

Linkage map saturation, construction, and comparison in four populations of *Prunus*

By E. ILLA¹, P. LAMBERT², B. QUILOT², J. M. AUDERGON², E. DIRLEWANGER³, W. HOWAD¹, L. DONDINI⁴, S. TARTARINI⁴, O. LAIN⁵, R. TESTOLIN⁵, D. BASSI⁶ and P. ARÚS^{1*}

¹IRTA, Centre de Recerca en Agrigenòmica CSIC-IRTA-UAB, Carretera de Cabrils Km 2, 08348 Cabrils, Spain

²INRA, UR1052, Unité de Génétique et Amélioration des Fruits et Légumes (GAFL), Domaine de St Maurice, B.P. 94, F-84143 Montfavet, France

³INRA, UR419, Unité de Recherches sur les Espèces Fruitières (UREF), B.P. 81, F-33140 Villenave d'Ornon, France

⁴Dipartimento di Coltura Arborea, University of Bologna, via Fanin 46, Bologna, Italy

⁵Dipartimento di Scienze Agrarie e Ambientali, University of Udine, Via delle Scienze 208, 33100 Udine, Italy

⁶Dipartimento di Produzione Vegetale, University of Milan, Via Celoria 2, 20133, Milano, Italy
(e-mail: pere.arus@irta.cat)

(Accepted 1 September 2009)

SUMMARY

One of the objectives of the ISAFRUIT Project was to perform genetic analyses in four populations of *Prunus*, two of peach (*P. persica*) and two of apricot (*P. armeniaca*), in order to identify major genes and quantitative trait loci (QTLs) for characters related to fruit quality. This required the construction of saturated marker maps in each of these populations. Marker maps were available for an intra-specific peach × peach F₂, a BC₂ peach × *P. davidiana* (using peach as the recurrent parent), and an apricot × apricot F₁. We have further saturated these maps mainly with SSR (simple sequence repeat) markers. A new map, constructed uniquely from SSRs was prepared for a fourth apricot × apricot F₁ population. Using anchor markers, we compared these four maps with the reference *Prunus* map, constructed using an almond × peach F₂ population. As previously observed, conservation of synteny and co-linearity were the general rule, providing additional evidence of the high level of similarity between all *Prunus* genomes. Comparisons of genetic distances between the maps suggested that those involving similar genomes had higher levels of recombination than those with more distant genomes, particularly the inter-specific crosses.

Linkage maps have been constructed in various *Prunus* species for genetic studies, synteny analysis, or for mapping major genes or quantitative trait loci (QTLs) (Arús *et al.*, 2005; Dirlewanger *et al.*, 2004). The development and use of SSR (simple sequence repeat) markers in these species has proved to be particularly effective for mapping, given their polymorphism and high level of transferability within the *Prunus* genus (Dirlewanger *et al.*, 2002). A simple and robust approach to mapping and map comparison within this genus is possible, based on the map positions of SSRs in the *Prunus* reference map (Dirlewanger *et al.*, 2004; Howad *et al.*, 2005), by selecting a subset of reference map markers that segregate in the progeny of interest and cover the complete genome, and using these for comparison with the reference map and other published maps.

The analysis of maps with common markers, constructed with different populations involving genotypes of seven *Prunus* species, has shown that their genomes are highly syntenic and co-linear, and so can be

considered as a single genome (Arús *et al.*, 2005; Dirlewanger *et al.*, 2004). This facilitates the location of genes or QTLs mapped in any population of any species at a single position in the *Prunus* genome (Dirlewanger *et al.*, 2004).

