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The inheritance of bract pigmentation and fleshy thorns on the globe artichoke capitulum

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Summary

The bracts of the globe artichoke inflorescence vary in their pigmentation and the extent of fleshy thorn development. Here, a genetic analysis of these two traits is presented, based on a pre-existing and well-characterized mapping population derived from a cross between a globe artichoke variety and a cultivated cardoon. While both traits appeared to be simply inherited when the number of trait classes was limited to three (pigmentation) or two (thorniness), extending the classification to a larger number of states generated continuous distributions appropriate for a quantitative trait locus (QTL) analysis. The seven QTL identified by this means, mapping to five different linkage groups, were all expressed across two growing seasons. The largest effect QTL mapped onto homologues linkage group in each parental maps, and explained up to 69% and 73% of the phenotypic variance respectively for bracts pigmentation and thorniness.

Keywords bract colour, bract thorniness, *Cynara cardunculus*, QTL analysis, trait inheritance

Introduction

The *Cynara cardunculus* complex includes three cross-compatible taxa: the progenitor var. *sylvestris* (wild cardoon) and the two cultivated forms var. *scolymus* (globe artichoke) and var. *altilis* (cultivated cardoon). Globe artichoke production has risen from about 1.5 Mt in 1993 to 1.8 Mt in 2013 (FAOSTAT 2013), with some 60% of this amount generated in Europe, predominantly Italy. The primary product of the globe artichoke is its inflorescence (more formally referred to as the capitulum), the inner bracts and the fleshy receptacle. Each plant produces various sizes of capitulum, with the largest formed on its central stem and the smaller ones on its lateral branches (Lanteri and Portis 2008). Compared to most vegetables, the globe artichoke capitulum harbours a high level of polyphenols (Moglia et al. 2008) some of which are of medicinal value (Wang et al. 2003; Pinelli et al. 2007; Lombardo et al. 2012; Pandino et al. 2012; 2013). As a result, and according to the definition of the European Commission on Functional Food Science in Europe (FuFoSE), the globe artichoke is considered as a functional food (Roberfroid 2000). Its non-food uses include the pharmaceutical exploitation of its polyphenols (Comino et al. 2007; 2009) and sesquiterpene lactones (Eljounaidi et al. 2014) extracted from in the foliage, while its roots and capitula contain inulin, a potent prebiotic and probiotic substance (Rijnierse et al. 2011). Its biomass has been suggested as a source of green forage, and the oil extracted from its seed is suitable for both edible and bioenergy purposes (Ierna and Mauromicale 2010; Portis et al. 2010; Ierna et al. 2012; Acquadro et al. 2013, Mauromicale et al. 2014).

Most commercial globe artichoke production relies on vegetatively reproduced autochthonous landrace materials, although in recent years seed propagated cultivars have begun to make an impact. Landraces are conventionally distinguished from one another by their capitulum shape, the presence/absence of spines and the colour of the bracts, although genotypic assays have shown a deal of within landrace heterogeneity (Lanteri et al. 2001;

Portis et al. 2005). The four major morphological groups recognized are the “spinosi”, which develop long, sharp spines on their bracts and leaves, the “violetti”, which produce violet coloured, moderately spiny capitula, the “romaneschi”, which develop spherical or near-spherical, non-spiny capitula and the “catanesi”, which produce small, elongated, non-spiny capitula (Porceddu et al. 1976). Pigmentation type (green or violet) is less robust as a descriptor, since colour intensity can vary substantially within a landrace and is also modulated by the growing environment.

Varietal improvement of globe artichoke has lagged behind that achieved in most vegetable crops, nevertheless, its genome organization has been explored in some detail (Scaglione et al. 2012) and its genome sequence is currently being acquired (http://compgenomics.ucdavis.edu/). As the species does not tolerate self-fertilization, populations developed for mapping purposes have been based on a double pseudo-test-cross approach (Lanteri et al. 2006; Acquadro et al. 2009), which has led elaboration of genetic maps covering all 17 major linkage groups (LGs). The most recently derived genetic maps have been generated from the progeny of a cross between the globe artichoke ‘Romanesco C3’ and the cultivated cardoon genotype ‘Altilis 41’ (Portis et al. 2009). The maps have been exploited to expose the mode of inheritance of precocity with respect to capitulum production (Portis et al. 2012), as well as to derive marker/trait associations involving a number of yield components (Portis et al. 2014). Here, the identification of genomic regions influencing bract colour and the presence of fleshy thorns on the bracts is described.

