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Abstract The genome organization of globe artichoke (*C. cardunculus* var. *scolymus*), unlike other species belonging to *Asteraceae* (= *Composite*) family (i.e. sunflower, lettuce and chicory), remains largely unexplored. The species is highly heterozygous and suffers marked inbreeding depression when forced to self-fertilize. Thus a two-way pseudo-testcross represents the optimal strategy for linkage analysis. We report here linkage maps based on the progeny of a cross between globe artichoke (var. *scolymus*) and cultivated cardoon (var. *altilis*). The population was genotyped using a variety of PCR-based marker platforms, resulting in the identification of 708 testcross markers suitable for map construction. The male map consisted of 177 loci arranged in 17 major linkage groups, spanning 1015.5cM , while female map was built with 326 loci arranged into 20 major linkage groups, spanning 1486.8cM. The presence of 84 loci shared between these maps and those previously developed from a cross within globe artichoke allowed for map alignment and the definition of 17 homologous linkage groups, corresponding to the haploid number of the species. This will provide a favorable property for QTL scanning; furthermore, as 23 mapped markers (7%,) correspond to coding regions, it has an additional values as functional map and might represent an important genetic tool for candidate gene studies in globe artichoke.

Key words: globe artichoke – cultivated cardoon - linkage map - AFLP- microsatellite

Introduction

Genetic maps provide a powerful means of analysing the inheritance of agronomic traits, many of which are under polygenic or oligogenic control. The establishment of linkage relationships between molecular marker loci represents the initial step in the identification of which chromosomal regions carry genes relevant for marker assisted breeding applications. The *Asteraceae* (*Compositae*) species *Cynara cardunculus* L. is native to the Mediterranean basin, and incorporates the *taxa* globe artichoke (var. *scolymus*), cultivated cardoon (var. *altilis*) and wild cardoon (var. *sylvestris*); the latter is by far the most widely distributed of these, thriving in warm, dry and low altitude environments. The globe artichoke makes a significant contribution to the agricultural economy of southern Europe, and is also cultivated across North Africa, the Middle East, South America, the USA and China (http://faostat.fao.org/). The cultivated cardoon is of some regional importance to local cuisine in Italy, Spain and southern France. The three *taxa* are sexually compatible with one another, producing fertile inter-*taxon* F_1 hybrids. Thus the wild and cultivated cardoon together represent a natural genetic resource for globe artichoke improvement. The species is an out-breeder, and is characteristically highly heterozygous. Its marked level of inbreeding depression inhibits the use of backcross, F_2 or recombinant inbred populations for mapping purposes. As haploid induction - via either andro- or gynogenesis - has till now not been achievable (Chatelet et al. 2005; Motzo and Deidda 1993; Stamigna et al. 2005), no possibility is presently available to generate doubled haploid populations. Thus, genetic mapping in globe artichoke has had to rely on a double pseudo-testcross approach, in which segregating F_1 progeny are derived from a cross between two heterozygous individuals.

The first genetic maps of *C. cardunculus* were provided by Lanteri et al. (2006), based on a cross between 'Romanesco C3' (a late-maturing non-spiny type as female) and 'Spinoso di Palermo' (an early-maturing spiny type as male). This population was genotyped using a number of PCR-based marker platforms, resulting in a ~1300cM female map consisting of 204 loci, divided into 18 linkage groups (LGs) and a ~1200cM male map comprising 180 loci and 17 LGs. The two maps shared 78 loci, which allowed for the alignment of 16 of the LGs. The maps have since been extended

by the inclusion of a number of microsatellite loci, of which 19 were represented in both maps (Acquadro et al. 2009). Three genes involved in the synthesis of caffeoylquinic acid have also been positioned on the maps (Comino et al. 2007, 2009; Moglia et al. 2009) .

The aims of the research described in this paper were to develop a genetic map based on a cross between the same female parent as previously ('Romanesco C3') and an accession of cultivated cardoon, and to align this map with the one already established.

Materials and methods

Plant material and DNA isolation

The mapping population was a set of F_1 progeny derived from a controlled cross between the globe artichoke 'Romanesco C3' and the cultivated cardoon 'Altilis 41' genotypes. Hybrid seeds were germinated in lightly moistened potting mix at room temperature. Emergence occurred within 10-12 days, and healthy seedlings were transferred to the field after about 30 days, at which time the seedlings had developed three true leaves. Two weeks after transplanting in the field, DNA was extracted following Lanteri et al. (2001) and the hybridity of each progeny was confirmed by genotyping with two microsatellite markers. Of the 154 true hybrids, a random selection of 94 was used for marker linkage analysis and genetic map construction, and the presence / absence of spines was scored on well developed leaves over two seasons (2006 and 2007).

Marker analysis

AFLP profiling followed Vos et al. (1995) with minor modifications as described by Lanteri et al. (2004). Parental and progeny DNA was digested with either *Eco*RI/*Mse*I (E/M), *Pst*I/*Mse*I (P/M) or *Eco*RI/*Taq*I (E/T), and ligated to standard adaptors. The ligation reaction was used as a template for pre-amplification, using primers

complementary to the adaptor sequences plus one selective nucleotide (*Eco*RI+A, *Pst*I+A, *Mse*I+C, *Taq*I+T). Selective amplification was performed using primers with two or three selective nucleotides. The same E/M and P/M AFLP primer combinations (PCs) were used as those chosen by Lanteri et al. (2006). A further 20 E/T PCs (five *Eco*RI primers x four *Taq*I primers) were applied to the parental and six of the progeny DNA templates in order to extend the number of informative PCs to 48 (18 E/M, 19 P/M and 11 E/T, see Table 1). Amplicons were electrophoretically resolved through 5% denaturing polyacrylamide gels and silver stained as described by Bassam et al. (1991).

The S-SAP fingerprinting method followed Waugh et al. (1997). The selective amplification used a fluorescence-labelled (IRD-700) cyre5 primer, designed to anneal to the long terminal repeat of a retroelement (Acquadro et al. 2006), in combination with an unlabelled AFLP primer with three selective nucleotides (Table 1). PCR products were separated on a DNA analyser Gene ReadIR 4200 (LI-COR) through 6.5% polyacrylamide gels (Sigma), as described by Jackson and Matthews (2000). The S-SAP primer pairs used by Lanteri et al. (2006) were implemented by the three most polymorphic E/T based PCs (Table 1).

A set of 114 microsatellite primer pairs was used to amplify template of the two parents and six progeny. Of these, 93 have been developed by our laboratory (Acquadro et al. 2003, 2005a, b, 2009). Eight SSRs were developed from the genic sequences SST (sucrose-sucrose 1 - fructosyltransferase), cyprosin (an aspartic proteinase), and phenylalanine ammonia-lyase (PAL) (De Paolis et al. 2008). Of the 61 genomic CELMS microsatellites (Acquadro et al. 2009), 27 contained at least one open reading frame and have been assumed to target genic sequence. Primer pairs identifying polymorphism in this screen were applied to the full mapping population. The PCR conditions were as detailed by (Acquadro et al. 2005a), and the amplicons were separated as described above for the S-SAP markers.

Single nucleotide polymorphism (SNP) assays were directed at the two acyltrasferase genes HCT and HQT (Comino et al. 2009; Comino et al. 2007) and the hydroxylase gene C3′H (Moglia et al.), assayed by a tetra-primer ARMS-PCR method (Ye et al. 2001; Chiapparino et al. 2004) and separated by 2% agarose gel electrophoresis.

All electrophoretic profiles were documented using the Quantity One Programme gel documentation system (BioRad). Each PCR was replicated once, and only unambiguous fragments were considered. AFLP and S-SAP profiles were treated as sets of dominant markers (presence / absence of fragment), and each markers was named according to the primer combination used to generate it, followed by the estimated molecular weight of the fragment; e.g. e33/t89-166 is an AFLP fragment of 166-bp length amplified by primer pair *Eco*+AAG/*Taq*+TGG. Microsatellite and SNP loci were identified by the primer pair used for their assay.