In the ISAFRUIT Project, we have taken advantage of the similarity among *Prunus* genomes to study the position of genes or QTLs involved in fruit quality in four populations. For three of these populations: a peach × peach F₂ (Dirlewanger *et al.*, 2006), a peach × *P. davidiana* backcross (Quilot *et al.*, 2004), and an apricot × apricot F₁ (Dondini *et al.*, 2007), maps were already constructed and several major genes and QTLs had been studied. We mapped additional markers and further saturated these three maps to improve their quality for QTL analysis. We constructed a new map based only on SSR markers in an additional apricot × apricot F₁ population. Using common markers, we compared the maps obtained for these four populations and the reference *Prunus* map, as a necessary first step prior to comparisons of the genome positions of genes and QTLs for fruit quality that will be obtained during the ISAFRUIT Project.

*Author for correspondence.

MATERIALS AND METHODS

Plant material

We used four populations with parents that had contrasting phenotypes for many fruit quality characters. The first population was 'Ferjalou Jalousia' × 'Fantasia' (J × F), a peach × peach F₂ mapping population (n = 208) previously used for QTL mapping of peach fruit quality (Dirlewanger *et al.*, 2006). The second was an advanced backcross progeny (Quilot *et al.*, 2004) from a cross between peach (cv. Summergrand) and *P. davidiana* (clone P1908). One of the resulting F₁ hybrids was backcrossed to 'Summergrand' to obtain a BC₁ progeny. A mixture of pollen from BC₁ individuals was used to pollinate a white-fleshed nectarine to generate this mapping population, named BC₂ (n = 163). The third mapping population consisted of 125 F₁ individuals from the cross between two apricot genotypes, 'Lito' and 'BO81604311', named L × B (Dondini *et al.*, 2007). The fourth population (G × M) was a progeny (n = 126) of F₁ plants derived from a cross between two apricot genotypes: the American cultivar 'Goldrich', and the Spanish cultivar 'Moniqui'.

DNA isolation

Samples of young expanded terminal leaves were collected and DNA was extracted following the methods described for J × F (Dirlewanger *et al.*, 2006), BC₂ (Quilot *et al.*, 2004), L × B (Dondini *et al.*, 2007), and for G × M (Lambert *et al.*, 2004).

Genotyping

Maps have been published for J × F (Dirlewanger *et al.*, 2007), BC₂ (Quilot *et al.*, 2004), and L × B (Dondini *et al.*, 2007). A map for the G × M population is presented here for the first time. SSR markers isolated from different *Prunus* species were used to further saturate the J × F, BC₂ and L × B maps using the mapped SSRs in the *Prunus* reference map (Dirlewanger *et al.*, 2004, Howad *et al.*, 2005), constructed with the 'Texas' almond × 'Earlygold' (T × E) peach F₂ population, where the positions of 449 SSRs have been established.

Given the low level of variability of J × F, AFLP markers were added to the J × F population (Dirlewanger *et al.*, 2006). For selective amplifications, *Pst* I primers with two selective nucleotides and *Mse* I primers with three selective nucleotides (named pXX-YYY; X being the selective nucleotides for the *Pst* I primers and Y the selective nucleotides for the *Mse* I primers) were used.

The SSR markers used for the construction of the G × M map were selected from those already described in various *Prunus* species including peach (Aranzana *et al.*, 2002; Cipriani *et al.*, 1999; Dirlewanger *et al.*, 2002; Sosinski *et al.*, 2000; Testolin *et al.*, 2000; Yamamoto *et al.*, 2002; 2005), almond (Mnejja *et al.*, 2005; Testolin *et al.*, 2004), apricot (Decroocq *et al.*, 2003; Hagen *et al.*, 2004; Lopes *et al.*, 2002; Messina *et al.*, 2004), and Japanese plum (Mnejja *et al.*, 2004). Most of the markers selected were already mapped in the T × E reference map.

PCR amplifications, electrophoresis, and DNA labelling were performed according to published protocols used in the authors' laboratories (Aranzana *et al.*, 2003; Dirlewanger *et al.*, 2006; Dondini *et al.*, 2007;

Lambert *et al.*, 2004). Mapping data were obtained by visual scoring of the band patterns.

