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QTL analysis for fruit yield components in table grapes (*Vitis vinifera*)

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Abstract A segregation population of 184 genotypes derived from a pseudo-testcross of table grapes (*Vitis vinifera*), together with 203 AFLP and 110 SSR markers was used to detect quantitative trait loci (QTLs) for fruit yield components. Diffferent QTLs, a low percentage of phenotypic variance explained by the QTLs detected and QTL instability over years were detected for each fruit yield component. These results confirm the complex genetic architecture of the yield components in grapevine due to the perennial nature of this species, which has to adapt to yearly variations in climate. Phenotypic correlation analyses between fruit yield components were also performed. The negative correlation between berry weight and the number of berries per cluster seems to have an indirect negative effect on cluster weight, as revealed by the path coefficient analysis; however, this negative correlation was not supported at the molecular level because no coincident QTLs were observed between these traits. Nonetheless, the possibility to select seedless genotypes with large berries without affecting cluster weight needs to be substantiated in future experiments because factors such as sample size and heritability might influence QTL identification in table grapes.

Introduction

Fruit yield is the most commonly measured but poorly understood trait in grapevine. It is an extremely complex quantitative character both because of the number of segregating loci controlling all of the traits involved in yield and of the influence of non-genetic factors. A multitude of investigations have been conducted on the inheritance of yield and yield components in fruit tree species using the classical biometrical approach, and while these studies have been useful for making predictions on the genetic progress occurring in plant breeding programs, they have not provided information on individual genes (or group of genes) influencing quantitative trait loci (QTLs). However, genetic studies for quantitative traits have recently been greatly facilitated by the development of molecular markers. Modern strategies for investigating the genetic basis of yield components or other quantitative traits are based on the construction of genetic linkage maps that have been constructed using the available molecular markers. Subsequent information gained from the constructed genetic linkage maps together with agronomic data collected from field experiments allow the identification of QTLs associated with variability of the agronomic trait under study. This approach may improve traditional methods of breeding, particularly in fruit tree species which have long juvenility periods, large plant size and show reproductive irregularities. To date, a number of QTL analyses have been reported in fruit tree species (Conner et al. 1998; Dirlewanger et al. 1999; Garcìa et al. 2000; King et al. 2000; Wang et al. 2000; Ballester et al. 2001; Quilot et al. 2004), including grapevine (Striem et al. 1996; Lahogue et al. 1998; Dalbò et al. 2001; Doligez et al. 2002; Fischer et al. 2004).

One of the major objectives of table grape breeding is the development of seedless genotypes with large berries, as all traditional seedless grape varieties develop smaller berries than their seeded counterparts. In *Vitis*, some QTL analyses have been carried out on the relationship between the seedless trait and berry weight (Striem et al. 1996; Lahogue et al. 1998; Doligez et al. 2002; Fischer et al. 2004), however there is not information available on the association of the seedless trait with the other fruit yield components. The success of a new table grape

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variety will depend not only on its seedlessness and berry size but also on the cluster weight and vine yield. Thus, knowledge of the genetic relationship among fruit yield components based on a QTL analysis is economically important in table grapes.

The objective of our investigation was to acquire information on the association between molecular markers and fruit yield components in table grapes in order to improve our understanding of the inheritance of these fruit traits and to facilitate the selection for seedless genotypes in breeding programs.

Materials and methods

Plant material and trait measurements

The plant material consisted of 184 progeny plants from a double pseudo-testcross between two table grape cultivars, Italia (seeded) × Big Perlon (seedless). The offspring of this cross are highly variable with respect to its fruit: approximately 50% seedless genotypes (including seedless genotypes with small seed traces and large seed traces) and 50% seeded genotypes. The plants were grown on their own roots (2 m between rows and 1 m within a row) under normal conditions of irrigation, fertilization and pest control. Environmental sources of variation between genotypes and between fruit within a genotype were minimized through pruning and cluster thinning. The plants flowered and fruited in 2000. The following fruit traits—vine yield, number of clusters per vine, cluster weight and number of berries per cluster (from two to three representative clusters), berry weight (from 100 random berries)—were measured for each genotype in three consecutive years (2002–2004).