Linkage analysis and map construction

Markers were grouped as either maternal testcross markers (segregating only within 'Romanesco C3') with an expected monogenic segregation ratio of 1:1; paternal testcross markers (segregating only within 'Altilis 41'); or intercross markers (segregating in both parents), with an expected segregation ratio of 3:1 for dominant markers, and 1:2:1 for co-dominant ones. Co-dominant markers showing three or four alleles (one parent *ab*, the other either *ac* or *cd*) , giving an expected segregation ratio of 1:1:1:1, were initially converted into 1:1 markers, according to the parental origin of the segregating alleles, and so were included within either the maternal or paternal data sets.

Independent framework linkage maps were constructed for each parent on the basis of the double pseudo-testcross mapping strategy (Weeden 1994), with only those markers in the testcross configuration being considered. One linkage map was generated for 'Romanesco C3', and a second for 'Altilis 41', by applying JoinMap v4.0 (Van Ooijen 2006) and treating the populations as a backcross. Goodness-of fit between observed and expected segregation was assessed using the χ^2 test. Markers fitting a Mendelian pattern closely ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.01}$) or with only a minor deviation ($\chi^2 > \chi^2_{\alpha=0.01}$) were used for map construction and for the estimation of genetic distances, when their presence did not alter surrounding marker order in the LG. Those for which the deviation was highly significant ($\chi^2 > \chi^2_{\alpha=0.01}$) were not immediately excluded but were handled with caution in subsequent analyses (see further). Markers with missing data for more than 30 of the 94 F_1 individuals were excluded. For both maps, LGs were

established on the basis of an initial threshold logarithm of odds ratio (LOD) of 6.0, with parameters set as follows: Rec=0.40, LOD=1.0, Jump=5.

Once the framework maps had been established, the intercross markers were added as accessory markers, by treating the population as a cross-pollination type. Intercross markers were associated with particular LGs, but were not used for the estimation of genetic distances. Additional accessory markers were subsequently added by lowering the LOD threshold to 4.0, with the inclusion of the ones departing from the Mendelian ratio at the $\alpha > 0.001$ level of confidence. They were not forced in the map to avoid potential artefact (major variation in marker orders and relative distances), but checked one by one and placed in their most likely position within LGs.

Markers deviating in their segregation only marginally from the expected Mendelian ratio were identified with one ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.05}$) two ($\chi^2_{\alpha=0.05} < \chi^2 \leq \chi^2_{\alpha=0.01}$) or three ($\chi^2 > \chi^2_{\alpha=0.01}$) asterisks (Fig. 1). LGs on the female map were named LG_C3, and those on the male map LG_Alt, with both numbered serially in descending order of genetic length (Fig. 1, Table 2).

Results

Genotyping

The 48 AFLP PCs produced 719 informative markers, of which 638 (89%) were testcross markers, and the remainder intercross markers. Per AFLP PC, the number of informative fragments ranged from 5 to 34, with a mean of 15. The most informative enzyme combination was E/T and the least P/M. The number of S-SAP markers ranged from two to eight per PC (mean 4.2), producing 42 mappable markers (38 testcross, four intercross).

Of the combined 676 AFLP and S-SAP testcross markers, 400 (59%) segregated in ‘Romanesco C3’ and 276 (41%) in ‘Altilis 41’. About 13% produced distorted segregation ratios ($\chi^2 > \chi^2_{\alpha=0.1}$), resulting in the discarding of 51 markers (44 testcross (22 for each parent) and seven intercross).

Of the 114 microsatellite primer pairs, 56 segregated in the F_1 population for at least one parent with major differences in their informativeness (70% of the CELMS markers, only 7% of the CsLib and none of the CsEST loci). Of the 22 which segregated in both parents, 21 segregated consistently with a 1:1:1:1 and the remaining one with a 1:2:1 ratio . The other 34 loci segregated within only one of the parents (29 female and five male only). Five loci suffered from minor segregation distortion ($\chi^2_{\alpha=0.05} < \chi^2 \leq \chi^2_{\alpha=0.01}$).

Only the female parent was heterozygous for the SNPs HCTsnp97, HQTsnp359 and C3H'snp447, all of which segregated consistently with a 1:1 ratio.

Phenotyping

The presence/absence of spines is controlled by a single gene with the two alleles *Sp* (dominant non-spiny) and *sp* (recessive spiny) (Lanteri et al. 2006). Spines were absent from both parents. As the character segregated consistently among the F_1 progeny with a 3:1 ratio (χ^2 = 0.35), both parents were clearly of genotype *Spsp*. To locate this gene within an LG, the data were treated as resulting from the segregation of a dominant intercross marker.

Map construction

From the 431 loci (359 AFLP, 19 S-SAP, 50 microsatellite and three SNP) segregating in the female parent, a map was generated which consisted of 326 loci grouped into 20 LGs (each with four or more loci), for a total genetic length of 1486.8cM (Table 2, Fig. 1A). A further nine loci formed one triplet and three doublets. LG length varied from 35.0 to 138.7cM, with the largest containing 49 loci. The bulk (77%) of map intervals were less than 7cM, with only eight gaps of >15cM. To evaluate the reliability of the LGs, for each marker pairs with gaps >10 cM, the specific LOD in support of the two-point placement were checked and reported in the Electronic supplementary table S1. The E/M, E/T and P/M AFLP loci were evenly distributed, without any noticeable clustering of loci generated by any one PC. Only two LGs (C3_6 and _18) were composed solely of AFLP loci. The 46 microsatellite loci which mapped within an LG

were distributed over 17 LGs. The 15 loci for which segregation was marginally distorted, mapped to nine LGs (eight at α=0.05 and seven at α=0.01). None of these distorted loci were linked to one another.

The male map was based on segregation at 280 loci (246 AFLP, eight S-SAP and 26 microsatellite). Here, 176 loci were distributed over 17 LGs, covering 1015.5cM, with four triplets and 11 doublets (Table 2, Fig. 1B). LG length varied from 17.4 to 117.7cM and the highest number of loci per LG was 26. Most of the genetic intervals (79%) were <10cM, with 11 gaps of >15cM, the largest of which was 20.1cM (on LG Alt_11, see Electronic supplementary table S1). The AFLP loci were evenly distributed over the 17 LGs, with no apparent clustering of markers generated by any one PC. Five LGs (Alt_8, _11, _13, _14 and _16) included only AFLP markers, and the 23 mapped microsatellite loci were distributed over 12 LGs. The ten loci showing minor segregation distortion mapped to six LGs (four at α=0.05 and six at α=0.01), and a group of linked distorted loci was present on LG_Alt_2.

Of 79 intercross markers , 25 (22 AFLP, one microsatellite, one S-SAP, *Sp/sp*; Table 3) were assigned to a specific LG, but were not ordered within their LG. These, together with 18 microsatellite loci, were used to identify 11 homologous LGs (Table 3). The number of common markers per homologous LG varied between one and nine. *Sp/sp* was assigned to LG C3_14 and to LG Alt_7 (Table 3).

Accessory markers not placed in LGs at the initial stringency (LOD ≥ 6), together with the highly distorted loci, were subsequently added to the maps when showing linkage only to a single LG and with a LOD score ≥ 4. Table 4 reports the most likely positions within LGs for the accessory testcross markers. As a result of this second stage of analysis, two doublets of the female map (Fig. 1A) were linked to LG C3_2 and C3_12 (Table 4). In the globe artichoke map, the most likely positioning of the highly distorted markers did not evidence clustering of distorted loci, while in the cultivated cardoon map a highly distorted locus was added to the cluster present at the end of LG Alt_2 (Table 4). A complete list of the accessory markers is reported in the Electronic supplementary table S2.

Map alignment

The female map was compared with the 'Romanesco C3' map produced by Lanteri et al. (2006) using 32 common microsatellite loci, three common SNP loci and 49 common AFLP/S-SAP loci. These bridge markers identified 17 LGs (I to XVII in Fig. 2). Between one and 12 loci were present on any one of these aligned LGs, with microsatellite loci on 11 LGs and at least one AFLP locus on all 17. Eleven of the LGs aligned readily. In LGs III, IV and VI two groups (major or minor) of the previous developed map joined and aligned with one group of the present map. On the other hand, in LGs XI and XII two groups of the present map joined and aligned with one group of the previous ones. LG XIII is formed by two LGs from the previous and the present maps, which might be merged on the basis of microsatellite CMAL-21 (Fig. 2). Although the mean genetic separation between pairs of loci and their relative order were mostly conserved across the two maps, twelve variation in marker order, affecting ten LGs, were detected.