Linkage map construction

Linkage maps were constructed using MapMaker/EXP Version 3.0 software (Lander *et al.*, 1987). In the case of the F₂ (J × F), we constructed a single map using the "f2 intercross" command of MapMaker and, for the BC₂ population, we used the "f2 backcross" command. Both apricot populations were F₁ segregating progenies, for which we constructed two maps, one for each parent, that were treated as first backcrosses for linkage analysis. The Kosambi function (Kosambi, 1944) was used to convert recombination units into genetic distances. The maps were drawn using Mapchart Version 2.1 software (Voorrips, 2002) with distances in centimorgans (cM). Linkage group terminology was the same as in the *Prunus* reference T × E map (Joobeur *et al.*, 1998).

Comparative mapping

Genetic distances between maps were compared using a paired *t*-test (two-tailed) of the difference between the map distances of the two furthest-apart anchor markers of each T × E linkage group, and that of the map compared with it (degrees of freedom = number of compared linkage groups minus one).

RESULTS AND DISCUSSION

The three available genetic linkage maps (J × F, BC₂ and L × B) were saturated mainly with SSR markers, then compared with the *Prunus* T × E map (Dirlewanger *et al.*, 2004). In addition, the first genetic linkage map for the cross between the apricot cultivars 'Goldrich' and 'Moniqui' is reported here.

The linkage map for J × F (Dirlewanger *et al.*, 2006) had a total length of 636.4 cM, with a total of 187 markers (37 RFLPs, 61 AFLPs, 82 SSR loci, six agronomical traits, and one isoenzyme gene) mapped to seven linkage groups. In addition, we have mapped 38 AFLPs and one microsatellite (CPPCT040; Figure 1) increasing the total number of loci to 208, with a mean marker density of 3.06 cM per marker. Linkage group 8 (G8) was not present because all known SSR markers located in this group were monomorphic. This suggests a case of "identity by descent" in this chromosome; a likely possibility considering that both parents were closely-related (Dirlewanger *et al.*, 2006). Despite the saturation, nine gaps longer than 15 cM were still present in J × F in linkage groups G1, G2, G3, G4, and G6 (Table I).

The genetic map for the BC₂ population contained 80 markers: 41 RFLPs, 29 AFLPs, and ten SSRs (Quilot *et al.*, 2004). The map covered most of the linkage groups from the *Prunus* reference map (Dirlewanger *et al.*, 2004). However, G8 was only represented by a single marker, and seven gaps greater than 15 cM remained. In order to saturate the existing map, we tested the polymorphism of 126 SSRs. Ninety-six (76.2%) of these microsatellites revealed a polymorphism between the two initial parents (P1908 and 'Summergrand'). Similar levels of polymorphism (70%) had previously been reported (Foulongne *et al.*, 2003). Fifty-nine segregating SSRs, located in regions with low marker density, were selected