The normality of each trait distribution was evaluated by the Shapiro-Wilk test and probability plots (SAS Institute 1988). The data were transformed (square-root) to fit a normal distribution. The repeated-measures analysis of variance (years, genotypes within year) was applied to estimate the repeatability over years (Falconer and Mackay 1996) for each fruit trait. The genotype stability across years was studied for each fruit trait by correlation analysis between years. Phenotypic correlations between traits were determined in each year. Path coefficient analysis (Li 1956) was also performed because it provides more information among variables since this analysis allows the direct and the indirect effect of correlated traits to be evaluated; the direct path coefficients were estimated by multiple regression analysis (SAS Institute 1988).

Molecular markers and QTL analysis

DNA extraction and the molecular marker detection were carried out as described in Fanizza et al. (2003) and Grando et al. (2003). The QTL analysis was based on individual parent linkage maps for Italia (I) and Big Perlon (BP) constructed using 203 amplified fragment length polymorphism (AFLP) and 110 simple sequence repeat (SSR) markers. The file maps were obtained by JOINMAP software (Van Ooijen and Voorrips 2001); the linkage groups were numbered according to the reference map of Riaz et al. (2004) and the international agreement achieved within the IGGP (International Grape Genome Program). Potential QTLs for each fruit yield component were detected using MAPQTL5 software (Van Ooijen 2004). Interval mapping analysis was initially performed to find regions with potential QTL effects, and then scored markers in those regions were used as co-factors in multiple QTL models (MQM analysis, also performed with MAQTL5). The threshold level at which a QTL was declared significant was determined by performing 1,000 permutations of the data, which maintained a chromosome-wise type error rate of 0.05 (Churchill and Doerge 1994). The amount of phenotypic variation simultaneously explained by all QTLs found for each continuous variable trait was determined using a stepwise regression analysis (SAS Institute 1988).

Results and discussion

Field trait analysis

The frequency distributions of the yield and fruit yield components are reported for only 1 year (Fig. 1) as these components showed approximately the same distribution for the 3 years of the investigation. For berry size, the weight of the berry is used (Fig. 1) as we detected a high correlation ($r = 0.97$) between berry volume and berry weight in the first year of observations and in other experimental tests. All traits showed a continuous variation, which is typical of quantitative traits, without any differentiation between seedless and seeded genotypes; the berry weight ranged from 1.5 g to 6 g for seedless genotypes and from 2.5 g to 9 g for seeded ones, while the number of berries per cluster ranges from 33 to 240 for the seedless genotypes and from 31 to 158 for the seeded ones. The data were transformed (square-root) to improve the normality and used in all subsequent analyses.

The repeatability, which also set the upper limit to the broad-sense heritability (Falconer 1996), was estimated for each fruit yield component over 3 years (Table 1). These analyses show that the yield components have a low to moderate repeatability, with the number of clusters per vine having the lowest repeatability (0.11) due to it being largely affected by the year environment variations. In-depth information is available in grapevine on the influence of the environmental conditions on bud fruitfulness and, consequently, on the number of clusters (Buttrose 1974; Perez and Kliewer 1990; Mullins et al. 1992). The other fruit yield components, such as the cluster weight, number of berries per cluster and berry weight, show moderate repeatability (Table 1), suggesting that there is some environment influence for

