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A microsatellite marker based framework linkage map of *Vitis vinifera* L.

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Abstract We have constructed a framework linkage map based on microsatellite markers for *Vitis vinifera* L., the European wine grape. The mapping population consisted of 153 progeny plants from a cross of *Vitis vinifera* cvs. Riesling × Cabernet Sauvignon. One hundred fifty-two microsatellite markers and one polymorphic EST marker have been mapped to 20 linkage groups (2*n*=38). The map covers 1,728 cM with an average distance between markers of 11.0 cM. Estimates of genome size, expected genome coverage, and observed genome coverage were determined with 135–140 markers. Genome length estimates differed between paternal and maternal data sets. Observed approximate genome coverage was 65% versus an expected coverage of 90%. Meiotic recombination rates were not significantly different between maternal and paternal parents. This map has been adopted as a reference map for the International Grape Genome Program.

Introduction

An ancient crop, the European wine grape *Vitis vinifera* L., is today grown throughout the temperate and tropical regions of the world for fresh fruit, dried fruit, juice, and wine. In contrast to families such as Solanaceae, Leguminoseae, Rosaceae, and Gramineae, *Vitis* is the only agriculturally important genus in the family Vitaceae. Because the genus is taxonomically isolated from other cultivated plants, most knowledge of the grape genome must come from studies of *Vitis* itself. The relatively small grape genetics research community has recently formed the International Grape Genome Program (IGGP) for the purpose of cooperation and coordination in increasing knowledge of the grape genome (http://www.vitaceae.org).

Among the interests of the IGGP is a reference linkage map to harmonize linkage groups resulting from individual mapping projects and as a resource for physical mapping. Such a map is also useful for targeting genomic regions for more intensive mapping efforts, such as for localizing quantitative trait loci (QTLs) and for marker-assisted selection. Because microsatellite markers are robust markers that are readily shared among laboratories, the grape genetics community worked cooperatively to develop a large number of these markers in the Vitis Microsatellite Consortium (VMC), a cooperative effort of 20 research groups in ten countries that was coordinated by AgroGene S.A. in Moissy Cramayel, France.

Of several cultivated *Vitis* species, *V. vinifera* is by far the most widely grown. Several other cultivated species in the genus are grown for fruit in regions not climatically suitable for *vinifera* or used as rootstocks.

Several grape linkage maps have previously been published, but most of the mapping populations have been interspecific hybrids, often chosen because the parents are sources of disease resistance (e.g., Lodhi et al. 1995; Dalbó et al. 2000; Grando et al. 2003; Zyprian et al. 2003). The recently published map by Doligez et al. (2002) employed a *vinifera* × *vinifera* cross, but the map includes only 44 microsatellite markers, consisting largely of AFLP markers that are not easily transferred between laboratories.

Our map is based on a *vinifera* × *vinifera* cross. Both parents are major cultivars that are grown in many countries. ‘Riesling’ (prime name ‘Riesling weiss’), one of the world’s most important white wine varieties, is especially important in wine-producing regions with colder climates, such as Germany, Canada, and the

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northeastern United States. 'Cabernet Sauvignon' is one of world's most widely distributed red wine varieties, grown throughout Europe and in all the New World wine-producing countries. Furthermore, 'Cabernet Sauvignon' has been selected by the IGGP as the target cultivar for cooperative efforts on physical mapping.

Materials and methods

Mapping population

The mapping population consists of 153 progeny plants from a 1994 cross between *V. vinifera* cvs. Riesling and Cabernet Sauvignon (M.A. Walker and C.P. Meredith, unpublished). Among economically important cultivars in the species, the parents are genetically relatively distant (Bowers 1998) and differ significantly in fruit morphology and flavor.

DNA isolation

DNA was extracted from young leaves and shoot tips of plants in the vineyard of the Department of Viticulture and Enology, University of California, Davis, by a modified CTAB method as previously described (Bowers et al. 1993) except that the protocol was performed at approximately 1/20th scale to reduce it to a volume suitable for microcentrifuge tubes.