Discussion

Map construction

Here we have applied the double pseudo-testcross mapping strategy to construct linkage maps of a globe artichoke and a cultivated cardoon genotypes. The efficiency of this strategy depends both on the level of heterozygosity present in the parents, and on the level of detectable polymorphism between the parents (Cervera et al. 2001; Kenis and Keulemans 2005). *C. cardunculus* is an out-crossing species, and thus is expected to be highly heterozygous. By intermating two different *taxa* it has been possible to create a population segregating for a number of significant agronomic traits (such as the size, shape, weight and form of the head, and biomass production), as well as for the content of a number of secondary metabolism products of nutraceutical and pharmaceutical interest (Comino et al. 2007; Lanteri and Portis 2008).

For the linkage analysis of populations in cross-pollinating species, dominant intercross markers can be highly non-informative in certain configurations, and very often generate zero estimates for recombination frequency (Maliepaard et al. 1997); a further problem concerning co-dominant markers is that 1:2:1 segregations do not allow for the deduction of the parental origin of the segregating alleles (Maliepaard et al. 1998). The inclusion of markers segregating within both parents produces an estimate for recombination frequency which is the average outcome of both male and female meiosis, so may differ from estimated testcross frequencies, which are based on either male or female meiosis. Conflicts can thus arise between marker orders. The usefulness of a map clearly depends on its faithful reflection of actual locus order, so a decision was made to build the framework maps by excluding intercross markers which segregated consistently with a 3:1 or a 1:2:1 ratio. The cross used to generate these maps was wider than the one used to develop the first *C. cardunculus* maps (Lanteri et al. 2006), so there was a decreased number of common alleles between the parents and fewer markers segregating either 3:1 or 1:2:1.

The number of informative loci was lower for the cultivated cardoon parent than for the globe artichoke one, suggesting that the latter parent was more heterozygous than the former. Of the 114 microsatellite loci, 26 were heterozygous in the male parent and and 50 in the female parent, giving estimates for the respective levels of heterozygosity of ~23% and ~44%, which is in broad agreement with the assessment of genetic variation previously detected in globe artichoke (Portis et al. 2005). 'Romanesco C3' is vegetatively propagated and has maintained its level of heterozygosity over time, whereas cultivated cardoon is seed-propagated and has probably been subjected to a limited degree of purifying selection aimed at stabilizing its production.

Framework maps were constructed using a high grouping threshold (LOD 6) along with an interval support LOD threshold of 1. The male parent framework map length (1015.5cM, 17 major LGs) was rather smaller than the female one (1486.8cM, 20 major LGs), and a higher frequency of unlinked triplets and duplets was generated, which suggests that certain genomic regions remain under-represented. Indeed, an higher efficiency in map construction of the most heterozygous parent has been previously reported in rubber tree (Lespinasse et al. 2000) and apricot (Hurtado et al. 2002). Despite the large number of markers used to construct the female map, the

number of LGs was greater than the known haploid number of 17. This may be because the mapping parameters were overly stringent, but may also be due a paucity of polymorphism in certain chromosomal regions. Although 43 intercross markers were assignable to an LG (Table 3), this number was insufficient to generate a genome-wide map, as only 11 LGs could be identified in this way.

Marker distribution and segregation ratio distortion

AFLPs were generated from restriction fragments produced by digestion with *Pst*I and *Mse*I (P/M), or *Eco*RI and either *Mse*I or *Taq*I (E/M, E/T). Although fewer E/M markers were obtained than E/T markers, their genomic distribution was more uniform. A globe artichoke map based solely on E/M PCs would give an higher coverage (862cM) than the one based on E/T PCs (757cM), making the former more suitable for mapping saturation. However their combination improves the density of the linkage map. Some gaps remain in the female map, such as the ~20cM ones on LGs C3_3, C3_11 and C3_18, and some of the LGs have a high mean inter-marker distance (>10cM; LGs C3_6, C3_11 and C3_18). These may reflect localized low recombination rates, such as characterize the centromeric chromosome regions (Tanksley et al. 1992) or regions containing an excess of repetitive DNA (Jeuken et al. 2001; Vuylsteke et al. 1999).

Microsatellite loci are represented on 17 of the 20 female LGs, and 12 of the 17 male LGs. Two of the mapped microsatellites lie within the known genes SST and PAL, and others within genes whose function has been identified in other species (Electronic supplementary table S3). The present results have confirmed the assignment of the HCT, HQT and C3'H genes (Comino et al. 2009; Moglia et al. 2009), involved in caffeoyl quinic acids biosynthesis, to specific globe artichoke LGs. The placement on the globe artichoke map of functionally annotated gene-derived markers may help to clarify the role of the genes which influence traits of interest, and is an essential step in the process of identifying candidate genes underlying the mechanisms of important morphological and physiological traits (Marino et al. 2009; Sargent et al. 2006; Vezzulli et al. 2008).

In the population derived from an intra-*taxa* (globe artichoke) cross (Lanteri et al. 2006), segregation distortion affected ~10% of loci, while in the present population, ~13% were affected. A greater degree of distorted segregation was not unexpected since it tends to increase with the genetic distance between the parents (Grandillo and Tanksley 1996; Verde et al. 2005). The basis of segregation distortion is not clearly understood and has been attributed to a number of causes including aneuploidy, chromosomal translocations, competition among gametes, and the inheritance of alleles affecting the viability of the embryo (Gonzalo et al. 2005). Scoring and sampling errors can also influence the assessment of the level of distortion (Echt and Nelson 1997; Hackett and Broadfoot 2003; Nikaido et al. 1999). Some studies reported that where distorted markers are ignored, a significant part of a linkage group can be excluded (Cervera et al. 2001; Lorieux et al. 2000), we have only included those deviating up to 1%, to reduce the probability of false linkage. Notwithstanding, highly distorted markers have been also included in a second stage of analysis and their most likely positioning established. In the previous 'Romanesco C3' map, distorted markers clustered on LGs 1, 5 and 10 (Lanteri et al. 2006), but in the present map they were scattered across different LGs. This difference may be cross-specific (Igarashi et al. 2008) and/or may reflect the stringent LOD threshold applied.

Alignment and comparison of globe artichoke maps

Map alignment and merging of LGs is commonly achieved by analysing additional populations derived from the same parents or, as here, populations with one parent in common (Pelgas et al. 2005). We have established a skeletal globe artichoke map on the basis of 84 loci, defining 17 LGs (Fig. 2) corresponding to the haploid number of *C. cardunculus*. The three SNP loci and 32 of the microsatellite loci are present on the 'Romanesco C3' map (Lanteri et al. 2006), while a further 14 microsatellite loci have been mapped here for the first time. A set of 49 AFLP fragments common to both populations was also identified and, as previously reported (Costa et al. 2000; Krutovskii et al. 1998; Laucou et al. 1998; Zraidi et al. 2007) they have been successfully used for map alignment. both here and in other studies. In general, marker order was conserved between the two maps, although some inconsistencies were noted

(Fig. 2). Re-ordering of closely linked markers is relatively commonplace (Cervera et al. 2001; Jeuken et al. 2001; Lespinasse et al. 2000; Lombard and Delourme 2001; Sebastian et al. 2000) and reflects the statistical nature of the estimation of map order. Variation in stringency (LOD thresholds) is a major cause of mapping inconsistency, as is the use of many intercross dominant markers (Fig. 2). Other potential sources of variation are genotyping errors, an excess of missing values and the mapping of distorted markers (Hackett and Broadfoot 2003).

The extensive polymorphism between the mapping population parents reflects their taxonomical distance and helps to explain the reduced mean inter-marker map distances. The total length of the original 'Romanesco C3' map is about 93% of the present one, despite an ~33% increase in the number of loci mapped. The increased coverage of the globe artichoke genome obtained here will enable the exploration of distal portions of LGs VI, IX, X, XII and XV which were previously unmapped, as well as linking previously identified minor LGs on LGIV and VI (Fig. 2).