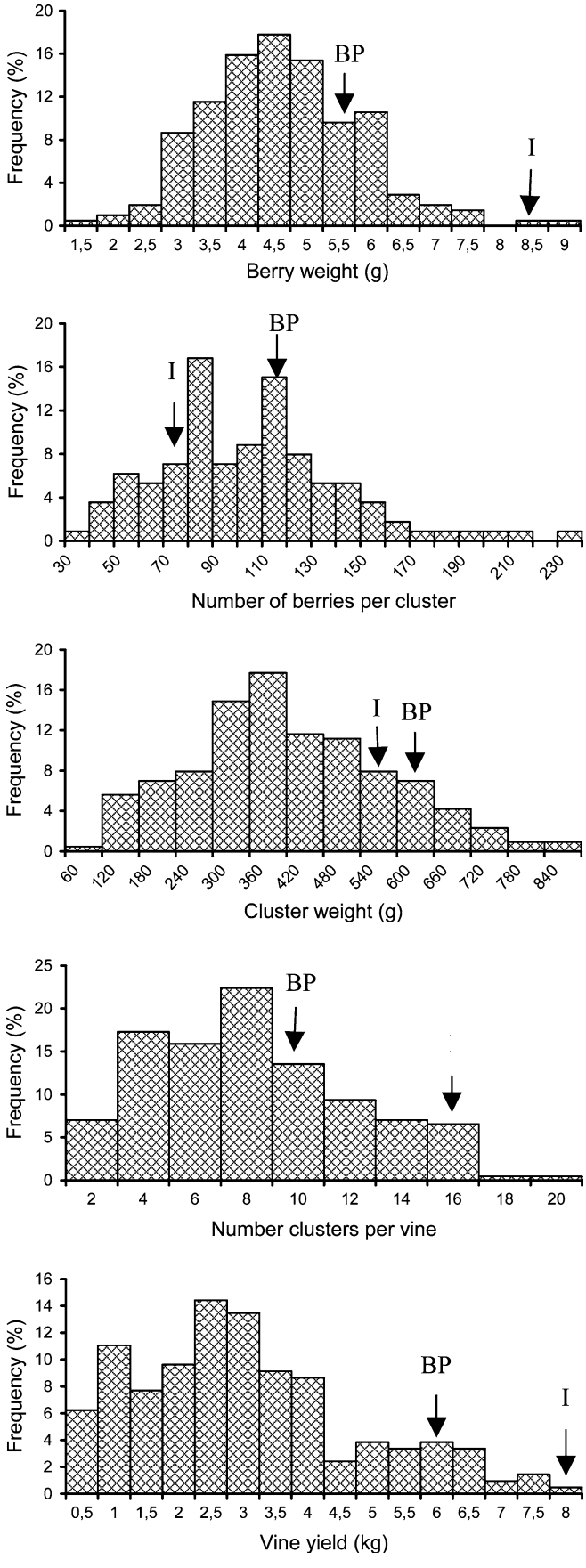

Fig. 1 Frequency distribution of 184 progeny plants for each trait. Parental phenotypes indicated by *arrows*. *I* Italia, *BP* Big Perlon

these traits also, although the degree of environmental influence is variety-dependent.

The differential genotypic sensitivity to year environment variation was estimated by phenotypic correlation of the same trait between years (Falconer and Mackay 1996) minimizing the environmental sources of variation between genotypes through pruning and cluster thinning. Low phenotypic correlations between years (Table 1) were observed for the number of clusters per vine (r ranges from 0.13 to 0.34) and for the number of berries per cluster (r ranges from 0.41 to 0.47), while higher correlation values were observed for the berry weight (r ranges from 0.63 to 0.77). Thus, the genotype × year interaction predominantly affects the number of clusters per vine and the number of berries per clusters; this is due to the differences in sensitivity each genotype shows to yearly climate variations, especially during the fruit bud formation and the berry set, which determine, respectively, the number of clusters per vine and the number of berries per clusters. Other investigators (Ewart et al. 1977; Mullins et al. 1992) have associated the yield variability of some grape varieties to the poor fruit-set caused by environmental factors.

Since genotypes react differently to yearly climate variations, the correlations between fruit yield components were determined in each year (Table 2). Positive correlations were detected between vine yield and number of clusters per vine (r varies from 0.73 to 0.77 in the 3 years) and cluster weight (r varies from 0.48 to 0.70). Thus, vine yield is correlated mainly to the number of clusters per vine and to some extent to the cluster weight. On the other hand, cluster weight is positively correlated to a larger extent with the number of berries per cluster (r ranges from 0.73 to 0.78) and to a less extent with the berry weight (r ranges from 0.36 to 0.52). Other authors (Smart et al. 1982; Dunn and Martin 2000; Lopez-Miranda and Yuste 2004) who have analysed fruit yield components within some grape varieties have reported that the most important trait responsible for cluster weight under normal cultural and climatic

Table 1 Phenotypic correlations between years and repeatability for each trait

Trait	Year	2002	2003	Repeatability
Yield/vine	2003	0.26**		0.15
	2004	0.06 NS	0.34**	
Number of clusters/vine	2003	0.34**		0.11
	2004	0.13 NS	0.28**	
Cluster weight	2003	0.53**		0.47
	2004	0.52**	0.53**	
Number of berries/cluster	2003	0.41**		0.35
	2004	0.44**	0.47*	
Berry weight	2003	0.63**		0.54
	2004	0.77**	0.72*	