Markers

The microsatellite markers used included some that have been previously published (Thomas and Scott 1993; Bowers et al. 1996, 1999) and many that were developed within the VMC (Sefc et al. 1999; Di Gaspero et al. 2000; and others not yet published) (Table 1). Four microsatellite markers derived from ESTs (Scott et al. 2000), and one polymorphic grape EST marker (obtained from Dr. Douglas Adams, Department of Viticulture and Enology, University of California, Davis) were also used. Primers were synthesized by Operon Technologies (Alameda, Calif., USA).

Amplification conditions

PCR amplifications were performed in a Perkin Elmer Model 480 thermal cycler in 20-μl reactions consisting of 10-ng template DNA, 10 pmol of each primer, 2.5 mM of each NTP, 2 μl 10× gold PCR buffer (Perkin Elmer), 0.5 unit AmpliTaq Gold DNA polymerase (Perkin Elmer), and 2 mM $MgCl_2$ solution. Amplification conditions were optimized individually for each marker. All markers were tested on a set of six DNA samples (including the 'Riesling' and 'Cabernet Sauvignon' parents) at two annealing temperatures (56° and 52°C), keeping all other conditions of the amplification protocol constant (2 min at 94°C; 40 cycles of 1 min at 92°C, 1 min at 56°C, and 2 min at 72°C; and 7 min at 72°C). Primers failing to amplify at 56° or 52°C were further tested at three more annealing temperatures (61°, 58°, and 50°C). All amplifications were confirmed by running 5.0 μl of the PCR reaction product on 2% agarose gels.

Amplification products were separated on denaturing 6% polyacrylamide sequencing gels and visualized by silver staining with a commercial kit (Promega, Madison, Wis., USA). Product sizes were determined by comparison to a standard sequencing reaction in adjacent lanes on the same gel. Only informative markers were used on the entire mapping progeny. For EST-derived microsatellite markers, reaction and cycling conditions were as described previously (Scott et al. 2000).

Scoring and data organization

Linkage analysis was performed with both MAPMAKER/EXP 3.0 (Lincoln et al. 1992) and JOINMAP 2.0 (Stam 1993; Stam and Van Ooijen 1995) and the data were organized accordingly. For MAPMAKER, two independent data sets were generated that separately contained the meiotic segregation information from each parent. In the absence of phase information, each segregating locus was paired with a dummy locus, resulting in a double data set (double pseudo-testcross strategy, Grattapaglia and Sederoff 1994). Data were thus combined into a single set in which genotypes were coded with two characters representing the two alleles (one from each parent).

Linkage analysis

For each parental data set, all markers were individually evaluated by the chi-square method to detect deviation of gametic segregation from the Mendelian 1:1 ratio ($P \leq 0.05$). Preliminary analysis for each parent was carried out with MAPMAKER. Linked markers were placed into groups using the "group" command with LOD$\geq$3.0, 4.0, and 5.0 with both Haldane and Kosambi mapping functions (Haldane 1919; Kosambi 1944). Linkage groups obtained from the doubled data set were then divided into two symmetrical sets of groups, and one set was chosen for further detailed analysis (Lodhi et al. 1995). The "first order" and "compare" commands were used to determine the probable order of all markers in each linkage group, which was further verified with the "ripple" command. These preliminary linkage groups were then visually aligned via markers common to both parents and, finally, unified into sets of homologous linkage groups.

The integrated linkage analysis to obtain the consensus map was performed with JOINMAP (LOD 5.0, recombination frequency 0.499). The "fixed sequence" command was used to determine the order of markers relative to the order obtained from the initial MAPMAKER analysis. Map units in centiMorgans were derived from the Kosambi mapping function.