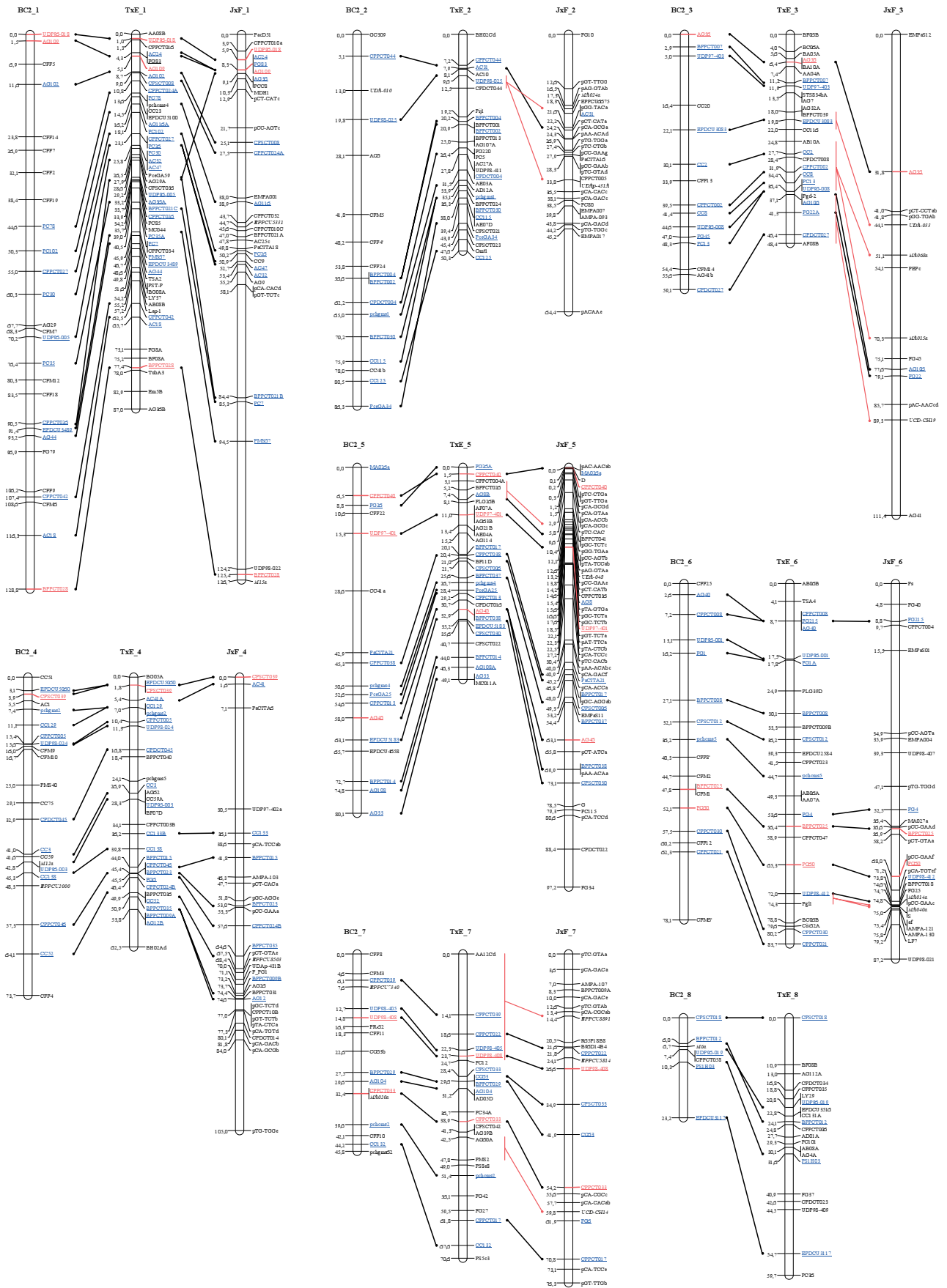


Fig. 1

Alignment of the two peach-based maps: BC₂ and J × F, further saturated in the present paper, and the ‘Texas’ almond × ‘Earlygold’ peach (T × E) map (Dirlewanger *et al.*, 2004). Common markers are underlined. Those markers present in all three maps are in red. Those markers that appear in two of the three maps are in blue. Markers bin-mapped in the T × E map (Howad *et al.*, 2005) are shown in italics.

TABLE I
Main characteristics of the four genetic maps of *Prunus*

Progeny name	Population size	Cross Type [†]	Length (cM)	Number of polymorphic markers	Mean distance between markers	Gaps (> 15 cM)
J × F	208	F ₂	636.4	208	3.06	9
BC ₂	163	BC ₂	575.1	139	4.14	1
L × B	125	F ₁ ('Lito')	715.0	161	4.44	7
		F ₁ ('BO81604311')	929.0	168	5.53	11
G × M	126	F ₁ ('Goldrich')	468.0	85	5.51	9
		F ₁ ('Moniquí')	706.8	63	11.22	15

[†]In parentheses, the name of the parent map for F₁ segregating populations.

and mapped using the whole BC₂ population. The resulting map (Table I; Figure 1) covered a total of 575.1 cM, with a density of 4.14 cM per marker, and contained 139 markers (41 RFLPs, 69 SSRs and 29 AFLPs) distributed in eight linkage groups. G8, previously with only one marker, now had seven microsatellites covering 23.2 cM. The same seven SSRs cover a distance of 54.7 cM in the *Prunus* reference map. The addition of 59 new markers therefore reduced the number of gaps longer than 15 cM from seven to one, located at the end of G6 between CPPCT021 and CFM6 (15.8 cM).