Materials and methods

Plant materials and trait evaluation

The C3 (Romanesco C3, female parent) x ALT (Altilis 41, male parent) mapping population (Portis et al. 2009) consists of 154 F_1 progeny. The population, along with six clones of each of C3 and ALT, was raised at the University of Catania (Sicily, Italy) Experimental Station (37°25'N; 15°30'E; 10m a.s.l) in both 2009-2010 (hereafter referred to as 2010) and 2010-2011 (2011) using standard agronomical practices. The area is representative of commercial globe artichoke cultivation, characterized by mild and wet winters and hot, dry summers. The two traits *bc* (bract colour) and *bt* (the extent of fleshy thorns developed on the bract) were assessed on capitula harvested prior to bract divergence, defined as "stage D" by Foury (1967). *bc* was initially evaluated by classifying the capitula as either 'green', 'uneven purple' or 'even purple', then refined by applying a 1 to 7 scale (1: green; 2: green with purple hue; 3: green-purple; 4: purple-green; 5: purple with green hue; 6: purple; 7: dark purple; Fig. 1A) was assigned to each individual. *bt* was initially classified using a simple presence/absence score, and subsequently refined to a 1 to 5 scale (1: absence; 2 to 5: from small and soft to fully developed; Fig. 1B).

Statistical analysis and quantitative trait locus (QTL) detection

Standard population metrics and trait correlations were obtained via algorithms implemented in R software (R Development Core Team 2006). Analyses of variance were based on treating each growing season as an independent replicate, following Zhang et al. (2010). Broad sense heritability was given by the expression $h_B^2 = y\sigma_g^2 / (\sigma_g^2 + \sigma_e^2)$, where σ_g^2 refers to the genetic variance and σ_e^2 to the error variance. The inter-trait correlation was calculated using the Spearman coefficient, and normality, kurtosis and skewness assessed

using the Shapiro-Wilks test (α=0.05). Segregation was considered as transgressive where at least one mapping population individual recorded a trait value differing from the relevant parental one by at least two standard deviations. QTL locations were, at first, based on the consensus genetic linkage map (Portis et al. 2012), which includes 694 markers and covers 1687.6 cM. by applying the Kruskal-Wallis (KW) non-parametric test in conjunction with the simple interval mapping procedure (SIM) (Lander and Botstein 1989) implemented in MapQTL v4.0 software (van Ooijen et al. 2002); subsequently the two separate parental maps were used for a re-analysis based on the BC1 algorithm, using both SIM and multiple QTL mapping (MQM) (Jansen and Stam 1994). Among the markers lying within a region harbouring a QTL, the one associated with the highest LOD score was used as a co-factor. For the MQM, a backwards elimination procedure was applied to select the appropriate co-factors. LOD thresholds for QTL significance were confirmed using a permutation test comprising 1,000 replications, which implies a genome-wide significance level of 0.05 (Churchill and Doerge 1994). Only those QTL associated with a LOD greater than either the genome-wide threshold or the LG threshold were considered. 1-LOD support intervals were determined for each LOD peak following van Ooijen (1992). The additive effect and the proportion of the overall phenotypic variance (PVE) associated with each QTL were both estimated from the MQM model. Linkage maps and QTL positions were drawn using MapChart (Voorrips 2002). Each QTL was designated by an abbreviated version of the trait name as a prefix, followed by the relevant LG.; so for example “bcC3_5” indicates a QTL underlying the bracts colour traits, mapping to the female linkage group C3_5.

Results

Phenotypic variation, heritability and frequency distributions of phenotypes

The population displayed a very high diversity of phenotype and some individuals displayed aspects of morphology not previously observed in cultivated types. A summary of trait performance and the associated heritability values is given in Table 1. C3 and ALT differed significantly from one another ($p<0.05$) in both 2010 and 2011 (Table 1). The former produced purple-green capitula (*bc* score of 4 corresponding to prevalence of purple over the green, see Fig, 1A) and lacked fleshy thorns (*bt* score of 1, see Fig, 1B), while the latter recorded a *bc* score of 3 (green-purple capitula, with prevalence of green over the purple) and a *bt* score of 2 (presence of small and soft thorns). A high broad sense hereditability was observed for both traits ranging from a minimum of 0.91 (*bt*) to a maximum of 0.94 (*bc*) (Table 1). There was no significant correlation between the traits in either season.