Table 1 Origins of the grape microsatellite markers used to construct the map

Source	Total markers	Amplified in our lab	Useful for this map	Reference
CSIRO, Australia	4	4	4	Thomas and Scott 1993
University of California, USA	25	24	17	Bowers et al. 1996, 1999
University of Agriculture, Vienna, Austria	19	18	11	Sefc et al. 1999
University of Crete, Greece	11	9	9	Lefort and Roubelakis-Angelakis 2000
University of Udine, Italy	16	8	8	Di Gaspero et al. 2000
Southern Cross University, Australia	13	7	4	Scott et al. 2000
Vitis Microsatellite Consortium	327	292	128	Unpublished[a]
Total	415	362	181	

[a] Unpublished markers will become available to the public before the end of 2004

Comparison of meiotic recombination rates among parents

Eighty-one markers common to both parents were selected in order to compare maternal and paternal recombination rates. For these markers, two data sets were prepared: one in which the maternal parent was coded as homozygous and the paternal parent was coded as heterozygous and a second data set in which the coding was reversed. Parental maps were re-calculated from those two data sets with JOINMAP. The "fixed sequence" command was used to determine the order of markers relative to the order obtained from the initial MAPMAKER analysis.

Fifty-seven pairs of linked markers were selected from both maps. Two point estimates of recombination and LOD scores indicating the likelihood of linkage were calculated for both parents. Chi-square values for differences in maternal and paternal recombination frequency were calculated by using a 2×2 contingency table for each marker pair. Standard deviation (SD) and standard error (SE) were calculated by standard statistical methods. A global test of difference in mean maternal and paternal recombination frequencies was performed from averages of marker pair intervals and standard deviation by the *Z*-test statistic.

Estimation of genome length and map coverage

The estimation of genome length was carried out by the method of moment estimator, $E(G)=M(M-1)X/K$ (Hulbert et al. 1988), where M is the number of markers, X is the maximum observed map distance among the locus pairs above a threshold LOD Z (Chakravarti et al. 1991), and K is the number of locus pairs having LOD values at or above Z. The values used for Z were 3, 4, and 5. The values of X and K were obtained from the inspection of a list of values generated by the "lods" function of MAPMAKER, using both the Haldane and Kosambi mapping functions. The confidence interval for G, $I_{\alpha}(G)$, was calculated from the equation

$$I_{\alpha}(G) = \hat{G}\left(1 \pm n_{\alpha}K^{-\frac{1}{2}}\right)^{-1} \quad (1)$$

where n_{α}=1.96 for an α of 5% (Gerber and Rodolphe 1994). The expected genome map coverage percentage, $E(C_n)$, was calculated from the equations

$$E(C_n) = 1 - P_{1,n} \quad (2)$$

and

$$P_{1,n} = \frac{2R}{n+1}\left[\left(1-\frac{X}{2G}\right)^{n+1} - \left(1-\frac{X}{G}\right)^{n+1}\right] + \left(1-\frac{RX}{G}\right) \times \left(1-\frac{X}{G}\right)^{n} \quad (3)$$

(Bishop et al. 1983) where R is the number of chromosomes, n is the number of markers, and X is the maximum centiMorgan distance when Z=5. Both Haldane and Kosambi mapping functions were used to calculate $E(G)$.

The observed genome map coverage, $C_{o,}$ was calculated from the equation

$$C_o = G_F + X(L - R) \quad (4)$$

where G_F is the total centiMorgan length of the framework map, X is that used for determining $E(C_n)$, and L is the total number of linkage groups, pairs, and unlinked loci (Nelson et al. 1994).

Results

Markers

Of the 362 primer pairs that amplified successfully, 181 were useful for this map (Table 1). Several markers that produced three to five bands per parent, suggesting that they amplified more than one locus, were excluded from the analysis. Other markers were excluded because they were either homozygous in both parents or difficult to score because of excessive stutter (results not shown). Some markers produced one band when amplified at a high annealing temperature, but two bands at a lower temperature. These markers were amplified at the most informative temperature.

Of the 181 microsatellite markers used on the entire progeny, 35 were fully informative (ab × cd), 73 had three alleles (ab × ac), and 73 had two alleles [68 (aa × ab) or (ab × aa) and 5 (ab × ab)]. Chi-square analysis indicated a distorted segregation ratio for 23 markers—15 (11%) for 'Cabernet Sauvignon' and 8 (6%) for 'Riesling' (data not shown). All markers were used for the MAPMAKER analysis, except those for which both parents were heterozygous for the same alleles (ab × ab). For JOINMAP analysis, all polymorphic SSR markers were used (markers with 1:1, 1:2:1 and 1:1:1:1 segregation patterns).

