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A reciprocal translocation between 'Garfi' almond and 'Nemared' peach

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Abstract A map with 51 markers (46 RFLPs and five isozymes) was constructed using an interspecific F_2 population between 'Garfi' almond (*Prunus amygdalus* Batsch.) and 'Nemared' peach [*Prunus persica* (L.) Batsch.]. This map was developed by selecting markers covering most of the distance of the eight linkage groups from previously constructed *Prunus* maps. The markers studied in this population mapped to seven linkage groups instead of the eight expected in *Prunus*. Markers belonging to groups 6 and 8 in previous maps formed a single group in the 'Garfi'×'Nemared' F_2 and several marker pairs placed in different groups in other maps exhibited tight linkages. The study of pollen fertility and chromosome behavior during meiosis in the F_1 generation allowed us to confirm the hypothesis that a reciprocal translocation exists between 'Garfi' and 'Nemared'. Based on independent evidence of linkage between markers and pollen fertility data in the F_2 population, we concluded that the breakpoint of the reciprocal translocation was placed between markers AC50 and AG26A in group 6 and between markers AG112A and FG230A in group 8.

Keywords *Prunus* · Mapping · Reciprocal translocation · RFLPs · Isozymes

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Introduction

The use of molecular markers for map construction and marker-assisted selection in *Prunus* fruit species began in the mid 1990s. Since then many maps have been constructed using various kinds of markers (Baird et al. 1996; Dirlewanger et al. 1998; Lu et al. 1998). One of them (Joobeur et al. 1998), constructed entirely with RFLP and isozyme markers in an almond×peach F_2, has an average density of 2.0 cM/marker and was considered to be saturated. A subset of markers can be selected from saturated maps to cover the whole genome at regular intervals in other populations segregating for different traits (Tanksley et al. 1989). Taking the map constructed by Joobeur et al. (1998) as a reference, 51 markers were selected covering the eight linkage groups of *Prunus* to construct a map in the interspecific F_2 population between the almond rootstock 'Garfi' and the peach rootstock 'Nemared' (the G×N population). This population segregates for various characters of breeding interest, including root-knot nematode resistance, that will be genetically analyzed with the help of this map.

Reciprocal translocations are one of the most common structural chromosome rearrangements and have been detected in many species through the study of pollen viability and chromosome pairing during meiosis (Garber 1972). Molecular markers provide an additional tool to these classical methods of genetic analysis. Comparison of the position of RFLP markers in linkage maps of the same or different species has made it possible to find and characterize reciprocal translocations between genotypes of the same species (Kianian and Quiros 1992; Fauré et al. 1993), between homoeologous chromosomes of polyploid species (Liu et al. 1992; Nelson et al. 1995), or between the genomes of different species (Dubcovsky et al. 1996; Brubaker et al. 1999). One of the consequences of a reciprocal translocation is pseudolinkage between loci of the two translocated chromosomes in the offspring of individuals heterozygous for the translocation. Pseudolinkage can be detected easily with molecular markers as it results in unexpected link-

ages between markers that are independent in other crosses (Tadmor et al. 1987; Hohmann and Lagudah 1993; Benito et al. 1994). In this paper, we report for the first time a reciprocal translocation in *Prunus* that was detected when constructing the G×N map with evidence based on marker linkage, pollen viability and meiotic chromosome behaviour.

Materials and methods

Plant material

A progeny of 113 plants derived from the open pollination of eight hybrid trees (GN1, GN2, GN3, GN7, GN9, GN15, GN17 and GN22) of the cross between the rootstock cultivars of almond ('Garfi') and peach ('Nemared') served as the mapping population. Hybrid individuals belong to the rootstock breeding program of S.I.A.-Zaragoza.

Isozymes

Enzyme extraction, electrophoresis and staining procedures were performed as described in Arús et al. (1994). Nine enzyme systems were examined for polymorphism in 'Garfi' and 'Nemared': aconitase (ACO), glucose-phosphate isomerase (GPI), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD) and shikimate dehydrogenase (SDH). Polymorphic enzymes were studied in the F_2 population.

