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The potential of *Prunus davidiana* for introgression into peach [*Prunus persica* (L.) Batsch] assessed by comparative mapping

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Abstract The potential for introgression of *Prunus davidiana*, a wild species related to peach, was evaluated with respect to problems of non-Mendelian segregation or suppressed recombination which often hamper breeding processes based on interspecific crosses. Three connected (F1, F2 and BC2) populations, derived from a cross between *P. davidiana* clone P1908 and the peach cultivar Summergrand were used. The intraspecific map of *P. davidiana* already established using the F1 progeny was complemented, and two interspecific maps, for the F2 and BC2 progenies, were built with a set of markers selected from the *Prunus* reference map. With the molecular data collected for the F2 map construction, regions with distorted marker segregation were detected on the genome; one third of all loci deviated significantly from the expected Mendelian ratios. However, some of these distorted segregations were probably not due to the interspecific cross. On linkage group 6, a skewed area under gametic selection was most likely influenced by the self-incompatibility gene of *P. davidiana*. Using anchor loci, a good colinearity between the three maps built and the *Prunus* reference map was demonstrated. Comparative mapping also revealed that homologous recombination occurred normally between *P. davidiana* and the *Prunus persica* genome. This confirmed the closeness of the two species. Higher recombination rates were generally observed between *P. davidiana* and *P. persica* than between *Prunus amygdalus* and *P. persica*. The consequences for plant breeding strategy are discussed. The three maps of the F1, F2 and BC2 progenies provide useful tools for QTL detection and marker-assisted selection, as well as for assessing the efficiency of the peach breeding scheme applied to introgress *P. davidiana* genes into peach cultivated varieties.

Keywords Interspecific cross · Distorted segregation · Comparative mapping · Recombination rate · Breeding strategy

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Introduction

Peach [*Prunus persica* (L.) Batsch] is one of the most important fruit crops in Europe with the second rank production after apple. As for many fruit and vegetable crops, consumer requests encourage the reduction of chemical inputs for pest management in peach (Byrne 2002), both to develop more environmentally friendly crop management and to avoid pesticide residues on fruit. As a result, breeding programs, focused on fruit quality until recently, extend to the improvement of resistance to pests and diseases.

Due to the narrow genetic base of peach commercial varieties (Scorza et al. 1985) leading to a low variability of resistance to pests and diseases in cultivar germplasm, breeders have to search for sources of resistance in related species. Several studies have illustrated the potential of wild related species such as *Prunus kansuensis* (Meader and Blake 1938, 1939), *Prunus davidiana* (Grasselly 1974) or *Prunus dulcis* (Gradziel 2002) in peach cultivar development.

P. davidiana, originating from China, was found to be resistant to several peach pests and diseases, including powdery mildew (Smykov et al. 1982), the green aphid (Massonié et al. 1982; Sauge et al. 1998), plum pox virus (Pascal et al. 1998) and leaf curl (Hesse 1975).

However, problems inherent to interspecific crosses were shown to hamper introgression from the wild species into cultivated peach varieties; poor hybrization due to

strong reproductive barriers and fertility issues, non-Mendelian segregations or lethal gamete association (Zamir and Tadmor 1986), and suppressed recombination (Rick 1969), are commonly reported in interspecific crosses.

The ability to produce vigorous and fertile *Prunus persica* × *P. davidiana* hybrids, i.e. the absence of strong reproductive isolation barriers, has already been demonstrated (Grasselly 1974). Nevertheless, no analysis of segregation or recombination frequencies in progenies derived from these hybrids (e.g. F2 and backcross progenies) has so far been reported, despite their implications in breeding strategies.

The aim of the present paper is to analyse segregation and recombination in F2 and BC2 progenies derived from one hybrid of a *P. persica* × *P. davidiana* F1 progeny. The development of molecular markers provides efficient tools to perform such analysis. Non-Mendelian segregation at marker loci may be directly detected with molecular data used to build genetic maps. Conversely, evidence for altered recombination, and comparison with other inter- or intra-specific linkage maps from the same or closely related species is necessary (Beavis and Grant 1991; Causse et al. 1994; Williams et al. 1995). Among the *Prunus* maps published over the last decade, the T × E map, established from the almond (cv Texas) × peach (cv Earlygold) interspecific F2 progeny by Joobeur et al. (1998) and complemented by Aranzana et al. (2002), seems particularly convenient for this purpose. It is composed of highly reproducible and easily transposable RFLP and SSR markers and is considered as a reference for the *Prunus* genus (Arús et al. 1994). An intraspecific genetic linkage map of *P. davidiana* (Dav Map) established by Viruel et al. (1998) is also worth considering: it was built with the same set of RFLP markers as the T × E map from the F1 progeny at the origin of our F2 and BC2 progenies.

A subset of markers from these two maps (T × E and Dav) was selected to develop interspecific maps for our F2 and BC2 populations. The molecular data collected were used to identify distorted segregation regions on the whole genome. Thanks to anchor markers, recombination events were compared between: (1) the two interspecific *P. davidiana* × peach and almond × peach F2 progenies, and (2) the three connected populations (F1, F2 and BC2) derived from *P. davidiana*. Consequences and perspectives for the peach breeding strategy are discussed.

Materials and methods

Mapping populations

Three related populations were studied.

(1) The F1 progeny of 77 hybrids was obtained from an interspecific cross between *P. persica*cv Summergrand and *P. davidiana*clone P1908. Summergrand is a yellow nectarine cultivar showing good agronomic performance. P1908 is an accession used as a source of resistance for several pests and diseases.

(2) The F2 progeny (called $SD40^2$) of 99 plants was generated by self-pollination of a single hybrid of the F1 progeny (hereafter referred to as SD40).

(3) A breeding scheme was carried out to obtain BC2 progenies: the hybrid SD40 was backcrossed with Summergrand to create a BC1 progeny. Mixtures of pollen from all BC1 hybrids resistant to powdery mildew on the one hand, and all BC1 susceptible hybrids on the other hand, were used to fertilize another commercial cultivar Zéphir and produce a BC2 progeny.

Genotyping

Three types of molecular markers, i.e. RFLPs, SSRs and AFLPs, were used. RFLP probes and SSR primers generate mostly codominant markers and allow the anchorage of the different maps with common markers. AFLP markers were added in order to saturate the maps.

Genomic DNA was extracted from young leaves according to the method of Viruel et al. (1995).

The RFLP probes employed (PC, AC, AG, CC and FG) were developed by the partners of the European Mapping Prunus Project (Arús et al. 1994) and used to establish the *Prunus* reference map (Joobeur et al. 1998). Some probes corresponding to known-function genes, i.e. malate dehydrogenase (GC308), citrate synthase (GC309), isocitrate dehydrogenase (GC310) and pyrophosphatase (GC311 and GC312), originating from a cDNA peach fruit library (Etienne et al. 2002) were also used. Hybridisation for the RFLP analysis was performed following the specifications of Viruel et al. (1995). Information about polymorphism between Summergrand and *P. davidiana*, collected for the elaboration of the Dav map (Viruel et al. 1998), allowed us to chose enzyme-probe pairs to apply to F2 progeny. All markers heterozygous in SD40 were retained. Overall, 63 RFLP probes were used on the $SD40^2$ progeny, together with five restriction enzymes (*Hin*dIII, *Eco*RI, *Bam*HI, *Dra*I and *Bgl*II).