Construction of parental maps

There was no difference in the number of mapped markers at LOD 3.0, 4.0, and 5.0 for both mapping functions; therefore, the complete analysis to determine the relative order of markers in each group was carried out only at LOD 5.0 with both mapping functions.

The maternal ('Riesling') map includes 140 markers in 20 linkage groups (19 groups expected, $2n$=38) with 2–15 markers per group (Table 2). The largest gap on the 'Riesling' map is 44 cM between VMC2e7 and VMC2e9a in group 3 (Fig. 1). The average distance between adjacent markers is 12.0 cM with the Haldane mapping function and 10.5 cM with the Kosambi mapping function.

The paternal ('Cabernet Sauvignon') map consists of 135 markers in 21 groups with 2–11 markers per group. The largest gap on the 'Cabernet Sauvignon' map is 43.3 cM between VMC1g3.2 and VMC8g6 in group 5 (Fig. 1). The average distance between adjacent markers is 12.2 cM with the Haldane mapping function and 10.6 cM with the Kosambi mapping function.

Table 2 Comparison of parental and consensus maps

Mapping software	Map	Number of linkage groups	Number of markers	
			Linked	Unlinked
MAPMAKER	'Riesling'	20	140	4
	'Cabernet Sauvignon'	21	135	4
JOINMAP	Consensus map	20	181	0

