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Note

An SSR-based genetic map of pepper (*Capsicum annuum* L.) serves as an anchor for the alignment of major pepper maps

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Of the Capsicum peppers (*Capsicum* spp.), cultivated *C. annuum* is the most commercially important, but has lacked an intraspecific linkage map based on sequence-specific PCR markers in accord with haploid chromosome numbers. We constructed a linkage map of pepper using a doubled haploid (DH) population derived from a cross between two *C. annuum* genotypes, a bell-type cultivar 'California Wonder' and a Malaysian small-fruited cultivar 'LS2341 (JP187992)', which is used as a source of resistance to bacterial wilt (*Ralstonia solanacearum*). A set of 253 markers (151 SSRs, 90 AFLPs, 10 CAPSs and 2 sequence-tagged sites) was on the map which we constructed, spanning 1,336 cM. This is the first SSR-based map to consist of 12 linkage groups, corresponding to the haploid chromosome number in an intraspecific cross of *C. annuum*. As this map has a lot of PCR-based anchor markers, it is easy to compare it to other pepper genetic maps. Therefore, this map and the newly developed markers will be useful for cultivated *C. annuum* breeding.

Key Words: pepper (*Capsicum annuum* L.), SSR markers, genetic map, 12 linkage groups.

Introduction

Cultivated *Capsicum* fruits are used as a source of vegetables, spice, colorant and for some medical applications. The genus is native to Central and South America (Pickersgill 1991) and includes the species *C. chinense*, *C. baccatum*, *C. frutescens*, *C. pubescens* and *C. annuum*. Of these five species, *C. annuum* is the most important one because it is cultivated in both tropical and temperate area in the world and it is the most versatile of the five species. In contrast, the other four species are cultivated in limited regions in the world or only in tropical areas and they are mainly used as spices.

Linkage maps of *Capsicum* have been constructed using both intraspecific *annuum* populations and interspecific crosses such as *C. annuum* × *C. chinense* (Kang *et al.* 2001, Lee *et al.* 2004, Livingstone *et al.* 1999, Yi *et al.* 2006) and *C. annuum* × *C. frutescens* (Ben-Chaim *et al.* 2006, Rao *et al.* 2003, Wu *et al.* 2009). Interspecific crosses benefit from a high level of marker polymorphism but suffer from low fertility, segregation distortion and major structural rearrangements (Lanteri 1991, Lanteri and Pickersgill 1993, Wu *et al.* 2009), which limit the power of the linkage analysis and restrict their relevance to marker-assisted selection (MAS) applications (Lefebvre *et al.* 2002).

Several intraspecific maps of *C. annuum* have been reported (Barchi *et al.* 2007, Caranta *et al.* 1997a, 1997b, Lefebvre *et al.* 1995, Minamiyama *et al.* 2006, 2007, Ogundiwin *et al.* 2005, Sugita *et al.* 2006). RFLP and RAPD markers were used for constructing some of the maps. However, RFLP markers have been largely replaced by a new generation of molecular markers (e.g. SSR, AFLP and CAPS) which offer tremendous advances in cost, efficiency, throughput and sensitivity for plant genomics. RAPD markers also have problem with reproducibility. The map position of highly reproducible, locus-specific, co-dominant PCR-based markers is of particular value for the integration of genetic information from different populations and will underpin much applied research in pepper, including gene mapping, quantitative trait loci (QTL) analysis, and marker-

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assisted selection. Previously, Minamiyama *et al.* (2006, 2007) have constructed a pepper map mainly by using SSR markers with high polymorphism information content. Nevertheless, these studies have not resulted in complete genetic maps of the pepper genome in which 12 linkage groups correspond to the haploid chromosome numbers. The maps are also not comparable in marker position to any other maps in pepper, since they have few common markers with other pepper maps. We constructed an SSR-based map which involved several QTLs such as bacterial wilt (*Ralstonia solanacearum*) resistance and growth traits in a previous study (Mimura *et al.* 2009b, 2010). However, our earlier map also described several chromosomes as segmented short linkage groups.

