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Development of a genetic linkage map and identification of homologous linkage groups in sweetpotato using multiple-dose AFLP markers

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Abstract Sweetpotato genomic research is minimal compared to most other major crops despite its worldwide importance as a food crop. The development of a genetic linkage map in sweetpotato will provide valuable information about the genomic organization of this important species that can be used by breeders to accelerate the introgression of desired traits into breeding lines. We developed a mapping population consisting of 240 individuals of a cross between 'Tanzania', a cream-fleshed African landrace, and 'Beauregard', an orange-fleshed US sweetpotato cultivar. The genetic linkage map of this population was constructed using Amplified Fragment Length Polymorphism (AFLP) markers. A total of 1944 ('Tanzania') and 1751 ('Beauregard') AFLP markers, of which 1511 and 1303 were single-dose markers respectively, were scored. Framework maps consisting of 86 and 90 linkage groups for 'Tanzania' and 'Beauregard' respectively, were developed using a combination of JoinMap 3.0 and MAPMAKER/EXP 3.0. A total of 947 single-dose markers were placed in the final framework linkage map for 'Tanzania'. The linkage map size was estimated as 5792 cM, with an average distance between markers of 4.5 cM. A total of 726 single-dose markers were placed in the final framework map for 'Beauregard'. The linkage map length was estimated as 5276 cM, with an average distance between markers of 4.8 cM. Duplex and triple-dose markers were used to identify the corresponding homologous groups in the maps. Our research supports the hypothesis that sweetpotato is an autopolyploid. Distorted segregation in some markers of different dosages in this study suggests that some preferential pairing occurs in sweetpotato. However, strict allopolyploid inheritance in sweetpotato can be ruled out due to the observed segregation ratios of the markers, and the proportion of simplex to multiple-dose markers.

Keywords Ipomoea batatas · Molecular marker · Molecular mapping · Polyploid mapping · Autopolyploid

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Introduction

Sweetpotato, *Ipomoea batatas* (L.) Lam. is the seventh most important crop in terms of production with more than 122 million metric tons produced annually worldwide (CIP 2005; FAOSTAT 2006). The polyploid nature of sweetpotato (2n = 6x = 90), outcrossing behavior, and numerous mating incompatibilities, make sweetpotato breeding difficult. Breeding efforts are complicated by the fact that most traits of economic significance exhibit quantitative inheritance (Collins et al. 1999; Jones 1986). The sweetpotato breeding community lacks a detailed genetic linkage map to facilitate the breeding process. To date, two independent genetic maps of sweetpotato have been reported (Kriegner et al. 2003; Ukoskit et al. 1997). However, neither of these maps identified all of the expected linkage groups, and as a result they have provided very little information on the genomic organization of this important crop.

Constructing genetic maps in polyploids has historically been challenging, and has most successfully been accomplished for allopolyploid species. This is due to their similarity to diploids in terms of the segregation patterns and chromosomal pairing (Hermsen 1984; Sybenga 1996). Genetic mapping in polyploids is difficult for several reasons. First, a large number of possible genotypes are expected in a segregating population due to the larger number of alleles combining in a particular event given the ploidy level of the genome. This is especially true in autopolyploid species. Second, the genotype of an individual is not always readily inferred through its marker phenotype. Third, the type of ploidy (allopolyploidy or autopolyploidy) of many crops is unclear, making it difficult to determine patterns of inheritance (Ripol et al. 1999; Wu et al. 1992). This latter aspect is particularly important, given that in an autopolyploid species, corresponding chromosomes in the different genome copies are homologs and, therefore, can pair randomly between each other. In contrast, for allopolyploids chromosomes may originate from 2 or more different genomes and during meiosis will pair preferentially to their homologs from the same genome, and in lower frequency to a homeologous chromosome (Ramsey and Schemske 2002; Sybenga 1996).

A commonly used approach to construct molecular genetic maps in polyploids is based on the use of single-dose fragments (SDF). Wu et al. (1992) illustrated this method using both autopolyploid and allopolyploid species with different ploidy levels. As single-dose markers are markers present in one parent in a single copy, during gamete formation only half will carry the marker. Thus, regardless of the ploidy of the genome, half the progeny will possess this fragment and half will not. SDFs combined with other mapping strategies such as testcross and pseudo-testcross approaches, have been used to construct linkage maps in several polyploid species, including potato, sugarcane, and eucalyptus (da Silva et al. 1993; Ghislain et al. 2004; Grattapaglia and Sederoff 1994; Hoarau et al. 2001; Ripol et al. 1999), and for sweetpotato (Kriegner et al. 2003; Ukoskit and Thompson 1997).

The identification of the homologous chromosomes is very important in genetic mapping analysis of polyploids, since only homologous chromosomes pair and recombine during meiosis. Thus, the identification of all homologous groups is crucial for understanding the genomic constitution of sweetpotato and its inheritance mechanisms. Sweetpotatoes have been characterized as allopolyploids (Jones 1965; Magoon et al. 1970; Ting and Kehr 1953) and as autopolyploids (Nishiyama et al. 1975; Ukoskit and Thompson 1997). More recently, Kriegner et al. (2003) using the segregation ratios of AFLP markers hypothesized that sweetpotatoes are auto-allopolyploids, that is mainly autopolyploids, but with some preferential pairing. Mwanga et al. (2002) in a study of resistance to *Sweetpotato Feathery Mottle Virus* in sweetpotato, after combining their molecular findings with observed greenhouse results, hypothesized a hexasomic or a tetradisomic inheritance.

In soybean, Cregan et al. (1999) used simple sequence repeats (SSR) to align homologous chromosomes, and they were able to organize the total number of groups into the basic number of chromosomes (2n = 2x = 40). Similarly, in sweetpotato Kriegner et al. (2003) using double-dose AFLP markers identified 13 and 10 homologous groups in the maps of Tanzania and Bikilamaliya, respectively. However, a single complete set of six homologous chromosomes as expected was not identified. In this study, we report on the development of framework genetic linkage maps of two sweetpotato cultivars based on SDF AFLP markers. Multiple-dose markers were then incorporated and used to identify homologous chromosomes. The long-term objectives of this

project are to use our molecular genetic linkage map to facilitate the introgression of desired traits into our breeding lines, and open the door for marker-assisted selection (MAS) for important traits in sweetpotato. The resulting genetic map will be used to perform QTL analyses of several economically important traits including yield, starch and beta-carotene content and root knot nematode resistance.

Materials and methods

Plant material

The mapping population consisted of a cross between the African landrace 'Tanzania' (female), and 'Beauregard' (male). 'Tanzania' is a sweetpotato landrace from sub-Saharan Africa, and is a cream-fleshed, high dry matter (ca. 30%) sweetpotato. 'Tanzania' is also resistant to root-knot nematodes (Cervantes-Flores et al. 2002a, b) and tolerant to *Sweet Potato Feathery Mottle Virus* (SPFMV) and *Sweetpotato Chlorotic Stunt Virus* which together lead to *Sweetpotato Virus Disease* (SPVD) (Mwanga et al. 2002). 'Beauregard' is the most widely grown sweetpotato in the US, and is an orange-fleshed, low dry matter (ca. 18%) cultivar. It is very susceptible to most root-knot nematode species (Cervantes et al. 2002a, b), and to SPFMV and SPCSV. Both 'Beauregard' and 'Tanzania' have been used extensively as parents in sweetpotato breeding programs in the US and east Africa, respectively. To develop the mapping population, crosses were made using 'Tanzania' as the female parent and 'Beauregard' as the male parent. Reciprocal crosses were not done due to low production of pollen in 'Tanzania'. A total of 250 progeny were selected randomly for genetic studies and construction of the genetic linkage map. Each clone in the mapping population was maintained in the greenhouse in order to conduct disease screenings and DNA analysis. The mapping population was also placed into tissue culture for long-term maintenance and future use by other sweetpotato breeding programs and researchers.

DNA preparation

Genomic DNA was extracted from young sweetpotato leaves for each progeny of the mapping population. The DNA was extracted using a modified CTAB DNA extraction procedure (Doyle and Doyle 1990; Murray and Thompson 1980). The quality and quantity of the DNA was determined by comparison with a standard weight Lambda DNA (New England Biolabs, Ipswich, Massachusetts) by electrophoresis on a 1% agarose gel stained with ethidium bromide and visualized under UV light. In order to perform AFLP analysis, the DNA concentration was adjusted to have 250–500 ng of DNA in 25 µl of dilution.

AFLP procedure

The AFLP procedure was conducted according to a modified protocol from Vos et al. (1995) (Myburg et al. 2001). Diluted DNA was digested with *Eco*RI and *Mse*I. After ligation of the adapters, pre-amplification was done using primers with one selective nucleotide, followed by amplification using primers with 3 selective nucleotides. The *Eco* primers in the selective amplification were IRDye™ labeled (LI-COR, Lincoln, Nebraska) for detection. Sample preparation for the LI-COR sequencers Models 4000 and 4200 (LI-COR, Lincoln, Nebraska) was done according to the manufacture's procedure with minor modifications as explained by Myburg et al. (2001). AFLP band separation and detection were performed by polyacrylamide gel electrophoresis using the LI-COR sequencers. Primer combinations were surveyed with the two parents and six progeny to select those combinations that produced patterns with a large number of polymorphic fragments. Selected primer combinations were used to develop AFLP markers in the mapping population.

