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New genetic maps for globe artichoke and wild cardoon and their alignment with an SSR-based consensus map

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Abstract An F1 mapping population was bred by crossing an accession of wild cardoon with a single Argentinian globe artichoke plant of the variety Estrella del Sur FCA with a view to generating new *Cynara cardunculus* linkage maps. Genotyping was conducting using a set of 553 SRAP, SSR, AFLP and SNP markers. The 1,465.5 cM map based on the segregation of alleles present in the wild cardoon parent comprised 214 loci distributed across 16 linkage groups (LGs), while the 910.1 cM globe artichoke-based map featured 141 loci falling into 12 LGs covering the total length. Three of the morphological traits (head spininess, leaf spininess and head color) for which the parents contrasted were inherited monogenically, and the genes conditioning them were mapped. A set of 48 co-dominant loci was used to align the LGs with those derived from a reference SSR-based consensus map of the species.

Keywords *Cynara cardunculus* · Globe artichoke · Cardoon · Molecular markers · Linkage groups · Genetic map

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Introduction

The Asteraceae species *Cynara cardunculus* L. ($2n = 2\times = 34$) includes two domesticated taxa, namely the globe artichoke (var. *scolymus*) and the cultivated cardoon (var. *altilis*), as well as the wild cardoon (var. *silvestris*), commonly considered to be the wild ancestor of both domesticated forms (Rottenberg and Zohary 1996; Lanteri et al. 2004). The species is highly heterozygous and suffers from inbreeding depression when self-fertilization is enforced (Cravero et al. 2002). Since inter-taxon hybrids are viable and fertile, globe artichoke improvement programmes can readily access germplasm across the whole species complex (Portis et al. 2009). Despite the impact of inbreeding depression, conventional breeding has succeeded in producing a number of high quality and genetically uniform seed-propagated globe artichoke varieties (Lopez Anido et al. 2010; Garcia et al. 2006).

As yet, the mode of inheritance of only a few traits (earliness, color, spininess and tightness of the head)

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has been investigated in any detail (Pecaut 1993; Lopez Anido et al. 1998; Mauromicale et al. 2000; Cravero et al. 2005; Lanteri et al. 2006; Portis et al. 2012). The acquisition of a genetic linkage map simplifies the genetic analysis of trait variation, particularly for those traits which are polygenically inherited. The definition of trait/marker linkages provides a tool for accelerated selection via marker-assisted selection (Young 1999). The first such map for globe artichoke was developed by Lanteri et al. (2006) and was based on 204 loci which fell into 18 linkage groups (LGs) for the female map and 180 loci distributed in 17 LGs for the male one. Since this time, the marker density of the original maps has been increased (Acquadro et al. 2006, 2009) and a number of other maps have been elaborated (Sonnante et al. 2011; Portis et al. 2012).

Building molecular-marker-based linkage maps has relied on a number of marker technologies. A particularly flexible and effective one, termed "sequence related amplified polymorphism" (SRAP), has been promoted by Li and Quiros (2001). Its advantages include simplicity, robustness, a reasonable throughput capacity and the ready sequencing of specific fragments included in the amplicon. The design of the primers ensures that the majority of polymorphisms arise due to variation in the length of intron, promoter and spacer regions (Lin et al. 2003). Approximately half of all SRAP markers are located within the genic portion of the genome (Lin et al. 2003; Sun et al. 2007).

Here, we present genetic linkage maps of *C. cardunculus* based on a cross between an accession of wild cardoon and a single plant belonging to the open-pollinated Argentinian globe artichoke variety Estrella del Sur FCA. Most of the genotypic data needed for linkage map construction were derived from SRAP analysis, although other PCR-based markers were also included to allow cross-referencing with the consensus map recently produced by Portis et al. (2012). The resulting maps were used to identify and locate the major loci controlling three key agronomic traits.

Materials and methods

Plant materials and DNA extraction

A mapping population was generated by pollinating a local accession of wild cardoon with a single plant of Estrella del Sur FCA (Est). The presumptive F_1 seeds were sown in a greenhouse, and seedlings at the fourth true leaf stage were transplanted, together with both crossing parents, into a loamy soil field at the Experimental Field Station of the Universidad Nacional de Rosario (33°1′S; 60°53′W). This site experiences a temperate climate and an average annual rainfall of 950 mm, and is typical of the zone in Argentina where most of the country's globe artichoke is produced (Cravero et al. 2010). The inter-row spacing was 1.4 m and the spacing between plants within each row was 80 cm. Genomic DNA of the presumptive hybrids and the parental genotypes was extracted from fresh leaf using a DNeasy Plant mini Kit (Qiagen). The hybrid status of each population member was verified by applying the two microsatellite (SSR, simple sequence repeat) markers CELMS-30 and -37 (Acquadro et al. 2009), resulting in the establishment of a set of 91 true F_1 hybrids.