*$P \leq 0.05$; **$P \leq 0.01$; NS, not significant

Table 2 Phenotypic correlations between traits in different years

Character	Year	Number of clusters/vine	Cluster weight	Number of berries/cluster	Berry weight
Yield/vine	2002	0.77**	0.48**	0.14 NS	0.15 NS
	2003	0.73**	0.65**	0.58*	0.22*
	2004	0.74**	0.70**	0.51*	0.39**
Number of clusters/vine	2002		−0.09 NS	−0.15 NS	−0.024 NS
	2003		0.10 NS	0.11 NS	−0.07 NS
	2004		0.10 NS	0.09 NS	0.018 NS
Cluster weight	2002			0.78**	0.36**
	2003			0.77**	0.39**
	2004			0.73**	0.52**
Number of berries/cluster	2002				−0.26**
	2003				−0.25**
	2004				−0.15 NS

*$P \leq 0.05$; **$P \leq 0.01$; NS, not significant

conditions is the number of berries per cluster. Conversely, a negative correlation was detected between the number of berries per cluster and berry weight (r varies from −0.15 to −0.26), which has a negative effect on the cluster weight. In fact, the path analysis (Table 3) shows that cluster weight is influenced indirectly either via the number of berries or via berry weight by this negative correlation. Thus, the selection of seedless genotypes with large berries and good cluster weight might be hampered by the negative correlation between the number of berries and the berry weight. Nonetheless, a better evaluation of the genetic relationships between the number of berries and berry weight and other fruit yield components can be obtained by means of the QTL analysis with the objective of searching for the coincidence of QTLs between traits.

QTL analysis

The results of the QTL analysis for the fruit yield components are presented in Table 4. Our results show that there were no stable QTLs across years for each of the components of fruit yield analysed. For the number of clusters per vine, different QTLs were detected in 2003 (*Cn3.1*, LOD score: 3.28; R^2: 7%) and in 2004 (*Cn4.1*, LOD: 4.23; R^2: 10%; *Cn4.2*, LOD: 4.17; R^2: 10%). For cluster weight, the same QTL was detected in 2003 (*Cw3.1*, LOD: 3.01; R^2: 1.3%) and in 2004 (*Cw4.1*, LOD: 3.32; R^2: 6.7%). For the number of berries per vine, several QTLs were detected, but none of these were observed in successive years. The same observations were made for the berry weight. Other investigators have detected stable QTLs for berry weight in table grapes (Doligez et al. 2002) and wine grapes (Fischer et al. 2004); however, the QTLs detected in these investigations were all different. These different results might be due to the different progenies used. In particular, the table grape progeny of Doligez et al. (2002) was derived from two partially seedless parents and included a large number of seedless genotypes with a relative uniform and medium-sized berry, while our progeny, derived from a seeded × seedless cross, showed a much higher variability for berry weight as well as a low repeatability over years. This variability in berry weight in the different progenies might have affected the detection of the QTLs and together with progeny size and heritability might play an important part in explaining the different results. Small sample size and medium-to-low trait heritability might have biased QTL detection (Beavis 1998; Melchinger et al. 2004). Nevertheless, the instability of QTLs over years has been reported in other fruit tree species (Conner et al.1998; Garcìa et al. 2000; Wang et al. 2000; Quilot et al. 2004).

The lack of QTL stability in different years for all of the traits analysed might be due to the presence of different genes or the differential expression of these genes as a result of differential genotypic sensitivity to yearly climate variations. Yearly variations in temperature had a considerable effect on the flowering and

Table 3 Path coefficients showing direct and indirect effects of the number of berries per cluster and berry weight on the cluster weight

Trait	Year	Direct effect[a]	Indirect effect via		Total correlation
			Number of berries/cluster	Berry weight	
Number of berries/cluster	2002	0.94		−0.15	0.79
	2003	0.91		−0.16	0.75
	2004	0.83		−0.10	0.73
Berry weight	2002	0.60	−0.24		0.36
	2003	0.63	−0.23		0.40
	2004	0.63	−0.12		0.51

[a]Residual effect = 0.14, 0.17 and 0.20, respectively, for 2002–2004

Table 4 Characteristics of the detected QTLs for each trait measured in different years