Marker scoring

Polymorphic markers were visually scored and recorded as 1 (present) and 0 (absent). Bands present in the two parents, but segregating in the progeny were similarly scored. Ambiguous bands were considered as missing data for map construction purposes. Band sizes were determined by comparison with the gel-mobility of the AFLP bands against an IRDye™ 50–700 bp Sizing Standard (LICOR, Lincoln, Nebraska). Band size estimations were done using the AFLP Quantar® software (Keygene products, Wageningen, Netherlands). All

scored markers were assigned a quality rating according to their band intensity, and only medium and high quality bands were considered for linkage analysis. The format for the marker names consisted of three parts: the code of the *Eco* primer (e.g., E32), the code of the *Mse* primer (e.g., M38) and the corresponding polymorphic band number (e.g., 2). Thus, in this example the resulting name would be E32M3802. Additionally, the band size in bp was recorded for each polymorphic band scored (data shown in Appendix A, available online). AFLP band sizes were not used in the marker nomenclature due to space constraints.

Segregation of markers

The mapping population was analyzed as a double pseudo-testcross (Grattapaglia and Sederoff 1994). Marker dosage of each AFLP marker was determined by analyzing the observed segregation ratios (presence vs. absence) of the markers in the mapping progeny, according to the predicted allele dosage as expected by four cytological hypotheses in sweetpotato as described by Jones (1967) (Table 1). All markers were analyzed for their goodness-of-fit to the appropriate expected segregation ratios using the χ^2 test ($\alpha = 0.01$) with 1 df. Markers were classified into four groups according to their segregation ratios: (a) Simplex or single dose, markers that are present in a single copy only in one parent and that segregate in a 1:1 (presence:absence) ratio in the progeny (segregation of these markers is not affected by the type of ploidy); (b) Duplex or double dose, markers present in one parent in two copies and that segregate in a hexasomic (4:1), tetrasomic (5:1) and disomic or tetradisomic (3:1) fashion; (c) Triplex or triple dose, markers present in one parent in three copies and that segregate in a hexasomic (19:1), tetradisomic (11:1) and disomic (7:1) ratio; and (d) Double simplex, markers present in both parents in a single-dose condition that segregate in a 3:1 ratio in the progeny.

Linkage analysis

As described by da Silva et al. (1993) using the pseudo-testcross mapping strategy, polymorphic markers derived from each parent were grouped into separate sets corresponding to each parent and were analyzed independently to construct separate framework maps. In each set, single-dose markers were analyzed and grouped into linkage groups using JoinMap® 3.0 (Van Ooijen and Voorrips 2001) and MapMaker EXP 3.0 (Lander et al. 1987) at a LOD 3.0 for each parent. Linkage grouping was confirmed at LOD's 4, 5, and 6, to assure consistency of results. Due to the large quantity of markers, we first analyzed the data using JoinMap® 3.0. Then, according to the grouping in JoinMap®, data

Table 1 Expected segregation ratios (presence:absence) for the inheritance of a dominant marker in hexaploid sweetpotato, according to four cytological hypotheses (Jones 1967)

Marker dosage	Hypothesis I		Hypothesis II and III		Hypothesis IV	
	Autohexaploid (hexasomic)		Tetradiploid (tetradisomic, tetrasomic, disomic)		Allohexaploid (disomic)	
Simplex	Aaaaaa	1:1	Aaaa aa	1:1	Aa aa aa	1:1
			aaaa Aa	1:1		
Duplex	AAaaaa	4:1	AAaa aa	5:1[b]	Aa Aa aa	3:1
			Aaaa Aa	3:1[c]	AA aa aa	1:0
			aaaa AA	1:0[a]		
Triplex	AAAaaa	19:1	AAAa aa	1:0	Aa Aa Aa	7:1
			AAaa Aa	11:1	AA Aa aa	1:0
			Aaaa AA	1:0		
Quadruplex	AAAAaa	1:0	AAAA aa	1:0	AA Aa Aa	1:0

[a] Disomic inheritance

[b] Tetrasomic inheritance

[c] Tetradisomic inheritance

(*Source*: Kriegner et al. 2003)

subsets of less than 1000 markers were prepared. This procedure was implemented due to the limitation of MapMaker to handle only up to 1000 markers. Subsets of markers were analyzed in MapMaker to obtain the final linkage groups at LOD 3.0.

The order of single dose markers was obtained by a two-point analysis (JoinMap®) and a multipoint analysis (MapMaker EXP) using the functions 'compare' or 'order', followed by a ripple analysis to confirm marker order. Marker order was assessed by both JoinMap® and MapMaker. The resulting maps were analyzed for marker order consistency between the output of the two programs, and those markers with ambiguous order or co-segregating were dropped. Two or more markers were considered co-segregating if they mapped to the same location in the map and their map distance was near to or equal to zero. The final marker set was re-analyzed with both programs and when the order of the SDF markers in the framework map was consistent and confirmed, their order was fixed for further analysis. All map distances were calculated according to the Kosambi mapping function (Kosambi 1944).

Duplex markers were incorporated into the fixed order of the simplex markers in the framework map. For this purpose, recombination fraction (r) and LOD scores for simplex/duplex and for duplex/duplex marker configurations were calculated under the assumption of hexasomic and tetrasomic genetic configurations. All single-dose markers were used for the calculations to avoid losing any relevant information. Calculations were performed under the assumption of random pairing of homologous chromosomes, and absence of double reduction by numerically maximizing the log-likelihood as follows:

$$L = X_{AB} \log p_{AB}(r) + X_A \log p_A(r) + X_B \log p_B(r) + X_0 \log p_0(r)$$

where L is the log-likelihood of the probability of the multiplex marker to be linked to the mapped SDF, r is the recombination fraction and X_{AB}, X_A, X_B, X_0 are the observed numbers of offspring in each phenotypic class. Phenotype probabilities for the marker pair are given in Table 2. LOD scores were calculated for each pair as: $\log_{10}$(likelihood for

Table 2 Marker pair configurations and expected phenotypic frequencies used in this study

Hexasomic inheritance marker-pair configuration[a]	Phenotype probabilities		Tetrasomic inheritance marker pair configuration	Phenotype probabilities	
Simplex/simplex coupling	AB	$1/2(1 - r)$	Simplex/simplex coupling	Equal to hexasomic inheritance	
AB/00/00/00/00/00 × 00/00/00/00/00/00	A	$1/2r$	AB/00/00/00 × 00/00/00/00		
	B	$1/2r$			
	0	$1/2(1 - r)$			
Simplex/duplex coupling	AB	$1/2 - 1/5r$	Simplex/duplex coupling	AB	$1/2 - 1/6r$
AB/0B/00/00/00/00 × 00/00/00/00/00/00	A	$1/5r$	AB/0B/00/00 × 00/00/00/00	A	$1/6r$
	B	$3/10 + 1/5r$		B	$1/3 + 1/6r$
	0	$1/5 - 1/5r$		0	$1/6 - 1/6r$
Duplex/duplex coupling	AB	$4/5 - 2/5r + 1/5r^2$	Duplex/duplex coupling	AB	$5/6 - 1/3r + 1/6r^2$
AB/AB/00/00/00/00 × 00/00/00/00/00/00	A	$2/5r - 1/5r^2$	AB/AB/00/00 × 00/00/00/00	A	$1/3r - 1/6r^2$
	B	$2/5r - 1/5r^2$		B	$1/3 - 1/6r^2$
	0	$1/5 - 2/5r + 1/5r^2$		0	$1/6 - 1/3r - 1/6r^2$
Simplex/triplex coupling	AB	$1/2 - 1/20r$	Simplex/triplex coupling	–	–
AB/0B/0B/00/00/00 × 00/00/00/00/00/00	A	$1/20r$			
	B	$9/20 + 1/20r$			
	0	$1/20 - 1/20r$			
Duplex/triplex coupling	AB	$4/5 - 1/4r + 1/20r^2$	Duplex/triplex coupling	–	–
AB/AB/0B/00/00/00 × 00/00/00/00/00/00	A	$1/10r - 1/20r^2$			
	B	$3/20 - 1/10r - 1/20r^2$			
	0	$1/20 - 1/10r + 1/20r^2$			

[a] Distribution of alleles of two loci in a base chromosome group (chromosomes are separated by "/"). "A": presence of band at locus A, "B": presence of band at locus B, "0": absence of band. (*Source*: Kriegner et al. 2003; Ripol et al. 1999)

$r = \hat{r}$) − $\log_{10}$(likelihood for $r = 0.5$). The estimation of recombination fractions (r) and LOD scores and the grouping of duplex and triplex markers were performed in R environment for statistical computing (Ihaka and Gentleman 1996) as described above. Duplex and triplex markers were selected on base of their close linkage ($r < 0.25$, LOD > 5) to the markers from the two individual linkage groups of the SD marker map.

The most likely positions of the duplex and triplex markers were defined by the JoinMap 3.0 (Van Ooijen and Voorrips 2001) 'Map' function using estimates for r and LOD from all simplex–simplex, simplex–duplex, simplex–triplex combinations. For this purpose, pairwise distance files were prepared for each linkage group, keeping the map order of the SD markers fixed. After placing every multiplex marker, a ripple analysis was performed. Two or more linkage groups were considered and declared homologous if they possessed the same multiple-dose markers within the same parental map (da Silva 1993).

The naming of the linkage groups of each parental map were constructed according to a format that consisted of three main parts: the code of the corresponding parental line (T = 'Tanzania' or B = 'Beauregard'), a number between 1 and 15 (identified as 01–15) corresponding to the homologous group that the linkage group belongs for that specific parental map, and then followed by a number between 1 and 90 (written as 01–90) representing the linkage group number. For example, T01.06 would refer to the linkage group 6 that belongs to the homologous group 1 in the Tanzania map. The last number was assigned consecutively depending on the homologous groups they belong. Linkage groups that could not be assigned to any homologous group in the parental maps, were named according to their map of origin (B or T), with the number 00 to indicate that no homologous group could be assigned, and a number not assigned previously (e.g., B00.90.)