Thirty eight *Prunus* SSRs previously developed by Cipriani et al. (1999), Sosinski et al. (2000) and Testolin et al. (2000) were analysed for polymorphism. Most of them were mapped on the T × E map (Aranzana et al. 2001). PCR reactions, radioactive labeling, electrophoretic separation and autoradiography were performed according to Cipriani et al. (1999).

On the F1 and the F2 progenies, AFLP genotyping was carried out as described by Lu et al. (1998), with *Eco*RI-*Mse*I primer combinations: E31-M47, E31-M48, E31-M49, E31-M52, E31-M59, E31-M62, E38-M54 and E40-M56. AFLP markers were coded by a three-capital-letter code followed by a small letter (e.g. CFFa), indicating the relative position of the polymorphic fragment on the sequencing gel (see correspondence with the Keygene denomination in the legend of Fig. 2).

The S-allele-specific PCR primer set AS1II-AmyC5R developed by Tamura et al. (2000) was also used on the F2 progeny.

The BC2 map was built only with RFLP markers. According to the information of the F2 map, 40 RFLP probes which generated codominant markers, a single locus profile and which made it possible to unambiguously distinguish the *P. davidiana* allele from the peach parent alleles, were chosen in order to cover all the genome.

For all mapping populations, genotypic data were scored independently by two persons and conflicting data were re-examined.

Data analysis and mapping strategy

Mapping procedure

On the F1 progeny, AFLP and SSR markers were included in the existing marker data set. Linkage analysis was performed using MAPMAKER/EXP V3.0 software (Lander et al. 1987), according to

the mapping strategy previously described for the Dav map construction (Viruel et al. 1998).

The genetic linkage map of the F2 progeny was constructed using MAPMAKER/EXP V3.0. Due to the existence of skewed loci in this population, the mapping procedure detailed by Joobeur et al. (1998) was applied to minimize the risk of the erroneous assignment of loci or biased recombination estimation. Because dominant markers with segregation distortion provided very poor information, only those which revealed anchor loci with other maps were retained and added in a second step of the mapping procedure.

For the BC2 map, the order of the markers was defined by MapManagerQTXb13 software (Manly et al. 2001). The "Advanced Backcross generation 2" design was applied to determine linkage groups and marker order within each linkage group, with stringent probability of the type I error ($p < 1{\cdot}10^{-4}$). Assuming that recombination rates in BC1 and BC2 were the same, recombination rates (r) were then calculated by the maximum-likelihood method.

For each map, the recombination rate was transformed into map distance using the Kosambi function.

Study of segregation distorsion

Segregation data were tested for deviation from expected Mendelian ratios with a chi-square test.

For the F2 progeny, the probable type of selection was determined on codominant markers according to the Lorieux et al. (1995) procedure.

Comparative mapping

Loci order and genetic distances were compared for each pair of maps ($SD40^2$-T × E, $SD40^2$-Dav, Dav-T × E and $SD40^2$-BC2).

Considering two maps, the comparison between distances was performed using a paired t-test applied to: (1) all segments bounded by two successive anchor markers belonging to the same linkage group (df = number of segments compared), and to (2) the two most-distant anchor loci of each linkage group (df = number of linkage groups compared). An analysis of the homogeneity of recombination rates between the two maps, on each common segment bounded by two successive anchor-markers, was performed by the Fisher scoring method described in Allard (1956) and detailed in Beavis and Grant (1991). The following statistic was used to test for significant differences of the recombination rate between populations:

$$\sum_{i=1}^{N} \frac{Li(r)^2}{Ii(r)} - \frac{Lp(r)^2}{Ip(r)}.$$

In this formula, r is the maximum-likelihood estimate of the recombination rate between the markers bounding the segment under consideration, computed after pooling data from all N populations. $Li(r)$ and $Ii(r)$ correspond to the logarithm of the likelihood equation and the information index, respectively, for population i, given r. Lp and Ip are respectively the sums of Li and Ii over all N populations. This statistic follows a χ^2 distribution with N – 1 degrees of freedom.

This method allowed us to compare populations differently derived, thanks to the independent determination of the likelihood equations for each population type.

Results

The number of markers studied in each progeny (F1, F2, BC2 and T × E) and the distribution of anchor loci for each map-pair are summarized in Fig. 1.