Conclusions

The 1C value of *C. cardunculus* has been estimated to be ~1078Mb (Marie and Brown 1993), thus the global relationship between physical and genetic distance is of the order of 1cM = 725kb. At present, none of the LGs can be assigned to a particular chromosome, a process which awaits the application of cytogenetic analysis. The current maps represent the most likely, but possibly not the actual arrangement of loci. An evenly spaced framework of markers based on the present set of LGs should facilitate genome-wide QTL scanning, and since 25 of the mapped markers (8%, Electronic supplementary table S3) identify coding regions, the present map supplies the basis for candidate gene studies within the species.

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Table 1 AFLP and SSAP primer combinations used for linkage analysis.

	Eco*RI*/Mse*I template*		*Eco*RI/*Taq*I template		*Pst*I/*Mse*I template	
	PC	**Code**	**PC**	**Code**	**PC**	**Code**
AFLP	E+AAT/M+CAG	e34/m49	E+AAC/T+TAC	e32/t80	P+AC/M+CAA	p12/m47
	E+AAT/M+CAT	e34/m50	E+AAC/T+TAG	e32/t81	P+AC/M+CAT	p12/m50
	E+ACA/M+CAA	e35/m47	E+AAC/T+TAT	e32/t82	P+AC/M+CTA	p12/m59
	E+ACA/M+CAC	e35/m48	E+AAG/T+TAC	e33/t80	P+AC/M+CTC	p12/m60
	E+ACA/M+CAG	e35/m49	E+AAG/T+TGG	e33/t89	P+AC/M+CTG	p12/m61
	E+ACA/M+CAT	e35/m50	E+ACA/T+TAC	e35/t80	P+AC/M+CTT	p12/m62
	E+ACA/M+CTT	e35/m62	E+ACA/T+TAG	e35/t81	P+AG/M+CAA	p13/m47
	E+ACC/M+CAA	e36/m47	E+ACA/T+TGG	e35/t89	P+AG/M+CAT	p13/m50
	E+ACC/M+CAC	e36/m48	E+ACT/T+TAC	e38/t80	P+AG/M+CTA	p13/m59
	E+ACC/M+CTA	e36/m59	E+ACT/T+TAT	e38/t82	P+AG/M+CTC	p13/m60
	E+ACG/M+CAG	e37/m49	E+AGA/T+TAC	e39/t80	P+AG/M+CTG	p13/m61
	E+ACG/M+CAT	e37/m50			P+AG/M+CTT	p13/m62
	E+ACG/M+CTG	e37/m61			P+ATG/M+CAA	p45/m47
	E+ACT/M+CAA	e38/m47			P+ATG/M+CAT	p45/m50
	E+ACT/M+CAT	e38/m50			P+ATG/M+CCA	p45/m51
	E+ACT/M+CTA	e38/m59			P+ATG/M+CTA	p45/m59
	E+AGA/M+CAT	e39/m50			P+ATG/M+CTC	p45/m60
	E+AGT/M+CAT	e42/m50			P+ATG/M+CTG	p45/m61
					P+ATG/M+CTT	p45/m62
S-SAP	Cyre5/E+AAG	cyre5/e33	Cyre5/T+TGA	cyre5/t87	Cyre5/P+AGT	cyre5/p42
	Cyre5/E+ACA	cyre5/e35	Cyre5/T+TGG	cyre5/t89		
	Cyre5/M+CAA	cyre5/m47	Cyre5/T+TGT	cyre5/t90		
	Cyre5/M+CAC	cyre5/m48				
	Cyre5/M+CAG	cyre5/m49				
	Cyre5/M+CAT	cyre5/m50				

Table 2 Characteristics of the globe artichoke (‘Romanesco C3’) and cultivated cardoon (‘Altilis 41’) linkage maps.

	Romanesco C3					Altilis 41			
Linkage group	**Size (cM)**	**N° of markers**	**Marker density**	**Gaps (>15 cM)**	**Linkage group**	**Size (cM)**	**N° of markers**	**Marker density**	**Gaps (>15 cM)**
C3_1	138.7	49	2.9	0	**Alt_1**	117.7	26	4.7	0
C3_2	116.3	32	3.8	0	**Alt_2**	103.9	22	4.7	0
C3_3	103.5	22	4.9	1	**Alt_3**	96.6	15	6.9	2
C3_4	102.0	14	7.8	0	**Alt_4**	78.2	20	4.1	0
C3_5	92.0	28	3.4	0	**Alt_5**	67.7	9	8.5	1
C3_6	80.6	8	11.5	2	**Alt_6**	66.7	20	3.5	0
C3_7	78.4	12	7.1	1	**Alt_7**	60.4	10	6.7	0
C3_8	76.2	24	3.3	0	**Alt_8**	56.5	6	11.3	0
C3_9	75.9	10	8.4	0	**Alt_9**	50.9	5	12.7	1
C3_10	72.8	11	7.3	0	**Alt_10**	47.9	12	4.4	0
C3_11	71.9	7	12.0	1	**Alt_11**	45.3	4	15.1	2
C3_12	67.3	22	3.2	0	**Alt_12**	44.6	6	8.9	0
C3_13	64.1	19	3.6	0	**Alt_13**	44.0	4	14.7	2
C3_14	61.0	13	5.1	1	**Alt_14**	41.5	5	10.4	0
C3_15	58.5	7	9.8	1	**Alt_15**	39.3	4	13.1	2
C3_16	58.0	16	3.9	0	**Alt_16**	36.9	4	12.3	1
C3_17	45.1	16	3.0	0	**Alt_17**	17.4	4	5.8	0
C3_18	45.4	4	15.1	1					
C3_19	44.1	6	8.8	0					
C3_20	35.0	6	7.0	0					
Average	74.3	16.3	4.6	0.4		59.7	10.4	5.7	0.6
Total	1486.8	326		8		1015.5	176		11.0

Table 3 Intercross and shared testcross markers assigned to LGs in both the globe artichoke (‘Romanesco C3’) and cultivated cardoon (‘Altilis 41’) genetic maps.