Results

Marker data

Primer pre-screening was performed on both parents and six progeny. Primers that produced good quality polymorphic bands segregating in this small subset of progeny were selected for evaluation in the entire mapping population. Of a total of 384 primer combinations screened, 342 were selected to develop AFLP fragments in the mapping population. Each primer combination yielded an average of 13 polymorphic markers, ranging from 1 to 28 scored markers per primer combination. Those primer combinations that yielded low quality or difficult to score fragments were rejected. Overall, the total number of AFLP markers scored was 4,499, of which 2,814 were single dose according to the χ^2 goodness of fit test. These single dose markers were used to construct the respective framework linkage maps in each parent.

For the 'Beauregard' map, 1,303 out of 1,751 markers (74.4%) were single dose ($P < 0.01$), and 219, 310 or 241 markers were duplex assuming disomic, tetradisomic and hexasomic inheritance, respectively. A total of 104 markers showed distorted segregation, accounting for 5.9% of the markers scored in 'Beauregard'. Also, six and four triple-dose markers, assuming tetradisomic and hexasomic inheritance, were scored.

For the 'Tanzania' map, 1,511 out of 1,944 markers (77.7%) were single-dose and 227, 302 and 188 were duplex assuming disomic, tetradisomic and hexasomic inheritance. Additionally, a total of 59 markers showed distorted segregation, accounting for 3% of the markers scored in 'Tanzania'. Similarly, seven markers were triple-dose assuming hexasomic inheritance.

Linkage analysis

The single-dose molecular markers of each parent were analyzed to form the genetic linkage groups using a combination of JoinMap and MapMaker as described above. Molecular markers were grouped into 90 and 86 linkage groups for 'Beauregard' and 'Tanzania', respectively. The grouping of markers was not affected at the different LOD score levels that were tested. AFLP markers were not distributed homogenously across linkage groups in both parents, but tended to be clustered. This was especially true for several groups, which had many markers clustering together or within short distances, such that several order arrangements were possible. The number of markers in the preliminary groups ranged from

2 to 34 markers in the Beauregard map, and from 2 to 51 markers in the Tanzania map.

In 'Beauregard', the preliminary framework map was constructed with 1,179 single-dose markers, leaving 124 markers unlinked. After exhaustive analysis of the mapping data and linkage grouping using the two mapping programs, and the removal of all markers with ambiguous order or that co-segregated with other markers, a total of 726 single-dose markers were ordered in the final framework linkage map. The linkage map length was estimated as 5276 cM, with an average distance between markers of 4.8 cM. The number of mapped SD markers in the genetic chromosomes of the final framework map ranged from 2 to 18 markers, and the estimated length of the chromosomes ranged from 8 to 97.8 cM, with an average size of 58.6 cM, with only 10 groups containing three or less single-dose markers (Fig. 1).

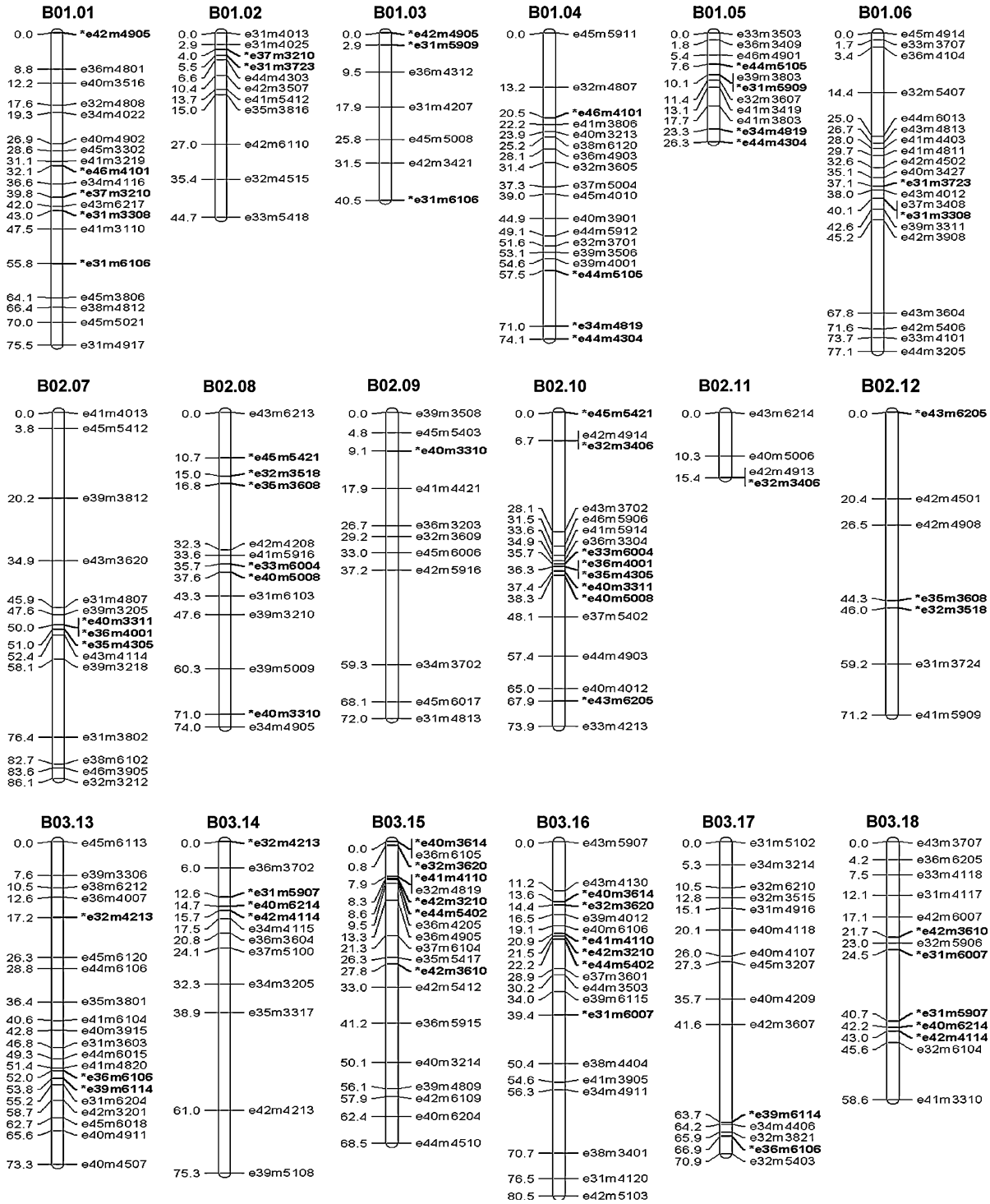
In 'Tanzania', the preliminary framework map was constructed with 1,359 single-dose markers with total of 152 markers remaining unlinked. Upon removal of the all markers with ambiguous orders or that co-segregated with other markers, a total of 947 single-dose markers were placed in the final framework linkage map. The linkage map size was estimated as 5792 cM, with an average distance between markers of 4.5 cM. The number of mapped SD markers in the genetic chromosomes of the final framework map ranged from 2 to 24 markers, with an estimated chromosomal length ranging from 2 to 130 cM, and an average size of 67.3 cM, with only seven linkage groups containing three or less single-dose markers (Fig. 2).

Duplex markers were analyzed against the fixed single-dose marker framework map of each parent using the approach explained above. The use of multiple-dose markers was explored for its application to highly heterozygous crops by Ritter et al. (1990) and later extended for autopolyploids by Ripol et al. (1999) and Meyer et al. (1998). Duplex markers enabled us to identify homologous chromosomes. As expected, most duplex markers aligned to only two different linkage groups, and by complementation these markers were able to align in most cases to six linkage groups per homologous group. In total, 234 duplex markers revealed 84 homologous relationships in 'Beauregard', and 216 duplex markers revealed 75 homologous relationships in 'Tanzania'. After completing the alignment, 15 homologous groups were identified with duplex markers in the 'Beauregard' map, and in the 'Tanzania' map. Additionally, homology of several groups in the 'Tanzania' maps was confirmed by 3 triplex markers, which mapped to two or three linkage groups. However, 6 and 11 linkage groups remained unassigned to any of the homologous groups in the 'Beauregard' and 'Tanzania' maps respectively.

Fig. 1 Linkage map of 'Beauregard' based on AFLP markers. ▶ Each linkage group is identified by parental map (B) and a nomenclature that identifies homologous groups (1–15) and linkage groups (1–90). Using this nomenclature, B01.01 refers to 'Beauregard' homologous group 1, linkage group 1. Duplex markers are shown in bold and preceded by an asterisk (*). Single-dose markers were analyzed and grouped into linkage groups using JoinMap® 3.0 (Van Ooijen and Voorrips 2001) and MapMaker EXP 3.0 (Lander et al. 1987) at a LOD 3.0 for each parent. Linkage grouping was confirmed at LOD's 4, 5, and 6, to assure consistency of results. Multiplex markers were incorporated into the fixed single-dose marker framework map

Discussion

The framework genetic maps presented in this paper represent the most comprehensive genetic linkage maps available for sweetpotato. Since the mapping population was derived from a broad cross between two very distinct sweetpotato cultivars, 'Beauregard' and 'Tanzania', which are important varieties in the US and East Africa, respectively and have been used as parental materials by breeders, we believe that the population represents a valuable genetic resource for the sweetpotato community. The significant differences between the parental phenotypes and the segregation of these traits in the progeny, will allow researchers to investigate and map a large number economically important traits. Currently, in our breeding program, we are using this population as our core mapping population to investigate the inheritance of root-knot nematode resistance, sweetpotato feathery mottle virus resistance, and of root quality traits such as beta-carotene content, dry matter content, as well as other traits. The use of 'Tanzania', which was also used in a previously published map (Kriegner et al. 2003) as a parental line of another cross with the clone 'Bikilamaliya', will allow sweetpotato breeders or geneticists to use that resource to construct an integrated map once codominant markers are available and mapped into our framework map.