As the population distributions for both traits were similar between years, only the 2010 data have been graphically presented (Fig. 1). On the basis of the initial three state classification of *bc*, the segregation in the mapping population was 39 green, 86 uneven purple and 29 even purple, fitting a 4:9:3 ratio ($\chi^2=0.01$, n.s.) predicted by the action of two independent genes interacting epistatically, as previously suggested by Cravero et al. (2005). The use of a 1-7 scale generated a continuous distribution in the mapping population, while each set of six clonally propagated individuals of both C3 and ALT was homogeneous. The mapping population mean value was close to the mid-parent value, but the distribution was skewed towards each parent, as F_1 capitula ranged from wholly green to dark purple (Fig. 1A). With respect to *bt*, the segregation pattern based on presence *vs* absence fitted the monogenic 3:1 ratio ($\chi^2=0.70$, n.s.) indicating that this trait is mainly controlled by a single gene. When the trait was scored on the 1-5 scale, the distribution became continuous, with

the population mean lying above the mid-parent value. About one third of the population recorded a higher *bt* score than ALT (Fig. 1B).

QTL identification

An independent QTL analysis was performed for each season (Table 2). The initial identification procedure highlighted three genomic regions influencing *bc* and two influencing *bt*. Each of the five QTL regions mapped to a different LG. The same QTL regions were identified in both seasons. The separate analysis of the C3 and ALT maps further validated the QTL regions; each of which was thus taken forward into the MQM procedure. The relationship between the two parental maps and the location of the *bt* and *bc* QTL are shown in Fig. 2. Table 2 documents the properties of each of the QTL: maximum LOD value, location on the genetic maps, additive marker value effects and proportion of phenotypic variance (PV) explained.

Considering bract pigmentation as a simple presence/absence trait (ignoring the effect of the proposed epistatic gene), the 9:4:3 ratio resolved into a monogenic 3:1 one (115 uneven or even purple *versus* 39 green). This pattern of segregation is consistent with the existence of a locus, termed *P*, present in the heterozygous state in both C3 and ALT; it was used as an intercross marker (ab x ab) and mapped onto the homologues LGs C3_5 and Alt_1, in the neighbourhood of two AFLP loci (Fig. 2). When the phenotypic data were treated as varying from 1 to 7, three QTL regions, each stable across the two seasons, were identified. One was represented in both parents (homologues QTL), one in C3 but not ALT, and the third in ALT but not C3. The largest effect QTL (PVE of 66-69%) mapped to C3_5/Alt_1, coincident with *P*. The C3 QTL (PVE of 16-17%) was located on LG C3_13 and the ALT QTL (PVE of 21-23%) mapped to Alt_11 (Fig. 2).

On the basis of the 3:1 segregation ratio detected for presence:absence of soft thorns, conventional linkage analysis located a gene underlying *bt* (denoted *Th*) on the same LG in both maps (C3_14/Alt_7). Scoring *bt* on a 1-5 scale identified a QTL (PVE of 68-73%) mapping in the same region as *Th*, along with a second locus (PVE of 11-12%) exclusive to ALT mapping to Alt_4, in the neighbourhood of a CAPS and a SSR marker (Fig. 2).

Discussion

Genetic control of capitulum colour

Differences in capitulum colour in globe artichoke reflect the content and distribution of anthocyanin. High levels of anthocyanin are considered to be a positive attribute of plant-based foods (Lattanzio et al. 2009) and pigmented globe artichoke capitula are well regarded by consumers. The synthesis and accumulation of anthocyanin are strongly affected by genotype, are developmental stage dependent and are influenced by temperature (Prior et al. 1998; Cohen et al. 2011; Yamane et al. 2011); the intensity of pigmentation in the capitulum is particularly sensitive to temperature (Foury 1969; Pochard et al. 1969; Basnizky and Zohary 1994). Nevertheless, the present experiments recorded a very high broad sense heritability for capitulum pigmentation. According to Pochard et al. (1969), pigmentation is determined by the presence of a dominant allele, interacting epistatically with an inhibitor. However, later evidence has suggested that a series of modifiers is additionally involved (Basnizki and Zohary (1994). The genetic model proposed by Cravero et al. (2005) on the basis of segregation patterns observed in various populations is that *bc* is determined by the two independent genes *P* and *U*, where plants of genotype *PP* or *Pp* produce purple bracts and the *pp* genotype produces green ones; meanwhile the *UU* or *Uu*

genotype confers an uneven distribution of pigment, while *uu* individuals form uniformly pigmented bracts. Superimposed on this simple genetic system is the action of various modifier genes, which result in a gradation of pigmentation intensity and the formation of colour streaks.