The linkage maps of the apricot accessions 'Lito' and 'BO81604311' (Dondini *et al.*, 2007) were also saturated with 44 markers: 18 (17 SSRs and one gene) in 'Lito' and 26 loci (22 SSRs and four genes) in 'BO81604311'. Of these, ten SSRs were common to both maps. The co-linearity of the maps of the two parents was confirmed by the relative positions of 93 co-dominant markers in both maps. Only a few inversions were observed in G1 and at the top of, or above G2 (Figure 1). This version of the 'BO81604311' and 'Lito' maps increased the number of gaps greater than 15 cM in both maps: from three to seven in 'Lito', and from six to 11 in 'BO81604311'. This almost certainly arose because these maps were previously constructed using JoinMap, which is known to produce shorter maps than Mapmaker (Stam, 1993; van Ooijen and Voorrips, 2002).

The two linkage maps constructed using the 'Goldrich' × 'Moniquí' population had the eight expected linkage groups and totalled 468.0 cM for 'Goldrich' and 706.8 cM for 'Moniquí' (Figure 2). A total of 85 SSR loci segregated in 'Goldrich' and 63 in the male parent 'Moniquí', corresponding to average marker densities of 5.51 cM per marker and 11.22 cM per marker, respectively. Nine gaps ≥ 15 cM were still present in

'Goldrich', and 15 in 'Moniquí'. Thirty-nine anchor markers in both maps showed the expected general synteny and co-linearity of the parental genomes (Figure 2). Inversions involving pairs of contiguous loci were observed in G1 and G3. However, the order of a group of five markers in the middle of G2 was different in the 'Moniquí' and 'Goldrich' maps. Four of these markers, which were common in the T × E *Prunus* map, had the same order as in 'Moniquí', but differed in the 'Goldrich' map, where they were located in a cluster of 12.5 cM.

Comparative mapping with the T × E *Prunus* reference map

Between 22 and 82 common markers (mostly SSRs and some RFLPs) were shared between the linkage maps of the four populations and the T × E reference map (Figure 1; Figure 2). The numbers of common markers for each of the six maps were as follows: J × F, 48; BC₂, 82; 'Lito', 27; 'BO81604311', 31; 'Goldrich', 32; and 'Moniquí', 22.

This analysis confirms that the linear order of markers is basically maintained across the different *Prunus* species, although comparisons of the maps with the T × E reference map showed a small number of markers that were not co-linear (Table II; Figure 1; Figure 2). Markers with a different order within the same linkage group were frequently contiguous, and separated by only a few cM, suggesting that these discrepancies were more likely to be due to sampling or scoring errors leading to slight differences in the order of loci than to chromosomal rearrangements.

Some SSR primer pairs amplified segregating fragments that mapped to unexpected positions when compared to other published *Prunus* maps (Dirlewanger *et al.*, 2006; 2004, Dondini *et al.*, 2007; Lambert *et al.*, 2004;

TABLE II
Comparison of *Prunus* linkage maps with the reference 'Texas' × 'Earlygold' (T × E) map