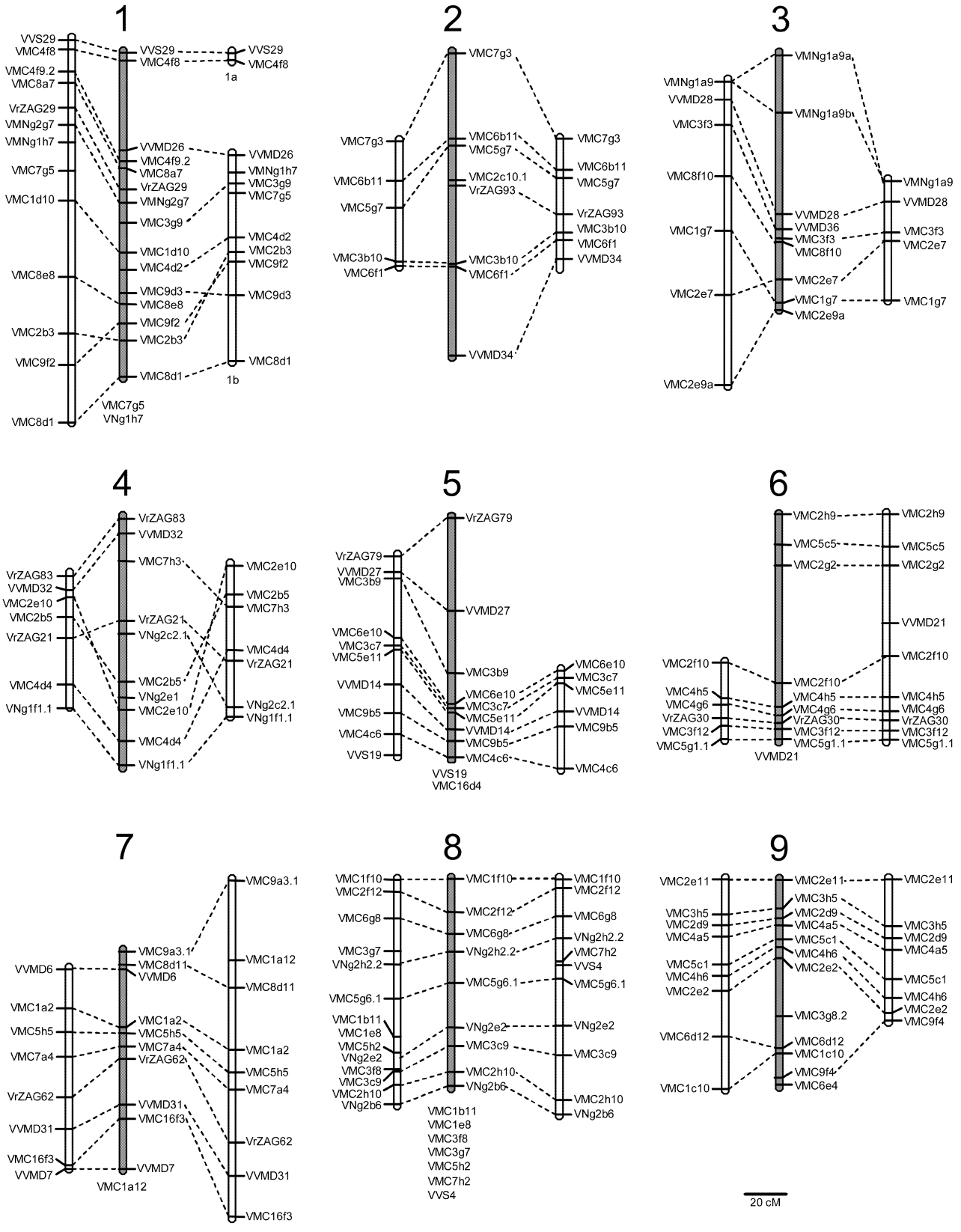

Fig. 1 Linkage map of *Vitis vinifera* 'Riesling' × 'Cabernet Sauvignon'. For each linkage group, the parental maps are shown on the *left* ('Riesling') and *right* ('Cabernet Sauvignon') and the consensus map is in the *center*. Markers common to parental and consensus maps are indicated by *dashed lines*. Linked, but unmapped, markers are listed below each group