In this study, we describe an SSR-based genetic map of cultivated *C. annuum* with the 12 pepper chromosomes by adding lots of reproducible markers in common with the maps of Minamiyama *et al.* (2006), Wu *et al.* (2009) and Yi *et al.* (2006). Moreover, we detected several QTLs related to economically important fruit traits. Therefore, the map developed through this study is useful for MAS and QTL in commercially important cultivated *C. annuum*.

Materials and Methods

Plant materials

Malaysian accession 'LS2341 (JP187992)' bearing small elongated, oval fruit and resistant to bacterial wilt (Mimura *et al.* 2009a) was used as the pollen donor. This accession was obtained from the National Institute of Agrobiological Sciences (NIAS) Genebank in Tsukuba, Japan. A sweet pepper cultivar, 'California Wonder (CW)' was employed as a seed parent. A segregating doubled haploid (DH) population ($n = 94$) was bred by anther culture of an F_1 individual (Mimura *et al.* 2009b).

Marker analysis and map construction

AFLP and SSR polymorphisms were scored according to a method described by Minamiyama *et al.* (2006). The SSR primer pairs used in this study were developed from genomic libraries and/or registered sequences at the databases (Huang *et al.* 2001, Lee *et al.* 2004, Mimura *et al.* 2010, Minamiyama *et al.* 2006, 2007, Nagy *et al.* 2007, Yi *et al.* 2006).

In order to converge the expected 12 linkage groups and to assign a few, yet unknown linkage groups, we also tried to use Conserved Ortholog Set II (COSII) markers (Wu *et al.* 2009). COSII markers are PCR-based markers developed from a set of single-copy conserved orthologous genes. In pepper, map positions of COSII markers have already been shown (Wu *et al.* 2009). Since most of the markers had no polymorphism between the parental lines, the PCR products were sequenced and we detected SNPs for designing as original CAPS or dCAPS markers. Mapping was performed using JoinMap 3.0 software with a population type code, DH1 (Van Ooijen and Voorrips 2001). Markers were grouped at an LOD score of 4.0, where map distances were calculated using the Kosambi function (Kosambi 1944).

Fruit trait QTLs

The parents and the 94 F_1DH lines were grown in a heated green house in Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Research Centre, Seika, Kyoto, Japan, and the fruit traits were studied during two growth seasons (May–Sep. 2007 and Jan.–May 2009).

The following traits were evaluated for each fruit:

(1) fruit length (FL)—the distance (in millimetres) from the pedicel attachment to its apex; (2) fruit diameter (FD)—measured at the maximum width (in millimetres); (3) fruit shape (FS)—the ratio of fruit length to fruit diameter.

Average scores of 5 to 10 fruits for each line were treated as trait data.

QTL mapping was performed using Map QTL 6.0 software (Van Ooijen 2009) under the multiple QTL model, which is equivalent to composite interval mapping.

Results and Discussion

Genetic map construction

The map in this study contains 151 SSR, 90 AFLP, 10 CAPS/dCAPS and 2 STS markers in 12 linkage groups, and covers 1,336 cM (Fig. 1). As for COSII markers, we tried 84 markers, and obtained PCR products from two parents of this study in 61 markers. Then, 12 of 61 markers were able to be modified as CAPS/dCAPS or indel STS markers with polymorphism (Table 1). Moreover, new 24 SSR markers have been mapped in this study. Their unique primer sequences and other information are shown in Table 2. Furthermore, previously reported 13 SSR markers were firstly mapped in this study (Fig. 1).

Comparison with other maps

The total map length of the present map is somewhat shorter than those of previous studies (Ben-Chaim *et al.* 2001, Livingstone *et al.* 1999, Wu *et al.* 2009, Yi *et al.* 2006). However, the map distance calculated by JoinMap is always shorter than that by Mapmaker (Bradeen *et al.* 2001). In addition, all the SSR markers, which had polymorphism in the DH population derived from F_1 between CW and LS2341, were mapped in this study. Then, there was no unlinked the SSR markers. This result suggests that the present map covers the majority of the pepper genome. The map of this study had 26, 12 and 36 common SSR and/or STS markers with the maps of Minamiyama *et al.* (2006), Wu *et al.* (2009) and Yi *et al.* (2006), respectively. The order of the SSR and STS markers was in good agreement with the maps of previous studies (Barchi *et al.* 2007, Lee *et al.* 2004, Minamiyama *et al.* 2006, Wu *et al.* 2009, Yi *et al.* 2006). Only a discrepancy of the position in the linkage group between our map (P1) and the Minamiyama *et al.* (2006) map (LG7) was identified; the order of the SSR markers CAMS460 and CAMS606 was the converse in the two