RFLPs

Five micrograms of genomic DNA of 'Garfi' and 'Nemared' were digested with five restriction enzymes (*Bam*HI, *Dra*I, *Eco*RI, *Hind*III and *Mva*I) and hybridized with 79 probes from several genomic and cDNA libraries of different *Prunus* species. Probe origin and terminology are those described in Joobeur et al. (1998). DNA extraction, digestion, Southern blotting, probe hybridization and labelling with ^{32}P-α-CTP or digoxygenin-11-UTP were as described by Viruel et al. (1995). After analyzing polymorphism in the parental genotypes, selected probes were studied in the F_2 progeny.

Choice of markers

The first criterion for marker selection was that the ensemble of markers chosen should cover most of the *Prunus* genome at intervals ≤25 cM, which was done using the information available from the almond×peach map (Joobeur et al. 1998). The second criterion was that, for all selected loci, the allele or alleles present in one parent had to be different to those present in the other parent. These markers are expected to segregate in a 1:2:1 ratio in the simplest and most frequent case (each parent homozygous for a different allele) or to segregate in a more complex ratio that can be converted into a 1:2:1 if the alleles of each of the parents are taken as a single allele. This second criterion was chosen because G×N consisted of progeny from various F_1 individuals from two non-inbred parents. Such a population can be treated as a conventional F_2 for inheritance and linkage analysis purposes if only markers expected to segregate 1:2:1 are used (Paterson 1996).

Inheritance analysis and map construction

A chi-square goodness-of-fit test of single-locus segregation ratios was carried out with LINKEM v.1.2. software (Vowden et al. 1995). LINKEM was also used to perform the chi-square tests using the contingency table for loci that had skewed segregations. Map construction was performed with MAPMAKER/EXP v. 3.0 (Lander et al. 1987). Linkage groups were established with the default criteria of LOD ≥3.0 and recombination fraction ≤0.3. The Kosambi mapping function was used to convert recombination units into genetic distances.

Cytology

Flower buds from F_1 hybrids GN1, GN9, GN15 and GN22 were fixed in Carnoy fluid II (6 absolute ethyl alcohol: 3 chloroform: 1 glacial acetic acid) with ferric chloride for 24 h and stained with 1% ferric aceto-carmine. Chromosome pairing in pollen mother cells was observed at metaphase-I as described in Salesses (1973). To test pollen fertility, 15–20 flowers at the "D" stage (Felipe 1977) were collected from 'Garfi', 'Nemared', the hybrids GN1, GN2, GN3, GN7, GN17 and GN22, and 72 plants from the F_2 progeny. Pollen fertility was evaluated from 500 grains stained with aceto-carmine. Fully stained and regularly shaped grains were considered to be viable.

Mapping the translocation breakpoint

Two different strategies were adopted. First, pollen fertility data were used to determine the translocation configuration of each individual. Fertile plants in the F_2 progeny should be homozygous for the translocation (*TT* or *tt*), and semi-sterile plants should be heterozygous (*Tt*). The estimation of recombination frequencies between codominant markers and the translocation break-point were calculated by the maximum-likelihood equation given by Tadmor et al. (1987). Second, the markers belonging to the two linkage groups involved in the translocation were submitted to additional analysis with MAPMAKER. Markers were first mapped as established in previous maps. Then the '*two point*' and '*try*' commands were used to determine the most probable position of the markers of one group within the other.

Results

Fifty one markers, including 46 RFLPs and five isozymes (*Pgm-2*, *Lap-1*, *6Pgd-1*, *6Pgd-2* and *Aco-2*), polymorphic between 'Garfi' and 'Nemared' and with an expected 1:2:1 segregation, were selected and studied in the G×N F_2 progeny. Twenty seven of them (53%) had segregations that deviated significantly from the 1:2:1 ratio. Their positions on the map are indicated in Fig. 1. All these loci had already been mapped in the almond×peach F_2 population used by Joobeur et al (1998) and covered 88% of the total distance of its map (which we will refer to as the T×E map). Seven linkage groups were detected. Six of them, G1, G2, G3, G4, G5 and G7 (Fig. 1a), were homologous to those found in T×E with identical locus order and similar distances. Fourteen markers belonging to the remaining two linkage groups of these maps (seven markers each for G6 and G8 of T×E), formed a single group in G×N when using the 'group' command of MAPMAKER. Ordering of this group (G6–8) was difficult and a linear order containing all loci could not be established. The map with the most markers included only 11 loci: all the G8 markers and four of the G6 markers (Fig. 1b). As shown in Table 1, 17 pairs of G6-G8 markers should be

