Theor Appl Genet (1997) 94: 674–681

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Identification and mode of action of quantitative trait loci affecting seedling height and leaf area in *Eucalyptus nitens*

Received: 1 August 1996 / Accepted: 25 October 1996

Abstract Regions of the genome influencing height and leaf area in seedlings of a three-generation outbred pedigree of *Eucalyptus nitens* have been identified. Three QTLs affecting height and two QTLs affecting leaf area were located using single-factor analysis of variance. The three QTLs affecting height each explained between 10.3 and 14.7% of the phenotypic variance, while the two QTLs for leaf area each explained between 9.8 and 11.6% of the phenotypic variation. Analysis of fully informative marker loci linked to the QTLs enabled the mode of action of the QTLs to be investigated. For three loci the QTL effect segregated from only one parent, while for two loci the QTL showed multiple alleles and the effect segregated from both parents in the pedigree. The two QTLs affecting leaf area were located in the same regions as two of the QTLs affecting height. Analysis of these regions with fully informative markers showed that both QTLs were linked to the same markers, but one had a similar size of effects and a similar mode of action for both height and leaf area, whilst the other showed a different mode of action for the two traits. These regions may contain two closely linked genes or may involve a single gene with a pleiotrophic effect on both height and leaf area. The QTL with the greatest effect showed multiple alleles and an intra-locus interaction that reduced the size of the effect. Assessment for two of the QTLs in a second related family did not show an effect associated with the marker loci; however, this was consistent with the mode of action of these QTLs and the pattern of inheritance in the second family.

Key words Eucalypts · Height · Leaf area · Genetic mapping · Pleiotrophy

Introduction

The majority of traits of interest to tree breeders for genetic improvement are quantitative rather than qualitative in nature. Plant breeders typically have little information about the number, the size of the effects, and the mode of action or interaction, of the genes that effect the expression of these quantitative traits (Stuber 1992a, b). The development of genetic linkage maps provide a powerful tool for the location of QTLs and the tagging of these loci with molecular markers. Identification of marker loci tagging these quantitative trait loci (QTLs) will facilitate a dissection of the genetic architecture of these traits. The dissection of quantitative traits into their individual genetic components will enhance their manipulation in breeding programs. In forest trees, QTLs affecting wood density, vegetative propagation traits, stem growth, form and spring leaf flush have been identified in pines, eucalypts and poplars (Groover et al. 1994; Bradshaw and Stettler 1995; Grattapaglia et al. 1995).

In contrast to crop plants, where the type of family structure generally results in the segregation of genetic markers in a 1 : 1 or 1 : 2 : 1 ratio, family structure in tree species is usually a result of outbred crosses. As a consequence, both molecular and quantitative loci can maintain numerous alleles and can show segregation of up to four alleles. In such cases it is important to determine the nature of the quantitative locus. This can be achieved using co-dominant markers to tag the QTL since analysis of an informative co-dominant linked marker locus can be used to infer the mode of action of the QTL. Identification of QTLs in outbreeding pedigrees has shown the presence of multiple alleles in loblolly pine and potato (Groover et al. 1994; van Eck

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Communicated by P. M. A. Tigerstedt

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et al. 1994) as well as an intra-locus interaction in loblolly pine (Groover et al. 1994).

The present study has located regions of the genome influencing two biomass production traits, height and leaf area, in 3-month-old seedlings of *Eucalyptus nitens*. Eucalypts are widely planted throughout the world for the production of timber, and pulp for paper manufacture. *E. nitens* is a major hardwood species grown in Australia, and is also grown in South Africa and Chile. Height and leaf-area are components of growth which are among the principal traits currently used for selection in tree-breeding programs (Eldridge et al. 1994). The seedlings used in this study are the progeny of a three-generation outbred pedigree, and a genetic linkage map has previously been constructed for this family (Byrne et al. 1995). This linkage map contains 210 RFLP loci of which 32% were fully informative showing segregation from both parents. Analysis of the mode of action of the QTL for height and leaf area was achieved using fully informative markers linked to the QTL. Identification of the QTL in a second related family was also investigated.