The pigmentation segregation pattern observed in the present mapping population was consistent with both C3 and ALT being of genotype *PpUu* as it was possible to identify the predicted three classes of capitulum colouration (uneven purple, green and even purple) segregating in the di-genic ratio of 4:9:3 [*ppU_* + *ppuu* (4)]: [*P_U_* (9)]: [*P_uu* (3)]. The pre-availability of the genome-wide genetic map allowed the placement of *P* onto LG C3_5 and Alt_1 (these two LGs are homologues) by analyzing its 3:1 monogenic segregation [(*P_U_* + *P_uu*): (*ppU_* + *ppuu*) = pigmented: green]. By treating the trait as a QTL showed that the most important locus (PVE of 66-69%) mapped to the same region of this LG. Following the strategy proposed by Monforte et al. (2004), the possibility that the other QTL (PVE of 16-23%) mapping to C3_13 and Alt_11 corresponded to *U* was tested by repeating the linkage analysis after excluding those individuals, which produced a green capitulum: the resulting segregation of uneven purple *versus* even purple fitted the segregation of a single dominant locus [*P_U_* (3)]: [*P_uu* (1)]. However, since the restricted size of this portion of the population hindered the placement of *U* on the map, it was not possible to confirm whether the minor *bc* QTL revealed on both C3_13 and Alt_11 was identical to *U*. The segregation of pigmentation among a population bred from a cross between a green capitulum wild cardoon and a purple capitulum globe artichoke variety was consistent with the two parents having the allelic constitution *ppUu* and *Ppuu,* as reported by Martin et al. (2013). On the resulting map associated with the wild cardoon parent, the presumptive location for *U* mapped to an LG corresponding with C3_10, rather than with C3_13. This lack of correspondence may reflect a number of factors, most notably the imprecision

associated with the detection of minor effect QTL (Beavis 1994). However, as other loci could be involved in the interaction, the number of modifier loci involved in the genetic control of anthocyanin distribution might be variable in different progenies.

Genetic control of the presence of fleshy thorns

The lack of both spines and fleshy thorns is a positive attribute for both the consumer and the processing industry. The genetic basis of spine formation relates to the allelic constitution at the *Sp* locus, with the spiny "thistle-like" phenotype determined by the recessive allele *sp* (Pochard et al. 1969; Basnizki and Zohary 1994); the map location of *Sp* has been reliably established with a few mapping exercises (Lanteri et al. 2006; Sonnante et al. 2011; Martin et al. 2013). Both C3 and ALT are non-spiny types; the lack of any segregation for spininess in the mapping population, together with its segregation among progeny derived from other crosses involved the same female parent (Lanteri et al. 2012), implies that the allelic constitution of the globe artichoke must have been *Spsp* and that of the cultivated cardoon *SpSp*. With respect to fleshy thorns, which can develop in non-spiny types either solely on the leaves or in some cases on both the leaves and capitulum (Lanteri et al. 2012), the discrete nature of its segregation is fully consistent with its monogenic control involving a gene *Th* mapping to LG C3_14/Alt_7. The dominant allele confers the absence of fleshy thorns, with C3 and ALT sharing the allelic constitution *Thth*. Unlike those of ALT, the capitula produced by C3 lack fleshy thorns; the simplest genetic model consistent with this phenotype is that C3 is homozygous for *i*, a recessive inhibitor gene, while ALT is homozygous for the dominant allele *I*. The variation observed with respect to the length of the fleshy thorn types suggests the existence of modifier genes, possibly related to the minor QTL (PVE=11-12%) identified on Alt_4.

