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Identification of quantitative trait loci influencing annual height- and diameter-increment growth in loblolly pine (*Pinus taeda* L.)

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Abstract Quantitative trait loci (QTLs) for annual height- and diameter-increment growth were estimated in each of two three-generation loblolly pine pedigrees. Annual height-increment was measured in three consecutive years in the *BASE* pedigree and in four consecutive years in the *QTL* pedigree. Annual diameter-increment was measured only in the *QTL* pedigree for two consecutive years. An interval mapping-approach was used to estimate the number of QTLs, the magnitude of QTL effects, and their position on genetic linkage maps. Thirteen different height-increment and eight different diameter-increment QTLs were detected, suggesting that these traits are, at least in part, controlled by a few genes of large effect. Little evidence was found for the expression of individual QTLs in multiple years or in multiple genetic backgrounds. These results were discussed in terms of the power of the experiment and their consequences for marker-assisted breeding.

Key words Quantitative trait locus mapping · *Pinus taeda* L. · Height- and diameter-increment

Introduction

It is now possible to map quantitative trait loci (QTLs) for growth and yield, wood quality, and adaptive traits in forest trees (Grattapaglia and Sederoff 1994; Groover et al. 1994; Bradshaw and Stettler 1995; Grattapaglia et al. 1995; Plomion et al. 1996; Knott et al. 1997). These studies demonstrate that individual QTLs of small to large effect are detectable in experimental mapping populations – even for growth and yield traits that are expected to be under polygenic control – and generally have low heritabilities. The knowledge of marker by QTL associations in tree genomes may eventually be applied toward marker-aided breeding in forest trees (Neale and Williams 1991). However, before the application of this technology is possible, verification experiments of several types must be performed (Strauss et al. 1992). Primarily, the effects of genetic background, environment, and developmental stages need to be assessed. This paper is a preliminary attempt to address these questions.

Annual height- and diameter-growth-increments are components of annual volume production and are important quantitative traits routinely evaluated in loblolly pine-breeding programs (Dorman and Zobel 1973). However, genetic evaluation of height- and diameter-growth is difficult because of the low heritabilities of these traits. Early selection of families can not be made reliably in pines because of weak correlations between the juvenile and mature performances of families in height- and diameter-growth (Lambeth 1980). Identification of quantitative trait loci with major effects on height- and diameter-increments would increase our understanding of the genetic control of these traits. This process might also be applied to a reduction of the breeding cycle time by developing efficient early selection programs, which would result in an increase of the overall efficiency of breeding in loblolly pine (Neale and Williams 1991).

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The objectives of the present study were to estimate the number of QTLs influencing height- and diameter-increment and the magnitude of their effects; determine developmental patterns of QTL expression for these traits; determine if QTLs influencing these traits will be different with respect to genetic background; and determine if there are QTLs affecting both annual height- and diameter-increment simultaneously.

Materials and methods

Mapping populations

Two unrelated, three-generation loblolly pine pedigrees (*BASE* and *QTL* pedigrees; Devey et al. 1994; Groover et al. 1994, respectively) were used for mapping QTLs. Pedigrees were constructed and maintained by the North Carolina State University Tree Improvement Cooperative and the Weyerhaeuser Company, and were evaluated for growth and wood quality traits. The *BASE* pedigree included 95 full-sib progeny grown at two test sites – 48 progeny in Hot Springs, Arkansas, and 47 progeny in Fort Towson, Oklahoma. The *QTL* pedigree included 172 progeny and was established in six Weyerhaeuser Co. evaluation test sites (four sites in coastal North Carolina, one in Arkansas, and one in Oklahoma).

Genotypic data and genetic linkage maps

Genetic linkage maps (maternal, paternal, and sex-averaged genetic maps) were constructed using segregation data from restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), and isozyme genetic markers for the *BASE* and *QTL* pedigrees (Devey et al. 1994; Groover et al. 1994; Sewell et al. 1999; Table 1 A).