Materials and methods

Plant materials

The plants relevant to this study were part of a larger experiment involving the progeny of four controlled crosses and open-pollinated seed from the same parents of *E. nitens*. The details of the two controlled cross families relevant to this study are shown in Fig. 1, and details of the natural distribution of the species is given in Byrne and Moran (1994). The seed was cold/moist stratified for 3 weeks and germinated in sand under mist. The seedlings were planted in 5-inch pots in a medium of sieved sand/vermiculite/perlite/peatmoss (1 : 1 : 1 : 1) that had been steam-air sterilized at 60°C for 1 h. Plants were grown in the glasshouse at 24°C day temperature and 16°C night temperature with individual pot irrigation using 1/5 Hoagland solution (Went 1957) with full-strength micro-nutrients and iron. Plants were positioned in the glasshouse according to a designed experiment to allow adjustments for possible glasshouse variation. A total of 465 plants were included in the experiment.

Height and leaf-area measurement

Height and leaf-area measurements were made at 55 days after planting out. Height was measured from the cotyledons to the terminal meristem of the seedling. The length and width of one leaf of all pairs of leaves were measured. Length was measured from the base to the tip of the leaf and width was measured at the widest point. The leaf-area for each seedling was calculated as 2 × width × length × 0.75, where the first term in this formula caters for the leaf pair and the last term approximates the oval shape of the leaves. The leaf-pair areas were then summed over all pairs.

DNA genotyping

The genotypes of 118 plants from Cross 1 and 60 plants from Cross 2 were determined. Leaves of the seedlings were sampled 3 months after planting out. DNA extractions were carried out as described in Byrne et al. (1993). The individuals of Cross 1 were genotyped for 210 RFLP loci, and linkage analysis and mapping of these loci was carried out as described in Byrne et al. (1995). The individuals of Cross 2 were genotyped for 30 RFLP loci.

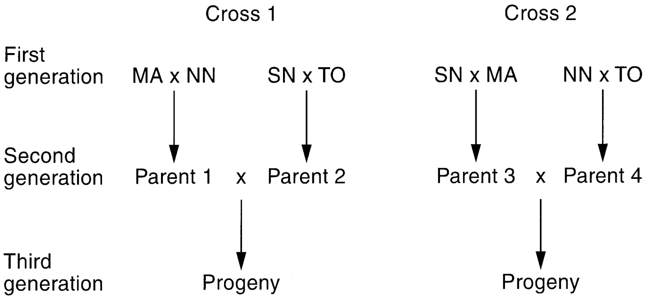


Fig. 1 Structure of the two families used to investigate QTL effects in *E. nitens*. The first-generation trees come from four different populations: *MA*, Macalister; *NN*, northern New South Wales; *SN*, southern New South Wales; *TO*, Toorongo

QTL analysis

Single-factor analyses of variance (Edwards et al. 1987) for the DNA genotypes and the phenotypic data were carried out separately for Cross 1 and Cross 2.

Results

Phenotypic data

The height and leaf-area data of Cross 1 and Cross 2 at day 55 showed normal distributions. No effects of glasshouse position were detected and no adjustments were made to the data. Narrow-sense heritability was calculated for the four fullsib families as 2 × additive variance/phenotypic variance (Falconer 1989). Narrow-sense heritability for height and leaf area were 0.19 and 0.36 respectively. The value for heritability of height obtained here is similar to an estimate of narrow-sense heritability for individuals in open pollinated families of *E. nitens* at 9 years ($h^2 = 0.23$) (Whiteman et al. 1992) and to estimates of narrow-sense heritability for controlled cross families of *E. grandis* at 3 months after planting ($h^2 = 0.27$; Griffin and Cotterill 1988).

QTL analysis

Height

Single-factor analysis of variance of the day-55 height measurement in Cross 1 identified 17 loci significant at the 5% level, five loci significant at the 1% level and two loci significant at the 0.1% level (Table 1). The genomic position of these loci was determined using the *E. nitens* map (Byrne et al. 1995), and showed clustering

Table 1 Loci that showed a significant association with height measurements in Cross 1. FI, fully informative; F, female segregation; M, male segregation; H, heterozygous for the same alleles. Linkage groups from the *E. nitens* map (Byrne et al. 1995)