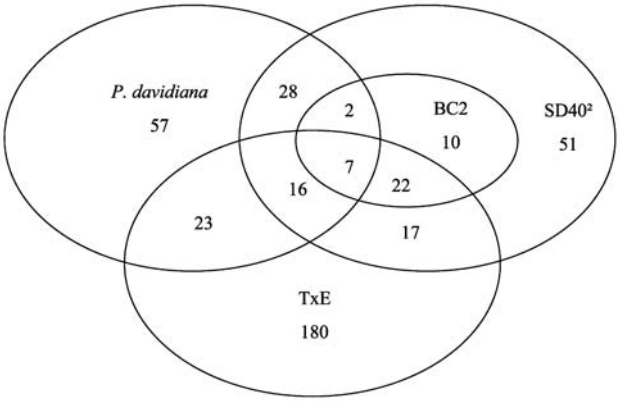


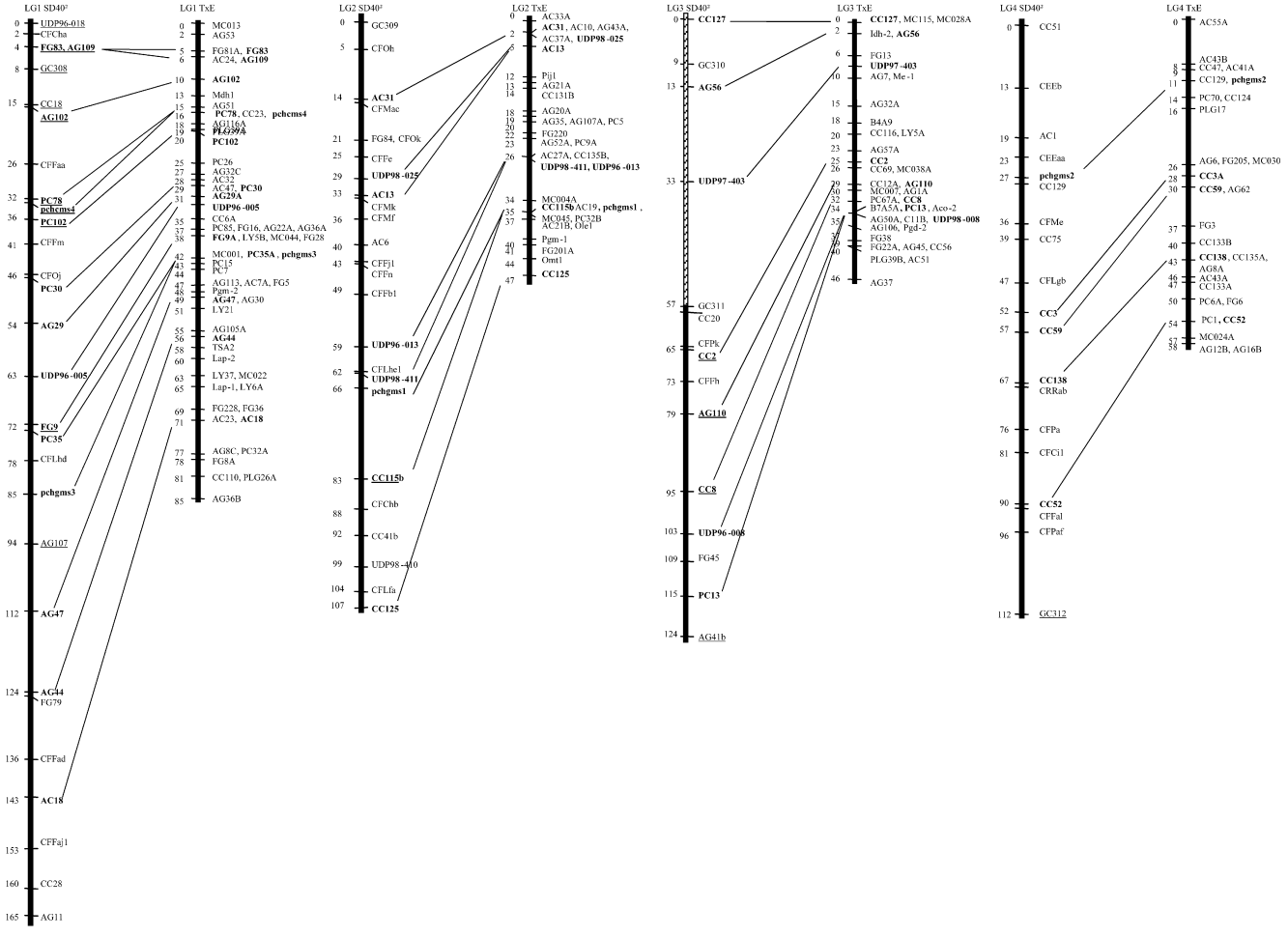
Fig. 1 Sharing of molecular markers between *P. davidiana*, $SD40^2$, BC2 and the T × E maps. *Numbers given in overlapping circles* refer to markers common to the different maps. *Numbers of markers unique to one map* are given in the non-overlapping portion of the circle

Construction of the $SD40^2$ linkage map

The genetic linkage map of $SD40^2$ (Fig. 2) was established using 153 markers. It covered 874 cM with an average 5.71-cM interval between markers. All markers coalesced into eight linkage groups (LG1 to LG8), corresponding to the number of chromosomes in peach (2n = 2x = 16). Linkage groups were assigned according to the *Prunus* reference map, using a subset of 62 anchor markers.

Among all the markers, 89 (58%) were codominant. Sixty six RFLPs (60 codominant, six dominant) were detected with 62 probes: AG41, CC41, CC63 and CC115 revealed two loci. Among the 35 peach SSR primers tested, 24 revealed polymorphism (70%) and generated SSR markers (22 codominant and two dominant). One hundred and three AFLP markers were identified using the eight primer combinations (12 markers per primer combination on average) but, due to ambiguous scoring or distorted segregation, only 61 of them (55 dominant, six codominant) were mapped. Whatever the type of marker considered, they were randomly dispersed over the whole map, without any clustering. One codominant PCR-marker was obtained with the AS1II-AmyC5R primer combination and was located on LG6. The phenotypic character, glabrous vs pubescent skin fruit, that distinguishes peach and nectarine (G-gene), scored on 75 $SD40^2$ hybrids, was located on linkage group 5.

The distribution of markers over the linkage groups was not uniform and marker coverage was low in a few regions. The highest number of markers was encountered on LG1 (29 markers) and the lowest on LG8 (ten markers). The average distance between markers ranged from 4.28 cM in LG2 to 8.2 cM in LG3. However, a chi-square test comparing the distribution of distances did not reveal significant differences between linkage groups. Overall, loci separated by 10 cM or less covered 79% of the map.


LG1 SD40²
LG1 TxE
LG2 SD40²
LG2 TxE
LG3 SD40²
LG3 TxE
LG4 SD40²
LG4 TxE
LG5 SD40²
LG5 TxE
LG6 SD40²
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LG7 TxE
LG8 SD40²
LG8 TxE