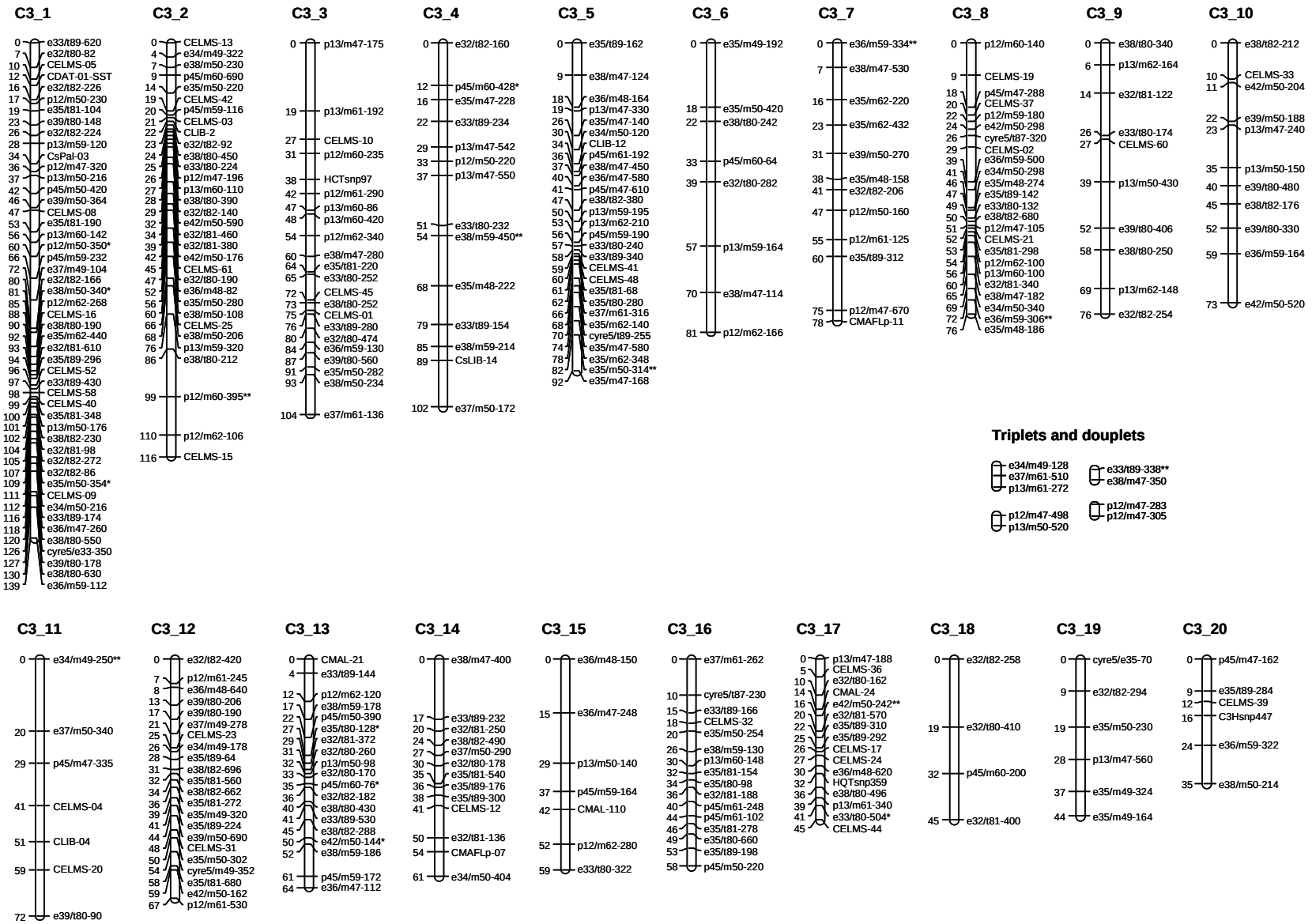
Romanesco C3 linkage group	Altilis 41 linkage group	Shared testcross markers	Intercross markers
C3_1	**Alt_2**	CELMS-05 CELMS-16 CELMS-52 CELMS-58	e35/t80-364 e36/m59-236 CELMS-26
C3_2	**Alt_4**	CELMS-13 CELMS-42 CELMS-25 CLIB-02	p12/m47-266 e33/t89-500 e36/m59-216 e33/t80-288 e32/t82-88
C3_3	**Alt_3**	CELMS-10 CELMS-01	e38/t80-154
C3_5	**Alt_1**	-	e32/t80-304 e35/t89-116
C3_7	**Alt_5**	-	e33/t80-206
C3_8	**Alt_10**	CELMS-37 CELMS-02	p12/m62-180 e35/t80-180 cyre5/m47-250
C3_9	**Alt_17**	CELMS-60	e33/t80-172 e33/t80-168
C3_11	**Alt_12**	CELMS-04	p45/m50-318
C3_14	**Alt_7**	CELMS-12 CMAFLP-07	p45/m47-142 e35/m62-102 Spines
C3_17	**Alt_9**	CELMS-17	
C3_20	**Alt_15**	CELMS-39	p12/m50-450 p13/m60-260 e35/t80-220 e33/t89-450

Table 4 Accessory testcross markers and specific LOD values in support of the two-point analysis with their linked loci. Markers showing significant levels of segregation distortion are indicated by one ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.05}$) two ($\chi^2_{\alpha=0.05} < \chi^2 \leq \chi^2_{\alpha=0.01}$) or three ($\chi^2 > \chi^2_{\alpha=0.01}$) asterisks. Markers reported as minor groups in Figure 1 are underlined.

LG	Accessory marker	Linked locus 1	LOD	Linked locus 2	LOD
C3_1	p45/m59-460	e33/t89-430	5.29	e35/t81-348	4.47
C3_2	e35/m47-340***	e38/t80-390	9.20	p13/m60-110	8.69
	p12/m60-116*	p12/m62-106	4.54	e38/t80-212	4.14
	e35/t89-496	e35/m50-220	4.87	CELMS-13	3.73
	e33/t89-338**	e38/m47-350	8.71	CELMS-15	4.12
	e38/m47-350	e33/t89-338**	8.71		
C3_3	e38/t82-214	p12/m62-340	5.11	e35/t80-252	3.71
C3_4	cyre5/m47-180***	P13/m47-542	5.44	p12/m50-220	4.97
	e39/t80-556***	e33/t80-232	4.13	e35/m48-222	4.03
C3_5	e38/t82-124	p13/m47-542	5.69	e35/m47-168	4.09
	e38/t80-504	e35/t89-162	5.21	p13/m47-330	4.14
	e35/m49-610	e36/m47-580	4.20	p13/m59-195	3.80
C3_6	p13/m60-162***	e35/m50-420	4.12	e38/t80-242	4.01
C3_8	e32/t80-230	p12/m60-140	4.02		
C3_10	e32/t82-118***	e39/t80-330	10.4	e38/t82-176	6.22
	e38/m47-144	e39/t80-330	4.99	e39/t80-480	3.47
C3_12	p12/m50-320***	e35/m50-302	4.65	e38/t82-696	4.15
	p12/m47-283	p12/m47-305	9.65	p12/m61-530	4.02
	p12/m47-305	p12/m47-283	9.65		
C3_13	e35/m47-682***	e32/t80-170	8.91	e32/t82-182	8.03
C3_15	e38/t82-600	p45/m59-164	5.03	e33/t80-322	4.25
Alt_1	e39/m50-186	p13/m47-335	4.35	p13/m50-690	3.88
Alt_2	e33/t80-340***	e32/t81-280	7.41	e35/t80-358	6.64
	e35/t89-144	e35/m47-590**	5.02	e38/m47-158*	4.66
Alt_5	cyre5/t89-110***	e33/t89-510	4.71	e39/t80-224	4.27
Alt_8	e33/t89-512***	e33/t89-190	7.39	e33/t80-178	4.74
Alt_9	cyre5/m49-170***	p13/m60-230	5.13	CELMS-17	4.06
	e38/m50-500	p13/m60-230	4.12	CELMS-17	3.34
Alt_13	e38/t82-78	e36/m47-290	5.19	p12/m62-455	4.66
	e32/t81-160	e33/t89-180	4.88	p12/m62-455	4.03
Alt_15	e37/m49-140	e35/m48-108	4.09		

Figure 1 Genetic maps of globe artichoke ‘Romanesco C3’ (A) and cultivated cardoon ‘Altilis 41’ (B). Marker names are shown to the right of each LG, with map distances (in cM) to the left. LGs with fewer than four markers are shown as ‘minor groups’. Markers showing significant levels of segregation distortion are indicated by asterisks (0.1 >*P ≥ 0.05; 0.05 >**P ≥ 0.01).

(A)



(B)