Locus	Segregation type	Linkage group	*F* probability
c077A	FI	7	0.043
c137	FI	2	0.017
c158	FI	1	0.050
c174	F	10	0.010
c326A	FI	1	0.049
c333	F	1	0.020
c340	M	6	0.046
c435	FI	1	0.049
c453	H	1	0.033
c457	FI	2	0.023
c480D	FI	10	0.039
c482	FI	10	0.039
c505A	FI	4	0.039
g092B	M	4	0.006
g233	M	4	0.016
g235B	FI	2	0.007
g250	F	10	0.013
g256	H	4	0.027
g258A	FI	4	0.007
g337	F	8	0.043
g373	FI	6	0.003
g402B	F	9	0.029
g418A	FI	4	< 0.001
g474	FI	4	< 0.001

of the loci in five regions of the map, on linkage groups 1, 2, 4, 6 and 10 . The markers with a probability of less than 0.01 were present in the clusters on groups 2, 4 and 6 (Fig. 2). This indicates the position of three putative QTLs affecting height located in these regions. The amount of phenotypic variation explained by these three QTLs was calculated for a marker flanking each QTL and ranged from 10.30% to 14.71% (see Table 3). The mean increase in height conferred on the genotypic class containing the QTL effect, compared to the mean height of all individuals, ranged from 6.68% to 11.46% (see Table 3). All regions were flanked by markers that were fully informative, i.e. segregation from both parents could be unambiguously determined, therefore the ancestry of the marker allele associated with the QTL effect could be traced in the grandparent generation. For the QTL on group 4 the direction of the effect was from one grandparent only (Toorongo), and therefore segregation of the effect was observed in the male parent only (see Table 3). For the QTL on linkage group 6 the direction of the effect was traced to two grandparents (Macalister and southern New South Wales) and the segregation of the QTL effect was seen in both parents (see Table 3). For the QTL on group 2 the direction of the effect could not be determined reliably. The marker loci showing a significant association in this region also showed significant segregation