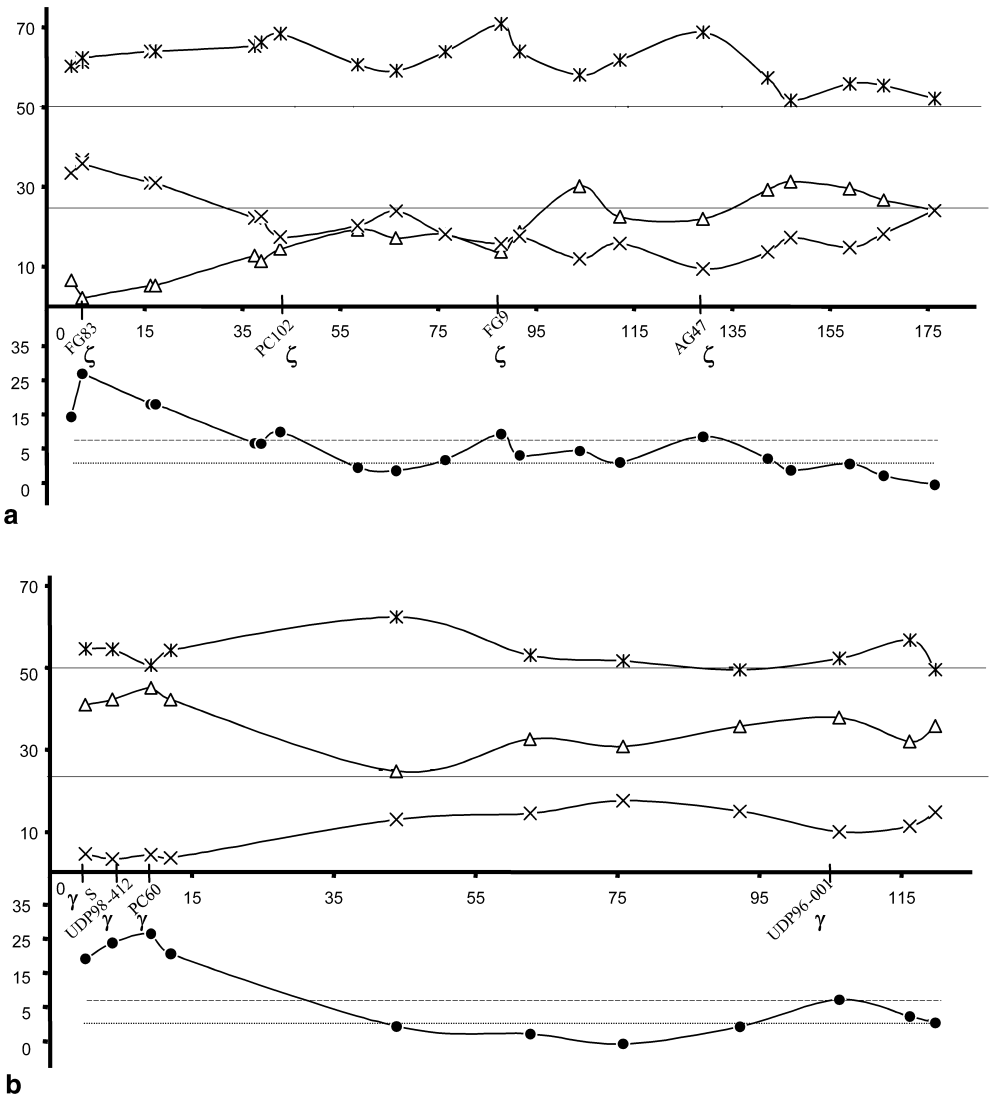


Fig. 3 Distribution of genotypes along **a** LG1 and **b** LG6 in the SD40^2 population. Frequencies in percentage at codominant marker loci are represented by ● for Summergrand homozygotes, by × for *P. davidiana* homozygotes and by * for heterozygotes. *Thin solid lines* indicate the expected ratios of homozygotes (25%) and heterozygotes (50%). In the lower part of the figure, goodness-of-fit test χ^2 values (●) comparing distribution to the expected 1:2:1 Mendelian ratio for codominant markers are given. *Dotted lines* indicate thresholds for $\alpha = 1\%$ (—) and $\alpha = 0.1\%$ (- - -). The most distorted markers for each distorted area are pointed out, together with the type of selection, gametic (γ) or zygotic (ζ), concluded from the statistical tests

Fig. 2 Alignment of the SD40^2 and the T × E maps. LG SD40^2 and LG T × E refer to the linkage group of the SD40^2 and the T × E maps respectively. The T × E map (linkage group on the right) has been already described in Joobeur et al. (1998), SSR anchor loci were added and located as in Aranzana et al. (2001). Concerning the SD40^2 map (linkage group on the left), AC-, AG-, CC-, FG-, GC- and PC- correspond to RFLP markers. Multiple loci detected by the same enzyme-probe pair are denoted with a *letter added to the name* (e.g. CC115a). UDP- and pch- correspond to SSR markers. AFLPs were named using a code for each *Eco*RI-*Mse*I primer combination followed by a *letter* corresponding to the molecular weight position (e.g. CFFa); CFF:E31-M47, CFP:E31-M48, CFO:E31-M49, CFM:E31-M52, CFC:E31-M59, CFL:E31-M62, CEE:E38-M54, CRR:E40-M56 (Keygene's primer denomination). Loci in *bold characters* are anchor points between the two maps, and are connected by lines. *Underlined loci* had distorted segregations (significant χ^2 test with $p < 0.01$). *Striped bars* correspond to regions where the locus order is not fully certain (see text for more details)

Analysis of marker segregation among the SD40^2 progeny

Among all the markers analysed, 46 (30%) presented significant deviations ($\alpha = 5\%$) from the expected Mendelian ratios 1:2:1 or 3:1. Some isolated loci (6%) showed distortion that could be attributed to difficult scoring of complex profiles, or the ambiguous pattern of homozygotes vs heterozygotes. Otherwise, distorted loci were not randomly distributed over all the genome, but were clustered (Fig. 2). On LG6, biased loci were located on both extremities, around markers UDP98-412 ($p = 3{\cdot}10^{-7}$) and UDP96-001 ($p = 9{\cdot}10^{-4}$), which were both highly distorted toward an excess of the *P. persica* allele (Fig. 3). The additional χ^2 tests revealed that gametic selection occurred on these two points ($p < 0.1\%$). Moreover, expected frequencies of phenotypes better fitted observed values if selection was assumed to occur only on male gametes. Linkage group 1 showed a large region with distorted loci, which covered more than 50 cM

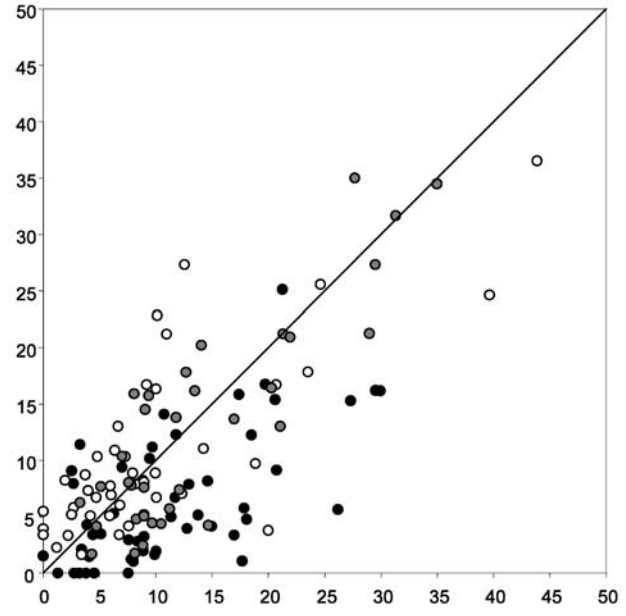


Fig. 4 Comparison of two-point distances (cM) of homologous segments of: (1) $SD40^2$ and T × E maps: 50 segments were considered (●); (2) $SD40^2$ and the *P. davidiana* map: 45 segments were considered (◯); (3) $SD40^2$ and BC2 maps: 34 segments were considered (*grey circles*)

Table 1 Comparison of recombination rates between the $SD40^2$ map and T × E, *P. davidiana* and BC2 maps: recombination rates in the two maps for common segments in which the difference is significant at the 5% level and the probability *p* associated to the χ^2 homogeneity test

LG	Segment	Recombination rates		*p*
		$SD40^2$	T × E	
1	AG102-PC78	0.137	0.051	$4{\cdot}10^{-2}$
1	PC30-AG29	0.078	0.012	$4{\cdot}10^{-2}$
1	AG29-UDP96 005	0.09	0.019	$2{\cdot}10^{-2}$
1	PC35-pchgms3	0.079	0.01	$2{\cdot}10^{-2}$
1	pchgms3-AG47	0.18	0.048	$3{\cdot}10^{-3}$
2	UDP96 013-UDP98 411	0.045	0	$2{\cdot}10^{-2}$
2	pchgms1-CC115b	0.17	0.011	$2{\cdot}10^{-4}$
3	CC127-AG56	0.098	0.017	$9{\cdot}10^{-3}$
3	AG56-UDP97 403	0.177	0.057	$7{\cdot}10^{-3}$
3	CC2-AG110	0.149	0.041	$1{\cdot}10^{-2}$
3	AG110-CC8	0.169	0.034	$4{\cdot}10^{-3}$
3	UDP96 008-PC13	0.075	0	$3{\cdot}10^{-2}$
4	CC138-CC52	0.207	0.09	$1{\cdot}10^{-2}$
5	pchgms4-AG46	0.127	0.039	$2{\cdot}10^{-2}$
6	PC73-PC60	0.033	0.114	$1{\cdot}10^{-2}$
6	UDP98 412-FG209	0.025	0.09	$2{\cdot}10^{-2}$
8	UDP98 409-AG49	0.261	0.056	$1{\cdot}10^{-4}$
		$SD40^2$	*P. davidiana*	
5	FG26-CFMn	0	0.055	$3{\cdot}10^{-2}$
6	pchcms5-CFFd	0.19	0.038	$9{\cdot}10^{-3}$
7a	CFOn- pchcms2	0	0.034	$4{\cdot}10^{-2}$
7b	UDP98 408-CFFg	0.123	0.273	$4{\cdot}10^{-2}$
		$SD40^2$	BC2	
2	CC41b-CC125	0.145	0.358	$6{\cdot}10^{-3}$
3	PC13-FG45	0.059	0.357	$4{\cdot}10^{-3}$
4	CC51-AC1	0.181	0.042	$6{\cdot}10^{-5}$
4	CC59-CC138	0.0986	0.044	$3{\cdot}10^{-2}$