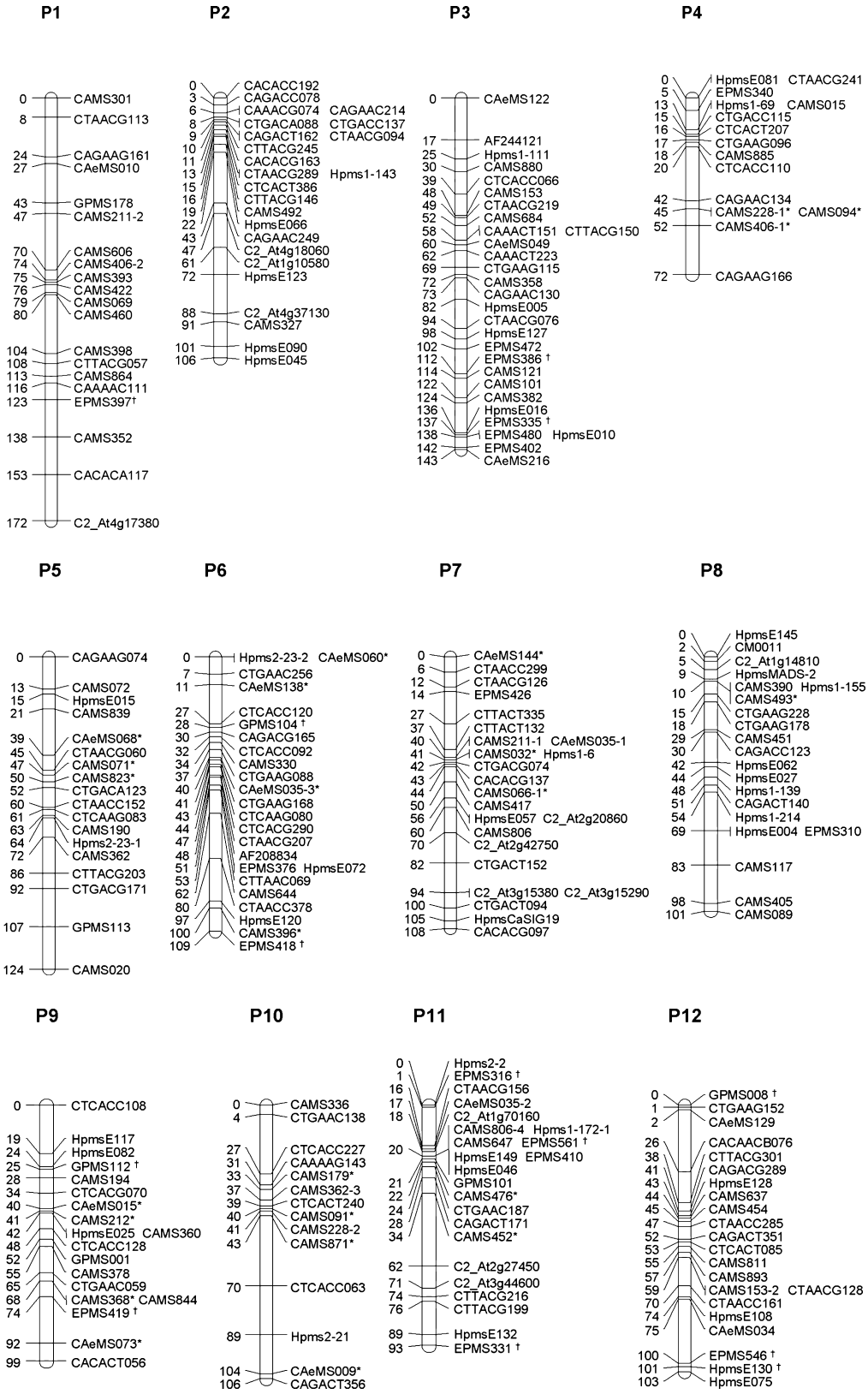

Fig. 1. A genetic linkage map of cultivated *C. annuum* genome. Nomenclature of linkage groups is referred to the consensus chromosome numbers (Wu *et al.* 2009). Marker names and the map distances (cM) are indicated on the right and left of linkage groups, respectively. Markers named AF__, CAeMS__, CAMS__, CM__, EPMS__, GPMS__, Hpms__ are SSR markers. COSII markers are represented by the name C2_At__ (Table 1). Others are AFLP markers. Newly used 24 SSR markers (Table 2) are indicated with asterisks (*). Previously reported but firstly mapped 13 SSR markers are indicated with daggers (†).

Table 1. CAPS/dCAPS and STS markers modified and used in this study

Marker name[a]	Forward primer (5′-3′)	Reverse primer (5′-3′)	Restriction enzyme	Chromo-some	Expected product size (bp)[b]	
					CW	LS
C2_At4g17380	caaggatgggaacaatggacag	gcaagttgaagaggtcaaactgcat	Tsp509 I	1	140	150
C2_At4g18060	tcaagcagtttagtgcaactggttatg	tgccttaacaatctctttctgaaaatc	Mse I	2	550, 300, 250, 100	550, 420, 250, 100
C2_At1g10580	agtaatgatggaagcaagtttttgac	agaagacaaacctccatcaggtgagaa	BsaB I	2	250	300, 200