Conclusions

The evolving *C. cardunculus* genetic map has sufficient resolution to identify the genomic region(s) influencing any heritable agronomic trait, such as the oligogenic traits (capitulum pigmentation and fleshy thorniness) described here. For the purpose of marker-assisted selection - and definitely for the QTL isolation where this may be of interest – a greater level of resolution is still needed. This goal should be accomplished in the near future given the recent preparation of a draft genome assembly (Acquadro et al. 2014; Scaglione et al. 2014), the large-scale re-sequencing of C3 and ALT and ongoing efforts to acquire low coverage genotyping-by-shotgun-sequencing of the mapping population.

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Figure legends

Figure 1:

Frequency distribution of *bc* and *bt* among the mapping population (2010 harvest). Parental perfomance ('C3': 'Romanesco C3', ALT: 'Altilis 41') indicated by arrows. A) Representative bracts illustrating the scale used to score bract pigmentation (bc). 1: green; 2: green with purple hue; 3: green-purple; 4: purple-green; 5: purple with green hue; 6: purple; 7: dark purple. B) Representative bracts illustrating the scale used to score fleshy thorns (bt). 1: absence; 2 to 5: from small and soft to fully developed.

Figure 2:

QTL mapping for bc and bt. Only those LGs harbouring relevant QTL are shown. C3 LGs shown in white, ALT LGs in grey. Bars represent 1-LOD support intervals; black bars indicate merged confidence intervals for QTL across both seasons.