between UDP96-018 and PC102, around the most distorted marker FG83 ($p = 6{\cdot}10^{-7}$) (Fig. 3). All the codominant markers in that region showed non-Mendelian ratios in favour of *P. davidiana* alleles and a significant excess of heterozygotes. Conversely, a significant deficit of *P. davidiana* alleles was observed for markers on the other extreme of LG1, around AG47 ($p = 2{\cdot}10^{-3}$). For all the distorted loci on LG1 mentioned previously, the hypothesis of zygotic selection was statistically retained. Other highly skewed loci were found on LG3 along which peach alleles were favoured, in particular for CC2 ($p = 5{\cdot}10^{-4}$) and CC8 ($p = 2{\cdot}10^{-3}$). Neither gametic nor zygotic selection was clearly demonstrated to explain the tendency of this linkage group.

Comparative mapping with the *Prunus* reference map

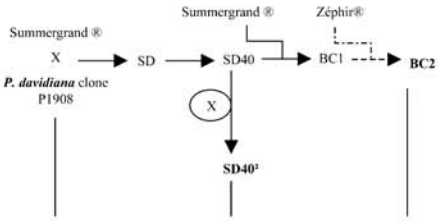
The $SD40^2$ map covered approximately 96% of the T × E map. Using the subset of the 57 markers common to the $SD40^2$ map and theT × E map, a quantitative and qualitative comparative mapping involving about 80% of the length of each map was performed.

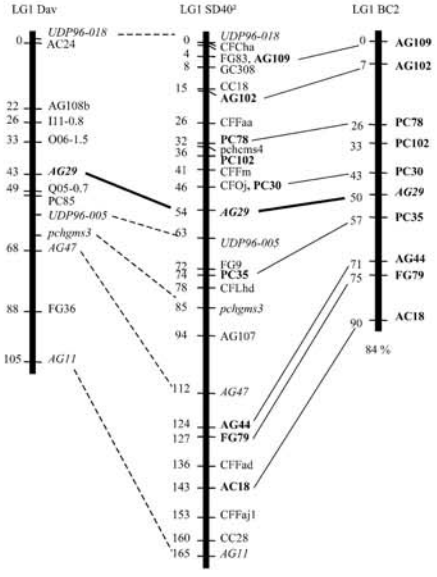
No significant difference in locus order was observed between the two maps (Fig. 2). On one end of LG3 and on LG8 linkage, analysis did not allow us to determine unambiguously the most likely order (i.e. the two possible orders differed by less than one LOD unit). The order in agreement with the T × E map was then retained. In both cases, mapping inaccuracy was mainly due to dominant markers involved in linkage analysis.

The distance of the $SD40^2$ map was, on average, 1.78-fold times the distance of the T×E map (Fig. 4). Among linkage groups, this rate ranged from 1.23 for LG8 to 2 for LG2 and LG3. The paired *t*-tests revealed significant differences on recombination rates between the T × E map and the $SD40^2$ map (Fig. 4), both for the 50 common segments ($t = 5.67$, $p = 8{\cdot}10^{-7}$, $df = 49$) and for the segments between the two most distant anchor loci of each linkage group ($t = 3.59$, $p = 9{\cdot}10^{-3}$, $df = 7$).

According to the homogeneity χ^2 test, recombination rates differed significantly between the two populations for 17 segments out of 50. The largest deviations between the two populations are reported in Table 1.

Fig. 5 Alignment of the *P. davidiana*, $SD40^2$ and BC2 maps. LG Dav, LG $SD40^2$ and LG BC2 refer to the linkage group of the *P. davidiana* map, the $SD40^2$ map and the BC2 map respectively. The *P. davidiana* map (on the left) has already been described by Viruel et al. (1998), only SSR and AFLP anchor loci were added. Markers encoded are as described in Fig. 2. Loci in *italic characters* are anchor points between *P. davidiana* and $SD40^2$ maps, and are connected by *dotted lines*. Loci in *bold characters* are anchor points between $SD40^2$ and BC2 maps and are connected by *full lines*. Loci common to the three maps are both *in italic and bold characters* and are connected by *bold lines*. For the BC2 map, the percentage of the $SD40^2$ map coverage is specified under each linkage group. The lack of data for BC2 LG8 and for *P. davidiana* LG7 is noted by a *dotted bar*


Summergrand ®
Summergrand ®
Zéphir®
X
SD
SD40
BC1
BC2
P. davidiana clone
P1908
X
SD40²


LG1 Dav
LG1 SD40²
LG1 BC2
UDP96-018
AC24
AG108b
I11-0.8
O06-1.5
AG29
Q05-0.7
PC85
UDP96-005
pchgms3
AG47
FG36
AG11
CFCha
FG83, AG109
GC308
CC18
AG102
CFFaa
PC78
pchcms4
PC102
CFFm
CFOj, PC30
FG9
PC35
CFLhd
AG107
AG44
FG79
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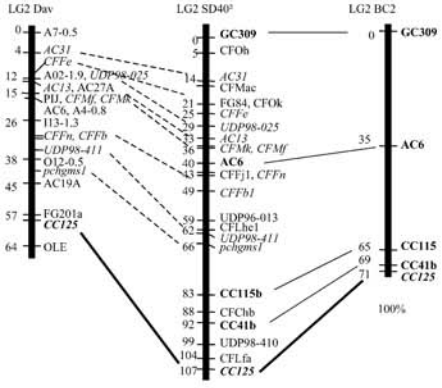
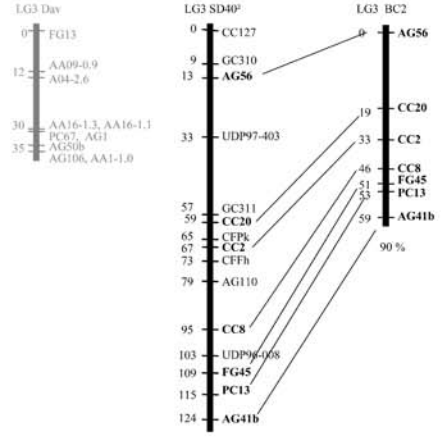
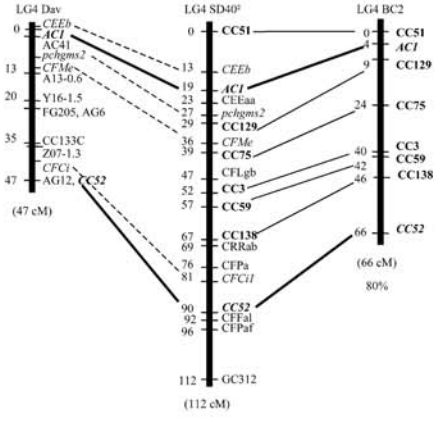
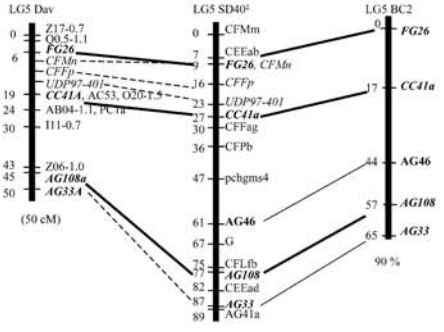
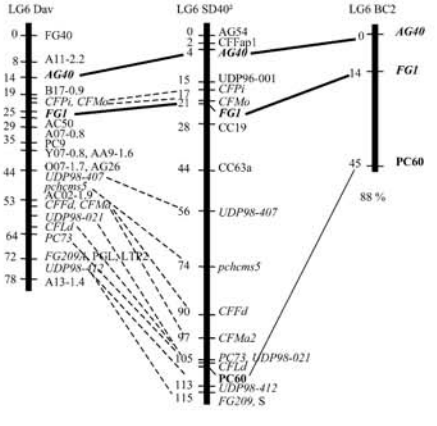
PC35
AG44
FG79
AC18
84 %