Phenotypic data

Total tree height was measured at ages 2, 3 and 4 for the *BASE* pedigree and at ages 4, 5, 6, and 7 for the *QTL* pedigree. Total tree diameter (diameter at breast height) was measured at ages 6 and 7 only in the *QTL* pedigree. Because height- and diameter-growth were cumulative, values for the growth traits, annual height- and diameter-increment values were determined and evaluated in QTL mapping analyses (Table 1 B). As a consequence of ongoing mortality in the test plantations, the number of progeny measured for each trait varied.

QTL mapping procedure

A multiple-marker interval mapping procedure designed for an outbred pedigree was used for mapping height- and diameter-increment QTLs (Knott et al. 1997). This method allows the use of a three-generation pedigree with four unrelated and heterozygous grandparents, and a least-squares analytical method permitting the simultaneous use of all markers in a linkage group. A three-generation pedigree is needed to calculate the additive and interaction coefficients for the four possible genotypes in the progeny (Haley et al. 1994; Knott et al. 1997). The QTL analysis was carried out in two stages. In the first stage, the probability of each offspring being one of the possible genotypes (line-cross probabilities) at fixed locations throughout the genome was calculated. In the second stage, the phenotypic values (trait values) were regressed on the line-cross probabilities (Knott et al. 1997). The probabilities of the possible genotypes at any given location along a linkage group were com-

Table 1 A Genetic markers and genetic linkage maps for the *BASE* and *QTL* pedigrees. **B** Phenotypic data collected in *BASE* and *QTL* pedigrees

A		
Item	<i>BASE</i> pedigree	<i>QTL</i> pedigree
Markers		
RFLP ^a	166	267
RAPD ^b	37	56
Isozymes	8	13
Total	211	336
Genetic linkage map		
Number of linkage groups	9	19
Number of mapped markers	62	173
Total map distance (cM)	689.9	1237.8
B		
Trait measured	Trait analyzed	Number of progeny
<i>BASE</i> pedigree		
Height-growth age	Height-increment year	
2 years ^c	1–2 (<i>htinc2</i>)	84
3 years	2–3 (<i>htinc3</i>)	84
4 years	3–4 (<i>htinc4</i>)	95
<i>QTL</i> pedigree		
Height-growth age	Height-increment year	
4 years	3–4 (<i>htinc4</i>)	171
5 years	4–5 (<i>htinc5</i>)	171
6 years	5–6 (<i>htinc6</i>)	144
7 years	6–7 (<i>htinc7</i>)	111
Diameter-growth age	Diameter-increment year	
6 years ^d	5–6 (<i>dinc6</i>)	84
7 years	6–7 (<i>dinc7</i>)	110

^a RFLP = Restriction fragment length polymorphism

^b RAPD = Random Amplified Polymorphic DNA

^c Height growth measured in meters

^d Diameter growth measured in centimeters

bined and additive and interaction effects were calculated for each progeny in terms of these probabilities. These values were used in a simple multiple linear regression model to determine the regions of linkage groups (possible QTL positions) that are responsible for the existence of variation in the phenotypic traits (Knott et al. 1997).

Two models were fitted, one assuming one QTL per linkage group, the other assuming two QTLs. In fitting both one QTL and two QTLs to each linkage group, estimates were made at 2-cM intervals. When fitting only a single QTL to a given linkage group, there is a chance of inaccurately mapping the QTL if there are in fact two QTLs on the same linkage group. Furthermore, when just one QTL is fitted, it is possible that a second QTL with major effect will pass undetected (Haley et al. 1994). Thus, two QTLs were fitted to all linkage groups in both pedigrees.

Permutation tests were conducted in a previous study (Knott et al. 1997) to empirically determine critical *F* values for estimating wood specific-gravity QTLs in the *QTL* mapping population. In the present study, a critical *F* corresponding to the 0.005 probability level was used. In the case of fitting one QTL, the degrees of freedom in the numerator (regression mean square for the *full model*) were three and in the denominator (residual mean square in the *reduced model*) ranged from 82 to 93 in the *BASE* pedigree and from 81 to 165 in the

QTL pedigree. When two QTLs were fitted for each linkage group, the degrees of freedom were six in the numerator and ranged from 81 to 165 for the denominator. The magnitude of each QTL effect on growth-increment traits was calculated by comparing the full model (assuming a QTL effect) with the reduced model (assuming no QTL effect) (cf. Haley et al. 1994 and Knott et al. 1997 for a discussion of full and reduced models). QTLs were positioned on a consensus linkage map that was constructed from the integration of linkage maps from the *BASE* and *QTL* pedigrees (Sewell et al. 1999).