Genotypic analysis

The mapping population was genotyped using SRAP, SSR, AFLP (amplified fragment length polymorphism) and SNP (single nucleotide polymorphisms) assays. The number of SRAP primer combinations (PCs, Table 1) was 25, and the protocol followed that

Table 1 SRAP primer sequences used for genotyping

Forward primer		Reverse primer	
Me1	5′-TGAGTCCAAACCGGATA-3′	Em1	5′-GACTGCGTACGAATTAAT-3′
Me2	5′-TGAGTCCAAACCGGAGC-3′	Em2	5′-GACTGCGTACGAATTTGC-3′
Me3	5′-TGAGTCCAAACCGGAAT-3′	Em3	5′-GACTGCGTACGAATTGAC-3′
Me4	5′-TGAGTCCAAACCGGACC-3′	Em4	5′-GACTGCGTACGAATTTGA-3′
Me5	5′-TGAGTCCAAACCGGAAG-3′	Em5	5′-GACTGCGTACGAATTAAC-3′

Table 2 AFLP primer combinations used for genotyping

*Eco*RI/*Taq*I template	
Primer combination	Code
E + ACC/T + TTT	1.800
E + ACG/T + TTT	1.700
E + ACC/T + TAC	2.800
E + ACG/T + TAC	2.700
E + ACC/T + TGT	3.800
E + ACG/T + TGT	3.700
E + ACC/T + TAG	4.800
E + ACG/T + TAG	4.700
E + ACC/T + TAT	5.800
E + ACG/T + TAT	5.700
E + ACC/T + TCC	6.800
E + ACG/T + TCC	6.700
E + ACC/T + TAA	7.800
E + ACG/T + TAA	7.700
E + ACC/T + TTA	8.800
E + ACG/T + TTA	8.700

given by Cravero et al. (2007), except that each reaction only contained 1 U *Taq* polymerase. The resulting amplicons were separated by electrophoresis through 6 % (w/v) denaturing polyacrylamide gels, and then visualized by silver staining (Bassam et al. 1991). The AFLP procedure followed that of Vos et al. (1995), as modified by Lanteri et al. (2004). Briefly, the genomic DNA was digested with *Eco*RI and *Taq*I and ligated to a standard adaptor oligomer. The product of the ligation reaction represented the template for a PCR driven by a pair of primers complementary to the adaptor sequences plus one selective nucleotide at their 3′ end (*Eco*RI + A and *Taq*I + T). A second PCR followed driven by one of 16 PCs (Table 2). The resulting amplicons were separated by electrophoresis through a 6.5 % denaturing polyacrylamide gel, and detected using a Gene ReadIR 4200 system (LI-COR) (Jackson and Matthews 2000). The set of SSRs comprised 247 loci, a combination of CELMS (Acquadro et al. 2009) and CyEM (Scaglione et al. 2009) assays. An initial screen was performed using as template DNA from the two parentals and six of the F_1 progeny, in order to identify those assays which were informative. Only these selected assays were applied to the full mapping population. The PCR conditions were applied followed the recommendations of the assay developer and the amplicons were separated in the same way as were the AFLP ones. SNP assays were directed at seven genes involved in the synthesis of caffeoylquinic acids, namely *HCT*, *HQT*, *C3′H*, *C4H*, *4CL*, *Acyltransf_1 and _2* (Comino et al. 2007, 2009; Moglia et al. 2009; Menin et al. 2010). The assay was based on a tetra-primer ARMS-PCR protocol (Ye et al. 2001), with the amplicons being separated by electrophoresis through 2 % w/v agarose gels and visualized by ethidium bromide staining.

Fragments generated by the SRAP and AFLP assays were treated as dominant markers, with each marker named according to the PC used to generate it (Tables 1 and 2) and the estimated size of the fragment; for example, locus 1.800.190 is an AFLP fragment of length 190 bp amplified by PC *Eco* + ACC/*Taq* + TTT. SSR and SNP loci were scored as co-dominant markers and identified by the primer pair used in the assay.

Phenotypic analysis

The parental lines differ from one another with respect to spininess of the leaf and head bracts, and by their head color: Est is non-spiny and forms purple heads, while the wild cardoon accession is spiny and forms green heads. The presence/absence of spines on well developed leaves and bracts, and head color was scored over two consecutive seasons (2008 and 2009). Goodness of fit between the observed and expected segregation behavior was evaluated using the χ^2 test.