FIGURE 1

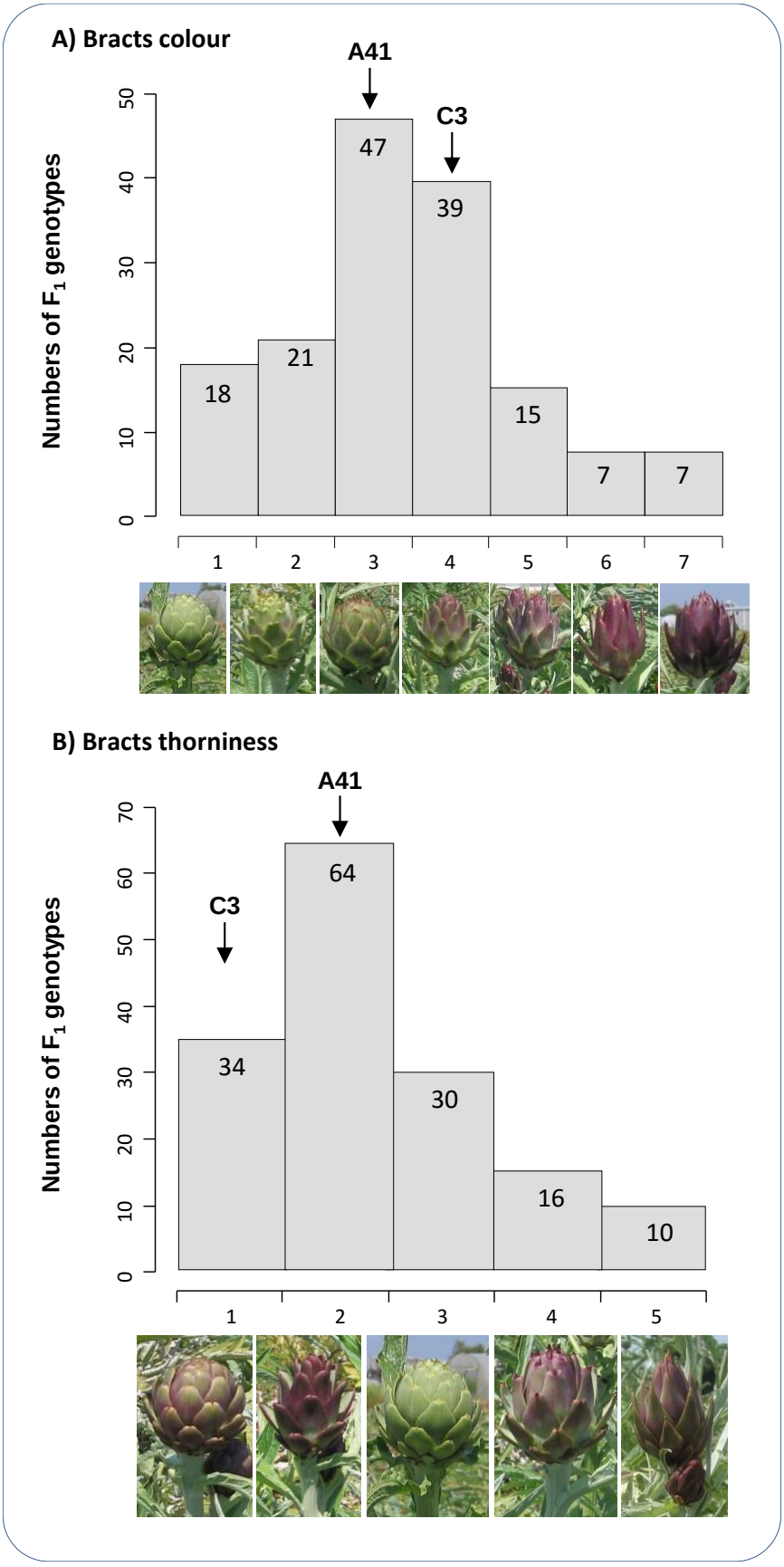
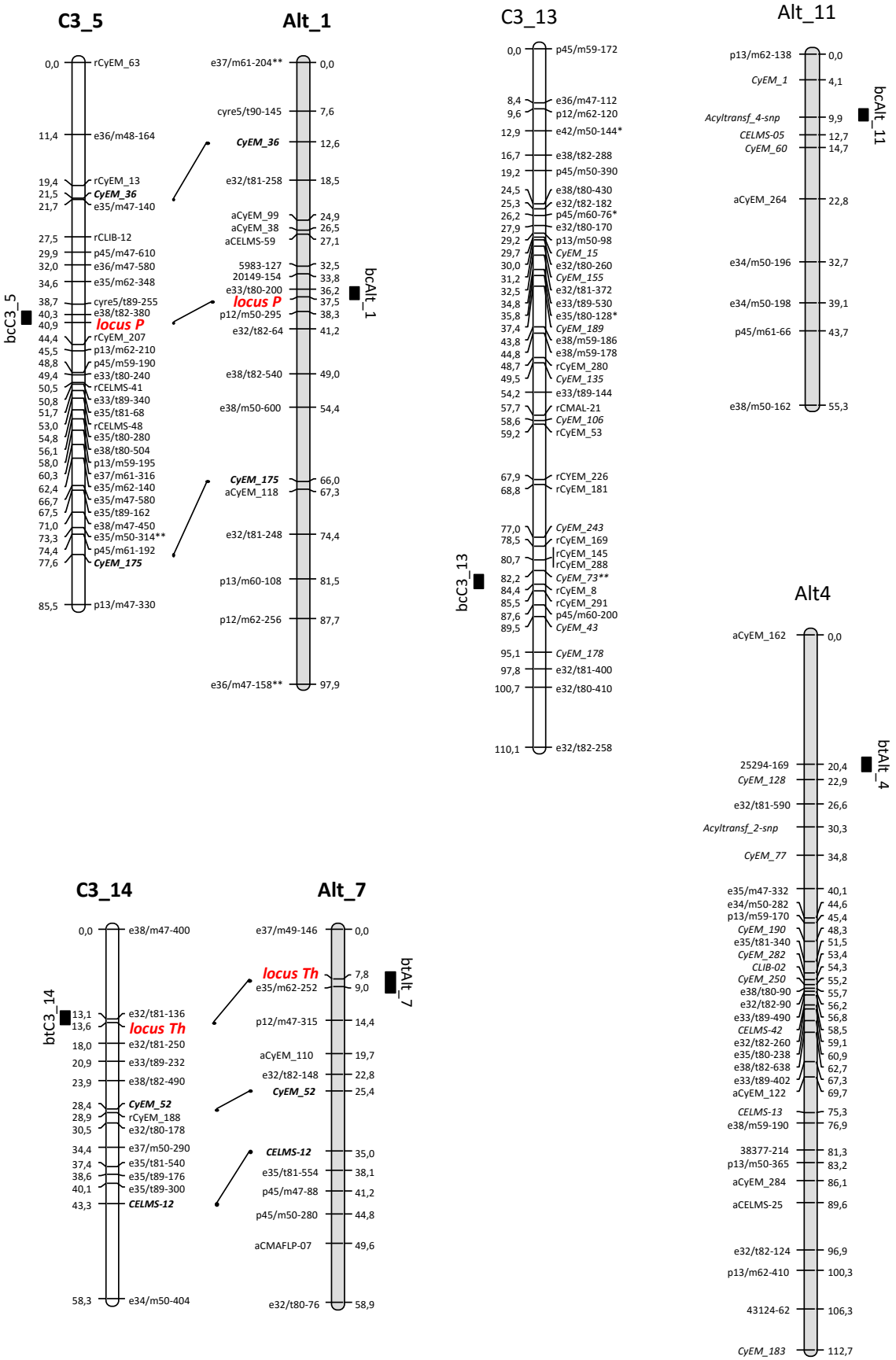