Results

BASE pedigree

One-QTL analysis

Two distinct QTLs for annual height-increment were identified in the *BASE* pedigree (Table 2A). These QTLs were located on linkage groups 8 (*htinc2*) and 9 (*htinc4*). They accounted for 20.0% and 12.6% of the phenotypic variance, respectively. No QTLs for annual height-increment at age 3 (*htinc3*) were detected.

Two-QTL analysis

Two tightly linked QTLs (44 cM and 46 cM) on linkage group 8 were detected for *htinc2* (Table 2B). These

appear to be QTLs of opposite effect and better explain the data than the one-QTL model.

For *htinc4*, two QTLs were detected both on linkage group 8 (18 and 22 cM) and on linkage group 9 (36 and 52 cM) (Table 2B). It is possible that the two tightly linked QTLs on linkage group 8 are of opposing effect because no QTL was detected in this region after the one-QTL analysis. In the case of the *htinc4* QTLs on linkage group 9, a QTL was detected at nearly the same position (52 vs 54 cm) in both the one- and two-QTL analysis, but an additional QTL was detected at position 36 in the two-QTL analysis. Fitting of this second QTL increased the proportion of the variance accounted for from 12.6% to 17.1% (Table 2B).

QTL pedigree

One-QTL analysis

Two distinct QTLs for annual height-increment at age 6 (*htinc6*) were identified in the *QTL* pedigree after the analysis of fitting the one QTL (Table 3A). The QTLs were located on linkage group 5 at 120 cM and linkage group 8 at 60 cM. These two QTLs accounted for 10.9% and 4.7% of the total phenotypic variation for *htinc6*, respectively (Table 3A). No QTLs for *htinc4*,

Table 2 Results of interval mapping of height-increment QTLs in *BASE* pedigree. **A** Results from fitting one QTL to each linkage group; **B** results from fitting two QTLs to each linkage group

Trait	Linkage group	Location (cM)	<i>F</i> -value (<i>df</i>)	Associated marker(s)	Paternal effect (SE)	Maternal effect (SE)	Paternal × maternal effect (SE)	Variance explained (%)
<i>htinc2</i> ^a	8	50	6.072*** (3, 83)	FI-2568.1, FI-616b	0.064 (0.016)	− 0.012 (0.013)	0.004 (0.018)	20.0
<i>htinc4</i>	9	54	5.46*** (3, 93)	PI-624.a	− 0.005 (0.022)	0.003 (0.022)	− 0.085 (0.023)	12.6
B								
Trait	Linkage group	Location (cM)	<i>F</i> -value (<i>df</i>)	Associated marker(s)	Paternal effect (SE)	Maternal effect (SE)	Paternal × maternal effect (SE)	Variance explained (%)
<i>htinc2</i>	8	44	5.11***	FI-2568.1	− 0.135 (0.091)	0.289 (0.145)	0.190 (0.082)	23.1
		46	3.56*** (6, 83)	FI-2568.1	0.195 (0.101)	− 0.307 (0.149)	− 0.199 (0.095)	
<i>htinc4</i>	8	18	3.39***	FI-1917.A, FI2568.1	− 0.016 (0.136)	0.070 (0.171)	− 0.472 (0.123)	13.4
		22	2.17*** (6, 93)		0.008 (0.152)	− 0.071 (0.183)	0.465 (0.145)	
<i>htinc4</i>	9	36	4.19***	FI-2323A, FI-669.b	0.029 (0.045)	0.161 (0.064)	− 0.048 (0.043)	17.1
		52	2.63*** (6, 93)	PI-624.a	− 0.011 (0.041)	− 0.096 (0.072)	0.124 (0.044)	