Construction of the linkage maps

The marker loci were either (1) maternal testcross markers which segregated only in the female (wild cardoon) gamete, giving a ratio of 1:1 in the F_1 population; (2) paternal testcross markers which segregated only in the male (globe artichoke) gamete, giving a ratio of 1:1 in the F_1 population; and intercross markers, which segregated in both gametes, producing a segregation ratio of either 3:1 (for the SRAP and AFLP markers) or 1:2:1 (SSR and SNP markers) in the F_1 population. The two-way pseudo-testcross mapping strategy described by Weeden (1994) and Grattapaglia and Sederoff (1994) was used to develop two independent linkage maps, one for each parental genotype. Goodness-of-fit between the observed and expected segregation ratios was determined by a χ^2 test. Only

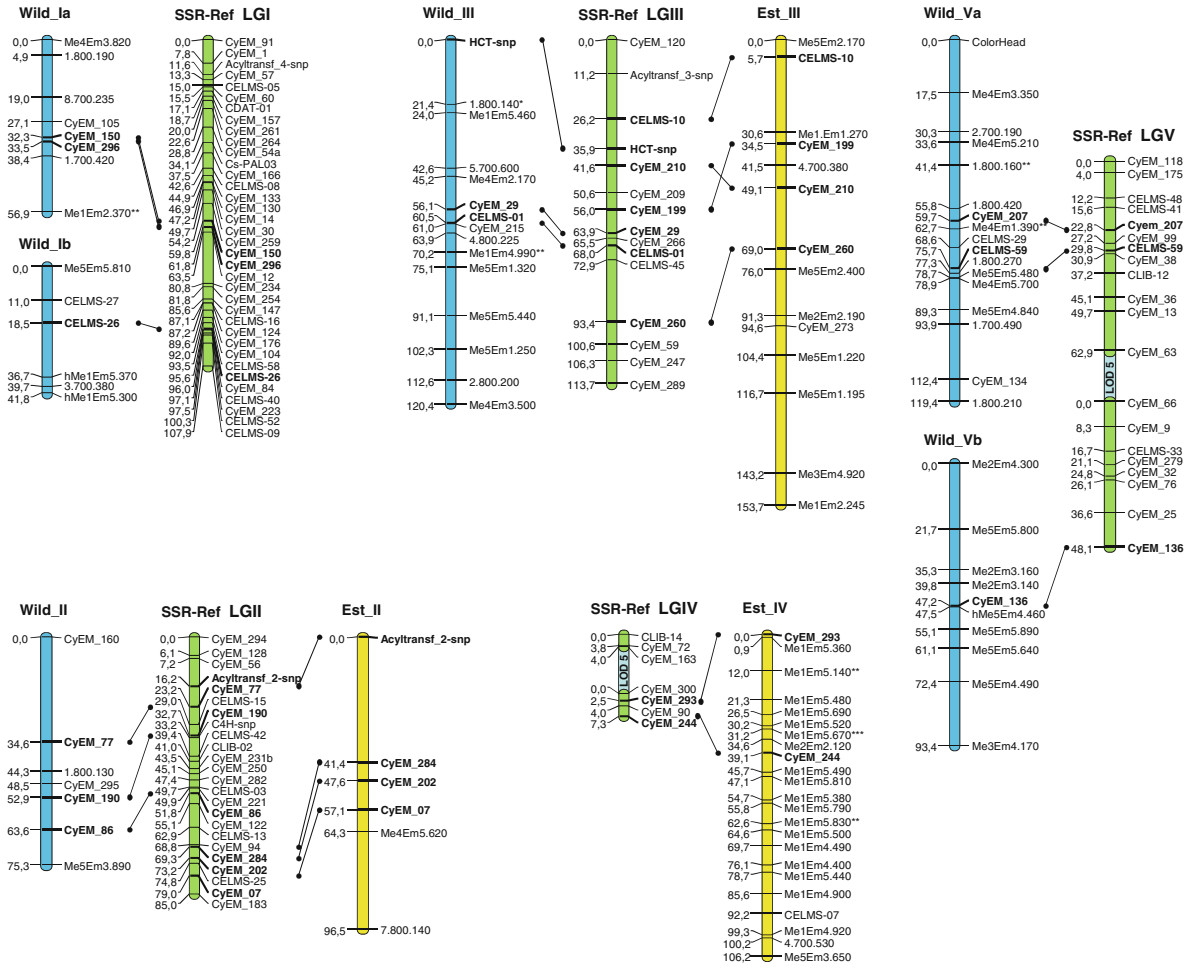

Fig. 1 **a**, **b**, **c** Genetic linkage maps of wild cardoon (*blue* LGs, shown on the *left*) and globe artichoke (*yellow* LGs, on the *right*) aligned with the reference SSR-based consensus map (*green* LGs in the *center*). Shared SSR and SNP loci are shown in *bold*, and their positions are connected by a *line*. Marker names are shown to the *right* of each LG, with map distances (in cM) to the *left*. Markers showing significant levels of segregation distortion are indicated by *asterisks* (*$0.1 > P > 0.05$, **$0.05 > P > 0.01$, ***$P < 0.01$)