B01.01
0.0 *e42m4905
8.8 e36m4801
12.2 e40m3516
17.6 e32m4808
19.3 e34m4022
26.9 e40m4902
28.6 e45m3302
31.1 e41m3219
32.1 *e46m4101
36.6 e34m4116
39.8 *e37m3210
42.0 e43m6217
43.0 *e31m3308
47.5 e41m3110
55.8 *e31m6106
64.1 e45m3806
66.4 e38m4812
70.0 e45m5021
75.5 e31m4917
B01.02
0.0 e31m4013
2.9 e31m4025
4.0 *e37m3210
5.5 *e31m3723
6.6 e44m4303
10.4 e42m3507
13.7 e41m5412
15.0 e35m3816
27.0 e42m6110
35.4 e32m4515
44.7 e33m5418
B01.03
0.0 *e42m4905
2.9 *e31m5909
9.5 e36m4312
17.9 e31m4207
25.8 e45m5008
31.5 e42m3421
40.5 *e31m6106
B01.04
0.0 e45m5911
13.2 e32m4807
20.5 *e46m4101
22.2 e41m3806
23.9 e40m3213
25.2 e38m6120
28.1 e36m4903
31.4 e32m3605
37.3 e37m5004
39.0 e45m4010
44.9 e40m3901
49.1 e44m5912
51.6 e32m3701
53.1 e39m3506
54.6 e39m4001
57.5 *e44m6105
71.0 *e34m4819
74.1 *e44m4304
B01.05
0.0 e33m3503
1.8 e36m3409
5.4 e46m4901
7.6 *e44m5105
10.1 e39m3803
*e31m6909
11.4 e32m3607
13.1 e41m3419
17.7 e41m3803
23.3 *e34m4819
26.3 *e44m4304
B01.06
0.0 e45m4914
1.7 e33m3707
3.4 e36m4104
14.4 e32m5407
25.0 e44m6013
26.7 e43m4813
28.0 e41m4403
29.7 e41m4811
32.6 e42m4502
35.1 e40m3427
37.1 *e31m3723
38.0 e43m4012
40.1 e37m3408
*e31m3308
42.6 e39m3311
45.2 e42m3908
67.8 e43m3604
71.6 e42m5406
73.7 e33m4101
77.1 e44m3205
B02.07
0.0 e41m4013
3.8 e45m5412
20.2 e39m3812
34.9 e43m3620
45.9 e31m4807
47.6 e39m3205
50.0 *e40m3311
*e36m4001
51.0 *e35m4305
52.4 e43m4114
58.1 e39m3218
76.4 e31m3802
82.7 e38m6102
83.6 e46m3905
86.1 e32m3212
B02.08
0.0 e43m6213
10.7 *e45m5421
15.0 *e32m3518
16.8 *e35m3608
32.3 e42m4208
33.6 e41m5916
35.7 *e33m6004
37.6 *e40m5008
43.3 e31m6103
47.6 e39m3210
60.3 e39m5009
71.0 *e40m3310
74.0 e34m4905
B02.09
0.0 e39m3508
4.8 e45m5403
9.1 *e40m3310
17.9 e41m4421
26.7 e36m3203
29.2 e32m3609
33.0 e45m6006
37.2 e42m5916
59.3 e34m3702
68.1 e45m6017
72.0 e31m4813
B02.10
0.0 *e45m5421
6.7 e42m4914
*e32m3406
28.1 e43m3702
31.5 e46m5906
33.6 e41m5914
34.9 e36m3304
35.7 *e33m6004
*e36m4001
36.3 *e35m4305
37.4 *e40m3311
38.3 *e40m5008
48.1 e37m5402
57.4 e44m4903
65.0 e40m4012
67.9 *e43m6205
73.9 e33m4213
B02.11
0.0 e43m6214
10.3 e40m5006
15.4 e42m4913
*e32m3406
B02.12
0.0 *e43m6205
20.4 e42m4501
26.5 e42m4908
44.3 *e35m3608
46.0 *e32m3518
59.2 e31m3724
71.2 e41m5909
B03.13
0.0 e45m6113
7.6 e39m3306
10.5 e38m6212
12.6 e36m4007
17.2 *e32m4213
26.3 e45m6120
28.8 e44m6106
36.4 e35m3801
40.6 e41m6104
42.8 e40m3915
46.8 e31m3603
49.3 e44m6015
51.4 e41m4820
52.0 *e36m6106
53.8 *e39m6114
55.2 e31m6204
58.7 e42m3201
62.7 e45m6018
65.6 e40m4911
73.3 e40m4507
B03.14
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6.0 e36m3702
12.6 *e31m5907
14.7 *e40m6214
15.7 *e42m4114
17.5 e34m4115
20.8 e36m3604
24.1 e37m5100
32.3 e34m3205
38.9 e35m3317
61.0 e42m4213
75.3 e39m5108
B03.15
0.0 *e40m3614
e36m6105
*e32m3620
0.8 *e41m4110
7.9 e32m4819
8.3 *e42m3210
8.6 *e44m5402
9.5 e36m4205
13.3 e36m4905
21.3 e37m6104
26.3 e35m5417
27.8 *e42m3610
33.0 e42m5412
41.2 e36m5915
50.1 e40m3214
56.1 e39m4809
57.9 e42m6109
62.4 e40m6204
68.5 e44m4510
B03.16
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11.2 e43m4130
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14.4 *e32m3620
16.5 e39m4012
19.1 e40m6106
20.9 *e41m4110
21.5 *e42m3210
22.2 *e44m5402
28.9 e37m3601
30.2 e44m3503
34.0 e39m6115
39.4 *e31m6007
50.4 e38m4404
54.6 e41m3905
56.3 e34m4911
70.7 e38m3401
76.5 e31m4120
80.5 e42m5103
B03.17
0.0 e31m5102
5.3 e34m3214
10.5 e32m6210
12.8 e32m3515
15.1 e31m4916
20.1 e40m4118
26.0 e40m4107
27.3 e45m3207
35.7 e40m4209
41.6 e42m3607
63.7 *e39m6114
64.2 e34m4406
65.9 e32m3821
66.9 *e36m6106
70.9 e32m5403
B03.18
0.0 e43m3707
4.2 e36m6205
7.5 e33m4118
12.1 e31m4117
17.1 e42m6007
21.7 *e42m3610
23.0 e32m5906
24.5 *e31m6007
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43.0 *e42m4114
45.6 e32m6104
58.6 e41m3310