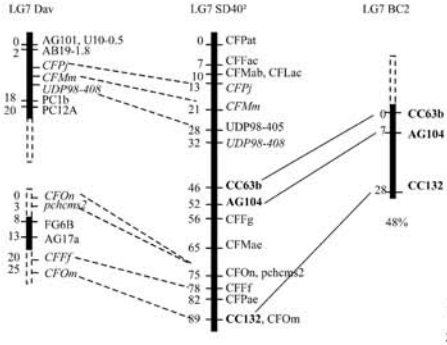

LG2 Dav
LG2 SD40²
LG2 BC2
A7-0.5
AC31
CFFe
A02-1.9, UDP98-025
AC13, AC27A
PU, CFMf, CFMh
AC6, A4-0.8
I13-1.3
CFFn, CFFb
UDP98-411
O12-0.5
pchgms1
AC19A
FG201a
CC125
OLE
GC309
CFOh
AC31
CFMac
FG84, CFOk
CFFe
UDP98-025
AC13
CFMk, CFMf
AC6
CFFj1, CFFn
CFFb1
UDP96-013
CFLhe1
UDP98-411
pchgms1
CC115b
CFChb
CC41b
UDP98-410
CFLfa
CC125
GC309
AC6
CC115
CC41b
CC125
100%


LG3 Dav
LG3 SD40²
LG3 BC2
FG13
AA09-0.9
A04-2.6
AA16-1.3, AA16-1.1
PC67, AG1
AG50b
AG106, AA1-1.0
CC127
GC310
AG56
UDP97-403
GC311
CC20
CFPk
CC2
CFFh
AG110
CC8
UDP98-008
FG45
PC13
AG41b
AG56
CC20
CC2
CC8
FG45
PC13
AG41b
90 %


LG4 Dav
LG4 SD40²
LG4 BC2
CEEb
AC1
AC41
pchgms2
CFMe
A13-0.6
Y16-1.5
FG205, AG6
CC133C
Z07-1.3
CFCi
AG12, CC52
(47 cM)
CC51
CEEb
AC1
CEEaa
pchgms2
CC129
CFMe
CC75
CFLgb
CC3
CC59
CC138
CRRab
CFPa
CFCi1
CC52
CFFal
CFPaf
GC312
(112 cM)
CC51
AC1
CC129
CC75
CC3
CC59
CC138
CC52
(66 cM)
80%


LG5 Dav
LG5 SD40²
LG5 BC2
Z17-0.7
Q0.5-1.1
FG26
CFMn
CFFp
UDP97-401
CC41A, AC53, O20-1.5
AB04-1.1, PC1a
I11-0.7
Z06-1.0
AG108a
AG33A
(50 cM)
CFMm
CEEab
FG26, CFMn
CFFp
UDP97-401
CC41a
CFFag
CFPb
pchgms4
AG46
G
CFLfb
AG108
CEEad
AG33
AG41a
FG26
CC41a
AG46
AG108
AG33
90 %


LG6 Dav
LG6 SD40²
LG6 BC2
FG40
A11-2.2
AG40
B17-0.9
CFPi, CFMo
FG1
AC50
A07-0.8
PC9
Y07-0.8, AA9-1.6
O07-1.7, AG26
UDP98-407
pchgms5
AC02-1.9
CFFd, CFMa
UDP98-021
CFLd
PC73
FG209A, PRU1-1.1T2
UDP98-012
A13-1.4
AG54
CFFap1
AG40
UDP96-001
CFPi
CFMo
FG1
CC19
CC63a
UDP98-407
pchcms5
CFFd
CFMa2
PC73, UDP98-021
CFLd
PC60
UDP98-412
FG209, S
AG40
FG1
PC60
88 %


LG7 Dav
LG7 SD40²
LG7 BC2
AG101, U10-0.5
AB19-1.8
CFPj
CFMm
UDP98-408
PC1b
PC12A
CFOn
pchcms2
FG6B
AG17a
CFFj
CFOm
CFPat
CFFac
CFMab, CFLac
CFPj
CFMm
UDP98-405
UDP98-408
CC63b
AG104
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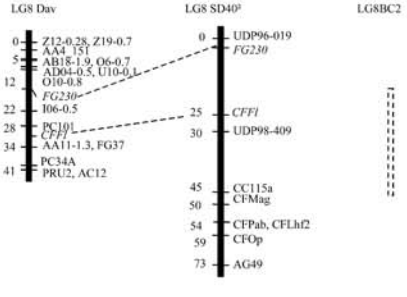
CFMae
CFOn, pchcms2
CFFf
CFPae
CC132, CFOm
CC63b
AG104
CC132
48%


LG8 Dav
LG8 SD40²
LG8BC2
Z12-0.28, Z19-0.7
AA4_151
AB18-1.9, O6-0.7
AD04-0.5, U10-0.1
O10-0.8
FG230
I06-0.5
PC101
CFFl
AA11-1.3, FG37
PC34A
PRU2, AC12
UDP96-019
FG230
CFFl
UDP98-409
CC115a
CFMag
CFPab, CFLhf2
CFOp
AG49

Alignment of the *P. davidiana*, SD40[2] and BC2 maps

Integration of new AFLP and SSR markers on the P. davidiana map

Fourteen SSR and 22 AFLP markers were added successfully within the existing framework of the *Dav* map (Fig. 5). However, the addition of new markers did not allow us to complete the genetic linkage map of *P. davidiana*, since linkage group 7 remained split into two parts. There were 53 anchor-markers between the SD40[2] map and the Dav map, spanning about 70% of each map. The highest number of anchor loci was (14) on LG6, whereas LG3 did not carry any. The conservation of the marker order between the Dav map and the SD40[2] map was verified.