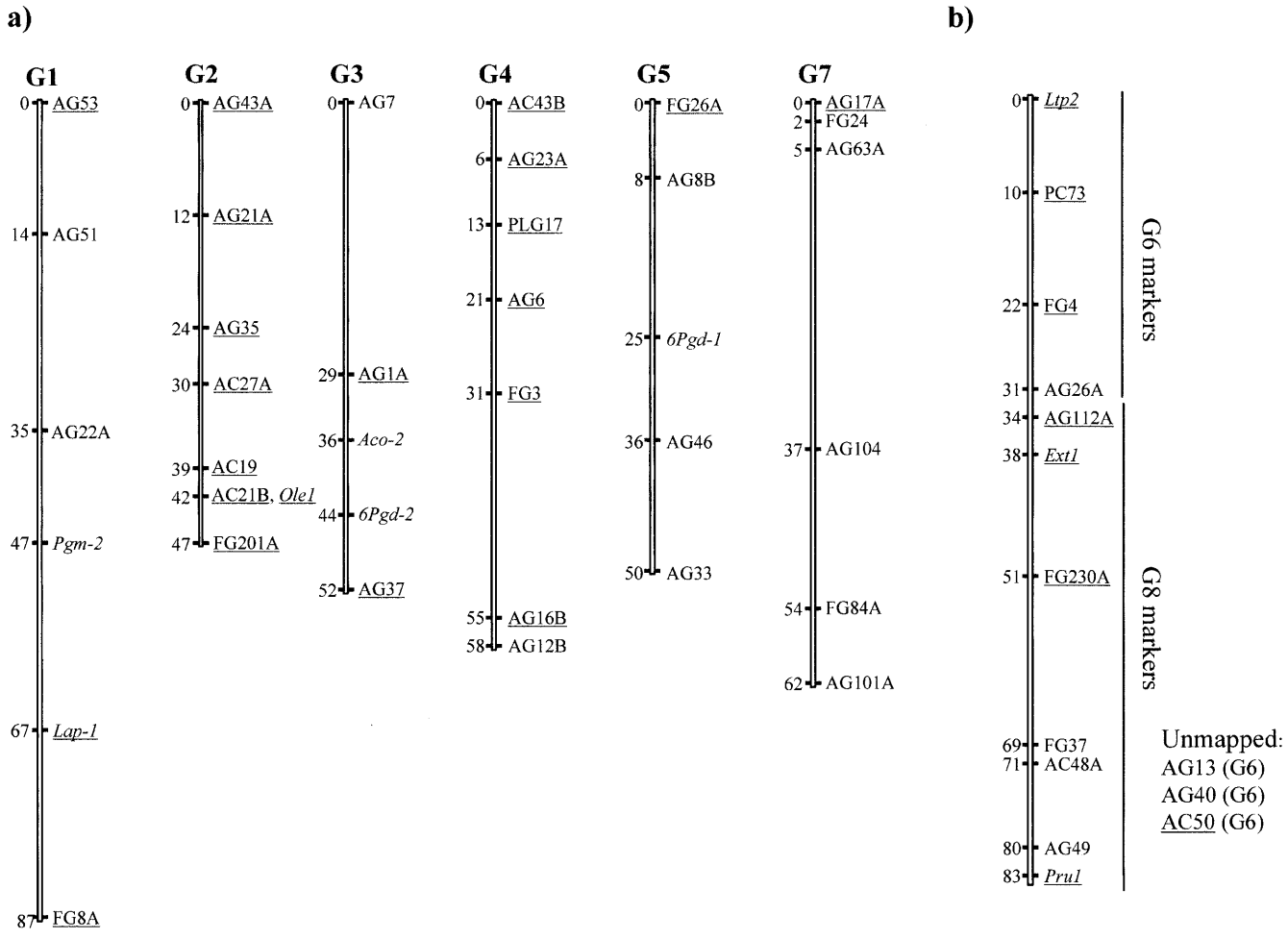

Fig. 1a, b Linkage map of the 'Garfi'×'Nemared' almond×peach F_2 population. Loci with distorted segregations are *underlined*. **a**) Groups homologous to those obtained in previous *Prunus* maps. **b**) Linkage group that includes markers of groups 6 and 8 of other maps