markers either fully consistent with monogenic segregation ($\chi^2 \leq \chi^2_{\alpha=0.1}$) or showing only minor distortion therefrom ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.01}$) were used for the construction of the maps. Those for which the segregation was highly distorted ($\chi^2 > \chi^2_{\alpha=0.01}$) were included in a second round of mapping only when their presence induced no alteration in local marker order. The LOD threshold for accepting an LG was 5.0, as estimated by JoinMap4.0 software (Van Ooijen 2006). The JoinMap settings applied were Rec = 0.40, LOD = 1.0 and Jump = 5. Recombination values were converted to genetic distances using the Kosambi (1994) mapping function. Intercross markers were used to identify homologous LGs. The LGs derived from the wild cardoon parent have been labeled "Wild" and those from the globe artichoke parent as "Est" (Fig. 1a–c; Table 3). Linkage maps were drawn using MapChart 2.2 software (Voorrips 2002).

Alignment of the "Wild" and "Est" LGs with the SSR-based consensus LGs

The SSR and SNP assays were used to align the de-novo LGs with those derived by Sonnante et al. (2011) and Portis et al. (2012). To achieve this, a consensus map, based exclusively on microsatellite and SNP markers, was assembled from the SSR and SNP segregation data collected from the Romanesco C3

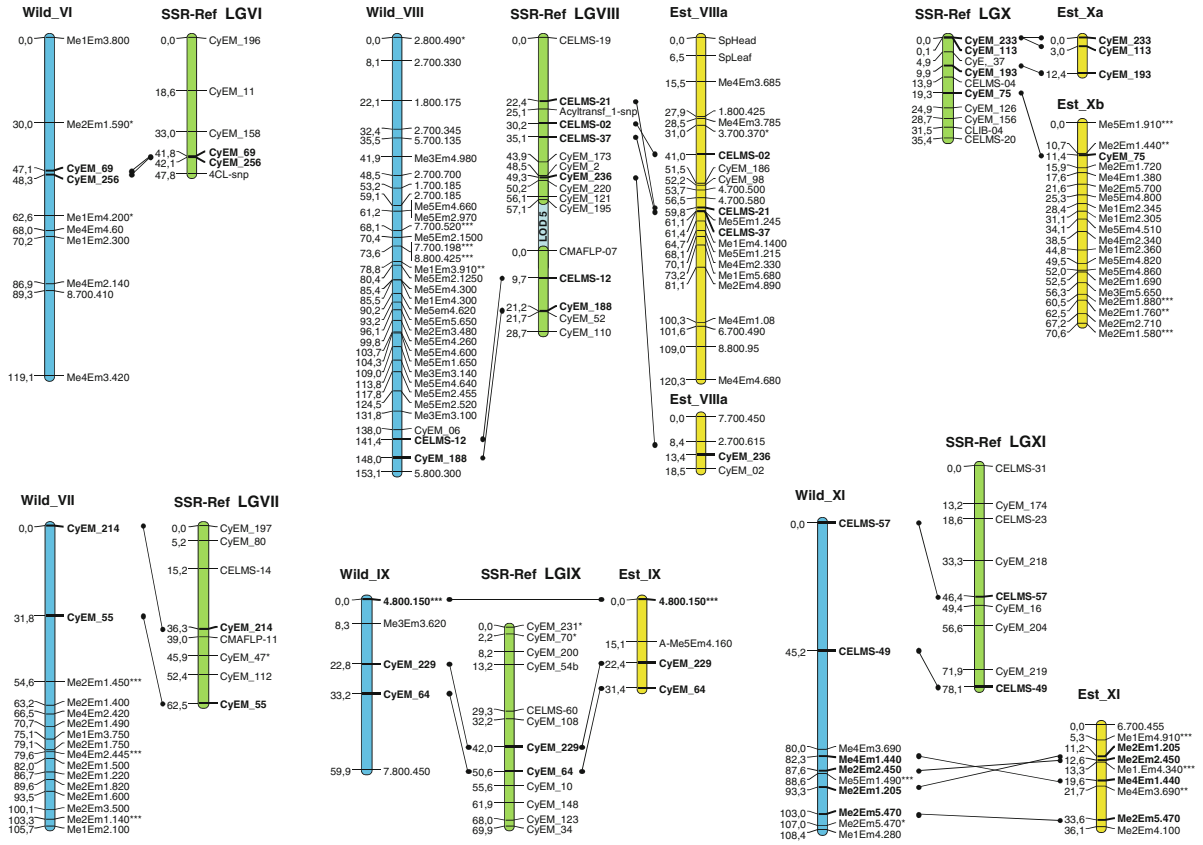

Fig. 1 continued

(globe artichoke) × Altilis 41 (cultivated cardoon) mapping population described by Portis et al. (2012). This SSR-based consensus map had an overall length of 1068.0 cM, comprising 217 SSR and ten SNP loci arranged into 20 LGs (LOD threshold >6.0). The haploid chromosome complement was recovered by lowering the LOD threshold to 5.0. These 17 SSR-based consensus LGs are hereafter referred to as "SSR-Ref_LGs", applying the same I–XVII numbering system employed by Portis et al. (2012). When bridge markers linked the "SSR-Ref_LGs" with the "Wild" and "Est" ones, the latter were numbered accordingly (Fig. 1a–c; Table 3).

Results

Genotypic segregation

The SRAP analysis generated 336 informative fragments, representing a mean of 13.4 (range 4–51) per PC. Of these, 186 segregated as expected in the maternal gametes, 130 as expected in the paternal gametes, while 20 were inferred to have been in the heterozygous state in both parental lines (intercross markers). The mean number of informative AFLP markers per PC was 8.4 (range 1–27), so that, in all, 135 loci segregated, of which 78 segregated only in the female gamete, 47 in the male gamete and the remaining ten were intercross markers. On the whole, of the combined 441 SRAP and AFLP testcross markers, 59.9 % segregated in the wild cardoon parental genotype, while 40.1 % segregated in "Est". The segregation of ~24 % of the SRAP and AFLP markers was distorted ($\chi^2 > \chi^2_{\alpha=0.01}$).

Of the 61 CELMS SSRs tested, 28 were informative between the parents; of these, 14 segregated only among the female gametes, 13 among the male, and only one was an intercross marker. Similarly, of the 186 CyEM SSRs tested, 25 segregated only among the female gametes, 17 among the male, and seven were intercross markers. Two of the SSR loci suffered a