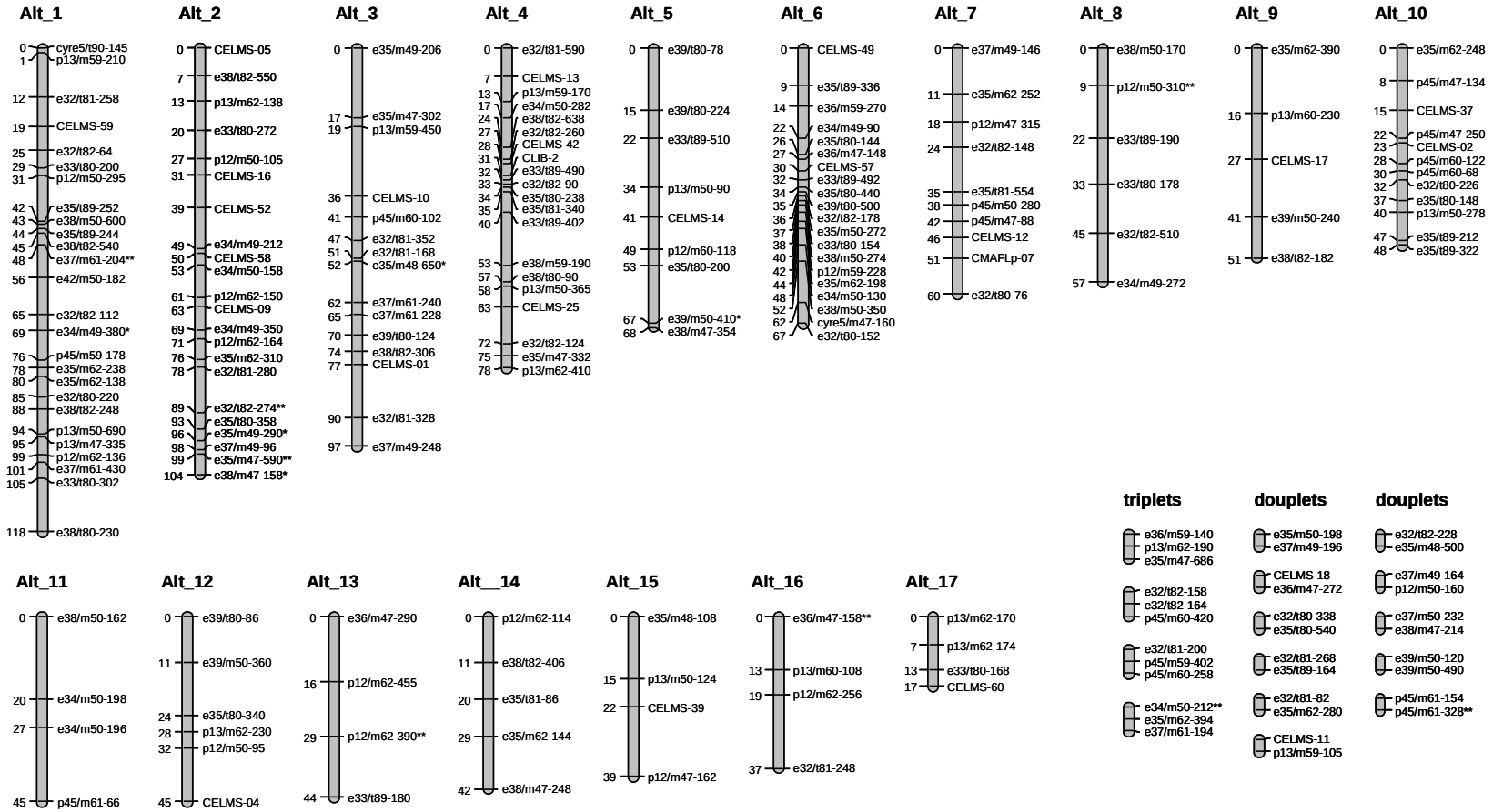
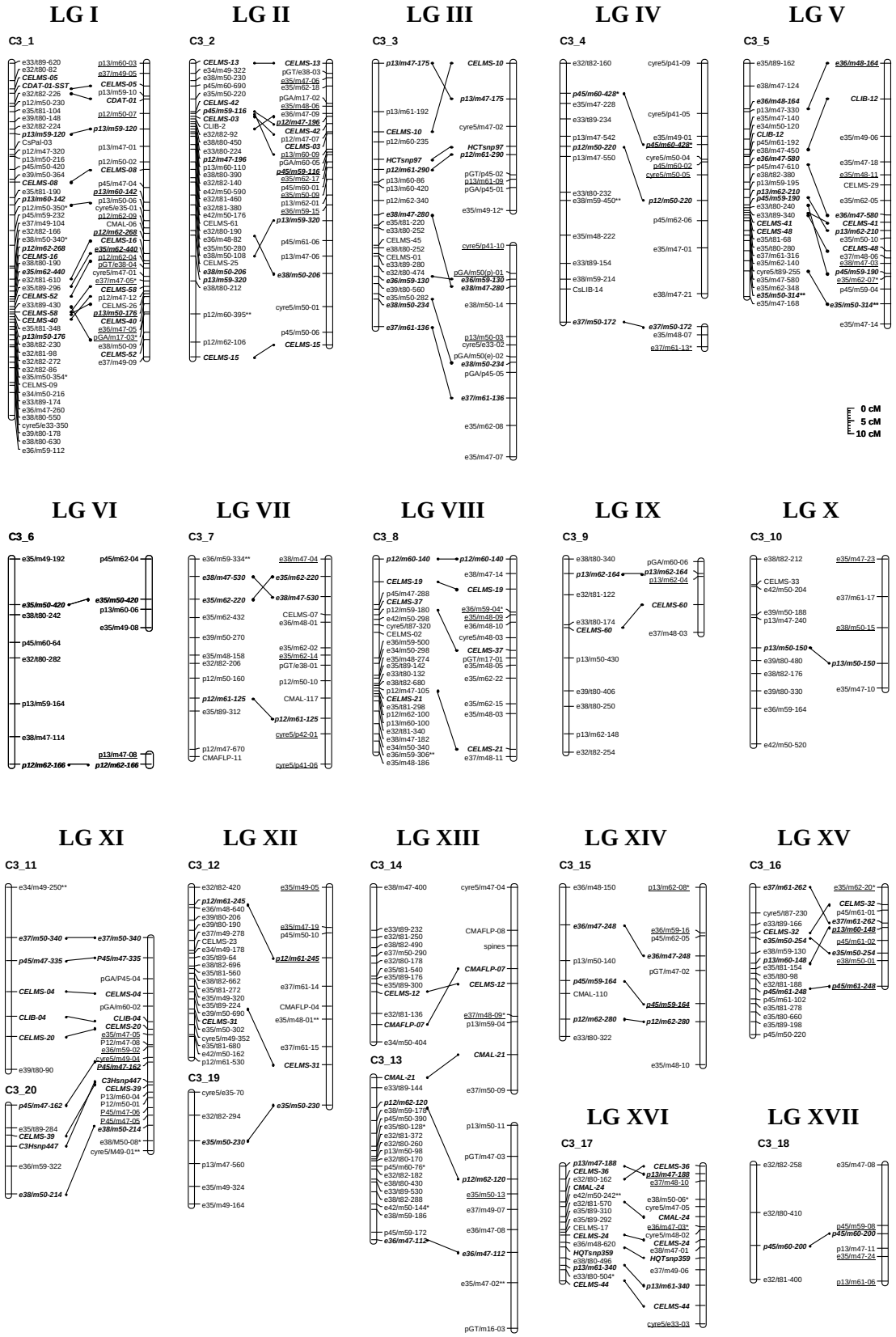