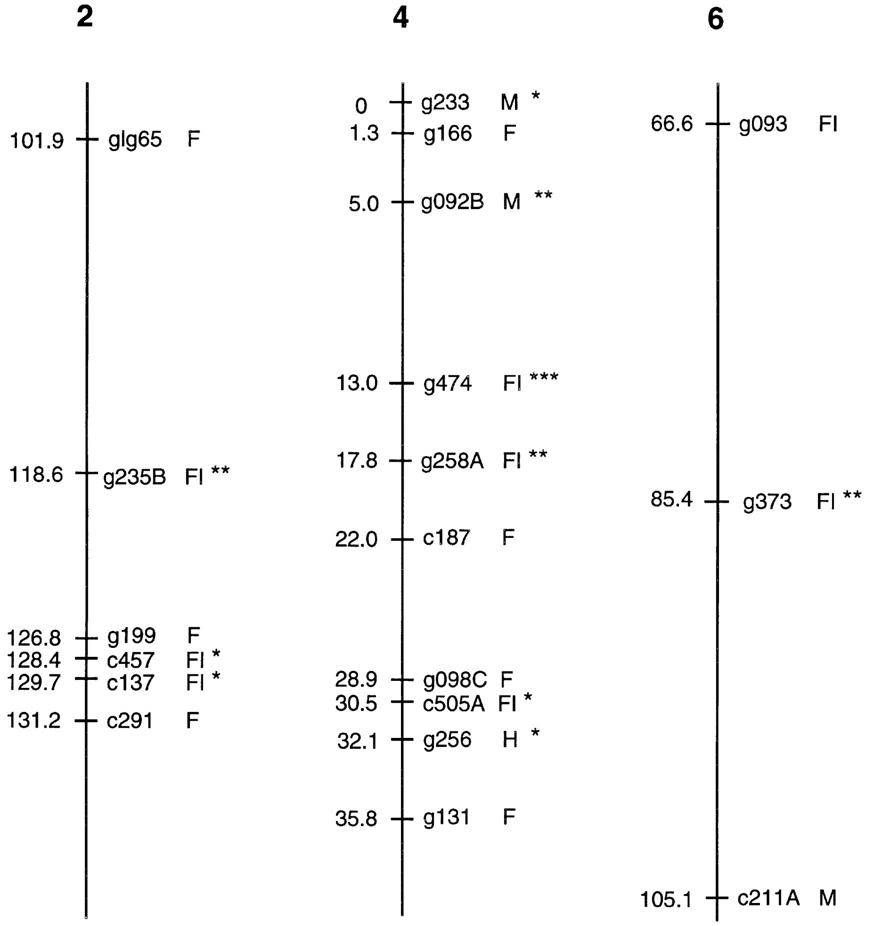


Fig. 2 Maps of the three regions where QTLs for height were located in Cross 1. *F*, locus segregating from the female parent; *M*, locus segregating from the male parent; *FI*, locus segregating from both parents; *H*, locus with both parents heterozygous for the same two alleles. ∗, significant at the 0.05% level; ∗∗, significant at the 0.01% level; ∗∗∗, significant at the 0.001% level

distortion from the male parent; therefore an analysis of these loci would not be reliable and was not pursued.

Leaf area

Single-factor analysis of variance of the day-55 surface leaf-area measurement in Cross 1 identified 16 loci significant at the 5% level and two loci significant at the 1% level (Table 2). The map position of these loci showed clustering of the loci in five regions of the map (Byrne et al. 1995), on linkage groups 1, 2, 4, 5 and 6. The markers with a probability of less than 0.01 were present in clusters on groups 2 and 4. This indicates the presence of two QTLs affecting leaf area located in these regions of the genome. These putative QTLs each explained between 9.86 and 11.68% of the phenotypic variation for leaf area in this family and gave a 7.04–14.31% mean increase in leaf area over the mean of all individuals (Table 3). Both of these QTLs were flanked by fully informative markers. The QTL on group 4 showed effects originating from the Toorongo grandparent with segregation from the male parent in the family. The QTL on group 2 showed segregation of the effect from the female parent and the effect was traced to the northern New South Wales grandparent.

Table 2 Loci that showed a significant association with leaf area measurements in Cross 1. FI, fully informative; F, female segregation; M, male segregation; H, heterozygous for the same two alleles. Linkage groups from the *E. nitens* map (Byrne et al. 1995)

Locus	Segregation type	Linkage group	*F* probability
c077A	FI	7	0.013
c137	FI	2	0.021
c165C	F	6	0.011
c291	F	2	0.031
c334A	F	5	0.045
c453	H	1	0.029
c457	FI	2	0.039
c505A	FI	4	0.017
g003	F	5	0.033
g063	F	6	0.011
g092B	M	4	0.013
g098A	F	1	0.024
g199	F	2	0.035
g235B	FI	2	0.009
g258A	FI	4	0.022
g417	FI	3	0.027
g418A	FI	4	0.011
g474	FI	4	0.003

Mode of action of QTLs for height and leaf area

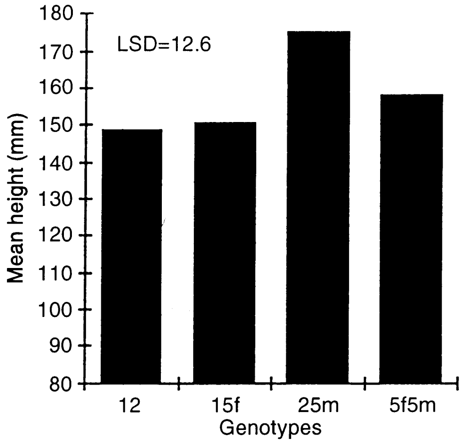
The QTL with the strongest effect on height was on linkage group 4. In this region the loci that were significantly correlated with height either showed segregation from the male side of the pedigree only or segregated on both sides of the pedigree, but the significant effect was only correlated with segregation from the male parent. The loci in this region that segregated on the female side of the pedigree did not show a significant correlation with height. The two loci that were significant at the 0.1% level were in this region and were fully informative loci. Analysis of these loci showed that one allele (allele 5 on marker locus *g474*) from the male parent was associated with a significant increase in height in the progeny that received that allele (Fig. 3). This allele contributed to a 16.9% increase in height compared to those individuals that inherited the alternative allele from the male parent. However, when this allele was combined with one of the alleles from the female parent (allele 5 on marker locus *g474*) the increase in height was reduced to only 5.5% (Fig. 3). Thus it appears that both parents in the cross are heterozygous for alleles at this QTL. If the two parents are heterozygous for the same two alleles at the QTL then two heterozygous genotype classes will have the same mean phenotypic values. No two classes have the same phenotypic values, and if the male allele 5 and the female allele 5 are both linked to the same QTL allele then a two-allele model shows that the two heterozygous classes (25 and 15) do not have the same value (Fig. 4). Therefore the parents of the cross are not heterozygous for the same two QTL alleles and it may be inferred that there are at least three QTL alleles present in this family. There is a significant interaction between two of the alleles at this QTL ($P < 0.05$). Genotyping of the grandparent trees of this cross enabled QTL alleles to be traced through three generations. The allele conferring the positive effect was inherited from the grandparent that came from the Toorongo provenance, while the allele that modified the effect was inherited from the grandparent that came from the northern New South Wales provenance.