*** Significant at $P < 0.005$

^a See Table 1 for definition of height-increment traits

Table 3 Results of interval mapping of height- and diameter-increment QTLs in the *QTL* pedigree. **A** Results from fitting one QTL to each linkage group; **B** Results from fitting two QTLs to each linkage group

Trait	Linkage group	Location (cM)	<i>F</i> -value (<i>df</i>)	Associated marker(s)	Paternal effect (SE)	Maternal effect (SE)	Paternal × maternal effect (SE)	Variance explained (%)
<i>htinc6</i> ^a	5	120	6.59*** (3, 138)	PI-2295.2	− 0.12 (0.04)	− 0.09 (0.04)	− 0.060 (0.04)	10.9
<i>htinc6</i>	8	60	7.74*** (3, 138)	MI-2738.A, MI-149.2	0.00	0.10 (0.03)	0.00	4.7
<i>dinc6</i>	1	70	4.96*** (3, 81)	MI-2782.13	0.26 (0.14)	0.28 (0.12)	0.40 (0.16)	12.8
<i>dinc6</i>	10	35	4.80*** (3, 81)	PI-pt3004.2, PI-1919.2	− 0.25 (0.11)	0.35 (0.11)	− 0.12 (0.12)	12.4
<i>dinc6</i>	9	10	5.41*** (3, 81)	FI-2479.1 PI-2323.A	0.00	− 0.77 (0.33)	0.00	5.2
B								
Trait	Linkage group	Location (cM)	<i>F</i> -value (<i>df</i>)	Associated marker(s)	Paternal effect (SE)	Maternal effect (SE)	Paternal × maternal effect (SE)	Variance explained (%)
<i>htinc5</i>	4	74	3.17***	FI-A2.C	− 1.03 (0.40)	0.16 (0.17)	− 0.59 (0.24)	7.3
		76	3.50*** (6, 165)	PI-2274.1	1.06 (0.44)	− 0.13 (0.17)	0.70 (0.026)	
<i>htinc6</i>	5	112	5.49****	MI-3026.A	− 0.05 (0.02)	9.42 (3.60)	9.36 (3.60)	14.0
		116	3.47**** (6, 138)	MI-3026.A, PI-2295.2	− 0.04 (0.01)	− 10.26 (3.89)	− 10.98 (4.21)	
<i>htinc7</i>	3	30	3.37***	PI-138.B	− 0.16 (0.11)	− 0.21 (0.13)	− 0.21 (0.13)	11.7
		88	2.77*** (6, 106)	MI-LP-5.A, MI-2889.12	0.20 (0.14)	− 0.14 (0.14)	− 0.46 (0.18)	
<i>dinc6</i>	1	82	5.91****	MI-2782.13	0.19 (0.22)	0.58 (0.17)	0.10 (0.26)	26.7
		114	5.92**** (6, 81)	MI-658.A	0.12 (0.23)	− 0.42 (0.14)	− 0.92 (0.21)	
<i>dinc6</i>	11	6	3.90***		− 5.10 (2.24)	− 0.07 (0.16)	10.12 (4.18)	15.2
		8	6.03*** (6, 81)	PI-2588.3, PI-1916.4	5.10 (2.31)	− 0.08 (0.16)	− 10.06 (4.18)	
<i>dinc7</i>	3	28	3.52***	MI-OP-J4-440 PI-138.B	− 0.42 (0.15)	− 0.19 (0.16)	− 0.17 (0.14)	12.5
		52	3.38*** (6, 107)	FI-2588.1, MI-2745.1	0.62 (0.18)	− 0.09 (0.15)	− 0.11 (0.16)	

*** Significant at $P < 0.005$; **** Significant at $P < 0.0001$

^a See Table 1 for definition of height- and diameter-increment traits

htinc5, and *htinc7* were detected with the one-QTL analysis.

Three QTLs for annual diameter-increment at age 6 (*dinc6*) were detected and located on linkage groups 1 at 70 cM, 10 at 35 cM, and 9 at 10 cM. They accounted for 12.8%, 12.4% and 5.2% of the total phenotypic variation for *dinc6*, respectively. No QTLs were detected for *dinc7* (Table 3 A).