Population	Map type [†]	Markers in common with T × E	Anchor marker % in same group as T × E [‡]	Non-colinear markers [§]	% T × E coverage [¶]	Common % distance [#]	Paired <i>t</i> -test comparison with T × E ^{¶¶}
'Texas' × 'Earlygold'	F ₂	562	100	0	100	100	—
'Ferjalou Jalousia' × 'Fantasia'	F ₂	48	96	1	61	141	2.95*
'Summergrand' × <i>P. davidiana</i>	BC ₂	82	100	4	85	117	0.96
'Goldrich' × 'Moniquí'	F ₁ ('Goldrich')	32	100	3	43	115	0.93
	F ₁ ('Moniquí')	22	95	1	29	185	5.62**
'Lito' × BO81604311	F ₁ ('Lito')	27	100	1	58	113	0.66
	F ₁ ('BO81604311')	31	97	0	57	176	2.16

[†]In parentheses, the name of the parent map for F₁ segregating populations.

[‡]Percentage of anchor markers located on the same linkage group as T × E.

[§]Number of markers placed on the same linkage group as T × E, but in a different order (generally pairs of markers in inverted order; only one marker is considered).

[¶]Percentage of the T × E map covered by the other map calculated as: distance of T × E covered x100 / total T × E distance.

[#]Relative size of the common maps: common distance covered in a map x 100 / total distance covered in T × E.

^{¶¶}Paired *t*-test of the comparison between the distances of the two furthest-apart common markers in each linkage group.

P* ≤ 0.05; *P* ≤ 0.01.