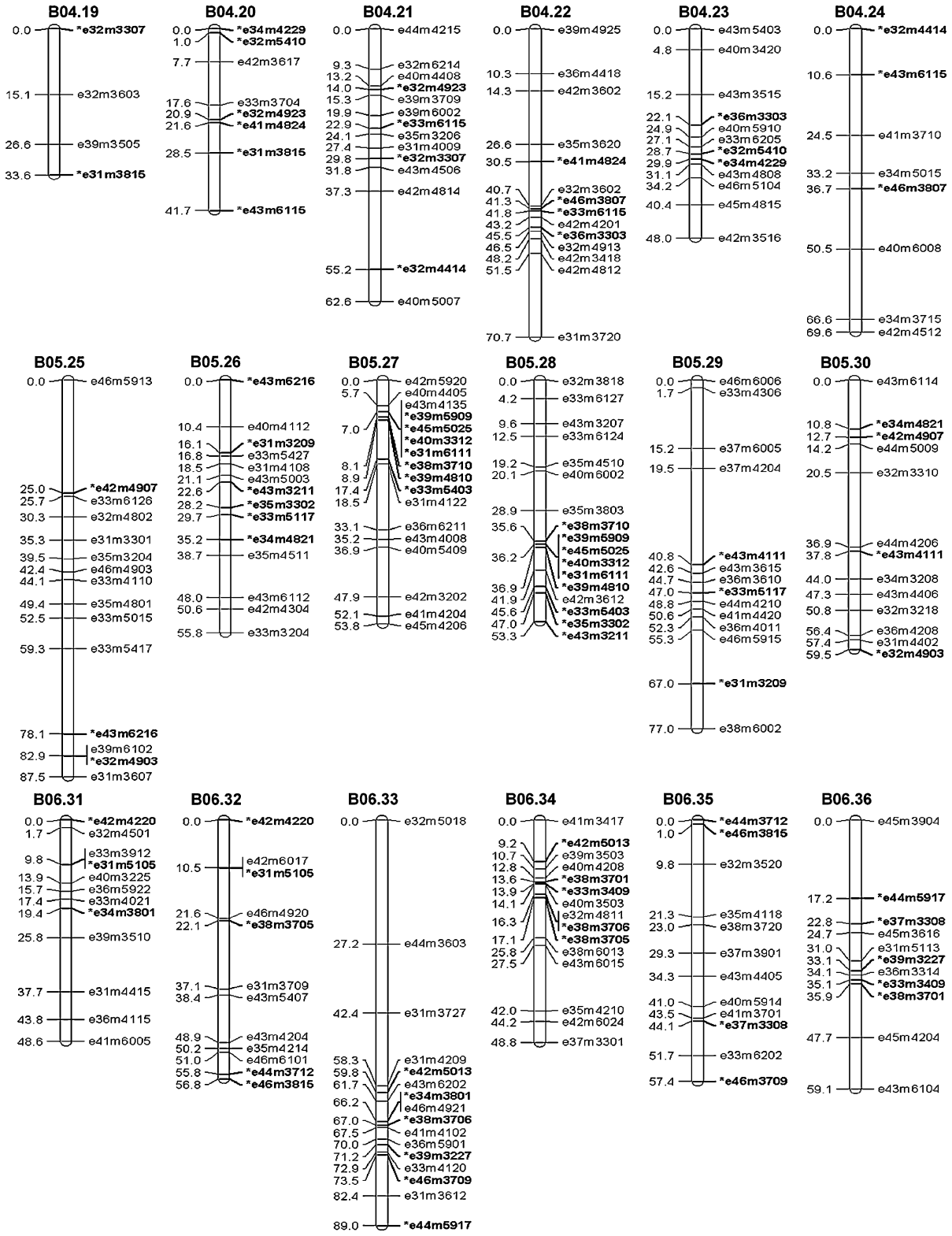


Fig. 1 continued

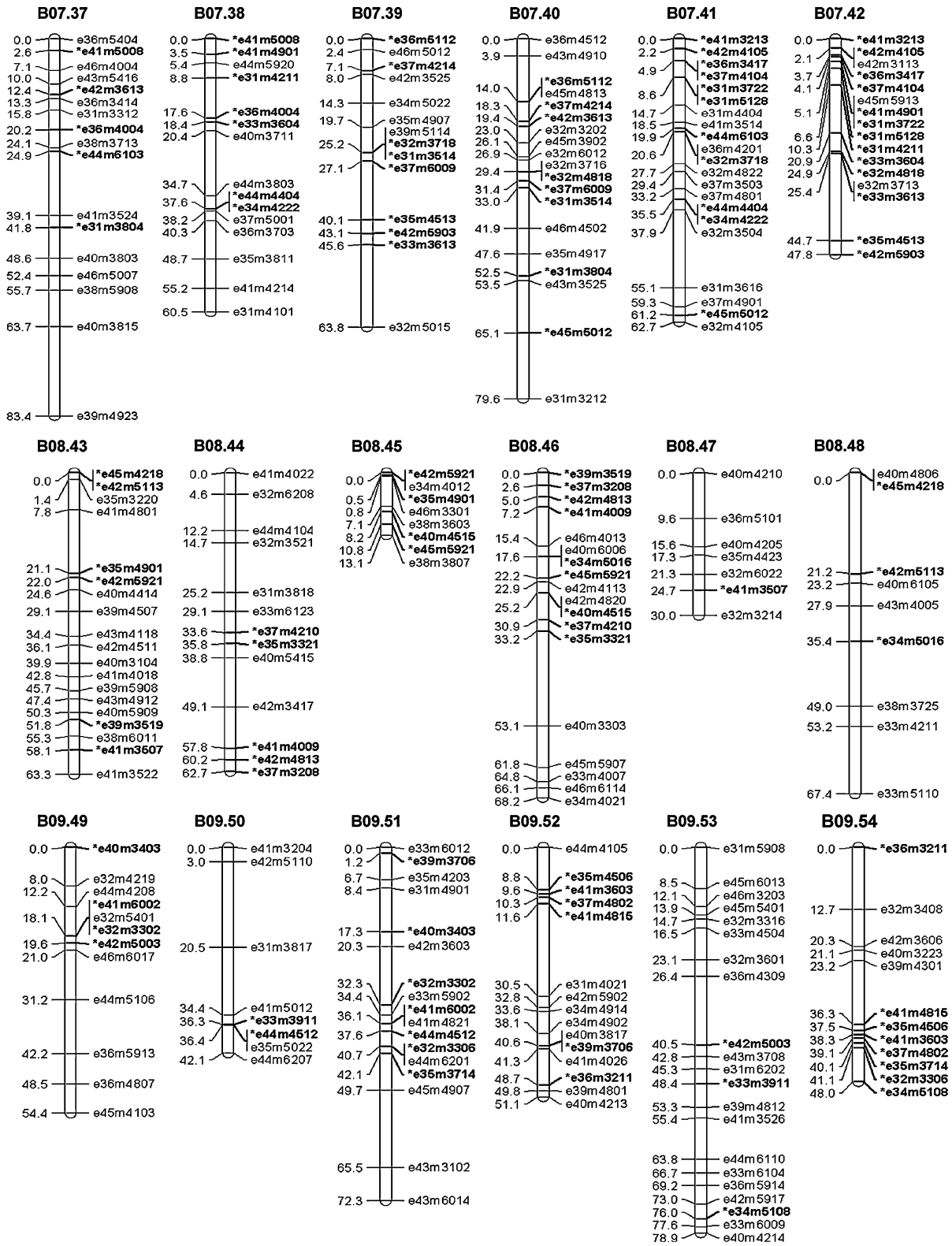


Fig. 1 continued

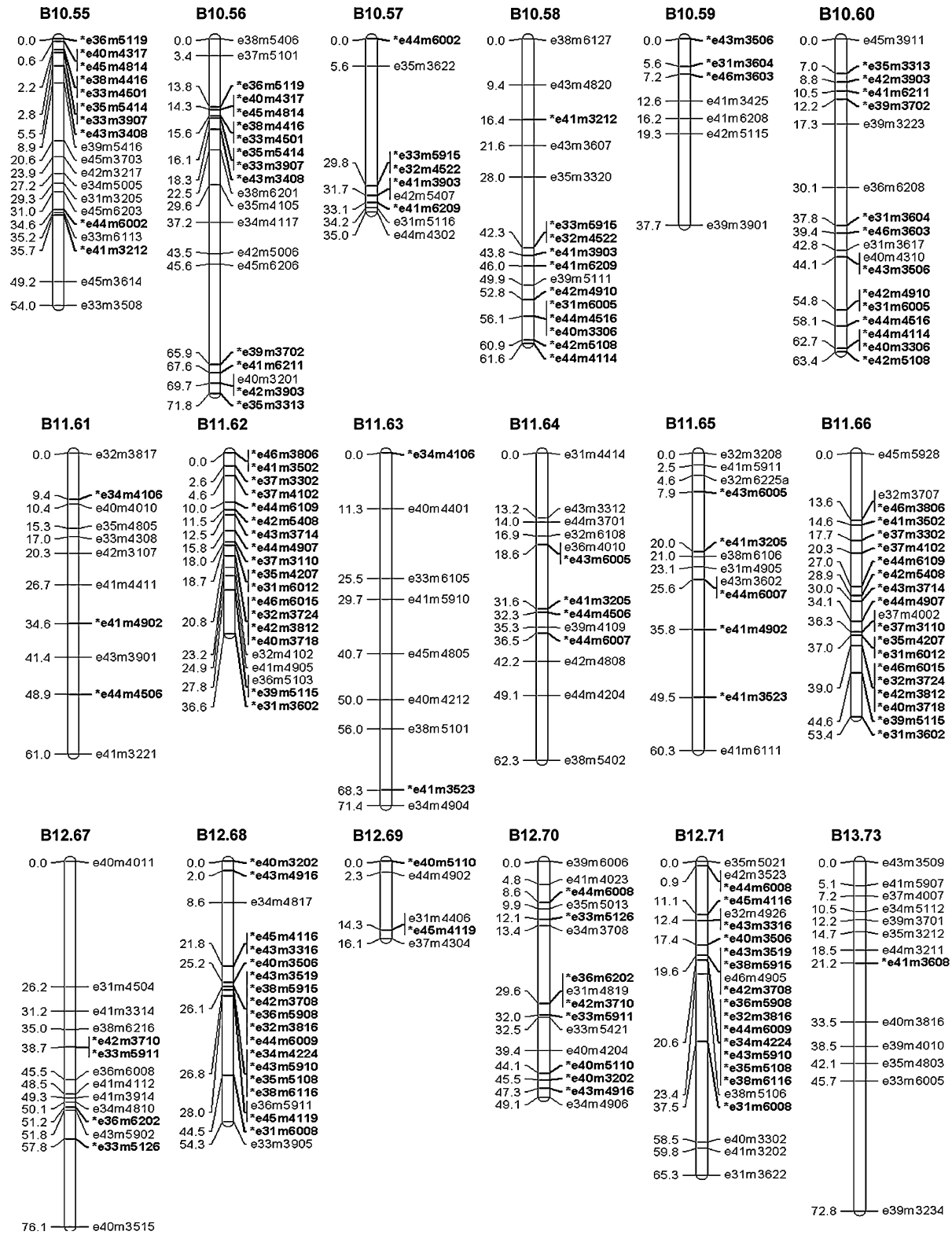


Fig. 1 continued

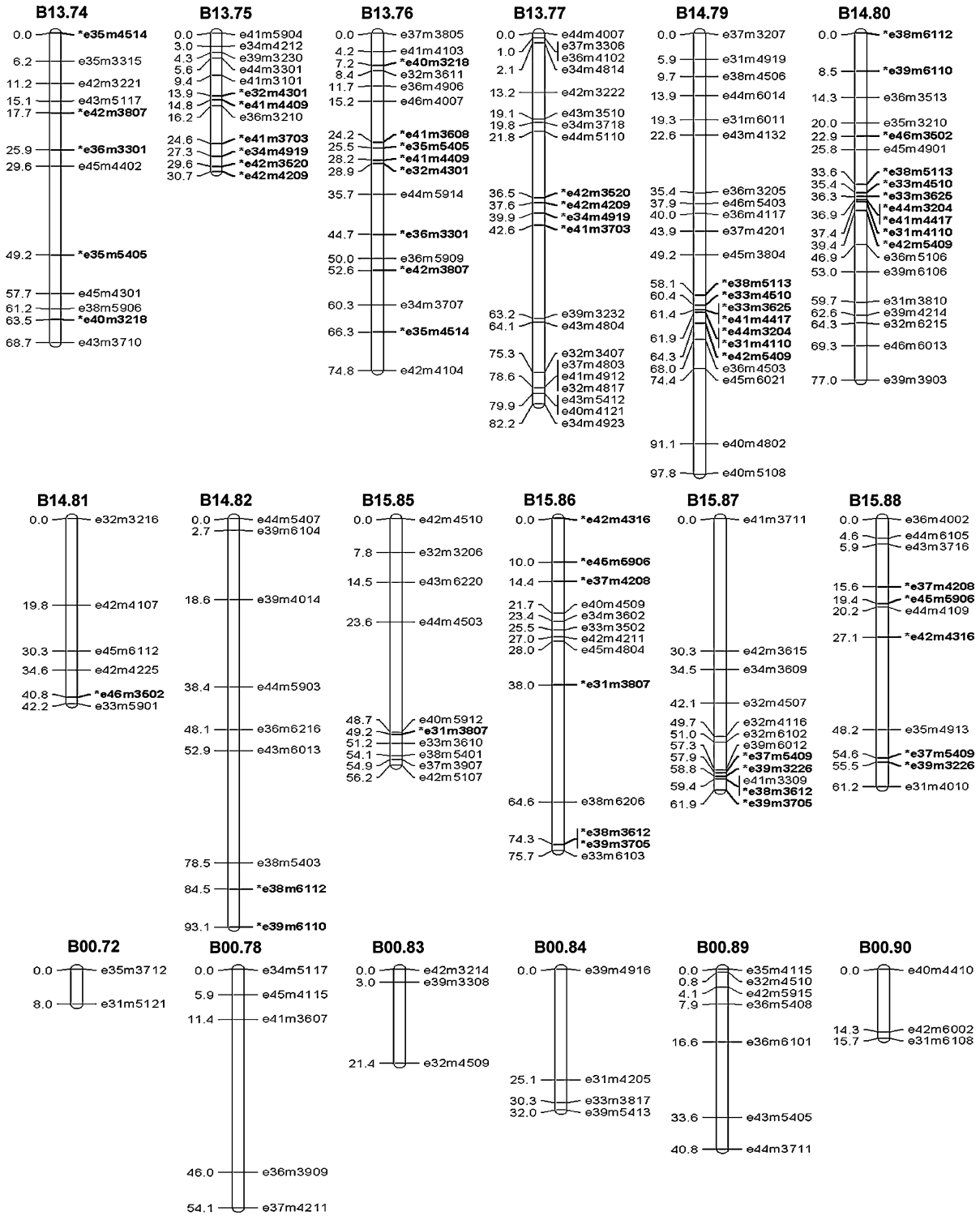


Fig. 1 continued

The size of the mapping population enabled us to evaluate a large number of recombination events, and the number of single-dose markers screened facilitated the construction of the framework maps with an average distance of 4.6 cM between markers. Our use of a combination of software packages to arrive at consensus framework maps based on single-dose AFLP markers increases our confidence in the output. In addition, by using duplex and triple-dose markers in both maps we were also able to identify nearly all 15 homologous chromosomal groups. This number is the expected number of homologous chromosomal groups in sweetpotato given that the basic number of chromosomes is 15. Thus, this provides a solid framework map and resource for further understanding the mode of inheritance and genetics of this important crop.

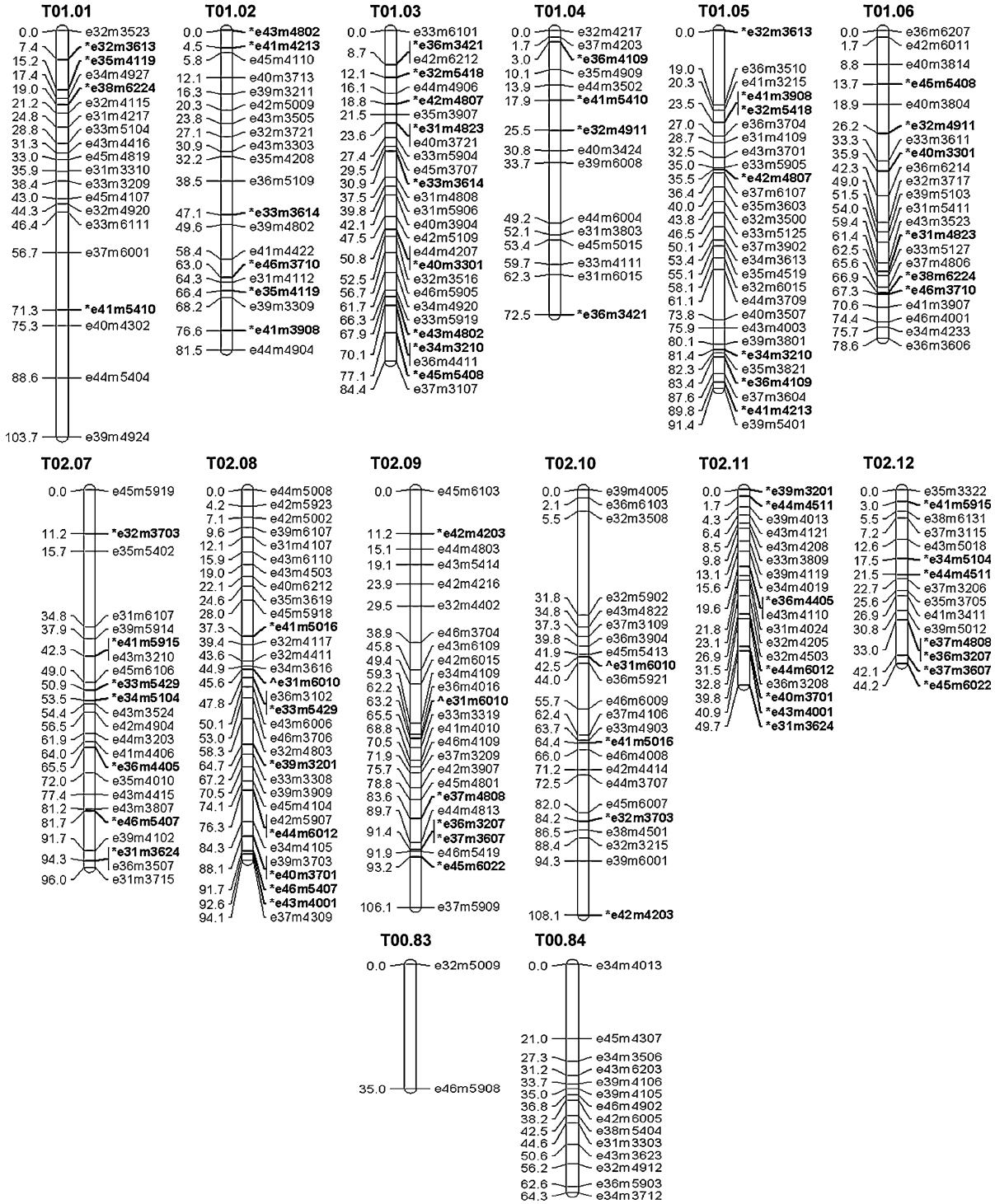
In developing the initial framework map, the amount of available single-dose molecular markers was critical, because during subsequent analyses approximately 40% of the markers were removed due to co-segregation or ambiguity. After the removal of markers with ambiguous order locations, consistency was achieved using either MapMaker or JoinMap software for calculating the marker order of the linkage groups. Inherently, linkage groups containing large numbers of markers are difficult to resolve, since most algorithms calculate precise ordering for linkage groups containing a small number of markers (Liu 1998).

The use of both JoinMap and Mapmaker was useful for handling the initial amount of data, especially considering that MapMaker can only handle data containing up to 999 markers. It was necessary to conduct extensive analyses of the data using the two programs to achieve consistent results. We observed one case in which the markers in