A) Bracts colour
A41
C3
Numbers of F1 genotypes
0
10
20
30
40
50
18
21
47
39
15
7
7
1
2
3
4
5
6
7
B) Bracts thorniness
A41
C3
Numbers of F1 genotypes
0
10
20
30
40
50
60
70
34
64
30
16
10
1
2
3
4
5

FIGURE 2


C3_5
Alt_1
C3_13
Alt_11
Alt4
C3_14
Alt_7
bcC3_5
bcAlt_1
bcC3_13
bcAlt_11
btC3_14
btAlt_7
btAlt_4
locus P
locus Th
0,0 rCyEM_63
11,4 e36/m48-164
19,4 rCyEM_13
21,5 CyEM_36
21,7 e35/m47-140
27,5 rCLIB-12
29,9 p45/m47-610
32,0 e36/m47-580
34,6 e35/m62-348
38,7 cyre5/t89-255
40,3 e38/t82-380
40,9 locus P
44,4 rCyEM_207
45,5 p13/m62-210
48,8 p45/m59-190
49,4 e33/t80-240
50,5 rCELMS-41
50,8 e33/t89-340
51,7 e35/t81-68
53,0 rCELMS-48
54,8 e35/t80-280
56,1 e38/t80-504
58,0 p13/m59-195
60,3 e37/m61-316
62,4 e35/m62-140
66,7 e35/m47-580
67,5 e35/t89-162
71,0 e38/m47-450
73,3 e35/m50-314**
74,4 p45/m61-192
77,6 CyEM_175
85,5 p13/m47-330
e37/m61-204** 0,0
cyre5/t90-145 7,6
CyEM_36 12,6
e32/t81-258 18,5
aCyEM_99 24,9
aCyEM_38 26,5
aCELMS-59 27,1
5983-127 32,5
20149-154 33,8
e33/t80-200 36,2
locus P 37,5
p12/m50-295 38,3
e32/t82-64 41,2
e38/t82-540 49,0
e38/m50-600 54,4
CyEM_175 66,0
aCyEM_118 67,3
e32/t81-248 74,4
p13/m60-108 81,5
p12/m62-256 87,7
e36/m47-158** 97,9
0,0 p45/m59-172
8,4 e36/m47-112
9,6 p12/m62-120
12,9 e42/m50-144*
16,7 e38/t82-288
19,2 p45/m50-390
24,5 e38/t80-430
25,3 e32/t82-182
26,2 p45/m60-76*
27,9 e32/t80-170
29,2 p13/m50-98
29,7 CyEM_15
30,0 e32/t80-260
31,2 CyEM_155
32,5 e32/t81-372
34,8 e33/t89-530
35,8 e35/t80-128*
37,4 CyEM_189
43,8 e38/m59-186
44,8 e38/m59-178
48,7 rCyEM_280
49,5 CyEM_135
54,2 e33/t89-144
57,7 rCMAL-21
58,6 CyEM_106
59,2 rCyEM_53
67,9 rCYEM_226
68,8 rCyEM_181
77,0 CyEM_243
78,5 rCyEM_169
80,7 rCyEM_145
rCyEM_288
82,2 CyEM_73**
84,4 rCyEM_8
85,5 rCyEM_291
87,6 p45/m60-200
89,5 CyEM_43
95,1 CyEM_178
97,8 e32/t81-400
100,7 e32/t80-410
110,1 e32/t82-258
p13/m62-138 0,0
CyEM_1 4,1
Acyltransf_4-snp 9,9
CELMS-05 12,7
CyEM_60 14,7
aCyEM_264 22,8
e34/m50-196 32,7
e34/m50-198 39,1
p45/m61-66 43,7
e38/m50-162 55,3
aCyEM_162 0,0
25294-169 20,4
CyEM_128 22,9
e32/t81-590 26,6
Acyltransf_2-snp 30,3
CyEM_77 34,8
e35/m47-332 40,1
e34/m50-282 44,6
p13/m59-170 45,4
CyEM_190 48,3
e35/t81-340 51,5
CyEM_282 53,4
CLIB-02 54,3
CyEM_250 55,2
e38/t80-90 55,7
e32/t82-90 56,2
e33/t89-490 56,8
CELMS-42 58,5
e32/t82-260 59,1
e35/t80-238 60,9
e38/t82-638 62,7
e33/t89-402 67,3
aCyEM_122 69,7
CELMS-13 75,3
e38/m59-190 76,9
38377-214 81,3
p13/m50-365 83,2
aCyEM_284 86,1
aCELMS-25 89,6
e32/t82-124 96,9
p13/m62-410 100,3
43124-62 106,3
CyEM_183 112,7
0,0 e38/m47-400
13,1 e32/t81-136
13,6 locus Th
18,0 e32/t81-250
20,9 e33/t89-232
23,9 e38/t82-490
28,4 CyEM_52
28,9 rCyEM_188
30,5 e32/t80-178
34,4 e37/m50-290
37,4 e35/t81-540
38,6 e35/t89-176
40,1 e35/t89-300
43,3 CELMS-12
58,3 e34/m50-404
e37/m49-146 0,0
locus Th 7,8
e35/m62-252 9,0
p12/m47-315 14,4
aCyEM_110 19,7
e32/t82-148 22,8
CyEM_52 25,4
CELMS-12 35,0
e35/t81-554 38,1
p45/m47-88 41,2
p45/m50-280 44,8
aCMAFLP-07 49,6
e32/t80-76 58,9