The region with the strongest effect for leaf area was also on linkage group 4 and also showed correlation with loci segregating on the male side of the pedigree. Analysis of the fully informative and significant loci in this region showed that the allele that contributed to an increase in height also contributed to an increase in surface leaf area of 17.5% compared to the alternative allele from the male parent (Fig. 3). A reduced effect of only 7.3% increase in leaf area was also observed when the same male allele was present in combination with a specific allele from the female parent (Fig. 3). Analysis of the phase relationships between the marker and the QTL also showed that the parents were heterozygous for at least three alleles at the QTL, as was seen in the analysis of the height QTL. As was observed for the height QTL, the allele conferring the effect was inherited from the grandparent from the Toorongo provenance and the allele modifying the effect was inherited from the grandparent from the northern New South Wales provenance.

Table 3 Location and effect of QTLs influencing (a) plant height in Cross 1 and (b) leaf area in Cross 1. Origin of effect is from grandparent: NN, northern New South Wales; SN, southern New South Wales; TO, Toorongo; MA, Macalister

Linkage group	Flanking marker	Segregation type	% variation explained	% Increase	Origin of effect
(a)					
2	*g235B*	FI	10.30	6.68	
4	*g474*	FI	14.71	11.46	TO
6	*g373*	FI	11.46	10.53	MA and SN
(b)					
2	*g235B*	FI	9.86	7.04	NN
4	*g474*	FI	11.68	14.31	TO

Fig. 3 Mean height and leaf area for genotype classes of 118 progeny of Cross 1 at marker locus *g474* which is associated with QTLs for height and leaf area. Parental genotypes are female 25, male 15. *5f* = allele 5 inherited from female parent, *5m* = allele 5 inherited from male parent



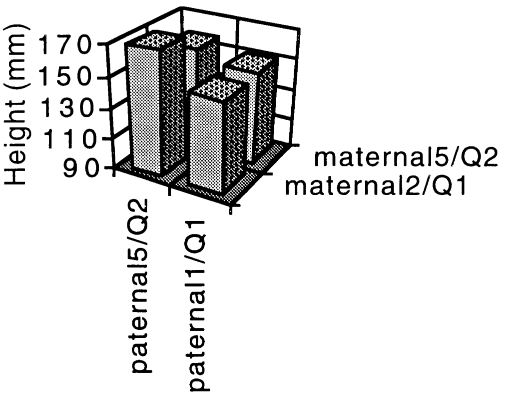


Fig. 4 Genotypic class-means for the marker locus associated with QTLs for height on linkage group 4. Genotypes are for a two-allele model, which is not consistent with the data. *Numbers* represent alleles for marker *g474*. Parental genotypes are female 25, male 15. *Q1* and *Q2* represent QTL alleles, *Q1* = QTL allele without an effect, *Q2* = QTL allele with an effect if a two-allele model is assumed

The QTL for height on group 6 showed effects segregating from both parents. If both parents are heterozygous for the same two alleles then the two heterozygous classes in the progeny should have similar mean values. The mean values of the two heterozygous classes are similar, namely classes 13 and 25 for *g373* in group 6 (Fig. 5). Where two parents are heterozygous for the same two alleles, the dominance or additivity of the alleles can be determined (Falconer 1989). In group 6, the mid point between the values of the two homozygous classes is 160.9 and the heterozygous classes show a mean value of 154.75, giving an a-value of 12.3 and a d-value of − 6.15. This indicates a partial dominance (d/a = − 0.5) of the allele without an effect at this locus.