Trait	Year	Linkage group[a]	Parent[b]	QTL[c]	Nearest marker	LOD score	LOD threshold[d]	R^2 (%)[e]
Number of clusters/vine	2003	19	I	*Cn3.1*	*m*CTC *e*ATC9	3.28	2.7	7
	2004	8	BP	*Cn4.1*	VVS4	4.23	2.5	10
		8	BP	*Cn4.2*	VMC7H2	4.17	2.5	10
Cluster weight	2002	12	I	*Cw2.1*	*m*CAC *e*ACA7	3.19	2.6	2.3
	2003	5	BP	*Cw3.1*	*m*CAT *e*AAG13	3.01	2.8	1.3
		16	I	*Cw3.2*	VMC1E11	2.98	2.5	4
	2004	5	BP	*Cw4.1*	*m*CAT *e*AAG13	3.32	2.7	6.7
		17	BP	*Cw4.2*	*m*CTC *e*ATG12	3.02	2.7	4
Number of berries/cluster	2002	8	BP	*Bn2.1*	*m*CAT *e*AAG4	3.72	2.6	5
		12	BP	*Bn2.2*	*m*CTG *e*ATT3	3.12	2.6	7
		17	I	*Bn2.3*	*m*CTG *e*ATC8	3.02	2.8	6
		2	I	*Bn2.4*	VVI055	3.19	2.8	1.2
	2003	5	BP	*Bn3.1*	*m*CAT *e*AAG137	4.09	2.7	4
		7	I	*Bn3.2*	*m*CAT *e*ATT1	3.01	2.7	4.5
	2004	7	BP	*Bn4.1*	VMC7A4	4.25	2.6	9
		7	BP	*Bn4.2*	*m*CAT *e*ATG15	4.25	2.6	1.5
		5	I	*Bn4.3*	*m*CAG *e*ATG15	3.32	2.2	2.8
		7	I	*Bn4.4*	VVMD7	3.02	2.2	5.7
		7	I	*Bn4.5*	VMC16F3	2.83	2.2	4
Berry weight	2002	5	I	*Bw2.1*	*m*CAT *e*ATT2	3.31	3	10
		16	I	*Bw2.2*	*m*CTA *e*AAG5	3.35	3	3
		5	BP	*Bw2.3*	VMC3B9	3.2	2.7	19
	2003	4	BP	*Bw3.1*	VMC7H3	3.13	2.5	5
		13	BP	*Bw3.2*	*m*CAG *e*AAG13	2.95	2.5	2
	2004	20	BP	*Bw4.1*	*m*CAT *e*AAG14	3.19	2.5	5.8
		20	I	*Bw4.2*	*m*CTG *e*AAG3	3.24	2.8	4.8

[a]Linkage group as International Grape Genome Program (*IGGP*)
[b]I, Italia; BP, Big Perlon
[c]QTLs are named using an abbreviation for the trait; the number is used to distinguish QTLs for year and order
[d]Determined by a permutation test at $P \leq 0.05$
[e]Coefficient of determination

berry set of some of the genotypes, affecting QTL stability of the number of berries per clusters and cluster weight. In addition, yearly variations in the amount of rainfall during the development of berries also had an effect on berry weight. On the other hand, the observed differences in QTL detection over years might be explained by alternate bearing due to the difficulty to regulating plant growth and the growth-yield balance of some genotypes, which is not uncommon in fruit tree species. If all these factors are taken into consideration, it is logical to imagine that a large number of genes and different physiological mechanisms might be involved in the determination of each fruit trait in response to yearly environmental variations. Thus, the detection of different QTLs for the same trait should be expected in different years because QTL detection will depend on the environmental conditions of that specific year. This will result not only in an increase in the number of QTLs but will also affect the detection of different QTLs across years for each fruit trait.