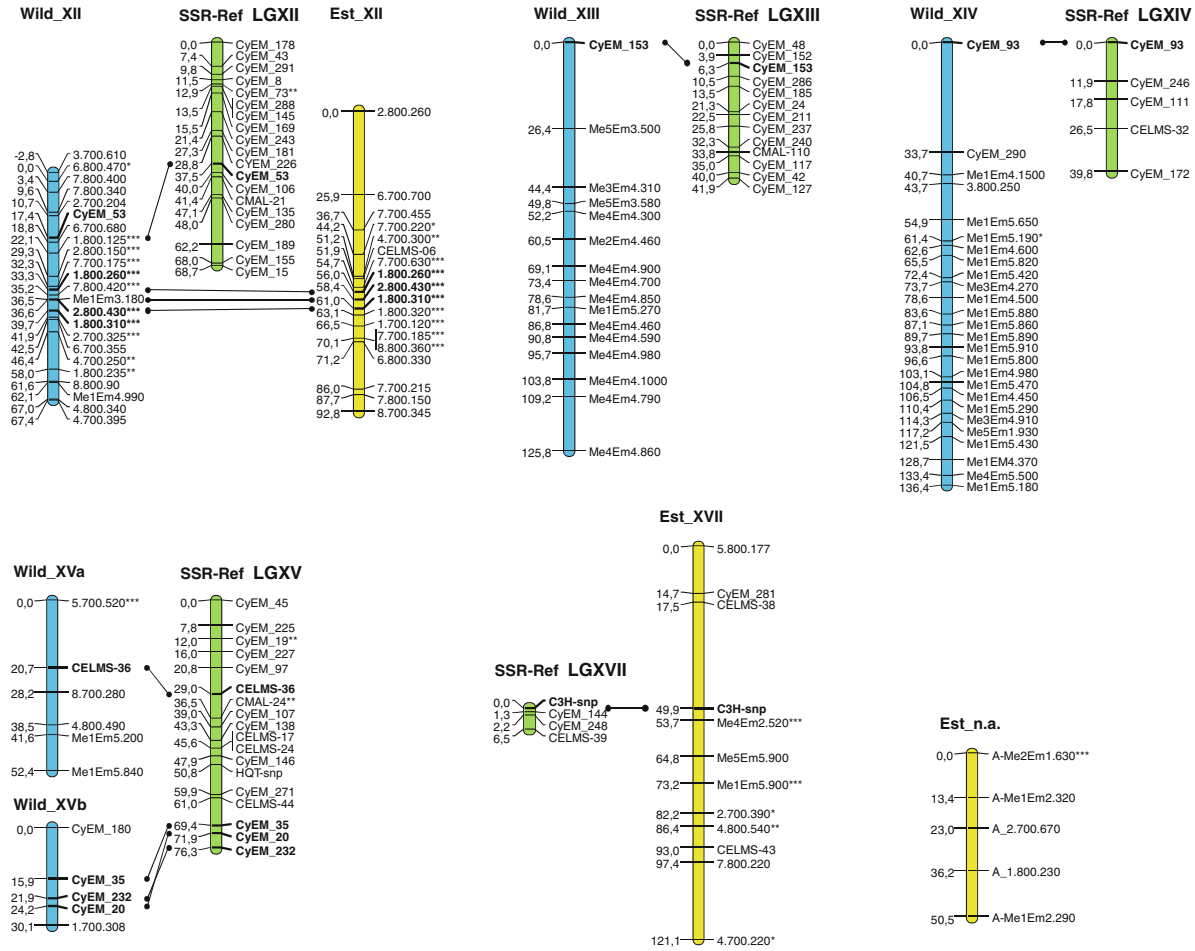

Fig. 1 continued

minor degree of segregation distortion ($\chi^2_{\alpha=0.1} < \chi^2 \leq \chi^2_{\alpha=0.01}$). Five out of the seven SNP loci genotyped segregated in the mapping population. The *HCT* assay segregated only among the female gametes, whereas those for *HQT*, *C3′H*, *4CL* and *Acyltranf_1* segregated only among the male gametes.

Phenotyping

The three morphological traits investigated all segregated consistently with the monogenic 1:1 ratio, suggesting that, in the analyzed progeny, all these traits are controlled by a single gene with two alternative alleles. The χ^2 values associated with these ratios were, respectively, 5.13 for the presence/absence of spines on the heads, 2.78 for the presence/absence of spines on the leaf, and 1.53 for purple-green versus purple heads.

Linkage maps construction and their alignment

Five hundred and fifty-six markers were used for map construction (553 molecular and three phenotypic markers). The genetic map constructed from the female gametes (the "Wild" map) was based on segregation at 344 loci, while that from the male gametes (the "Est" map) was based on 250. The number of intercross markers was 38. The linkage analysis resulted in the placement of 345 loci across both maps, comprising 187 SRAP markers, 89 AFLP markers, 64 SSR loci, three SNP loci and three phenotypic traits.

The "Wild" map featured 214 loci distributed over 16 LGs, each defined by between five and 34 loci (mean 13.4), their length ranging from 30.1 to 153.1 cM (mean 91.6 cM). The overall map length was 1,465.5 cM and the mean inter-marker distance