C2_At4g37130	ttacagcaaactgtagcaagatttgag	tgctgttttcattgattcaatgtactg	Alu I	2	1000	600, 210, 190
C2_At2g20860	aaatgaggagctggtggtcacat	taggtatcgcttaactgatggtg	Rsa I	7	180	100, 80
C2_At2g42750	gggaaaatggtgagatggcaaagttag	caagtataatcctccacgtgtcattg	Afa I	7	110, 50	160
C2_At3g15380	ttgtttggcggctattgggc	agcattacgattcacagatttgatgg	Msp I	7	380, 200	500
C2_At3g15290	tctgctattttggcttctaatacaag	acaatatgtgtcttctgatgtatctgc	Bsp1286 I	7	1500	680
C2_At1g14810	gcattagtggtgttggaccaca	gacaggcaaggctatgtgacag	Indel	8	150	140
C2_At1g70160	acatgtggaacgaagctctgaataa	tggaggtaaagaaggacaattctcattc	Alu I	11	900, 200	600, 200
C2_At2g27450	gaatttctgtatctcatttggattc	acccctaataaaaaagagtcac	Taq I	11	160	180
C2_At3g44600	tcctttataccgacttgaagctattg	agattctatgtttcttgaaagcacagc	Indel	11	500	530

[a] Restriction Sites were detected in PCR-amplified fragments from the population of this study and several primer pairs were newly designed. However, the marker names are the same as the original COSII markers to facilitate comparison with other maps.
[b] CW = allele from California Wonder, LS = allele from LS2341.