the 'Tanzania' map were grouped together in JoinMap and split into two groups using MapMaker, even at a very low LOD value. After the removal in JoinMap of some of the markers localized to a different group by Mapmaker, the linkage grouping was the same in Joinmap. The framework map was considered reliable when both software outputs were consistent in terms of grouping and marker order. Map distances were not considered relevant when assessing consistency, due to the inherent difference in the algorithms used by each program.

Similar to the observation in most species (Cregan et al. 1999; Fregene et al. 1997; Grattapaglia and Sederoff 1994; Tanksley et al. 1992), and in previous maps of sweetpotato (Kriegner et al. 2003), disregarding the type of marker technology used, we observed that approximately 28% of the single-dose AFLP markers mapped into clusters in our maps. Tanksley et al. (1992) suggested that clustering of markers might have a biological basis reflecting suppressed or reduced genetic recombination in heterochromatic regions surrounding the centromeres and/or telomeric regions. This reduction or suppression at such regions has been observed in several cytological studies conducted in different organisms (Gill et al. 1996; Lefevre 1970; Roberts 1965). Also, as observed in other crops (Isidore et al. 2003; Truco et al. 2007) AFLP markers generated by the enzymatic combination Eco RI/Mse I tend to cluster due to the uneven distribution across the genome. Clustering is likely observed because the A–T rich regions that EcoRI recognizes are more frequent in the pericentromeric heterochromatin, where suppression of recombination may occur (Isidore et al. 2003). These clustered markers were the main source of disagreement on marker ordering, but these differences were solved after removal of close and/or low quality markers. The minimum distance between single-dose markers in our framework map was 1 cM, because at this distance all remaining markers could be placed at a unique order in their respective linkage groups.