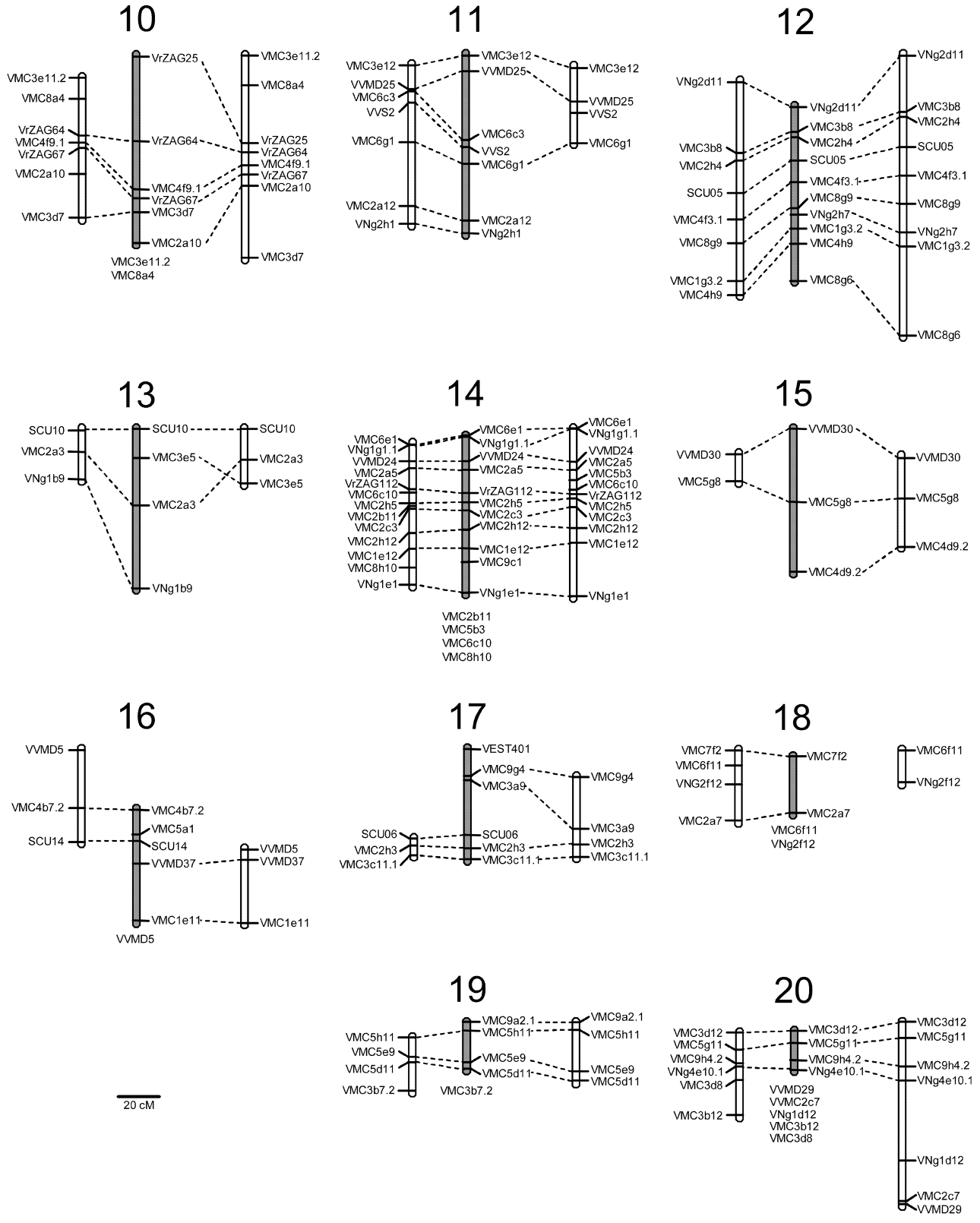

Fig. 1 (continued)

Table 3 Test of deviation between maternal and paternal recombination rates (*SD* standard deviation, *SE* standard error)

Parent	Number of intervals	Mean recombination frequency	SD	SE	*Z*- test
Maternal	57	10.20	6.24	0.81	0.87 ns
Paternal	57	11.37	8.06	1.05	–

Table 4 Estimated genome length and expected and observed map coverage with Haldane and Kosambi mapping functions

	'Riesling'	'Cabernet Sauvignon'	Mean	Consensus map
Number of meioses	153	153	–	–
Number of loci	140	135	–	153
Haldane (*Z*=5.0)				
K [a]	396	334	–	–
X [b]	49.0	44.7	–	–
Estimated genome length (cM)	2,374	2,385	2,379	–
Confidence interval (95%)	2,165–2,633	2,154–2,671	2,157–2,652	–
Expected genome map coverage	91%	89%	90%	–
Observed genome map coverage	1,664	1,634	1,649	1,882
	70%	68%	69%	–
Kosambi (*Z*=5.0)				
K	402	336	–	–
X	44.0	43.3	–	–
Estimated genome length (cM)	2,130	2,331	2,230	–
Confidence interval (95%)	1,940–2,361	2,106–2,610	2,023–2,485	–
Expected genome map coverage	91%	89%	90%	–
Observed genome map coverage	1,469	1,431	1,450	1,728
	69%	61%	65%	–

[a] Number of pairs at LOD threshold *Z*
[b] Maximum distance between markers

Of the 93 markers common to both parental maps, all are co-linear except for three pairs (VMC1g7 and VMC2e7 in group 3, VrZAG21 and VMC4d4 in group 4, and VrZAG112 and VMC6c10 in group 14). Group 21 of 'Cabernet Sauvignon' showed homology to group 1 of 'Riesling' and so was designated "1a" (Fig. 1).

Construction of the consensus map

The consensus map was developed with 181 markers at LOD 5.0 threshold with the Kosambi mapping function (Table 2). The markers formed 20 linkage groups consisting of 152 mapped microsatellite markers, one mapped EST marker and 28 linked but unmapped microsatellite markers (Fig. 1). Linkage groups were numbered according to their length in centiMorgans. The mapped microsatellite markers span 1,728 cM with an average distance between markers of 11.0 cM. With the exception of four pairs of markers, in groups 1, 3, 4, and 10, respectively, marker order on the consensus map was the same as on the parental maps (Fig. 1).