Table 3 Key characteristics of the wild cardoon ("Wild") and globe artichoke ("Est") linkage maps and their alignment

LG name		Size (cM) "Wild"	Size (cM) "Est"	Total no. of markers	Marker density	Portis et al. (2012)		Sonnante et al. (2011)	
Wild cardoon	Estrella del Sur					Aligned LGs	Shared markers	Aligned LGs	Shared markers
Wild_Ia		56.9		8	8.1	I	2	I	2
Wild_Ib		41.8		6	8.4		1		0
Wild_II		75.3		7	12.6	II	3	II	2
	Est_II		96.5	6	19.3		4		1
Wild_III		120.4		15	8.6	III	3	III	1
	Est_III		153.7	14	11.8		4		0
	Est_IV		106.2	23	4.8	IV	2	VI	2
Wild_Va		119.4		17	7.5	V	2	V	2
Wild_Vb		93.4		10	10.4		1	X	1
Wild_VI		119.1		10	13.2	VI	2		0
Wild_VII		105.7		16	7.0	VII	2	XVIII	2
Wild_VIII		153.1		34	4.6	VIII	2	XV	1
	Est_VIIIa		120.3	23	5.5		3	VIII	1
	Est_VIIIb		18.5	4	6.2		1	VIII	2
Wild_IX		59.9		5	15.0	IX	2	IX	2
	Est_IX		31.4	4	10.5		2		2
	Est_Xa		12.4	3	6.2	X	3	XI	1
	Est_Xb		70.6	20	3.7		1		1
Wild_XI		108.4		10	12.0	XI	2		0
	Est_XI		36.1	9	4.5		0		0
Wild_XII		67.4		23	3.1	XII	1	IV	1
	Est_XII		92.8	18	5.5		0		1
Wild_XIII		125.8		16	8.4	XIII	1	XIV	1
Wild_XIV		136.4		26	5.5	XIV	1	XIII	1
Wild_XVa		52.4		6	10.5	XV	1	XVI	1
Wild_XVb		30.1		5	7.5		3		3
	Est_XVII		121.1	12	11.0	XVII	1		0
	Est_n.a.		50.5	5	12.6		0		0

was 7.4 cM (range 3.1–15.0 cM). The placement of one SNP and 28 SSR loci allowed the alignment of the 16 LGs with 13 consensus SSR-based map LGs (Table 3; Fig. 1a–c); three pairs of "Wild" LGs (Ia and Ib, Va and Vb, XVa and XVb) each corresponded with a single consensus SSR-based one. Among the loci showing segregation distortion, 28 were successfully integrated within ten of the LGs. Clusters of distorted loci were detected on Wild_VIII (four loci) and Wild_XII (ten loci) (Fig. 1b, c).