From the data presented in Table 4, it is clear that the detected QTLs explain a low percentage of the phenotypic variance for each fruit yield component. The QTLs with the highest R^2 values were detected for berry weight (*Bw2.3* and *Bw2.1* with $R^2 = 19\%$ and 10%, respectively). Only a few other QTLs with a relatively high R^2 (about 9–10%) were observed: for number of berries per cluster (*Bn4.1*) and for number of clusters per vine (*Cn4.1* and *Cn4.2*). However, most of the detected QTLs had low R^2 values. The main explanation for the low percentage of phenotypic variance accounted for by the detected QTLs is the large number of QTLs with small effect; most of these remain undetected and will not contribute to an explanation of the phenotypic variance. Consequently, estimates of QTL number should be considered as lower bounds. In addition, part of the unexplained variance might be attributable to the interaction between QTLs, which was not determined in this experiment. Limitations in QTL statistical methodology and in the experimental designs might lead to biased results in the estimation of both QTL number and the phenotypic variance explained by the detected QTLs. Sample size and heritability are the most relevant factors in QTL detection. As the variance explained by a QTL decreases, the number of progeny must increase, as suggested by Lander and Bolstein (1989). When the trait heritability is low, the size of a population must be relatively large—100–1,000 individuals (Staub et al.1998). Simulation and experimental studies (Beavis 1998; Melchinger et al. 2004) have shown that the results for the number of QTLs and for the proportion of explained variance by the detected QTLs are biased when a small sample size and a medium-to-low trait heritability are used. This underscores the importance of interpreting QTL mapping results with caution when the sample size is not large and there is a medium-to-low heritability or repeatability.

In our investigation, we also analysed the relationships between fruit yield components by looking for the simultaneous expression of QTLs between correlated traits. In the past, associations between fruit traits in grapevines have usually been tested by comparing either unrelated genotypes or various treatments within a single genotype. Using these approaches, it is difficult to show if two traits are causally related or if they merely vary in association. By identifying coincident QTLs between traits, it might be hypothesised that these traits are controlled by closely linked genes or a unique gene with pleiotropic effect. This is important in plant breeding because trait selection can be affected. In our study, even though berry weight and number of berries per cluster were negatively correlated (Tables 2, 3), we did not detect any coincidence of the QTLs (Table 4) between these traits. This might indicate that the genes controlling berry weight and the number of berries per cluster function independently of each other. If this were to be the case, there is the possibility of selecting seedless genotypes with large berries without affecting the cluster weight. Nonetheless, this needs to be confirmed in follow-up experiments because the lack of QTL coincidence between the number of berries and berry weight might be due to other factors—sample size, heritability, etc.—which might influence the QTL identification.

In conclusion, this study draws a complex picture of the genetic architecture of the fruit yield components of grapevine due to the perennial nature of this species, which has to adapt to yearly variations in climate. The detection of different QTLs, the low percentage of the phenotypic variance explained by the detected QTLs and QTL instability over years for each fruit yield component confirm the quantitative genetic model of the yield components in grapevine. In addition, the negative phenotypic correlation between berry weight and number of berries per cluster, which might hamper the possibility of selecting for seedless genotypes with large berries without affecting the cluster weight, is not supported at the molecular level because of the lack of QTL coincidence between these traits. Nevertheless, this needs to be substantiated in future experiments because other factors such as sample size and heritability might influence the identification of QTLs.

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References

Ballester J, Socias I Company R, Arus P, De Vicente MC (2001) Genetic mapping of a major gene delaying blooming in almond. Plant Breed 120:268–270

Beavis WD (1998) QTL analyses: power, precision and accuracy. In: Paterson AH (ed) Molecular dissection of complex traits. CRC Press, Boca Raton, pp 145–162

Buttrose MS (1974) Climatic factors and fruitfulness in grapevines. Hortic Abstr 44:319–326

Conner PJ, Brown SK, Weeden NF (1998) Molecular-marker analysis of quantitative traits for growth and development in juvenile apple trees. Theor Appl Genet 96:1027–1035

Churchill GA, Doerge RW (1994) Empirical threshold values for quantitative trait mapping. Genetics 138:963–971

Dalbò MA, Ye GN, Weeden NF, Wilcox WF, Reich BI (2001) Marker-assisted selection for powdery mildew resistance in grapes. J Am Soc Hortic Sci 126:83–89

Dirlewanger E, Moing A, Rothan C, Svanella L, Pronier V, Guye A, Plomion C, Monet R (1999) Mapping QTLs controlling fruit quality in peach (*Prunus persica* (L.) Batsch). Theor Appl Genet 98:18–31

Doligez A, Bouquet A, Danglot Y, Lahogue F, Riaz S, Meredith CP, Edwards KJ, This P (2002) Genetic mapping of grapevine (*Vitis vinifera* L.) applied to the detection of QTLs for seedlessness and berry weight. Theor Appl Genet 105:780–795