Comparison of parental meiotic recombination rates

Of the 57 pairs of linked markers in which parental recombination rates were compared, statistically significant ($P \leq 0.05$) differences were observed in only three. Recombination was higher in the maternal parent for two pairs (VMC9f2-VMC2b3 in group 1 and VMC6b11-VMC5g7 in group 2) and higher in the paternal parent for the pair VMC3c9-VMC2h10 in group 8. Recombination rates were not significantly different for the other marker pairs. The overall mean recombination rate was higher in the paternal parent but the difference was not significant (Table 3).

Genome length

Estimates of genome length for both parents are shown in Table 4. The average estimated total length is 2,379 cM and 2,230 cM for the Haldane and Kosambi mapping functions, respectively. The average estimated genome coverage is 90% with both mapping functions. The average observed coverage is 69% and 65% with the Haldane and Kosambi functions, respectively (Table 4).

Discussion

Because microsatellite markers can be readily used across different mapping populations (Powell et al. 1996), this map (hereafter referred to as the "R × CS map") is a useful resource from which markers can be selected for other mapping projects and as the basis for an eventual high-density consensus map. The high-density map

required for the fine resolution of QTLs is prohibitively expensive for any one group to develop, but a common marker system facilitates pooling of information from different mapping populations into an integrated consensus map, as has been done in *Arabidopsis*, soybean, and pine (Hauge et al. 1993; Cregan et al. 1999; Mitchell et al. 1999).

Marker order on the consensus map differed from the parental maps for four marker pairs in four different linkage groups. We speculate that the order differences might be related to differences in recombination frequency in some regions, although parental recombination differences were significant for only one of those four groups (group 1). Significant recombination differences were also observed between marker pairs in groups 2 and 8, but marker order in those groups was consistent between the parental and consensus maps (Fig. 1). The increased fragmentation observed in the paternal map (21 linkage groups of which four contained only two or three markers) might also be related to the slightly higher, albeit non-significant, overall recombination frequency in the male parent.

Markers segregating in only one parent might also contribute to differences in marker order. For example, group 8 includes eight unmapped markers, of which six segregate only in 'Riesling' and two only in 'Cabernet Sauvignon'. When the marker order obtained from the maternal and paternal maps was used as the fixed order for the consensus map, it was not possible to establish a comparable marker order for this group. However, when all markers not common to both parents were removed, a comparable marker order could be established for the consensus map. In group 20, two groups of markers were separated by a gap greater than 50 cM. We retained the group that included markers common to both parents, leaving five unmapped markers.

The non-uniform marker distribution in many of the linkage groups (Fig. 1) could be a consequence of uneven distribution of recombination or to non-random sampling of the genome. The latter is unlikely, however, because in general, microsatellite sequences are randomly distributed among coding and non-coding areas of the genome; furthermore, the microsatellite markers used here were developed from five different genomic libraries [Thomas and Scott 1993; Bowers et al. 1996, 1999; Sefc et al. 1999; and two VMC libraries (K. Edwards, unpublished)]. Clustering of markers at the ends of groups 5 and 6 was also observed (Fig. 1), as has been previously noted in grape by Lodhi et al. (1995) and Dalbó et al. (2000). This is consistent with studies in tomato and *Drosophila* that showed suppressed recombination at the telomeres of some chromosomes (Tanksley et al. 1992; Lefevre 1970).

Heterogeneity in recombination throughout the genome has practical implications. High-resolution genetic maps are much easier to develop for regions of higher recombination. Mapping areas of suppressed recombination, on the other hand, requires much larger progeny sizes to allow the observation of infrequent crossover events necessary for constructing detailed genetic maps (Tanksley et al. 1992).

The genetic map for the maternal parent showed slightly greater coverage than the paternal map (Table 4), but this may be unrelated to sex. Our map suggests the presence of recombination hot spots in both parents, so sex-independent genetic background may influence recombination events. In other plants, however, meiotic recombination differences between the parents are well established. In maize and *Arabidopsis*, for example, male parents have higher recombination rates than females (Robertson 1984; Vizir and Korol 1990). In tomato, however, female parents have higher recombination rates (de Vincente and Tanksley 1991). For coniferous tree species, the recombination rate is 40% greater in male gametophytes and extensive data suggest that the difference is sex-dependent (Moran et al. 1983; Groover et al. 1995). Among angiosperm tree species, Hemmat et al. (1994) reported high recombination rates for males in apple. In grape, Lodhi et al. (1995) observed approximately 280 cM greater map length for the male and concluded that the difference was due to higher recombination rate in the male.