The "Est" map comprised 141 loci grouped into 12 LGs, which covered a genetic distance of 910.1 cM. The individual LGs varied in length from 12.5 to 153.7 cM (mean 75.9 cM), containing between three and 23 (mean 11.8) loci. The mean inter-locus distance was 7.1 cM (range 3.7–19.3 cM). The placement of 19 SSR and two SNP loci allowed 11 of these LGs to be aligned with nine of the reference LGs (Table 3; Fig. 1a–c). Two pairs of "Est" LGs (VIIIa and VIIIb, Xa and Xb) each corresponded with a single consensus SSR-based one. The remaining LG was labeled "Est_n.a." (n.a. = not aligned) in Table 3 and Fig. 1c. Among the loci showing segregation distortion, 29 were successfully integrated within eight of the LGs. Two clusters of distorted loci were detected on Est_Xb (one comprising two and the other three loci), along with one cluster on Est_XII (ten loci) and a further one on Est_XVII (three loci) (Fig. 1b, c).

The genes underlying the presence/absence of head spines (Sp_{Head}) and the presence/absence of leaf spines (Sp_{Leaf}) were represented on the "Est" map (LG VIIIa), and the one responsible for head color (*ColorHead*) was located on LG Wild_Va.

Ten of the 38 intercross markers (four SRAP, four AFLP and two SSR) were assignable to a specific LG in both maps (three each on IX and XII and four on XI), which aided the identification of homology between the "Wild" and "Est" LGs. Another three pairs (II, III and VIII) were identified as being homologous, based on their alignment with the reference SSR-based map (Table 3; Fig. 1a–c). The distribution across 12 "Wild" and nine "Est" LGs of the 31 markers shared with the map generated by Sonnante et al. (2011) is also shown in Table 3.

Discussion

A population arising from the cross between wild cardoon and a globe artichoke variety was generated with a view to constructing a linkage map and locating the genes underlying the presence/absence of spines on the heads and leaf, and pigmentation of the heads. The high level of inbreeding depression experienced by *C. cardunculus* (Cravero et al. 2002) prevents either backcross, F_2 or recombinant inbred line populations being used for mapping quantitative traits, so instead the double pseudo-testcross approach was taken, as also successfully used by Lanteri et al. (2006), Portis et al. (2009) and Sonnante et al. (2011). Mapping population individuals obtained from other globe artichoke × wild cardoon crosses have been shown to vary widely with respect to both quantitative and qualitative characters (Sonnate et al. 2011; Lanteri et al. 2012), confirming that a high level of heterozygosity has been retained in both wild and cultivated germplasm (Portis et al. 2005a, b; Mauro et al. 2009, 2012).

The present linkage maps were based on a variety of molecular marker types. The choice of SRAP PCs reflected prior experience (Cravero et al. 2007) and, as SRAP genotyping generated most of the markers applied, these loci constituted the major backbone of the two maps. Since its development some 10 years ago, SRAP genotyping has been deployed in a range of plant species for estimating levels of genetic diversity (Cravero et al. 2007; Esposito et al. 2007; Aneja et al. 2012), gene tagging (Martin et al. 2008; Zhang et al. 2011) and map construction (Lin et al. 2003; Sun et al. 2007; Xue et al. 2010). However, here we report its first usage for genetic mapping in *C. cardunculus*.

A comparison of heterozygosity between the mapping parents used by Portis et al. (2009) showed that fewer loci were informative in the cultivated cardoon than in the globe artichoke variety Romanesco C3. An explanation for this difference lies in the fact that while the latter is propagated vegetatively, the former is a seed-propagated variety. Clonal propagation allows the maintenance of heterozygosity, but seed propagation can introduce an element of purifying selection to stabilize production. In contrast, the parental lines used by Sonnante et al. (2011) (one a globe artichoke, the other a wild cardoon) produced a pair of maps in which the cultivated parent map include more loci than the wild parent one. In the present case, the wild cardoon-based map was based on a higher number of loci than the globe artichoke one (214 vs. 141 markers) and was some 50 % longer (1,465.5 vs. 910.1 cM), implying that the level of heterozygosity in the wild cardoon parent is rather higher than in the domesticated type. Indeed, the latter was selected from an open-pollinated population on the basis of some key commercial traits (Garcia et al. 2006), and it was expected that this selection would have reduced its global level of heterozygosity.