The mode of action of the QTL for height on group 2 could not be determined; however, the QTL for leaf area on the same group has a different mode of action. For leaf area, loci segregating from the female parent, and showing no segregation distortion, were significantly associated with the QTL. Since the loci segregate from one parent only, no assessment of dominance/additivity or allelic interaction could be made.

Epistasis

To test for epistatic interactions between QTLs a pairwise analysis of variance was carried out using the fully informative marker locus that showed the most significant association for each QTL. There was no significant interaction between any combination of two of the three QTLs or between the three QTLs taken together.

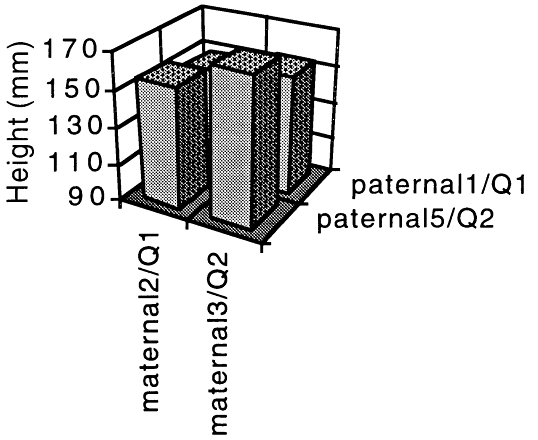


Fig. 5 Genotypic class-means for QTLs for height on linkage group 6. Genotypes are for marker *g373* on linkage group 6. *Q1* = QTL allele without an effect; *Q2* = QTL allele with an effect

Analysis of cross 2

To test the proposed mode of action of the QTL on group 4 in a second related family, the loci that were significantly associated with height and leaf area on linkage group 4 in Cross 1 were also genotyped on 60 individuals from Cross 2. This second cross has the same four grandparents as Cross 1, but different parents. Single-factor analysis of variance for these loci and other loci randomly distributed throughout the genome did not identify any that were significantly correlated with height or leaf area at day 55. Analysis of the fully informative locus on linkage group 4 showed that the male parent in Cross 2 inherited the alternative allele from the Toorongo grandparent and not the allele that conferred the increase in height and leaf area in Cross 1.

The proposed mode of action for the QTL on group 6 was also tested in Cross 2. In Cross 2 at the marker locus for the QTL on group 6 (*g373*) the female parent possesses the marker alleles linked to the QTL allele with the effect from both the MA and SN grandparents, while the male parent possesses the alternate alleles. Thus, under the proposed mode of action at this QTL, Cross 2 involves a homozygote for the QTL allele with the effect and a homozygote for the QTL allele without the effect, so all progeny will be heterozygous for the QTL effect. An analysis of variance showed no significant association for the *g373* locus and height in Cross 2.

Discussion

Regions of the genome containing QTLs influencing height and leaf area have been identified in a cross of *E. nitens*. Three QTLs affecting height and two QTLs affecting leaf area were located in this family. Both of the QTLs that influenced leaf area were in the same regions as the QTLs that influenced height. One QTL showed the same mode of action of the alleles for both height and leaf area, whilst the other QTL showed a different mode of action. The presence of QTLs for both height and leaf area identified in the same regions may be due to the presence of two genes closely linked, or to one gene with a pleiotrophic effect on both height and leaf area. The same mode of action of the QTL on group 4 for both height and leaf area suggests the presence of a single gene with a pleiotrophic effect on both traits in this genomic region. The QTL identified in this family may involve genes that have a general effect on biomass production which can be most readily observed in height and leaf-area traits. QTLs with pleiotrophic effects on height and other traits associated with biomass production have been identified in some crop species. Pleiotrophy has been observed between dwarfing and heading-date in barley (Barua et al. 1993), and between height and yield, tiller number, panicle size and leaf area in sorghum (Pereira and Lee 1995). The QTL on group 2 suggests the presence of two tightly linked genes in this region.