The small differences in meiotic recombination frequency between parents were also evident from the estimates of genome length. The paternal segregation data produced slightly longer estimates of genome length than the maternal data (Table 4).

The Kosambi mapping function takes into consideration interference from other crossover events. Haldane, on the other hand, ignores the interference of other crossovers, resulting in an overestimation of the distance between markers and the total distance covered. Observed genome coverage was also greater with the Haldane mapping function, where 137 markers covered about 69% of the genome versus 65% with the Kosambi function (Table 4). This suggests that 200–250 microsatellite markers could theoretically provide coverage of the whole genome.

Co-dominant microsatellite markers can provide good coverage of the *Vitis* genome with a smaller number of markers than dominant markers of other types. Lodhi et al. (1995) reported coverage of 1,300 cM with 443 RAPD markers, Doligez et al. (2002) reported 1,002 cM with 250 AFLP and 44 SSR markers, and Grando et al. (2003) observed 1,639 cM with 312 AFLP markers and 39 microsatellite markers. By contrast, the consensus map presented here covered 1,728 cM with only 152 microsatellite markets and one polymorphic EST marker (Table 4).

With respect to linkage groups, considerable agreement exists between the R × CS map and several other *Vitis* maps. The 38 microsatellite markers shared with the MTP3140 consensus map of Doligez et al. (2002), produced from a cross between two *V. vinifera* breeding lines, are in the same linkage groups except that our groups 13 and 18 are not represented. A *V. vinifera* 'Syrah' × 'Grenache' consensus map produced by the same group (Roux et al. 2002) has 101 markers in

common with the R × CS map, and all are in the same linkage groups, except that our group 13 is not represented on their map. One group shares 12 markers, one shares 11, and 12 additional groups share at least four markers.

The two parental maps produced from a *V. vinifera* 'Moscato bianco' × *V. riparia* cross by Grando et al. (2003) share 40 markers with our map. The linkage groups are consistent for all but one marker, Scu05, which is in our group 12, but on their map is linked to markers that are in our group 14.

Only 14 markers are shared with the Dalbó et al. (2000) map. Nine of those markers fall into three linkage groups of two or more, and all three are consistent with our groups. However, their group I contains two markers (VVS4 and VVS19) that are not linked on our map. The population used for the Dalbó map was a cross between two interspecific hybrids, and this complex genetic background may have influenced recombination frequencies. Inversions and other chromosomal variations that differentiate species are known to cause regional suppression of meiotic recombination and thus clustering of markers on a linkage map resulting in less overall coverage of the genome (Tanksley et al. 1992).

Marker order is less consistent among the maps. Of the six groups on the MTP3140 map (Doligez et al. 2002) that share at least three mapped markers with the R × CS map, marker order is consistent for four groups (R × CS groups 2, 3, 8, and 11). On the 'Syrah' × 'Grenache' map (Roux et al. 2002), marker order is the same for only seven of the 15 comparable groups (groups 2, 4, 8, 16, 17, 19, and 20) and similar for one other (group 3). The number of comparable groups is too small for marker order comparisons with the Dalbó and Grando maps. The inconsistencies in marker order among the grape maps produced to date reflect the limitations inherent in the small population sizes on which the maps are based and the statistical method by which the segregation data are combined. Pooling of segregation data from several segregating populations may lead to a more accurate integrated map.

In August 2002, the map presented here was adopted as a reference map by the IGGP (http://www.vitaceae.org). The map was made possible by the existence of the VMC, which provided a platform for rapid exchange of information among the grape genetics community and resulted in the development of a large number of grape microsatellite markers. Although most of these markers are currently restricted to members of the Consortium, they will become publicly available by the end of 2004.

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