Segregation distortion is commonplace in mapping populations, including an intra-taxon one in *C. cardunculus*, where it affected ~10 % of the loci (Lanteri et al. 2006). Here, the segregation of some 19 % of mapped loci was distorted, and this higher level may simply reflect the greater genetic separation between the parents of the population (Grandillo and Tanksley 1996; Verde et al. 2005). Clusters of distorted markers were detected in both the "Wild" and the "Est" maps. Since the direction of segregation bias within each cluster was unidirectional, the suggestion is that the basis of the phenomenon is biological, rather than it being due to scoring error or chance (Fishman et al. 2001).

The mapping of the three morphological traits considered was consistent with each being determined by a single gene. The spininess of the head trait has been known for some time to be determined by the gene *Sp*, where the dominant allele determines lack of spininess (Pochard et al. 1969; Basnitzki and Zohary 1994). The wild cardoon parent used here was therefore presumably of genotype *spsp*, while that of

"Est" was *Spsp*. The homozygous state prevented its location in the "Wild" map, but it was successfully located to LG VIIIa on the "Est" map. The gene underlying the presence/absence of leaf spines (Sp_{Leaf}) appeared to be tightly linked to *Sp*. The presence of recombinants in the F1 progeny indicates that this trait is therefore controlled by a locus distinct from *Sp*. The non-spiny type is conditioned by the presence of at least one dominant allele (Sp_{Leaf}-), while the recessive homozygote $sp_{Leaf}sp_{Leaf}$ produces spiny leaves. At the genetic level, therefore, the wild cardoon accession was $spsp/sp_{Leaf}sp_{Leaf}$ and "Est" was $Spsp/Sp_{Leaf}sp_{Leaf}$. With respect to head color, Cravero et al. (2005) showed that within globe artichoke, two independent genes act epistatically to determine the trait; in the absence of dominant alleles at *P* the inflorescence bracts remain green (*pp*), while the genotype *P-U-* develops purple-green bracts and *P-uu* uniformly purple bracts. The segregation for head color observed in the present mapping population was consistent with homozygosity composition in both parents at locus *P*, which determines the presence/absence of anthocyanic pigments (*pp* in "Wild" and *PP* in "Est"), while "Wild" was *Uu* and "Est" was *uu*, suggesting that the second locus, which determinates anthocyanin distribution, segregated. The *U* locus mapped to Wild_Va on the maternal map.

The alignment and integration of independently generated linkage maps is desirable, but problematical where different marker types and/or population types are involved (Sun et al. 2007). Here, we relied on a set of 48 co-dominant markers for the alignment with the Portis et al. (2012) Romanesco C3 × Altilis 41 consensus map. This allowed 16 of the "Wild" and 11 of the "Est" LGs to be matched with 16 out of the 17 consensus LGs. Six of the reference LGs could be simultaneously aligned with both the "Wild" and "Est" LGs, leaving seven aligned only with the "Wild" map and four only with the "Est" map. The number of bridging markers per LG required for this exercise varied from one to four, and their linear order was mostly conserved. The exceptions related to three of the CELMS and four of the CyEM SSRs, which appeared to identify small inversions within LGs III, VIII and XV. Such minor differences may be due to mapping imprecisions (Lombard and Delourne 2001), to differences in recombination frequencies of marker pairs in different populations (Studer et al. 2010), or might be attributed to different population sizes (Spiller et al. 2011). Other potential sources of variation are genotyping errors, an excess of missing values and the mapping of distorted markers (Hackett and Broadfoot 2003). Given the probabilistic nature of genetic maps, the re-ordering of tightly linked markers will generally produce a version of the map only marginally less probable than the most probable one, so this practice is quite frequently followed to improve alignment quality (Cervera et al. 2001; Jeuken et al. 2001; Lespinasse et al. 2000; Lombard and Delourne 2001; Sebastian et al. 2000). The further alignment of the "Wild" and "Est" LGs with 15 of the Sonnante et al. (2011) globe artichoke × wild cardoon LGs using 31 common markers evidenced the assignment of 14 SSR loci (ten CyEM, four CELMS) to a specific LG for the first time in a *C. cardunculus* map.

Given that the parents of the present mapping population differ widely with respect to a number of both qualitative and quantitative traits such as shape and weight of the heads, number of head per plant, height and shape of the plant, and days to first harvest, opportunities are now available to investigate the inheritance of some important agronomic characteristics. Moreover, these are the first linkage maps of *C. cardunculus* developed from Argentinean genotypes of wild cardoon and globe artichoke. The enrichment of these maps with additional markers, like CAPS and SNPs recently developed by Scaglione et al. (2012a, 2012b), will improve their utility for the localization of major genes and quantitative trait loci.

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