Alt_1
0 cyre5/t90-145
1 p13/m59-210
12 e32/t81-258
19 CELMS-59
25 e32/t82-64
29 e33/t80-200
31 p12/m50-295
42 e35/t89-252
43 e38/m50-600
44 e35/t89-244
45 e38/t82-540
48 e37/m61-204**
56 e42/m50-182
65 e32/t82-112
69 e34/m49-380*
76 p45/m59-178
78 e35/m62-238
80 e35/m62-138
85 e32/t80-220
88 e38/t82-248
94 p13/m50-690
95 p13/m47-335
99 p12/m62-136
101 e37/m61-430
105 e33/t80-302
118 e38/t80-230
Alt_2
0 CELMS-05
7 e38/t82-550
13 p13/m62-138
20 e33/t80-272
27 p12/m50-105
31 CELMS-16
39 CELMS-52
49 e34/m49-212
50 CELMS-58
53 e34/m50-158
61 p12/m62-150
63 CELMS-09
69 e34/m49-350
71 p12/m62-164
76 e35/m62-310
78 e32/t81-280
89 e32/t82-274**
93 e35/t80-358
96 e35/m49-290*
98 e37/m49-96
99 e35/m47-590**
104 e38/m47-158*
Alt_3
0 e35/m49-206
17 e35/m47-302
19 p13/m59-450
36 CELMS-10
41 p45/m60-102
47 e32/t81-352
51 e32/t81-168
52 e35/m48-650*
62 e37/m61-240
65 e37/m61-228
70 e39/t80-124
74 e38/t82-306
77 CELMS-01
90 e32/t81-328
97 e37/m49-248
Alt_4
0 e32/t81-590
7 CELMS-13
13 p13/m59-170
17 e34/m50-282
24 e38/t82-638
27 e32/t82-260
28 CELMS-42
31 CLIB-2
32 e33/t89-490
33 e32/t82-90
34 e35/t80-238
35 e35/t81-340
40 e33/t89-402
53 e38/m59-190
57 e38/t80-90
58 p13/m50-365
63 CELMS-25
72 e32/t82-124
75 e35/m47-332
78 p13/m62-410
Alt_5
0 e39/t80-78
15 e39/t80-224
22 e33/t89-510
34 p13/m50-90
41 CELMS-14
49 p12/m60-118
53 e35/t80-200
67 e39/m50-410*
68 e38/m47-354
Alt_6
0 CELMS-49
9 e35/t89-336
14 e36/m59-270
22 e34/m49-90
26 e35/t80-144
27 e36/m47-148
30 CELMS-57
32 e33/t89-492
34 e35/t80-440
35 e39/t80-500
36 e32/t82-178
37 e35/m50-272
38 e33/t80-154
40 e38/m50-274
42 p12/m59-228
44 e35/m62-198
48 e34/m50-130
52 e38/m50-350
62 cyre5/m47-160
67 e32/t80-152
Alt_7
0 e37/m49-146
11 e35/m62-252
18 p12/m47-315
24 e32/t82-148
35 e35/t81-554
38 p45/m50-280
42 p45/m47-88
46 CELMS-12
51 CMAFLp-07
60 e32/t80-76
Alt_8
0 e38/m50-170
9 p12/m50-310**
22 e33/t89-190
33 e33/t80-178
45 e32/t82-510
57 e34/m49-272
Alt_9
0 e35/m62-390
16 p13/m60-230
27 CELMS-17
41 e39/m50-240
51 e38/t82-182
Alt_10
0 e35/m62-248
8 p45/m47-134
15 CELMS-37
22 p45/m47-250
23 CELMS-02
28 p45/m60-122
30 p45/m60-68
32 e32/t80-226
37 e35/t80-148
40 p13/m50-278
47 e35/t89-212
48 e35/t89-322
triplets
e36/m59-140
p13/m62-190
e35/m47-686
e32/t82-158
e32/t82-164
p45/m60-420
e32/t81-200
p45/m59-402
p45/m60-258
e34/m50-212**
e35/m62-394
e37/m61-194
douplets
e35/m50-198
e37/m49-196
CELMS-18
e36/m47-272
e32/t80-338
e35/t80-540
e32/t81-268
e35/t89-164
e32/t81-82
e35/m62-280
CELMS-11
p13/m59-105
douplets
e32/t82-228
e35/m48-500
e37/m49-164
p12/m50-160
e37/m50-232
e38/m47-214
e39/m50-120
e39/m50-490
p45/m61-154
p45/m61-328**
Alt_11
0 e38/m50-162
20 e34/m50-198
27 e34/m50-196
45 p45/m61-66
Alt_12
0 e39/t80-86
11 e39/m50-360
24 e35/t80-340
28 p13/m62-230
32 p12/m50-95
45 CELMS-04
Alt_13
0 e36/m47-290
16 p12/m62-455
29 p12/m62-390**
44 e33/t89-180
Alt__14
0 p12/m62-114
11 e38/t82-406
20 e35/t81-86
29 e35/m62-144
42 e38/m47-248
Alt_15
0 e35/m48-108
15 p13/m50-124
22 CELMS-39
39 p12/m47-162
Alt_16
0 e36/m47-158**
13 p13/m60-108
19 p12/m62-256
37 e32/t81-248
Alt_17
0 p13/m62-170
7 p13/m62-174
13 e33/t80-168
17 CELMS-60

Figure 2 A comparative genetic linkage map of globe artichoke 'Romanesco C3'. LGs derived from the current population (on the left) aligned with the corresponding LGs defined by Lanteri et al. (2006) (on the right) on the basis of common microsatellite and AFLP loci. Common marker loci are shown in **bold**, and their positions are connected with a line. Intercross markers positioned in the LGs of the first map are underlined.



Electronic supplementary table S1. List of the marker pairs with gaps >10 cM for the female and the male maps. Distances in centimorgan (cM) and specific LOD values in support of the two-point analysis were reported.

Female map (Romanesco C3)				
LG	**Marker pairs**		**cM**	**LOD**
C3_2	e38/t80-212	p12/m60-395**	13.5	10.11
	p12/m60-395**	p12/m62-106	10.9	7.6
C3_3	p13/m47-175	p13/m61-192	19.3	7.21
	e38/m50-234	e37/m61-136	10.5	4.27
C3_4	e37/m50-172	CsLIB-14	13.1	9.75
	e33/t89-154	e35/m48-222	10.2	8.65
	e35/m48-222	e38/m59-450**	14.6	4.87
	e33/t80-232	p13/m47-550	14.1	8.07
	p45/m60-428*	e32/t82-160	11.8	11.19
C3_6	e35/m49-192	e35/m50-420	17.5	6.86
	e38/t80-242	p45/m60-64	10.4	10.89
	e32/t80-282	p13/m59-164	17.5	4.16
	p13/m59-164	e38/m47-114	13.2	6.49
	e38/m47-114	p12/m62-166	10.8	5.02
C3_7	e35/t89-312	p12/m47-670	15.2	6.82
C3_9	p13/m62-148	e38/t80-250	11.6	8.23
	e39/t80-406	p13/m50-430	12.6	10.31
	p13/m50-430	CELMS-60	12.1	11.78
	e33/t80-174	e32/t81-122	11.8	12.66
C3_10	e42/m50-204	e39/m50-188	10.8	6.42
	p13/m47-240	p13/m50-150	12.2	7.46
	e36/m59-164	e42/m50-520	13.9	5.35
C3_11	e34/m49-250**	e37/m50-340	19.6	7.09
	p45/m47-335	CELMS-04	11.7	5.07
	CELMS-04	CLIB-04	10.4	8.62
	CELMS-20	e39/t80-90	13.2	9.92
C3_14	e38/m47-400	e33/t89-232	16.5	6.04
C3_15	e36/m48-150	e36/m47-248	15.3	4.06
	e36/m47-248	p13/m50-140	13.8	9.22
	CMAL-110	p12/m62-280	10.3	13.15
C3_18	e32/t82-258	e32/t80-410	18.7	6.89
	e32/t80-410	p45/m60-200	13.6	9.44
	p45/m60-200	e32/t81-400	13.1	12.96
C3_20	e38/m50-214	e36/m59-322	10.7	9.31

Male map (Altilis 41)				
LG	**Marker pairs**		**cM**	**LOD**
Alt_1	p12/m50-295	e35/t89-252	10.5	6.85
	e33/t80-302	e38/t80-230	13.1	9.24
Alt_2	CELMS-52	e34/m49-212	10.4	4.88
	e32/t81-280	e32/t82-274**	10.9	6.9
Alt_3	e35/m49-206	e35/m47-302	16.9	5.42
	p13/m59-450	CELMS-10	17.2	6.02
	CELMS-01	e32/t81-328	12.3	8.3
Alt_4	e38/m59-190	e33/t89-402	13.1	5.39
Alt_5	e39/t80-78	e39/t80-224	15.1	8.86
	e33/t89-510	p13/m50-90	11.6	8.79
	e35/t80-200	e39/m50-410*	14.1	7.42
Alt_6	e38/m50-350	cyre5/m47-160	10.6	6.24
Alt_7	e35/t81-554	e32/t82-148	11.0	8.18
	e35/m62-252	e37/m49-146	10.7	9.03
Alt_8	p12/m50-310**	e33/t89-190	12.8	11.1
	e33/t89-190	e33/t80-178	11.1	8.56
	e33/t80-178	e32/t82-510	12.1	6.5
	e32/t82-510	e34/m49-272	11.5	4.89
Alt_9	e35/m62-390	p13/m60-230	16.3	8.99
	p13/m60-230	CELMS-17	10.7	5.43
	CELMS-17	e39/m50-240	14.0	4.03
Alt_11	e38/m50-162	e34/m50-198	20.1	6.65
	e34/m50-196	p45/m61-66	18.2	8.38
Alt_12	e39/t80-86	e39/m50-360	11.0	8.05
	e39/m50-360	e35/t80-340	13.4	9.7
	p12/m50-95	CELMS-04	12.7	8.12
Alt_13	e36/m47-290	p12/m62-455	16.1	5.68
	p12/m62-455	p12/m62-390**	12.6	9.09
	p12/m62-390**	e33/t89-180	15.3	6.75
Alt_14	p12/m62-114	e38/t82-406	11.1	11.53
	e35/m62-144	e38/m47-248	12.7	9.62
Alt_15	p12/m47-162	CELMS-39	17.0	5.11
	p13/m50-124	e35/m48-108	15.2	9.15
Alt_16	e36/m47-158**	p13/m60-108	13.2	10.46
	p12/m62-256	e32/t81-248	17.7	6.48

Electronic supplementary table S2. List of the accessory marker for the female (LG_C3) and the male (LG_Alt) maps.