Suppressed recombination of chromosomal regions could have strong implications in sweetpotato breeding, since many genes could be located in regions that rarely recombine. In several cases, during breeding one might observe significant linkage drag, reducing the likelihood of obtaining superior genotypes that contain certain specific traits of interest without carrying other undesirable alleles (Tanksley

Fig. 2 Linkage map of 'Tanzania' based on AFLP markers. ▶ Each linkage group is identified by parental map (T) and a nomenclature that identifies homologous groups (1–15) and linkage groups (1–90). Using this nomenclature, T01.01 refers to 'Tanzania' homologous group 1, linkage group 1. Multiplex markers shown in bold fonts and preceded by: (*) duplex markers and (^) triplex markers. Single-dose markers were analyzed and grouped into linkage groups using JoinMap® 3.0 (Van Ooijen and Voorrips 2001) and MapMaker EXP 3.0 (Lander et al. 1987) at a LOD 3.0 for each parent. Linkage grouping was confirmed at LOD's 4, 5, and 6, to assure consistency of results. Multiplex markers were incorporated into the fixed single-dose marker framework map


T01.01
0.0 e32m3523
7.4 *e32m3613
15.2 *e35m4119
17.4 e34m4927
19.0 *e38m6224
21.2 e32m4115
24.8 e31m4217
28.8 e33m5104
31.3 e43m4416
33.0 e45m4819
35.9 e31m3310
38.4 e33m3209
43.0 e45m4107
44.3 e32m4920
46.4 e33m6111
56.7 e37m6001
71.3 *e41m5410
75.3 e40m4302
88.6 e44m5404
103.7 e39m4924
T01.02
0.0 *e43m4802
4.5 *e41m4213
5.8 e45m4110
12.1 e40m3713
16.3 e39m3211
20.3 e42m5009
23.8 e43m3505
27.1 e32m3721
30.9 e43m3303
32.2 e35m4208
38.5 e36m5109
47.1 *e33m3614
49.6 e39m4802
58.4 e41m4422
63.0 *e46m3710
64.3 e31m4112
66.4 *e35m4119
68.2 e39m3309
76.6 *e41m3908
81.5 e44m4904
T01.03
0.0 e33m6101
8.7 *e36m3421
e42m6212
12.1 *e32m5418
16.1 e44m4906
18.8 *e42m4807
21.5 e35m3907
23.6 *e31m4823
e40m3721
27.4 e33m5904
29.5 e45m3707
30.9 *e33m3614
37.5 e31m4808
39.8 e31m5906
42.1 e40m3904
47.5 e42m5109
50.8 e44m4207
52.5 *e40m3301
56.7 e32m3516
61.7 e46m5905
66.3 e34m4920
67.9 e33m5919
70.1 *e43m4802
77.1 *e34m3210
84.4 e36m4411
*e45m5408
e37m3107
T01.04
0.0 e32m4217
1.7 e37m4203
3.0 *e36m4109
10.1 e35m4909
13.9 e44m3502
17.9 *e41m5410
25.5 *e32m4911
30.8 e40m3424
33.7 e39m6008
49.2 e44m6004
52.1 e31m3803
53.4 e45m5015
59.7 e33m4111
62.3 e31m6015
72.5 *e36m3421
T01.05
0.0 *e32m3613
19.0 e36m3510
20.3 e41m3215
*e41m3908
23.5 *e32m5418
27.0 e36m3704
28.7 e31m4109
32.5 e43m3701
35.0 e33m5905
35.5 *e42m4807
36.4 e37m6107
40.0 e35m3603
43.8 e32m3500
46.5 e33m5125
50.1 e37m3902
53.4 e34m3613
55.1 e35m4519
58.1 e32m6015
61.1 e44m3709
73.8 e40m3507
75.9 e43m4003
80.1 e39m3801
81.4 *e34m3210
82.3 e35m3821
83.4 *e36m4109
87.6 e37m3604
89.8 *e41m4213
91.4 e39m5401
T01.06
0.0 e36m6207
1.7 e42m6011
8.8 e40m3814
13.7 *e45m5408
18.9 e40m3804
26.2 *e32m4911
33.3 e33m3611
35.9 *e40m3301
42.3 e36m6214
49.0 e32m3717
51.5 e39m5103
54.0 e31m5411
59.4 e43m3523
61.4 *e31m4823
62.5 e33m5127
65.6 e37m4806
66.9 *e38m6224
67.3 *e46m3710
70.6 e41m3907
74.4 e46m4001
75.7 e34m4233
78.6 e36m3606
T02.07
0.0 e45m5919
11.2 *e32m3703
15.7 e35m5402
34.8 e31m6107
37.9 e39m5914
*e41m5915
42.3 e43m3210
49.0 e45m6106
50.9 *e33m5429
53.5 *e34m5104
54.4 e43m3524
56.5 e42m4904
61.9 e44m3203
64.0 e41m4406
65.5 *e36m4405
72.0 e35m4010
77.4 e43m4415
81.2 e43m3807
81.7 *e46m5407
91.7 e39m4102
94.3 *e31m3624
96.0 e36m3507
e31m3715
T02.08
0.0 e44m5008
4.2 e42m5923
7.1 e42m5002
9.6 e39m6107
12.1 e31m4107
15.9 e43m6110
19.0 e43m4503
22.1 e40m6212
24.6 e35m3619
28.0 e45m5918
37.3 *e41m5016
39.4 e32m4117
43.6 e32m4411
44.9 e34m3616
45.6 ^e31m6010
e36m3102
47.8 *e33m5429
50.1 e43m6006
53.0 e46m3706
58.3 e32m4803
64.7 *e39m3201
67.2 e33m3308
70.5 e39m3909
74.1 e45m4104
e42m5907
76.3 *e44m6012
84.3 e34m4105
88.1 e39m3703
*e40m3701
91.7 *e46m5407
92.6 *e43m4001
94.1 e37m4309
T02.09
0.0 e45m6103
11.2 *e42m4203
15.1 e44m4803
19.1 e43m5414
23.9 e42m4216
29.5 e32m4402
38.9 e46m3704
45.8 e43m6109
49.4 e42m6015
59.3 e34m4109
62.2 e36m4016
63.2 ^e31m6010
65.5 e33m3319
68.8 e41m4010
70.5 e46m4109
71.9 e37m3209
75.7 e42m3907
78.8 e45m4801
83.6 *e37m4808
89.7 e44m4813
91.4 *e36m3207
*e37m3607
91.9 e46m5419
93.2 *e45m6022
106.1 e37m5909
T02.10
0.0 e39m4005
2.1 e36m6103
5.5 e32m3508
31.8 e32m5902
34.8 e43m4822
37.3 e37m3109
39.8 e36m3904
41.9 e45m5413
42.5 ^e31m6010
44.0 e36m5921
55.7 e46m6009
62.4 e37m4106
63.7 e33m4903
64.4 *e41m5016
66.0 e46m4008
71.2 e42m4414
72.5 e44m3707
82.0 e45m6007
84.2 *e32m3703
86.5 e38m4501
88.4 e32m3215
94.3 e39m6001
108.1 *e42m4203
T02.11
0.0 *e39m3201
1.7 *e44m4511
4.3 e39m4013
6.4 e43m4121
8.5 e43m4208
9.8 e33m3809
13.1 e39m4119
15.6 e34m4019
19.6 *e36m4405
e43m4110
21.8 e31m4024
23.1 e32m4205
26.9 e32m4503
31.5 *e44m6012
32.8 e36m3208
39.8 *e40m3701
40.9 *e43m4001
49.7 *e31m3624
T02.12
0.0 e35m3322
3.0 *e41m5915
5.5 e38m6131
7.2 e37m3115
12.6 e43m5018
17.5 *e34m5104
21.5 *e44m4511
22.7 e37m3206
25.6 e35m3705
26.9 e41m3411
30.8 e39m5012
33.0 *e37m4808
*e36m3207
42.1 *e37m3607
44.2 *e45m6022
T00.83
0.0 e32m5009
35.0 e46m5908
T00.84
0.0 e34m4013
21.0 e45m4307
27.3 e34m3506
31.2 e43m6203
33.7 e39m4106
35.0 e39m4105
36.8 e46m4902
38.2 e42m6005
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62.6 e36m5903
64.3 e34m3712