Table 1 Genetic distances in cM (upper number) and LOD score values (lower number) between markers of linkage groups 6 (G6) and 8 (G8) in 'G×N'. Shadowed areas include pairs of markers with LOD scores >3.0

		G6						
		AG13	AG40	AC50	AG26A	FG4	PC73	*Ltp*2
G8	*Ext1*	–	39.4	18.5	5.8	12.8	22.2	32.6
		–	2.1	9.9	27.4	16.5	8.2	3.8
	AG112 A	53.6	34.1	14.2	3.3	12.5	23.0	37.7
		0.7	3.1	13.6	33.5	16.6	7.4	2.4
	FG230 A	53.6	35.4	16.0	8.8	17.4	24.0	39.6
		0.5	2.7	10.6	20.3	10.6	6.3	2.1
	FG37	–	50.0	39.2	27.7	36.6	50.0	–
		–	1.2	2.1	5.2	2.8	1.0	–
	AC48 A	–	55.9	43.0	30.9	41.4	53.6	–
		–	0.7	1.5	3.9	1.9	0.8	–
	AG49	–	50.1	32.1	32.0	47.2	–	–
		–	0.6	2.2	2.4	0.8	–	–
	Pru1	–	59.2	44.4	34.2	43.6	–	–
		–	0.5	1.5	3.2	1.7	–	–