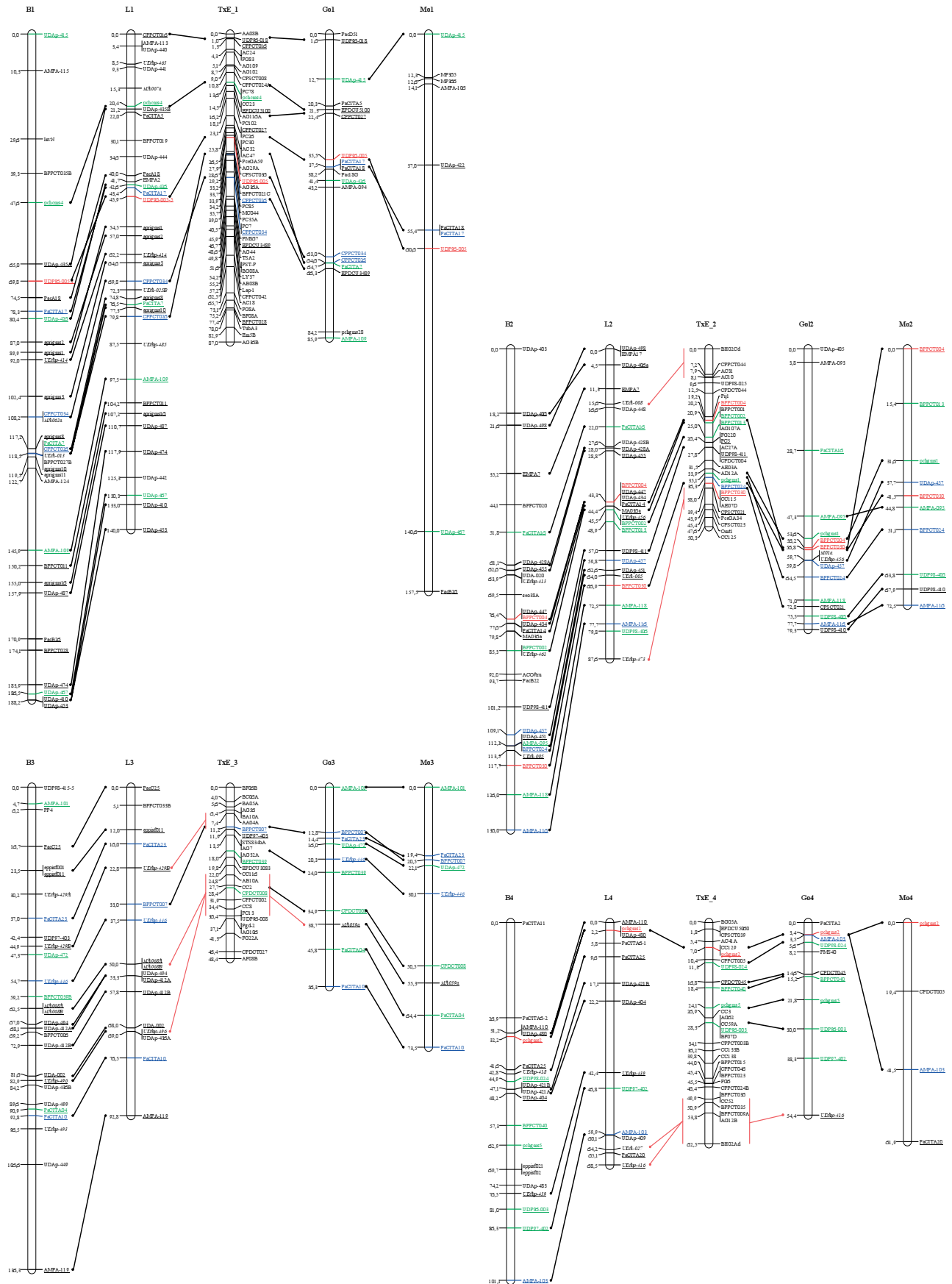


FIG. 2 (continued overleaf)

Alignment of the different apricot-based maps: ‘Lito’ (L), ‘BO81604311’ (B), ‘Goldrich’ (Go), and ‘Monique’ (Mo), and the ‘Texas’ almond × ‘Earlygold’ peach (T × E) map (Dirlewanger *et al.*, 2004). Common markers are underlined. Those markers present in all five maps are in red. Those markers that appear in four of the five maps are in blue, and those markers that appear in three of the five maps are in green. Markers bin-mapped in the T × E map (Howad *et al.*, 2005) are shown in italics.