Investigation of the QTL effects in a second related cross allowed the testing of the proposed mode of action of the QTLs detected in Cross 1. The QTLs on group 4 and 6 identified in Cross 1 were not identified in Cross 2. However, analysis of the allele structure in Cross 2 shows that in both cases lack of identification of the QTLs in this cross could be explained since for one QTL the allele with the effect is not present in the parents of Cross 2, and in the other QTL one parent is homozygous for the allele with the effect and hence the progeny do not show segregation of the QTL effect. Whilst this investigation does not positively confirm the presence of the QTL in the other cross, the results are consistent with those expected under the proposed mode of action of the QTLs detected in the first cross.

The QTLs each explained between 10 and 15% of the phenotypic variation. No previous infomation was available on the relative growth charactistics of the parents in this family; therefore it was not known whether QTLs would be located in this family. However, it may be that there is generally sufficient variation in outbred pedigrees for the effects of QTLs to be detected. In other outbreeding tree species QTLs have been detected with effects of 5.6% phentotypic variation explained for wood specific gravity in loblolly pine (Groover et al. 1994), 6.0–21.0% phenotypic variation explained for vegetative propagation traits in *E. grandis* and *E. urophylla* (Grattapaglia et al. 1995), and 24.4–33.4% phenotypic variation explained for growth traits in poplars (Bradshaw and Stettler 1995). However, both studies that have detected QTLs with large effects (Bradshaw and Stettler 1995; Grattapaglia et al. 1995) have been in inter-specific hybrid crosses which may be expected to display large differences in the segregation of traits. No epistasis was detected between the QTLs located in this study, and epistasis has not been detected for QTLs in loblolly pine or poplars (Groover et al. 1994; Bradshaw and Stettler 1995).

In an outcrossed pedigree up to four alleles can segregate at a locus. The family used in this study originates from a wide inter-population cross and thus may be expected to segregate for multiple alleles at QTLs. The use of fully informative marker loci in these pedigrees enables the identification of the effects of multiple alleles at QTLs. All the QTLs were flanked by fully informative marker loci, enabling the mode of action of these QTLs to be investigated. Multiple alleles were observed at one of the QTLs which affected both height and leaf area. One allele was associated with a positive effect, but showed an interaction with an allele segregating from the alternate parent. Analysis of this locus indicated the presence of at least three alleles with a significant interaction between two of them. Multiple alleles at QTLs have been identified in other outbreeding species where outbred pedigree structures have been used. Three alleles were identified at a QTL for tuber shape in potato (van Eck et al. 1994), and three alleles with intralocus interaction at a QTL for wood specific gravity were reported in loblolly pine (Groover et al. 1994). The identification of intra-locus interactions is important for an understanding of the mode of action of QTLs, particularly where selection based on markers flanking QTLs will be undertaken. Lack of identification of the intra-locus interaction that reduced the positive effect of the allele for the QTL on linkage group 4 in this family would have resulted in half of the selected individuals not realising the expected increase in height and leaf area. Depending on the arrangement of alleles in the parents, lack of identification of a similar intra-locus interaction in another family may result in up to two thirds of the selected individuals not realising the expected gain.

The other QTL identified showed segregation for two alleles, with one allele giving a positive effect. For one locus both the parents were heterozygous for the same alleles and deviation from purely additive effects with partial dominance of the non-effect allele was observed. Most QTLs where the mode of action has been identified have shown some dominance effects. In poplars, dominance effects were observed in most of the QTLs detected for growth, form and spring bud flush, although two loci showed additive gene action (Bradshaw et al. 1995). Dominance was observed in four QTLs for height identified in sorghum (Pereira and Lee 1995). A range of additive to overdominant gene action was observed in analyses of a large number of traits in maize (Edwards et al. 1987, 1992), and mainly dominant or overdominant gene action was observed in QTLs identified for yield traits in maize (Stuber et al. 1987, 1992). Mainly dominant gene action was also observed in QTLs identified for 18 traits in tomato with overdominance at the QTL for plant height (Weller et al. 1988), although additivity was observed in the QTL for fruit traits (Paterson et al. 1991).

The progeny of the crosses have been planted in the field and will be assessed for growth traits in future years. This will enable monitoring of the temporal expression of the QTLs identified in this study. It will be of interest to determine if genes affecting growth at the seedling stage are the same as those influencing later age growth, or whether there are a suite of genes affecting growth that influence different stages in the development of the tree.

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