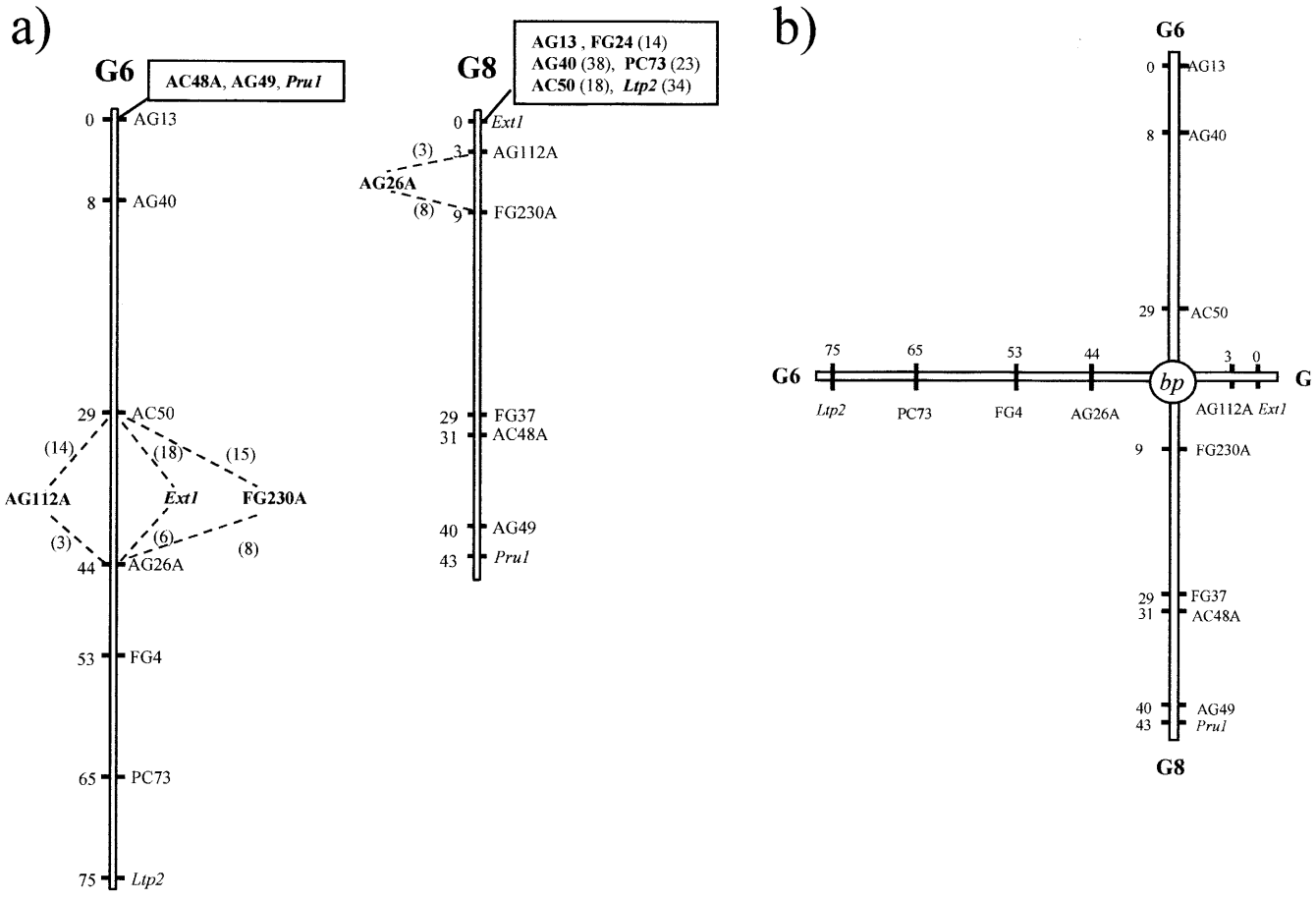

Fig. 2 **a**) Most probable position of markers from G6 in G8 and from G8 in G6. Distances in parenthesis if ≤40 cM. **b**) Diagrammatic representation of G6-G8 translocation and position of the breakpoint (*bp*)

considered as linked (LOD ≥3.0). The tightest linkage was that observed for markers AG112A (G8) and AG26A (G6) with a LOD=33.5 and a distance of 3.3 cM. When markers of group G6–8 were mapped separately as G6 and G8, marker order was identical and genetic distances were comparable to those obtained in T×E (Fig. 2a).

In order to explain these results, we tested several hypotheses. First, we considered the possibility that the distorted segregations found in some markers of G6–8 (see Fig. 1b) could have resulted in the incorrect assignment of markers between G6 and G8 because the adjustment to Mendelian segregations is a requirement of the model when using LOD scores as a statistic for linkage detection (Lorieux et al. 1995). To avoid this problem, we used the chi-square test with the contingency table for all the pairs of G6–G8 loci with a LOD ≥3.0 because this test is robust against skewed segregations (Bailey 1949). In all cases we found significant (P<0.001) χ^2 values, so we rejected this hypothesis. A second possible cause for the apparent linkage between G6 and G8 markers could have been due to errors in the interpretation of banding patterns. If two bands are considered to be allelic but belong to two independent loci, incorrect linkage is then detected between the groups where these two loci lie. To test this hypothesis, bands produced by codominant markers segregating 1:2:1 in G6 and G8 and linked, were re-scored as if they were two separate markers segregating 3:1 (band presence vs absence). The G6–8 linkage obtained previously was confirmed from these data, and this second potential cause of anomalous linkage was also discarded.

Finally, we considered the hypothesis that our results were due to pseudolinkage as a consequence of a reciprocal translocation between the chromosomes corresponding to G6 and G8 in the two parents of this cross. In this case, (1) multivalents should be found in the meiosis of translocation heterozygotes (F_1 generation), and (2) due to unequal chromosome pairing at meiosis, these individuals should be semi-sterile and their offspring (F_2 progeny) should segregate for semi-sterile vs fertile plants in a 1:1 ratio.

To test prediction (1), we studied chromosome pairing at metaphase-I in pollen mother cells of four F_1 hybrids (GN1, GN9, GN15 and GN22) and observed configurations with 6II+1IV or 6II+1III+1I in all of them (Fig. 3). For prediction (2), we verified that F_1 hybrids were semi-sterile while ‘Garfi’ and ‘Nemared’ were fully fertile. Viable pollen percentage results for the F_1 hybrids analyzed were: 56% in GN1, 45% in GN2, 57% in GN3, 69% in GN7, and 51% in both GN17 and GN22.