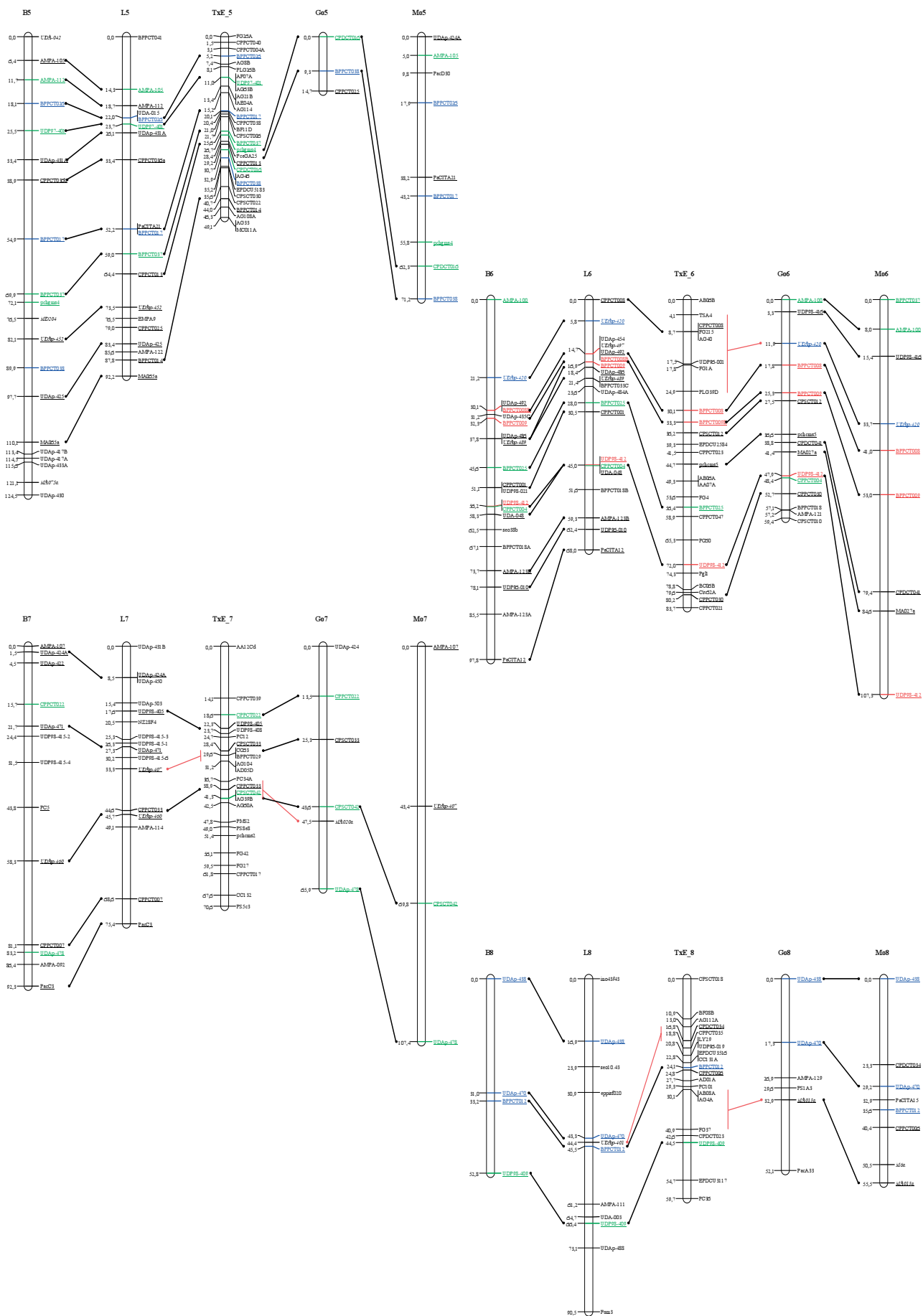


FIG. 2 (continued from previous page)

Verde *et al.*, 2005; Vilanova *et al.*, 2003). Seven (BPPCT006, BPPCT019, BPPCT020, BPPCT033, BPPCT035, UDA-025, and UDAp-415) have been described as SSRs detecting multiple loci located in different chromosomes (Dondini *et al.*, 2007). Similarly, an additional locus for BPPCT037 was detected in apricot, placed on top of G6 in the 'Moniquí' map. Nine markers from the UDA (UDA-002, UDA-003, UDA-015, and UDA-048) and UDAp series (UDAp-412, UDAp-426, UDAp-431, UDAp-435, and UDAp-471) mapped to linkage groups different from their positions established by bin-mapping (Howad *et al.*, 2005). Finally, in the J × F map, CPPCT005 was assigned to G2; while, in the T × E map, it was in G4. In addition, the FG6 marker was located on G7 of J × F, but was in the middle of G4 in the T × E map.

All six maps were longer than the T × E map (Table II), which was expected, given the overall reduction in recombination associated with its inter-specific nature. The same has been found in previous comparisons between *Prunus* maps (Arús *et al.*, 2005) and in other species (Gebhardt *et al.*, 1991). Length differences were significant in only two intra-specific crosses: the peach F₂ (J × F), and the apricot 'Moniquí'. These were expected

to be the most homozygous genomes among those studied in this work. The F₁ hybrid plant, J × F, was a seedling of the cross between two related genotypes of peach, the least variable *Prunus* species; and 'Moniquí,' a cultivar of Spanish origin, was known to have one of the lowest levels of heterozygosity in apricot (de Vicente *et al.*, 2002). Based on a comparison of a sample of 16 *Prunus* maps, Arús *et al.* (2005) concluded that the specific composition of each individual for genes affecting recombination was the major cause of the differences in genetic distance observed between homologous genome regions. Our results suggest that the similarity between the two homologous genome components in each individual may also play a significant role in its level of recombination.

The ISAFRUIT Project is funded by the European Commission under Thematic Priority 5 – Food Quality and Safety of the 6th Framework Programme of RTD (Contract No. FP6-FOOD-CT-2006-016279).

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