Two-QTL analysis

After the analysis of fitting two QTLs simultaneously, QTLs were detected for *htinc5* on linkage group 4 at

positions 74 and 76 cM, for *htinc6* on linkage group 5 at positions 112 and 116 cM, and for *htinc7* on linkage group 3 at positions 30 and 88 cM. No QTLs were detected for *htinc5* and *htinc7* in the single-QTL analysis, therefore the pair of QTLs for *htinc5* and *htinc7* may be of opposite effect. The two-QTL analysis detected QTLs for *htinc6* on linkage group 5 at positions 112 cM and 116 cM, whereas a QTL at position 120 cM was detected in the one-QTL analysis. It is possible that there are two QTLs of weak opposite effect in this region or else there is only a single QTL.

QTLs for diameter-increment were also detected following the analysis of fitting two QTLs simultaneously (Table 3 B). Two QTLs for *dinc6* at positions 82 and

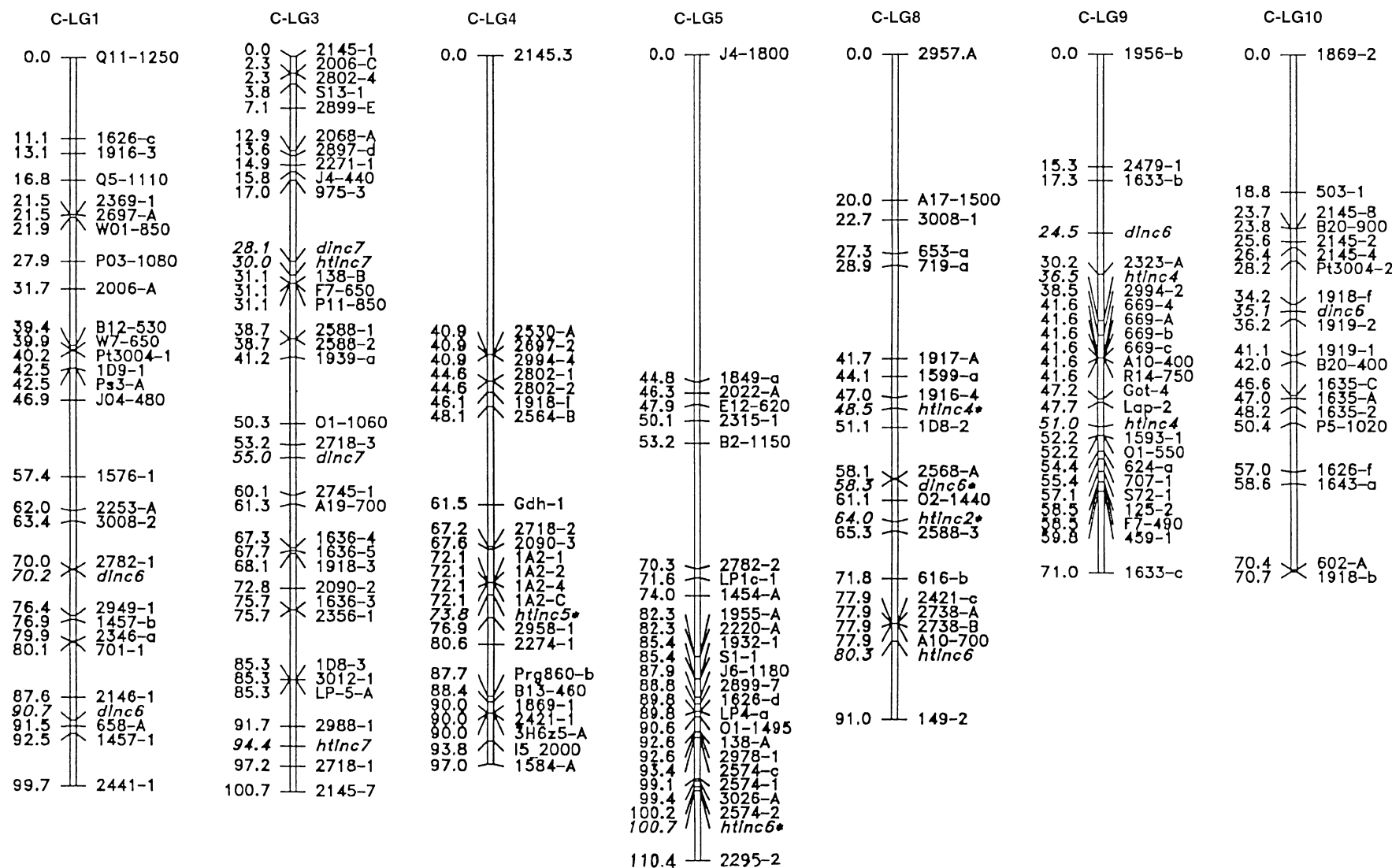


Fig. 1 Map position of height- and diameter-growth-increment QTLs on a loblolly pine consensus map (Sewell et al. 1999). Numbers of the left side of linkage groups are the distances between markers in cM and designations on the right are genetic markers and QTLs (shown in *italics*). QTLs followed by "*" represent positions where two closely-linked QTL were detected. With the exception of linkage group C-LG3, the markers positioned near 0 cM were not given since no QTLs were mapped in these regions. For the same reason, markers mapped on the locations greater than 100 cM on the linkage groups were not provided [see Sewell et al. (1999) for the complete linkage map]

Table 4 Total variance explained by height- and diameter increment QTLs in *BASE* and *QTL* pedigrees

Pedigree	Trait	Number of QTLs	Total phenotypic variance explained by QTLs (%)
<i>BASE</i>	<i>htinc2</i> ^a	2	23.1
	<i>htinc4</i>	4	30.5
<i>QTL</i>	<i>htinc5</i>	2	7.3
	<i>htinc6</i>	3	18.7
	<i>htinc7</i>	2	11.7
	<i>dinc6</i>	6	59.5
	<i>dinc7</i>	2	12.5

^a See Table 1 for definition of height- and diameter-increment traits

