relation to productivity. Forestry and Forest Products Research Institute, Ibaraki, Japan, pp 359–381

Isebrands JG, Nelson ND (1982) Crown architecture of short-rotation, intensively cultured *Populus*. II. Branch morphology and distribution of leaves within the crown of *Populus* 'Tristis' as related to biomass production. Can J For Res 12:853–864

Isebrands JG, Ceulemans R, Wiard B (1988) Genetic variation in photosynthetic traits among *Populus* clones in relation to yield. Plant Physiol Biochem 26:427–437

Knapp AK, Vogelmann TC, McClean TM, Smith WK (1988) Light and chlorophyll gradients with *Curcurbita* cotyledons. Plant Cell Environ 11:257–263

Larson PR, Isebrands JG (1972) The relation between leaf production and wood weight in first-year root sprouts of two *Populus* clones. Can J For Res 2:98–104

Leopold LB (1971) Trees and streams: the efficiency of branching patterns. J Theor Biol 31:339–354

Namkoong G (1979) Introduction to quantitative genetics in forestry. USDA Tech Bull No 1588

Nelson ND, Burk T, Isebrands JG (1981) Crown architecture of short-rotation, intensively cultured *Populus*. I. Effects of clones and spacing on first-order branch characteristics. Can J For Res 11:73–81

Ridge CR, Hinckley TM, Stettler RF, van Vokenburgh E (1986) Leaf growth characteristics of fast-growing poplar hybrids *Populus trichocarpa P. deltoides*. Tree Physiol 1:209–216

Rogers DL, Stettler RF, Heilman PE (1989) Genetic variation and productivity of *Populus trichocarpa* and its hybrids. III. Structure and pattern of variation in a 3-year field test. Can J For Res 19:372–377

Scarascia-Mugnozza G (1991) Physiological and morphological determinants of yield in intensively cultured poplars (*Populus* spp.). PhD thesis, University of Washington, Seattle, Wash.

Sprugel DG (1989) The relationship of evergreenness, crown architecture, and leaf size. Am Nat 133:465–479

Tomlinson PB. (1983) Tree architecture. Am Sci 71:141–149

Vogelmann TC (1989) Penetration of light into plants. Photochem Photobiol 50:895–902

Vogelmann TC, Bornman JF, Josserand S (1989) Photosynthetic light gradients and spectral regime within leaves of *Medicago sativa*. Philos Trans R Soc London Ser B 323:411–421

Wang M-X, Huang M-R, Wu R-L (1991) Recent progress in research on genetic improvement in *Populus*. J Word For Res (China) 4:20–27

Wu R-L (1993) Simulated optimal structure of a photosynthetic system:Implication for the breeding of forest crop ideotype. Can J For Res 23:1668–1675

Wu R-L (1994) Quantitative genetics of yield breeding for *Populus* short rotation culture. II. Genetic determination and expected selection response of tree geometry. Can J For Res 24:155–165

Wu R-L, Wang M-X, Huang M-R (1989) Study of new clones of the *Aigeriros* Section. VI. Early selection. J Nanjing For Univ 11:1–12 (Chinese, English abstr)

Wu R-L, Wang M-X, Huang, M-R (1992) Quantitative genetics of yield breeding for *Populus* short rotation culture. I. Dynamics of genetic control and selection model of yield traits. Can J For Res 22:175–182

Zobel B, Talbert J (1984) Applied forest tree improvement. John Wiley & Son, New York