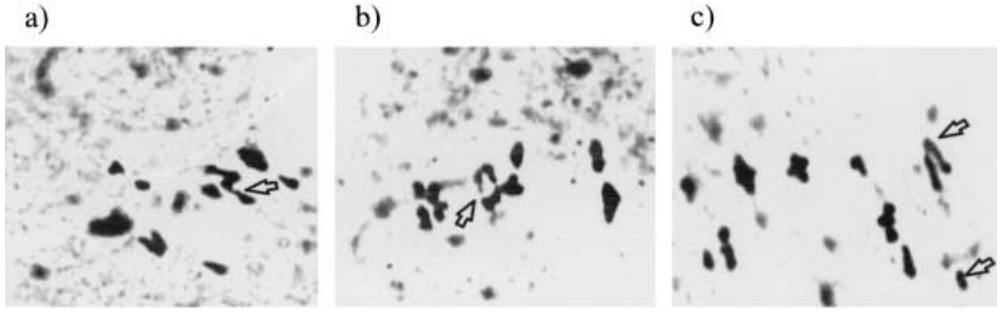

Fig. 3a–c Chromosome pairing in metaphase-I in three hybrids between 'Garfi' and 'Nemared'. **a**) 6II+1IV in GN15; **b**) 6II+1IV in GN9; **c**) 6II+1III+1I in GN22. *Arrows* point to tetravalents in **a**) and **b**) and to a trivalent and a monovalent in **c**)

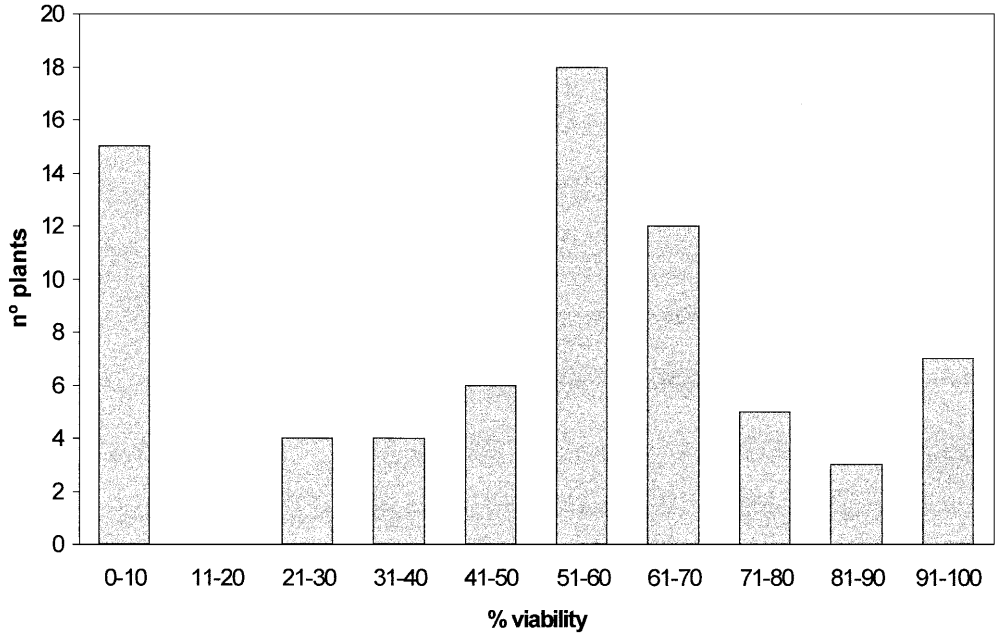

Fig. 4 Histogram with the % of pollen viability from 74 plants of the 'Garfi'×'Nemared' F_2 population