Table 2. Twenty four SSR markers newly used in this study

Marker name	Forward primer (5′-3′)	Reverse primer (5′-3′)	Motif	Chromo-some	Expected product size (bp)[a]	
					CW	LS
CAMS094	tgtagctcacatcgtctccact	gcattgcatttcacttgcat	(ta)5(tg)13	4	190	188
CAMS228	gagggctaagcaaagcagaa	tgcatgtttcccttagtttcc	(ta)5(tg)13	4	241	239
CAMS406	taaaaatcgcggaaagttgc	gtcgttctatgcggcatttt	(ga)8	4	184	182
CAeMS068	atcaaatctcaacacatggtggct	gtttactgtatctccggccctgtca	(cct)5ctt(cct)3	5	169	166
CAMS071	aatgggatctgcatgagaca	ttccctaaaagatggtgattcc	(ac)11	5	172	166
CAMS823	tcctcctccttctcgtgttc	aaagaagcagcaggtgaaga	(ctt)5	5	226	228
CAeMS035	aggtctatcggaaacagcctttct	gtttgatcacatcccagtcgaatccta	(tgt)5	6	183	181
CAeMS060	atcaagacaacaacatcatgggga	gtttcgcctatcaacaatggcaaataca	(ta)10	6	286	292
CAeMS138	acacacacaatttccctcactcac	gtttctctcaaatccctccgttgttc	(ag)5...(ag)5...(ga)3...(ag)3	6	250	244
CAMS396	gtcggccgtcattcactatt	agcttgatgcacctggtctt	(ag)12	6	240	244
CAeMS144	ataactttgattcctagttcggcg	gtttgaacccccaatcatcatatcctca	(gaa)5	7	222	219
CAMS032	tgccacataggttggctttc	caaagccaatgcacataatca	(gt)13	7	233	245
CAMS066	aaaaacatgcaccagtcctt	caaccgcctgaattttctct	(ac)11	7	157	153
CAMS493	tcgatgacgaaaaagtgtgaa	agggcaaaagacccattctt	(ag)6	8	225	223
CAeMS015	atgccttggtggtggttaaatctg	gtttagcggtatggactgcgtacatctt	(caa)7	9	273	270
CAeMS073	atgcttctaagaaaccccacaaca	gtttctcataaaggggttgggattga	(tat)7	9	234	230
CAMS212	ttccctttcccaacatggta	acacccgaagatgggttaga	(tg)10	9	154	150
CAMS368	gagtggataagcaaggacgttt	tttgcttccctttttgcttc	(ag)23	9	206	180
CAeMS009	acgcaccaacgaatatctatctca	gtttccgtccagatctacttttcctgc	(ag)4...(ag)8	10	246	232
CAMS091	tgctaaacttggttccctatcc	cgaagatggattagcgggta	(ta)6(tg)10	10	180	172
CAMS179	catgtcatgaagttgataagacaatg	tgttccagtgaaaggcttctt	(ac)13(at)9	10	228	224
CAMS871	acaaagcatcggctgaaaat	gcgaccaagtaccaacaggt	(gaa)14	10	–	150
CAMS452	gaagtctgggacctcttttgg	ttcattttgatcttcacgaacg	(ga)11	11	161	163
CAMS476	ttttccctttccagttgttca	atgggtgaagtgtgaaaagaa	(tc)5	11	156	164

[a] CW = Allele from California Wonder, LS = Allele from LS2341.

maps, although the distance of the two markers was estimated to be less than 10 cM.

Conflict of linkage groups P1 and P8 in cultivated Capsicum annuum

In the map of Yi *et al.* (2006), linkage group 8 was missing and fused with linkage group 1. As a result, the linkage group 1 represented two pepper chromosomes, P1 and P8. Such a pseudolinkage may occur resulting from reciprocal translocation of the two chromosomes between the parents of the mapping population (*C. annuum* and *C. chinense*), as proposed by Wu *et al.* (2009). These two chromosomes have

Table 3. QTLs detected for the fruit traits in this study

Trait	Test	Marker[a]	Chromosome	Position[b]	LOD	R2[c]	Additive[d]	Threshold[e]
Fruit length	2007	C2_At1g10580	P2	63.7	3.0	6.7	6.6	3.0
	2007	C2_At4g37130	P2	84.1	3.6	7.9	7.5	3.0
	2007	CAAACT151	P3	58.0	14.5	51.2	−16.8	3.0
	2009	C2_At4g37130	P2	82.1	3.6	8.1	6.6	2.9
	2009	HpmsE045	P2	105.7	3.7	8.2	5.8	2.9
	2009	CAAACT151	P3	58.0	14.4	52.2	−14.3	2.9
Fruit diameter	2007	GPMS178	P1	38.4	4.2	11.7	3.2	3.0
	2007	CAAACT151	P3	58.0	9.6	37.9	5.0	3.0
	2009	CAeMS010	P1	33.4	5.0	14.2	2.8	3.1
	2009	CAAACT151	P3	58.0	9.1	37.1	4.0	3.1
	2009	CAMS451	P8	28.9	4.4	12.7	2.4	3.1
	2009	CTCACC227	P10	29.3	3.6	10.4	2.3	3.1
Fruit shape	2007	CAAACT151	P3	58.0	23.1	68.2	−7.9	2.9
	2009	CAAACT151	P3	58.0	18.5	61.3	−0.76	3.0
	2009	CAMS493	P8	11.6	3.9	6.9	−0.27	3.0