114 cM on linkage group 1 were detected, suggesting that the two-QTL model may be more likely than the one-QTL model fitted at position 70 cM. Two QTLs for *dinc6* were detected on linkage group 11 at positions 6 and 8 cM, which may again be two tightly linked QTLs of opposite effect (Table 3 B). There were a total of six QTLs for *dinc6* detected on linkage groups 1, 9, 10, and 11 which together accounted for 59.5% of the total phenotypic variation in this trait (Tables 3 A and B). Two QTLs for *dinc7* were also detected at positions 28 and 52 cM on linkage groups 3 accounting for 12.5% of the total phenotypic variation in this trait (Table 3 B).

Discussion

Quantitative traits such as height and diameter growth in loblolly pine are assumed to be under polygenic control. The infinitesimal model assumes that such traits are under the control of many genes of small and additive effect. The results of the present study suggest that the infinitesimal model may not be completely true for height- and diameter-increment growth in loblolly pine and that these traits may be in part controlled by a few genes of large effect. The number of QTLs influencing the annual growth-increment varied from two to four for height-increment and from two to six for diameter-increment. Within a given year and pedigree, the portion of total phenotypic variation attributable to individual QTLs ranged from 7.3 to 30% for annual height-increment and from 12.5 to 59.5% for annual diameter-increment (Table 4). The power and precision of these estimates is, however, likely to be low and the effects of the QTLs may have been over estimated as a result of small progeny sizes, large amounts of environmental variation due to multiple test sites, and incomplete genetic maps (Beavis 1994).

QTLs for height- and diameter-increment were not detected in consecutive growing seasons in either

pedigree, and in some years no QTLs were detected at all. Considering the complex nature of height- and diameter-growth, it was not expected to detect the same QTLs in all years. Plomion et al. (1996) observed similar results for QTLs influencing height-growth over developmental stages in *Pinus pinaster* and suggested that different sets of loci may be involved in the genetic control of height-growth at different ages. There are also reports that some QTLs expressed in plants are specific to environments where the plants are grown (Beavis 1994; Paterson et al. 1991). Thus, if the progeny in the present study were grown in a single environment, we might have expected more stable expression of QTLs influencing annual height- and diameter-increment over the different ages.