As part of the testing of prediction (2), and to map the translocation breakpoint, we analyzed pollen fertility in the F_2 progeny. The range of observed sterility was very broad as can be observed in Fig. 4. Fifteen plants were completely sterile or almost so (pollen fertility ≤10%), and were not used. Plants with pollen fertility in the range of 21–60% were considered to be semi-sterile and heterozygous for the translocation break-point (*Tt*) and those with pollen fertility ≥70% were considered to be fertile and homozygous for the translocation (*TT* or *tt*). Twelve more plants with fertility ranging from 61 to 70% were also discarded in order to avoid misclassification. The segregation ratio obtained with the remaining plants was of 32 semi-sterile to 15 fertile plants which differs significantly from the expected 1:1 segregation (χ^2=6.15; $P \leq 0.01$). Genetic distances obtained between the linkage-map estimate of the translocation breakpoint and the eight codominant markers from G6–8 are shown in Table 2. Markers AG26A (G6) and AG112A (G8) were placed at 8.2 and 8.1 cM respectively from the translocation breakpoint while the rest of the markers were further away (≥15 cM) or unlinked. Given that most of the markers of these regions presented skewed segregations, a χ^2 test of independence was performed and was found to be significant in the loci previously detected as linked by the MLE test with maximum values for AG26A and AG112A. The analysis of linkage between markers (Table 1) detected the tightest pseudolinkage between markers AG26A and AG112A (3.3 cM), suggesting also that they were the closest to the breakpoint. Using the 'try' command of MAPMAKER (Fig. 2), we found that AG26A was most probably positioned between AG112 and FG230A of G8, while the

Table 2 Distances between markers of linkage groups 6 and 8, and the translocation breakpoint and χ^2 values of independence

Marker	Group	Distance (cM)	χ^2	
AG40	6	–[a]	1.2	n.s.
AC50	6	16.9**	15.0	**
AG26A	6	8.2**	29.2	**
FG4	6	32.8 n.s.	7.9	*
Ext1	8	15.7**	18.9	**
AG112A	8	8.1**	29.1	**
FG230A	8	16.5**	15.1	**
AC48A	8	–	2.3	n.s.

* $0.05<P<0.01$; ** $P<0.01$; n.s. non significant
[a] –, unlinked loci

rest of the pseudolinked markers of G6 were placed at the extreme *Ext1* end of this linkage group, suggesting that the most-likely position of the breakpoint is between these loci. Similar analyses with G8 markers in G6 detected the interval AG26A–AC50 as being the most-probable location of the breakpoint, since AG112A, *Ext1* and FG230 A were most probably located in this chromosome fragment.

Discussion

A genetic map was constructed in an almond×peach F_2 population using previous information from the saturated T×E map reported by Joobeur et al. (1998). This strategy allowed us to obtain a new map for a population expected to segregate for characters of interest for rootstock breeding with moderate effort, since only 51 markers were sufficient to cover most (88%) of its length. The locus order for six of the linkage groups was the same as that obtained in the previous map and distances were also similar. Unexpectedly, loci from the two remaining linkage groups (G6 and G8) appeared as a single one, although when linkage analysis was performed only with loci of either G6 or G8, loci order was again identical to that in the corresponding homologous groups of the saturated map.

The fusion of G6 and G8 observed in G×N was attributed to the presence of a reciprocal translocation between the parents of this population, the 'Garfi' almond and the 'Nemared' peach. Three levels of evidence support this hypothesis. First, the linkage observed between markers of G6 and G8 is consistent with the pseudolinkage expected between loci of the two chromosomes involved in the translocation in the regions proximal to the translocation breakpoint. Second, almond and peach are related species whose hybrids are fully fertile (Layne and Sherman 1986) and eight bivalents are found during metaphase-I (Salesses and Bonnet 1971). The observation of multivalents (tetravalents or trivalents plus univalents) at metaphase-I in four hybrids between 'Garfi' and 'Nemared' was also expected if these hybrids were heterozygous for a reciprocal translocation. Third, only half of the pollen of heterozygous individuals for the translocation is expected to be viable due to the unbalanced gametes that are produced during meiosis. Both parents 'Garfi' and 'Nemared' were fully fertile, but all hybrids between them were semi-sterile.

Another expected consequence of the reciprocal translocation was that the F_2 progeny would segregate for fertile and semi-sterile plants, corresponding to homozygotes (*TT* and *tt*) and heterozygotes (*Tt*) for the translocation, respectively. We found considerable variation for pollen fertility in the F_2 that would correspond to a tri-modal distribution with maxima in the classes 0–10%, 51–60% and 91–100% pollen viability. We interpreted the plants falling into the two latter categories as corresponding to the semi-sterile and fertile plants. Fully sterile individuals may have been produced by the presence of a homozygous recessive sterility allele that was heterozygous in one of the parents and in some F_1 individuals. If this was the case, then it would be difficult to find linkage between this gene and the rest of the markers of the map, and we did not find it. Other hypotheses of a more complex nature are also posssible but they were not testable with our data.