The paired *t*-tests did not reveal significant differences in recombination rates between the Dav map and the SD40[2] map (Fig. 4), either for the 45 common segments ($t = -1.14$, $p = 0.25$, $df = 44$) or the segments between the two most distant anchor loci of each linkage group ($t = -1.64$, $p = 0.15$, $df = 7$). The homogeneity χ^2 tests detected only four significant differences in recombination rate (Table 1). Conversely, the distances on the T × E map were significantly smaller than those of the Dav map ($t = -2.89$, $p = 6{\cdot}10^{-3}$, $df = 37$).

BC2 genetic linkage map

The BC2 map composed of 41 RFLP markers (Fig. 5) was organized into seven linkage groups. Linkage group 8 was not represented because none of the RFLP markers located on the SD40[2] map could be used on the BC2 progeny: CC115 revealed several loci, FG230 was dominant and with AG49, the *P. davidiana* allele could not be clearly differentiated from the Zephir allele. For the other groups, the coverage of the SD40[2] map ranged from 84% to 100%, except for LG7, with a coverage of 48%. This arose from the fact that more than half of LG7 of the SD40[2] maps was covered only by AFLPs and SSRs. The overall BC2 map-coverage for the comparison with the SD40[2] map was 73%. The average distance between markers was 9.41 cM, ranging from 6.43 cM for LG3 to 12.33 cM for LG6. Indeed, a large gap of 31 cM was located on this last group, between FG1 and PC60. Other gaps were also observed on LG3 between GC309 and AG6, and between AG6 and CC115a.

For each linkage group, the order of the markers established by the mapping algorithm of MapManager QTX software was the same as the SD40[2] map-order (Fig. 5). As illustrated in Fig. 4, the paired *t*-test did not reveal any significant difference in recombination rates between the SD40[2] map and the BC2 map ($t = 0.36$, $p = 0.72$, $df = 30$).

Discussion

Analysis of distorted segregation

From our results, the use of *P. davidiana* as a genitor in crosses with *P. persica* does not seem to drastically affect the allele transmission rate in the progeny.

The observed percentage of markers exhibiting significant transmission distortion (30% at $\alpha = 5\%$) in our F2 population, appears to be in the lower part of the range reported for interspecific F2 populations in the various genera reviewed by Jenczewski et al. 1997) as well as in *Lactuca* (Jeuken et al. 2001), in *Tetramolopium* (Whitkus et al. 1998) and in *Lycopersicon* (Paterson et al. 1991). Higher proportions of skewed loci, 37% (Foolad et al. 1995) and 42% (Joobeur et al. 1998), were observed in two almond × peach F2 progenies.

The distortions equally affected alleles from the two species. Depending on the part of the genome considered, either *P. persica* or *P. davidiana* alleles were underrepresented. Unidirectional deviations against the wild genotype, as reported in some interspecific maps (Whitkus 1998; Ky et al. 2000; Fishman et al. 2001; Jeuken et al. 2001), did not occur in the analysis of the SD40[2] progeny. Furthermore, the distortions observed did not lead to the elimination of either *P. davidiana* or *P. persica* alleles. The most pronounced deviations, 2.1% for the homozygous *P. persica* genotype and 3.3% for the homozygous *P. davidiana* genotype instead of the 25% expected, were quite similar to those reported in other cases: 3.2% in the *japonica* × *indica* rice cross (Harushima et al. 1996) or 1.7% in almond × peach progeny (Joobeur et al. 1998). In addition, the type of selection observed was not likely to cause the elimination of one type of allele. Zygotic selection, which occurred most frequently, resulted in an excess of the heterozygous genotype, which allows the preservation of both alleles. Gametic selection, which has a more direct effect than zygotic selection on allele frequencies, was also observed on LG6 but, since it probably acted only on one sex, its effect was attenuated.

Skewed loci were concentrated in some specific regions, suggesting local rather than global selection events. Such a pattern has been commonly described in either intraspecific or interspecific crosses (reviewed by Jenczewski et al. 1997). As noted by Zamir and Tadmor (1986) and Lyttle (1991), this configuration suggests the presence of a small number of loci under strong selection pressure influencing flanking marker transmission by linkage. Simulations on our data confirmed that selection on a few loci could lead to the pattern of distortion observed (data not shown). Distorting factors have been described as deleterious recessive alleles, pre- or post-syngamic selected allelic combinations, self-incompatibility alleles or even structural rearrangement (Lyttle 1991). The detailed examination of the genotype frequencies allowed us to put forward some hypotheses about the mechanisms leading to transmission-ratio distortion.

Among the various biological events liable to explain zygotic selection, lower fitness of recombinant genotypes, resulting from the breaking of associations of co-adapted genes (Jenczewski et al. 1997), seems unlikely to act at both extremities of LG1. Under this assumption, both parental forms should be predominantly favoured over recombinants. In our study, only unidirectional bias against one or the other parent was observed on this linkage group.

Deficits of carrier parent homozygotes in the F2 population may more probably be due to a lethal or semi-lethal recessive allele. Such an allele, heterozygous in one parent and transmitted to the F1 hybrid, would cause differential zygote mortality after selfing and segregation. Thus zygotic selection would be a consequence of inbreeding depression rather than an interspecific cross. Such a phenomenon is particularly conceivable for *P. davidiana* which is preferentially allogamous and highly heterozygous.

The gametic selection effects noted on LG6 could result from several mechanisms. For example, abnormal pairing of chromosomes or meiotic irregularities could affect the proportion of viable gametes in F1 hybrids (Lyttle 1991). Otherwise, the differential fertilization success of viable F1 gametes could also affect the transmission ratio. Under competition conditions, variation in pollen-tube growth rate could be observed and thus constitute a prezygotic barrier (Rieseberg and Carney 1998). Genetic factors, controlling sterility or self-incompatibility, could also affect fertilization success. Our data allowed us to consider this last mechanism more thoroughly. Indeed the self-incompatibility process could explain selection detected on one end of LG6, around marker FG209, and concerning 16% of the distorted loci. Such a causal relationship between the self incompatibility locus and segregation deviation has been hypothesized previously (e.g. Lashermes et al. 1996; Lorieux et al. 2000). Several points support such a hypothesis in our case: (1) on the basis of phenotypic observations, the self-incompatibility gene of almond (SI) was located by Ballester et al. (1998) on one extreme on LG6 and 5 cM from Pgl1, i.e. between UDP98-412 and FG209 on the $SD40^2$ map, according to the position of anchor loci between $SD40^2$ and the T × E maps; (2) the use of the primer-set specific to the self-incompatibility allele of almond (Tamura et al. 2000) revealed a segregating marker in our F2 population co-located with FG209; (3) FG209 showed a strong unbalanced ratio between homozygotes, with a deficit of *P. davidiana* alleles; (4) selection on FG209 is likely to be due to gametic selection acting only on one sex, which is expected in the case of gametophytic self-incompatibility; (5) self-incompatibility studied in other *Prunus* species (almond, cherry, apricot) was found to be gametophytic; and (6) self incompatibility has not been formally described in *P. davidiana,* but this species is known to be preferentially allogamous.