There are large differences between genetic backgrounds in the expression of growth-increment QTLs, although these comparisons are confounded by differences in the environments of the test sites. In fact, there is no evidence suggesting the existence of QTLs common to both pedigrees (Fig. 1). Clearly, large experiments with minimal environmental variation will be needed to identify growth-increment QTLs common to multiple genetic backgrounds versus those specific to certain genotypes.

There is also little evidence from this experiment for the presence of pleiotropic growth-increment QTLs, although close linkage of height- and diameter-increment QTLs on linkage groups 3 and 8 suggests that there may be QTLs affecting both traits (Fig. 1). Bradshaw and Stettler (1995) reported in poplar that QTLs controlling basal stem area growth and sylleptic branch habit are probably controlled by the same genes. Again, larger experiments and more precise mapping of QTLs will be need to positively identify QTLs acting pleiotropically.

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References

- Beavis WD (1994) The power and deceit of QTL experiments: lessons from comparative QTL studies. In: 49th Annual Corn and Sorghum Industry Research Conference ASTA. Washington, D.C., pp 250–266
- Bradshaw HD, Stettler RF (1995) Molecular genetics of growth and development in *Populus*. 4. Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139:963–973

- Devey ME, Jermstad KD, Tauer CG, Neale DB (1991) Inheritance of RFLP loci in a loblolly pine three-generation pedigree. *Theor Appl Genet* 83:238–242
- Devey ME, Fiddler TA, Liu BH, Knapp SJ, Neale DB (1994) An RFLP linkage map for loblolly pine based on a three-generation outbred pedigree. *Theor Appl Genet* 88:273–278
- Dorman KW, Zobel BJ (1973) Genetics of loblolly pine. USDA For Serv Res Pap WO-19
- Edwards MD, Stuber CW, Wendel JF (1987) Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. *Crop Sci* 27:639–648
- Grattapaglia D, Sederoff RR (1994) Genetic linkage maps of *Eucalyptus grandis* and *E. uruphylla* using a pseudo-testcross mapping strategy and RAPD markers. *Genetics* 137:1121–1137
- Grattapaglia D, Bertolucci FL, Sederoff RR (1995) Genetic mapping of QTLs controlling vegetative propagation in *Eucalyptus grandis* and *E. uruphylla* using a pseudo-testcross strategy and RAPD markers. *Theor Appl Genet* 90:933–947
- Groover A, Devey M, Fiddler T, Lee J, Megraw R, Mitchel-Olds T, Sherman B, Vujic S, Williams C, Neale D (1994) Identification of quantitative trait loci influencing wood specific gravity in an outbred pedigree of loblolly pine. *Genetics* 138:1293–1300
- Haley CS, Knott SA, Elsen J-M (1994) Mapping quantitative trait loci in crosses between outbred lines using least squares. *Genetics* 136:1195–1207
- Knott SA, Neale DB, Swell MM, Haley CS (1997) Multiple marker mapping of quantitative trait loci in an outbred pedigree of loblolly pine. *Theor Appl Genet* 94:810–820
- Lambeth CC (1980) Juvenile-mature correlations in *Pinaceae* and implications for early selection. *For Sci* 26:571–580
- Lander ES, Botstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics* 121:185–189
- Neale DB, Williams CG (1991) Restriction fragment length polymorphism mapping in conifers and applications to forest genetics and tree improvement. *Can J For Res* 21:545–554
- Paterson AH, Damon S, Hewitt JD, Zamir D, Rabinowitch HD et al. (1991) Mendelian factors underlying quantitative traits in tomato: comparisons across species, generations, and environments. *Genetics* 127:181–197
- Plomion C, Durel, C-E, O'Malley DM (1996) Genetic dissection of height in maritime pine seedlings raised under accelerated growth conditions. *Theor Appl Genet* 93:849–858
- Sewell MM, Sherman BK, Neale DB (1999) A consensus map for loblolly pine (*Pinus taeda* L.). I. Construction and integration of individual linkage maps from two independent three-generation pedigrees. *Genetics* (in press)
- Strauss SH, Lande R, Namkoong G (1992) Limitations of molecular-marker-aided selection in forest tree breeding. *Can J For Res* 22:1050–1061