Data from pollen fertility and marker linkage analysis allowed us to locate the translocation breakpoint between markers AC50 and AG26A in G6 and between AG112A and FG230 A in G8. Genetic distances calculated using pollen fertility data were higher than expected considering the distances calculated with the markers. These results may be due to a few errors in the classification of semi-sterile and fertile plants leading to an overestimation of recombination frequencies. The presence of additional factors involved in pollen fertility may have contributed to the masking some of the data on pollen viability, leading to the erroneous classification of a few plants. Seven plants with an unexpected viability classification considering their marker genotype were detected. Their true genotype for the translocation may be clarified after further cytogenetic analysis.

The presence of this translocation can be studied in various maps constructed with homologous markers. Almond cultivars Texas, Ferragnes, Tuono, Felisia and Bertina had the same genotype (which we will call 'standard') for the translocation (Viruel et al. 1995; Ballester 1998; Joobeur et al. 1998). The standard genotype also occurs in 'Earlygold' peach (Joobeur et al. 1998) and in the *Prunus davidiana* genotype used by Dirlewanger et al. (1996). Thus, the translocation is not a distinctive genetic rearrangement of the genome of any of these three species and, instead, it appears to be a mutation that occurs with unknown frequency within at least one of them.

While we have been able to document that 'Garfi' and 'Nemared' differ by a reciprocal translocation, our data cannot determine which of them has the standard genotype and which has the rearrangement. Both cultivars are fully fertile, indicating that they are each homozygous for a different chromosome arrangement. If 'Garfi' is homozygous for the translocation, this implies that it should be present simultaneously in its two parents, the 'Garrigues' almond and the unknown almond that pollinated it. With the data available the probability of such an event appears to be low, given that the translocation was not found in any of the five known almond genotypes, suggesting that, if present in almond, the translocation would exist at low frequency. On the other hand, 'Nemared' was selected in the F_3 of a cross between a red leaf peach seedling and 'Nemaguard' (Ramming and Tanner 1983). The red leaf character comes from 'Bound Brook', which derives from the peach germplasm called Tennessee naturals, considered to be one of the first introductions of *Prunus persica* in the USA, and geneticall-ly different from the most-widespread germplasm origi-

nated after the introduction of 'Chinese Cling' during the nineteenth century (Hesse 1975). 'Nemaguard' originated from a cross between peach and *P. davidiana* (Hesse 1975). Then, the translocation could have been introduced either from *P. davidiana*, from the peach line used to produce 'Nemaguard' or from the red leaf genotype and fixed in 'Nemared' after a few generations of inbreeding. All these considerations make 'Nemared' a more-probable candidate for having the translocation than 'Garfi'. To prove this, 'Nemared' and 'Garfi' could be crossed with almond or peach genotypes which we know have the standard arrangement. In the F_1 hybrid obtained from the translocated progenitor, semi-sterility and multivalents in meiosis should be detected in contrast with fertility and normal chromosome pairing in the hybrid derived from crossing two plants with the same chromosomal arrangement. Results would then be available 2 to 3 years later.

The translocation between 'Garfi' and 'Nemared' was noticed because the map constructed in its F_2 was based on reference maps already developed with markers that can be easily transferred to other populations of the same or related species such as RFLPs. Another map obtained with an F_2 population involving 'Nemared' ('Lovell'×'Nemared') was recently constructed mainly with AFLPs by Lu et al. (1998). The lack of reference maps and common markers has made it impossible to determine whether the reciprocal translocation reported here is also segregating in this population, making our results not comparable with theirs at the present stage. The information provided by markers has enormously increased our knowledge of tree genetics within the last decade. Any initiative towards unifying results obtained by different research groups in various populations of *Prunus* and *Malus* would be synergic. New high quality markers such as SSRs are being developed rapidly in *Prunus* (Cipriani et al. 1999). They appear to be ideal tools for map merging in this genus once they have been analyzed in different mapping populations.

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