[a] The marker on or in the vicinity of the LOD score peak.
[b] Position of the LOD score peak in the linkage group in cM.
[c] Percentage of phenotypic variation explained.
[d] Additive effect of QTLs of the 'California Wonder' allele.
[e] The significance threshold for detecting QTL by 1,000 permutations at $P < 0.05$.

been split into the expected linkage groups in the present map (Fig. 1, P1 and P8), though the linkage assignment was exchanged between P1 and P8 previously (Mimura *et al.* 2009b). This was because our previous assignment was done based on the integrated map by Paran *et al.* (2004) through the map by Yi *et al.* (2006), where Paran *et al.* (2004) made the assignments of P1 and P8 in a direction opposite to those of the more recent maps (Barchi *et al.* 2009, Wu *et al.* 2009). Here we concluded that the linkage group which was formerly expressed as P1 by Mimura *et al.* (2009b) was shifted to P8 in this map and *vice versa*.

Phenotypic variations and QTLs of fruit traits

The ranges of FL, FD and FS values were 32–137 mm, 19–61 mm and 0.89–4.91, respectively. The narrow sense heritabilities were higher than 94% in all traits.

A QTL for FL located on P3 had the largest effect in both years, explaining 51% and 52% of the total phenotypic variation in 2007 and 2009, respectively (Table 3). The 'CW' allele on P3 decreased the FL. Two additional QTLs were identified on P2. The QTL on P3 also brought about the largest effect for FD and FS, explaining 37–38% and 61–68% of total phenotypic variation, respectively (Table 3). Three additional QTLs for FD and one for FS were also detected. The major QTLs for the three traits were located on the same position of marker 'CAAACT151' on P3. The position may overlap with that of a QTL cluster of 'fl3.1', 'fd3.1' and 'fs3.1' (Ben-Chaim *et al.* 2001), because the cluster locus located at the 65 cM interval involves the 'CAAACT151' locus between the markers 'AF244121' and 'HpmsE005' on our map, when we compare the two maps using the map by Yi *et al.* (2006). Moreover, Ben-Chaim *et al.* (2001) and this study used similar *C. annuum* parent pairs, Bell type pepper and small elongated pepper from South-East Asia. Then, the FS QTLs of P3 in both studies also explained similar proportions of phenotypic variation, 63–67% and 61–68%, respectively. While the other study reported the high ratio of contribution in other chromosome (Ben-Chaim *et al.* 2003). However, the correspondence is unclear because of no PCR-based anchor marker in the vicinity of the QTL cluster.

Utility of the map in this study

Linkage groups P1 and P8 in cultivated *C. annuum* have important QTLs such as fruit related traits (Ben-Chaim *et al.* 2001), growth traits (Barchi *et al.* 2009, Ben-Chaim *et al.* 2001, Mimura *et al.* 2010) and several disease resistances (Mimura *et al.* 2009b, Ogundiwin *et al.* 2005, Sugita *et al.* 2006). The map in this study firstly revealed 12 linkage groups representing the 12 chromosomes in cultivated *C. annuum* with a lot of PCR-based anchor markers. Especially in P1 and P8, map length was comparable to those of previous studies (Wu *et al.* 2009, Yi *et al.* 2006). In addition, this map enables us to estimate a lot of CAMS (SSR) markers (Minamiyama *et al.* 2006) in other major maps. Moreover, the map has newly developed SSR and CAPS markers, and contains culturally important QTLs which affect fruits, growth and bacterial wilt resistance traits (Mimura *et al.* 2009b, 2010). In practice, breeding programmes involve lots of crossing between two cultivated *C. annuum.* Therefore, the map developed through this study is useful for MAS in breeding.

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