Tables

Table 1. Variation for *bc* and *bt* between C3 and ALT and across the mapping population in both seasons.

Trait	Trait code	Year	Parental genotypes			F_1 population [1]			
			C3	ALT	Wilcoxon test	Mean	Range	s.e.	h_B^2
Bracts colour	bc	2010	4.00	3.00	p<0.05	3.42	1 – 7	0.119	0.94
		2011	4.00	3.00	p<0.05	3.57	1 – 7	0.101	
Bracts thorniness	bt	2010	1.00	2.00	p<0.05	2.38	1 – 5	0.174	0.91
		2011	1.00	2.00	p<0.05	2.41	1 – 5	0.185	

[1] s.e.: standard errors; h_B^2: broad sense heritability based on two years' data.

Table 2. QTL underlying *bc* and *bt* inferred from the C3 and ALT maps.

Trait	Map	LG	QTL	2010						2011					
				GW	Locus	cM	LOD	PVE	Add	GW	Locus	cM	LOD	PVE	Add
Bracts colour	C3	C3_5	bcC3_5	6.9	e38/t82-380	40.3	18.0	67.2	3.89	7.3	e38/t82-380	40.3	20.6	69.3	3.92
		C3_13	bcC3_13		CyEM_8	25.8	7.2	15.6	1.18		CyEM_43	20.7	7.5	17.5	1.03
	ALT	Alt_1	bcAlt_1	6.3	e33/t80-200	36.2	15.2	66.1	3.56	6.1	e33/t80-200	36.2	17.1	68.1	3.29
		Alt_11	bcAlt_11		Acyltransf_4-snp	30.3	7.7	23.6	-2.26		Acyltransf_4-snp	30.3	6.9	21.1	-2.09
Bract thorniness	C3	C3_14	btC3_14	8.1	e32/t81-250	18.0	11.0	68.1	5.44	7.9	e32/t81-250	18.0	8.7	71.3	4.99
	ALT	Alt_7	btAlt_7	9	e35/m62-252	9.0	14.0	73.2	5.63	8.7	e35/m62-252	9.0	12.5	71.2	5.51
		Alt_4	btAlt_4		25294-169	20.4	9.4	12.5	3.12		25294-169	20.4	8.8	11.3	2.96

Each QTL name is formed by the abbreviation of the trait followed by the relevant LG. The table indicates genome-wide LOD thresholds (GW) as determined by a permutation test at $p \leq 0.05$, the closest linked markers (Locus) and their map location (cM), the estimated LODs at the QTL peak (LOD), the proportions (%) of the total variance explained (PVE), and the additive effects (Add).