Clearly, no single genetic mechanism could account for the patterns of transmission-ratio distortion observed. Further investigations on the effects of differential gamete viability, pollen competition, the self-incompatibility process or zygote mortality on the biased transmission, would be necessary to confirm our hypotheses. However, our results indicate that the possible effect of heterospecific genome interactions on segregation is minimized, and that the whole genome of *P. davidiana* could be transmitted to further generations in an introgression programme context.

Analysis of recombination through comparative mapping

Comparative mapping revealed that the interspecific hybrids *P. davidiana* × *P. persica* could normally recombine along the whole genome, allowing easy genetic information exchange. Consensus order observed between the $SD40^2$ map and the T × E map suggested that no major structural rearrangement, such as that reported by Jauregui et al. (2001) in a F2 progeny issued from an interspecific cross between peach and almond, occurred between *P. davidiana* and *P. persica*. Moreover, the alignment of the two maps demonstrated the occurrence of uniform recombination without suppressed recombination areas between *P. davidiana* and *P. persica*, since marker loci were spread randomly on the entire genome and no marker cluster was revealed. These results were also confirmed by the colinearity observed between the maps of the three generations.

Comparative analysis of recombination rates performed herein suggested that *P. davidiana* is very close to *P. persica*. Whereas, due to a lower homology between DNA strands inducing a reduction in chiasma frequency, reduced recombination rates in interspecific mapping populations have been often reported (Causse et al. 1994; Lefebvre et al. 1995; Ky et al. 2000), the recombination rates in the intraspecific *P. davidiana* map were quite similar to the recombination rates in the interspecific $SD40^2$ map. Accordingly, the recombination rates in our BC2 map did not differ statistically from recombination rates in the $SD40^2$ map, whereas the recombination rate was often observed to increase in advanced backcross generations due to a progressive return to the recipient genome (Rick 1969).

Through the comparison of recombination rates, *P. davidiana* appeared to be closer to peach than *Prunus amygdalus*. Even though the loci order was conserved between the $SD40^2$ map and the reference map, large differences in the recombination estimation were pointed out. The recombination rate in $SD40^2$ was on average 1.78-times the recombination rate in T × E, in coherence with the ratio of map lengths (874 cM in the $SD40^2$ map vs 491 cM in the T × E map). Although intra- and interspecific map sizes have been frequently compared, few results were reported concerning comparisons of recombination rates: 1.4-fold to 2-fold ratios in maize (Tulsieram et al. 1992; Williams et al. 1995) and a 1.12 ratio in *Ceratotropis* (Kaga et al. 2000). Compared to available data, the difference observed between $SD40^2$ and T × E is

relatively high. The difference observed between the two interspecific maps may result from a lower genome homology between almond and peach than between *P. davidiana* and peach. In tomato, such differences associated to closeness between species were observed. With similar population sizes and the same number of mapped markers, Fulton (1997) obtained a map length of 865 cM (*Lycopersicon esculentum* × *Lycopersicon peruvianum*), whereas, with closer parents (*L. esculentum* × *Lycopersicon pimpenellifolium*), Grandillo and Tanksley (1996) constructed a map of 1,279 cM in length. However, a low recombination rate inherent to the almond genome could also explain the difference between the $SD40^2$ map and the T × E map. This has been already put forward to explain the shortness of both the intraspecific almond map (Viruel et al. 1995) and the interspecific almond × peach map (Joobeur et al. 1998).

Altogether, these results confirmed the hypothesis based on morphological characters, that *P. davidiana* is more closely related to *P. persica* than *P. amygdalus*. In Rehder's (1949) classification, the subgenus *Amygdalus* is subdivided into three species, *persica, davidiana* and *amygdalus*, but, interestingly, the older classification of Miller (1768) distinguished the subgenus *Amygdalus* and the subgenus *Persica* which includes *P. persica* (L.) Batsch and *P. davidiana*. The closeness of the two species was also hypothesized by Hedrick (1917) who considered *P. davidiana* as the ancestor of the current peach varieties on the basis of morphological characters. A recent study using SSR molecular markers confirmed, by another approach, that *P. davidiana* is closer to peach than almond (Martinez-Gomez et al. 2002).

Consequences in plant breeding strategy

The efficient use of the genetic variation available in related species such as almond or *P. davidiana* appeared essential to monitor peach breeding schemes. In an introgression programme, since the objective is to obtain recombinants possessing the favourable genes of the wild parent, and genes from the cultivated species at the other loci, recombination ability is a critical factor to consider. The comparison of recombination rates in $SD40^2$ and T × E progenies suggests that the main difficulties could be different when introgressing genes from almond or *P. davidiana* into peach. Using almond as a progenitor, due to the low recombination rate with peach, the main concern would be to reduce the length of the donor segment around the gene(s) of interest. With *P. davidiana*, linkage drag on the carrier chromosome is expected to be lower. Conversely, due to the possible dispersal of small unfavourable donor segments along the whole recipient chromosome, the background selection could be difficult, all the more if it is delayed after several generations of back- or inter-crossing. If marker-assisted selection is used, "controlling" markers physically closer to the gene(s) or QTLs of interest with *P. davidiana* than with almond donors will be required to avoid disruptive recombination and consecutive loss of the gene(s) to be introgressed in advanced generations.

Distortions of segregation were shown to affect a few regions of the genome. The knowledge of the type of selection leading to transmission-ratio distortions and the location of biased parts of the genome should allow us to more thoughtfully monitor breeding experiments. Indeed, consequences for breeding programmes will depend on the effects of *P. davidiana* alleles on agronomic characters for genes located in those regions, and on the type of selection encountered. Natural selection against *P. davidiana* alleles may hamper the introgression of resistance factors. This might occur on LG3, where a QTL for resistance to *Myzus persicae* has been evidenced near marker AG50A (Sauge et al. 2001), and on LG6, where a major QTL of resistance to powdery mildew has been detected in the F1 progeny (Dirlewanger et al. 1996). In both locations, selection strongly acted against individuals homozygous for the *P. davidiana* allele, whereas the number of heterozygotes was little affected. If the effects of the QTLs mentioned above are purely additive, the more desirable individuals, i.e. individuals homozygous for *P. davidiana* alleles, will be difficult to obtain. Conversely if resistance factors are dominant, the frequency of desirable individuals, i.e. individuals either homozygous for *P. davidiana* alleles or heterozygous, will be less reduced. Natural selection against *P. davidiana* alleles may be helpful if it accelerates the elimination of factors detrimental to agronomic characters brought by *P. davidiana*. If selection for *P. davidiana* alleles occurs, as on LG1, introgression of resistant factors will be facilitated, but elimination of possible poor-agronomic genes will be more difficult.

The present study demonstrated the potential of *P. davidiana* to introgress characters of interest into peach. The three maps obtained in this study on the F1, F2 and BC2 generations provide efficient tools to perform the genetic study of *P. davidiana* and to develop an efficient introgression programme. Analysis on F2 progeny will give additional information on the inheritance of agronomic traits to complement the genetic study of *P. davidiana* already undertaken on the F1 progeny (Dirlewanger et al. 1996). The molecular data collected on the BC2 progenies will make it possible to evaluate the percentage of the wild genome introgressed, as in the study performed in tomato (Fulton et al. 1997), and to identify the unfavourable *P. davidiana* alleles for fruit and tree characteristics.

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