Dunn GM, Martin SR (2000) Do temperature conditions at budburst affect flower number in *Vitis vinifera* L. cv. Cabernet sauvignon?. Aust J Grape Wine Res 6:116–124

Ewart A, Kliewer WM (1977) Effects of controlled day and night temperatures and nitrogen on fruit-set, ovule fertility, and fruit composition of several wine grape cultivars. Am J Enol Vitic 28:88–95

Falconer DS, Mackay TDC (1996) Introduction to quantitative genetics. Prentice Hall, Pearson Education, Harlow

Fanizza G, Chaabane R, Lamaj F, Ricciardi L (2003) AFLP analysis of genetic relationships among aromatic grapevines (*Vitis vinifera*). Theor Appl Genet 107:1043–1047

Fischer BM, Salakhutdinov I, Akkurt M, Eibach R, Edwards KJ, Topfer R, Zyprian EM (2004) Quantitative trait locus analysis of fungal disease resistance factors on a molecular map of grapevine. Theor Appl Genet 108:501–515

Garcìa MR, Asins MJ, Carbonell EA (2000) QTL analysis of yield and seed number in *Citrus*. Theor Appl Genet 101:487–493

Grando MS, Bellin D, Edwards KJ, Pozzi C, Stefanini M, Velasco R (2003) Molecular linkage maps of *Vitis vinifera* L. and *Vitis riparia* Mchx. Theor Appl Genet 106:1213–1224

King GL, Maliepaard C, Lynn JR, Alston FH, Durel CE, Evans KM, Griffon B, Laurens F, Manganaris AG, Schrevens E, Tartarini S (2000) Quantitative genetic analysis and comparison of physical and sensory descriptors relating to fruit flesh firmness in apple (*Malus pumila* Mill.). Theor Appl Genet 100:1074–1084

Lahogue F, This P, Bouquet A (1998) Identification of a codominant scar marker linked to the seedlessness character in grapevine. Theor Appl Genet 97:950–959

Lander ES, Bolstein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199

Li CC (1956) The concept of path coefficients and its impact on population genetics. Biometrics 12:190–210

Lòpez-Miranda S, Yuste J (2004) Influence du Nombre de Fleurs par grappe pourcentage de nouaison et poids de la baie sur le poids de la grappe du cèpage Verdejo (Vitis vinifera L.). J Int Sci Vigne Vin 38:41–47

Melchinger AE, Utz HF, Schon CC (2004). QTL analyses of complex traits with cross validation, bootstrapping and other biometrical methods. Euphytica 137:1–11

Mullins MG, Bouquet A, Williams LE (1992) Biology of the grapevine. Cambridge University Press, Cambridge

Perez J, Kliewer WM (1990) Effect of shading on bud necrosis and bud fruitfulness of Thompson Seedless grapevines. Am J Enol Vitic 41:168–175

Quilot B, Wu BH, Kervella J, Gérard M, Foulogne M, Moreau K (2004) QTL analysis of qualitative traits in an advanced backcross between *Prunus persica* cultivars and the wild relative species *P. davidiana* Theor Appl Genet 109:884–897

Riaz S, Dangl GS, Edwards KJ, Meredith CP (2004) A microsatellite marker based framework linkage map of *Vitis vinifera* L. Theor Appl Genet 108:864–872

SAS Institute (1988) SAS language guide for personal computers, 6.03 edn. Cary, N.C.

Smart RE, Shaulis NJ, Lemon ER (1982) The effect of Concord vineyard microclimate on yield. II. Interrelations between microclimate and yield expression. Am J Enol Vitic 33:109–116

Staub JE, Serquen FC, Gupta M (1996) Genetic markers, map construction, and their application in plant breeding. HortScience 31:729–741

Striem MJ, Ben-Hayyim G, Spiegel-Roy P (1996) Identifying molecular genetic markers associated with seedlessness in grape. J Am Soc Hortic Sci 121:758–763

Van Ooijen JW (2004) MAP QTL5, software for the mapping of quantitative trait loci in experimental populations. Kyazma B.V., Wageningen, The Netherlands

Van Ooijen JW, Voorrips RE (2001). JOINMAP 3.0, software for the calculation of genetic linkage maps. Plant Research International, Wageningen, Netherlands

Wang D, Karle R, Iezzoni AF (2000) QTL analysis of flower and fruit traits in sour cherry. Theor Appl Genet 100:535–544