LG	TESTCROSS MARKERS		INTERCROSS MARKERS		
	(4<LOD<6)	**Highly distorted markers (LOD >4)**	**(LOD > 6)**	**(4<LOD<6)**	**Highly distorted markers (LOD >4)**
C3_1	p45/m59-460		e35/t80-364 e36/m59-236 CELMS-26	e32/t80-274 p12/m62-134 p45/m50-105	
C3_2	e35/t89-496 p12/m60-116* e33/t89-338** e38/m47-350	e35/m47-340***	p12/m47-266 e33/t89-500 e36/m59-216 e33/t80-288 e32/t82-88		p13/m62-610***
C3_3	e38/t82-214		e38/t80-154		
C3_4		cyre5/m47-180*** e39/t80-556***		e38/t80-540 p45/m60-432	
C3_5	e35/m49-610 e38/t80-504 e38/t82-124		e32/t80-304 e35/t89-116	e32/t82-98 e35/m62-98 e38/t80-138 e38/t80-140 p45/m50-250	p13/m62-282***
C3_6		p13/m60-162***		e32/t80-102	
C3_7			e33/t80-206		
C3_8	e32/t80-230		p12/m62-180 e35/t80-180 cyre5/m47-250		
C3_9			e33/t80-172 e33/t80-168	e32/t82-168	e32/t82-58***
C3_10	e38/m47-144	e32/t82-118***		e32/t82-98 e35/m62-98 e38/t80-138	

C3_11			p45/m50-318		
C3_12	p12/m47-283 p12/m47-305	p12/m50-320***		e35/m47-136 p13/m59-510	
C3_13		e35/m47-682***		e33/t80-220	
C3_14			p45/m47-142 e35/m62-102 Spines		
C3_15	e38/t82-600				
C3_16				e32/t80-310	
C3_17				e35/t89-220	
C3_20			p12/m50-450 p13/m60-260 e35/t80-220 e33/t89-450	e35/m47-380 p12/m59-320 p45/m47-170	
Alt_1	e39/m50-186		e32/t80-304 e35/t89-116	e32/t82-98 e35/m62-98 e38/t80-138 e38/t80-140 p45/m50-250	p13/m62-282***
Alt_2	e35/t89-144	e33/t80-340***	e35/t80-364 e36/m59-236 CELMS-26	e32/t80-274 p12/m62-134 p45/m50-105	
Alt_3			e38/t80-154		
Alt_4			p12/m47-266 e33/t89-500 e36/m59-216 e33/t80-288 e32/t82-88		p13/m62-610***
Alt_5		cyre5/t89-110***	e33/t80-206	e32/t81-468	
Alt_6				e35/m47-136	

Alt_7			p45/m47-142 e35/m62-102 Spines		
Alt_8		e33/t89-512***			
Alt_9	e38/m50-500	cyre5/m49-170***		e35/t89-220	
Alt_10			p12/m62-180 e35/t80-180 cyre5/m47-250	p45/m47-142	
Alt_12			p45/m50-318	e36/m59-158	
Alt_13	e32/t81-160 e38/t82-78				
Alt_15	e37/m49-140		p12/m50-450 p13/m60-260 e35/t80-220 e33/t89-450	e35/m47-380 p12/m59-320 p45/m47-170	
Alt_17			e33/t80-172 e33/t80-168	e32/t82-168	e32/t82-58***

Electronic supplementary table S3. List of 25 "genic markers" (microsatellites and SNPs) located in the linkage groups of the male and female genetic maps. Similarity (using MegaBlast) with globe artichoke ESTs or among other Asteraceae species is reported (e-value in brackets). Protein functions were the ones reported in Acquadro et. al (2009) and re-analysed using the Gene ontology platform (www.geneontology.org), with the *Arabidopsis thaliana* annotated genes.

Locus name	LG	Marker type	Marker position	Globe artichoke gene or putative Asteraceae ortholog	Function
C3H'	C3_20	SNP	SNP in CDS	FJ225121, globe artichoke	*p*-coumaroyl 3' hydroxylase (CYP98A49)
HCT	C3_3	SNP	SNP in CDS	DQ104740, globe artichoke	hydroxycinnamoyltransferase
HQT	C3_17	SNP	SNP in CDS	DQ915589, globe artichoke	hydroxycinnamoyltransferase
CDAT-01	C3_1	genic SSR	SSR after CDS	A86530, globe artichoke	Fructosyl polymerase
CsPal-03	C3_1	genic SSR	SSR in CDS	AM497826, AM418586, globe artichoke	phenylalanine ammonia-lyase
CELMS-03	C3_2	genic SSR	SSR after CDS	-	CLC-C (chloride channel C)
CELMS-04	C3_11 - Alt_12	genic SSR	SSR after CDS	GE577454, globe artichoke EST (0.0)	BLH1 (BLH1)
CELMS-05	C3_1 - Alt_2	genic SSR	SSR in CDS	EL399062, *C. tinctorius* (9 e^{-62})	Peptidoglycan-binding LysM domain-containing protein
CELMS-10	C3_3 - Alt_3	genic SSR	Uncertain position	-	Kelch repeat-containing ser/thr phosphoesterase
CELMS-12	C3_14 - Alt_7	genic SSR	Uncertain position	GE605411, globe artichoke EST (0.0)	Transcribed locus
CELMS-15	C3_2	genic SSR	SSR after CDS	-	Transducin/WD-40 repeat family protein
CELMS-16	C3_1 - Alt_2	genic SSR	SSR before CDS	GE597437, globe artichoke EST (e^{-141})	Transcribed locus
CELMS-17	C3_17 - Alt_9	genic SSR	SSR in CDS	-	MSI1 (Multicopy suppressor of IRA1)
CELMS-19	C3_8	genic SSR	SSR in CDS	-	LRR transmembrane protein kinase
CELMS-20	C3_11	genic SSR	SSR in CDS	GE593071, globe artichoke EST (7 e^{-21})	LUG (LEUNIG); Transcriptional corepressor
CELMS-31	C3_14	genic SSR	SSR in CDS	GE609927, globe artichoke EST (0.0)	Zinc finger protein
CELMS-33	C3_10	genic SSR	SSR in CDS	EL456618, *H. tuberosus* (5 e^{-93})	SEC14 cytosolic factor/phosphoglyceride transfer family
CELMS-37	C3_8 - Alt_10	genic SSR	SSR in CDS	-	LRR plant protein
CELMS-44	C3_17	genic SSR	SSR between 2 CDS	-	MSH7 (Muts Homolog 6-2)
CELMS-48	C3_5	genic SSR	SSR in CDS	EH757759, *C. solstitialis* (3 e^{-71})	Transcribed locus
CELMS-49	Alt_6	genic SSR	SSR in CDS	CX944987, *H. annuus* (1 e^{-29})	Transcribed locus
CELMS-52	C3_1 - Alt_2	genic SSR	SSR before CDS	EH739359, *C. maculosa (* 4 e^{-75})	Putative NMT2
CELMS-57	Alt_6	genic SSR	SSR after CDS	-	TF (Squamosa promoter-binding-like protein 16 - SPL16)
CELMS-60	C3_9 - Alt_17	genic SSR	SSR in CDS	-	C2 domain containing protein
CELMS-61	C3_2	genic SSR	SSR between 2 CDS	GE600199, globe artichoke (2 e^{-21})	3-keto acyl-coA thiolase