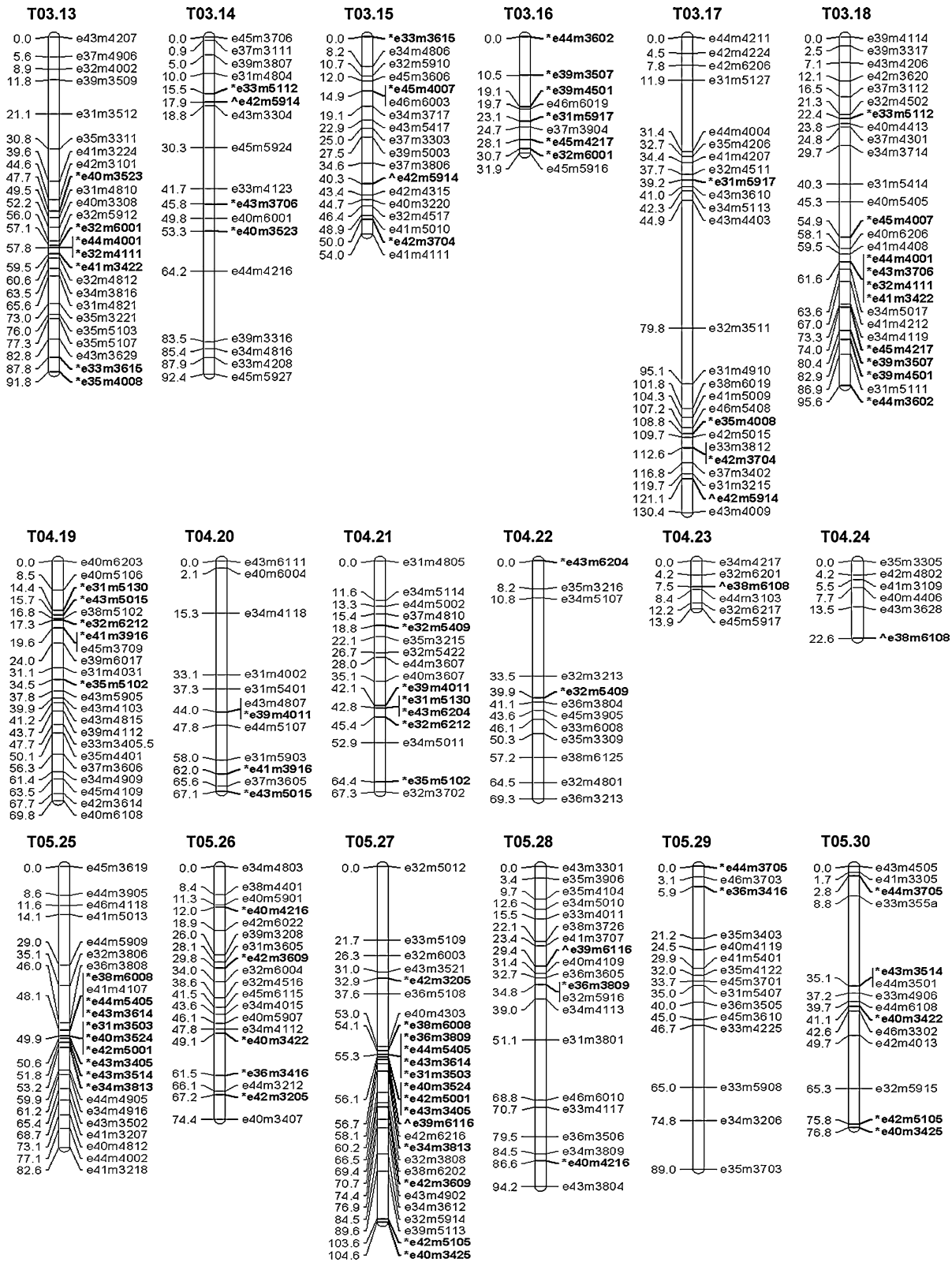
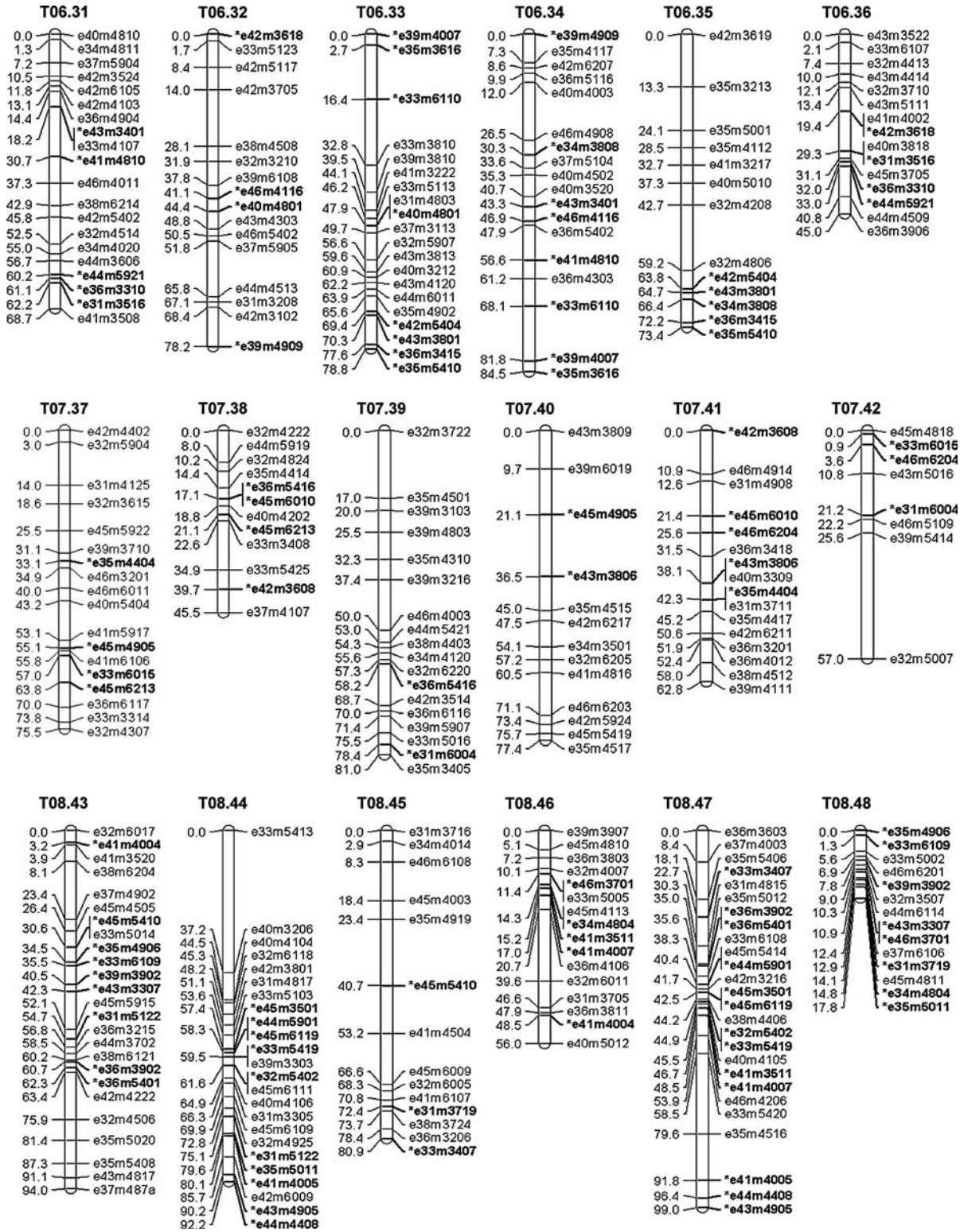


Fig. 2 continued



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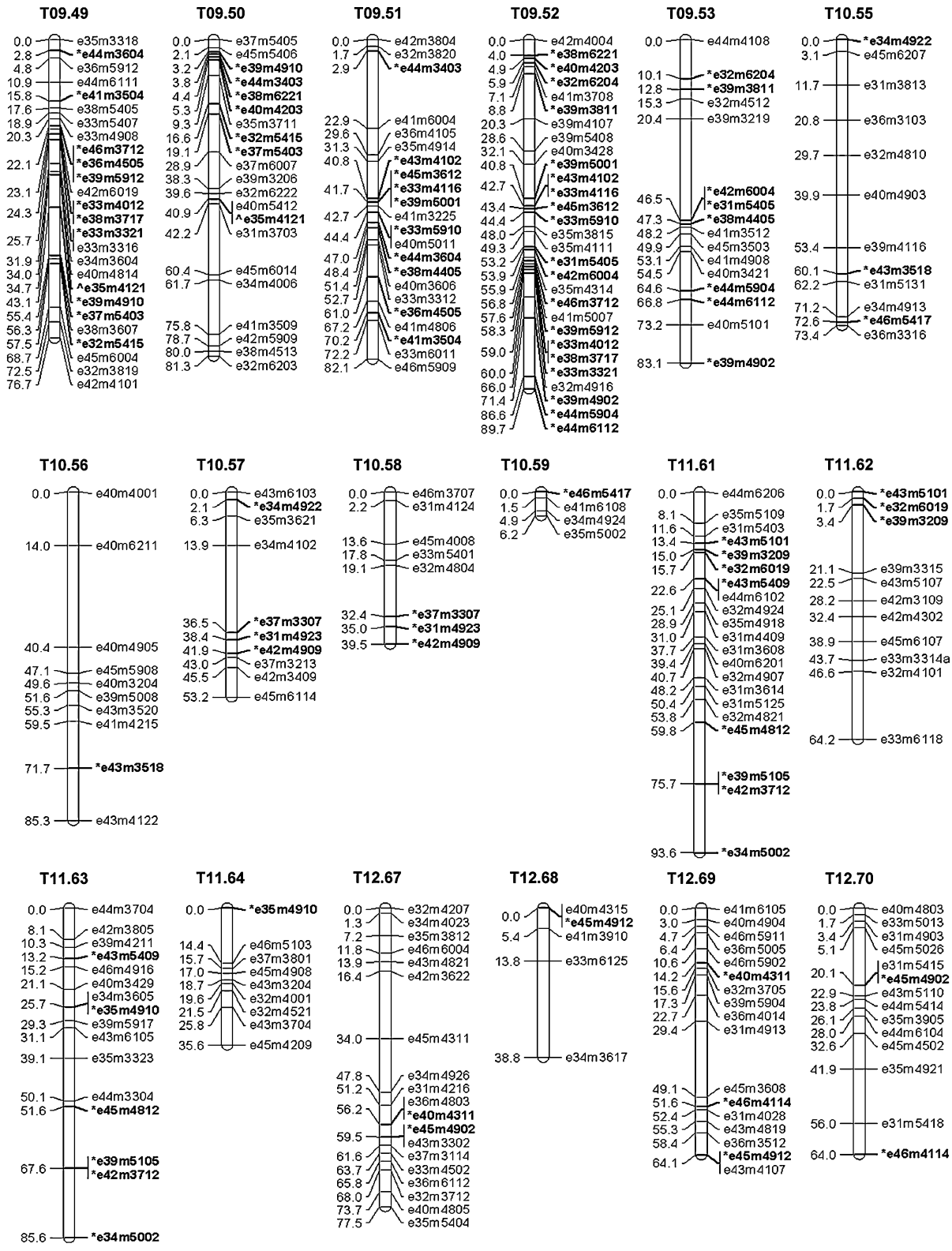

Fig. 2 continued

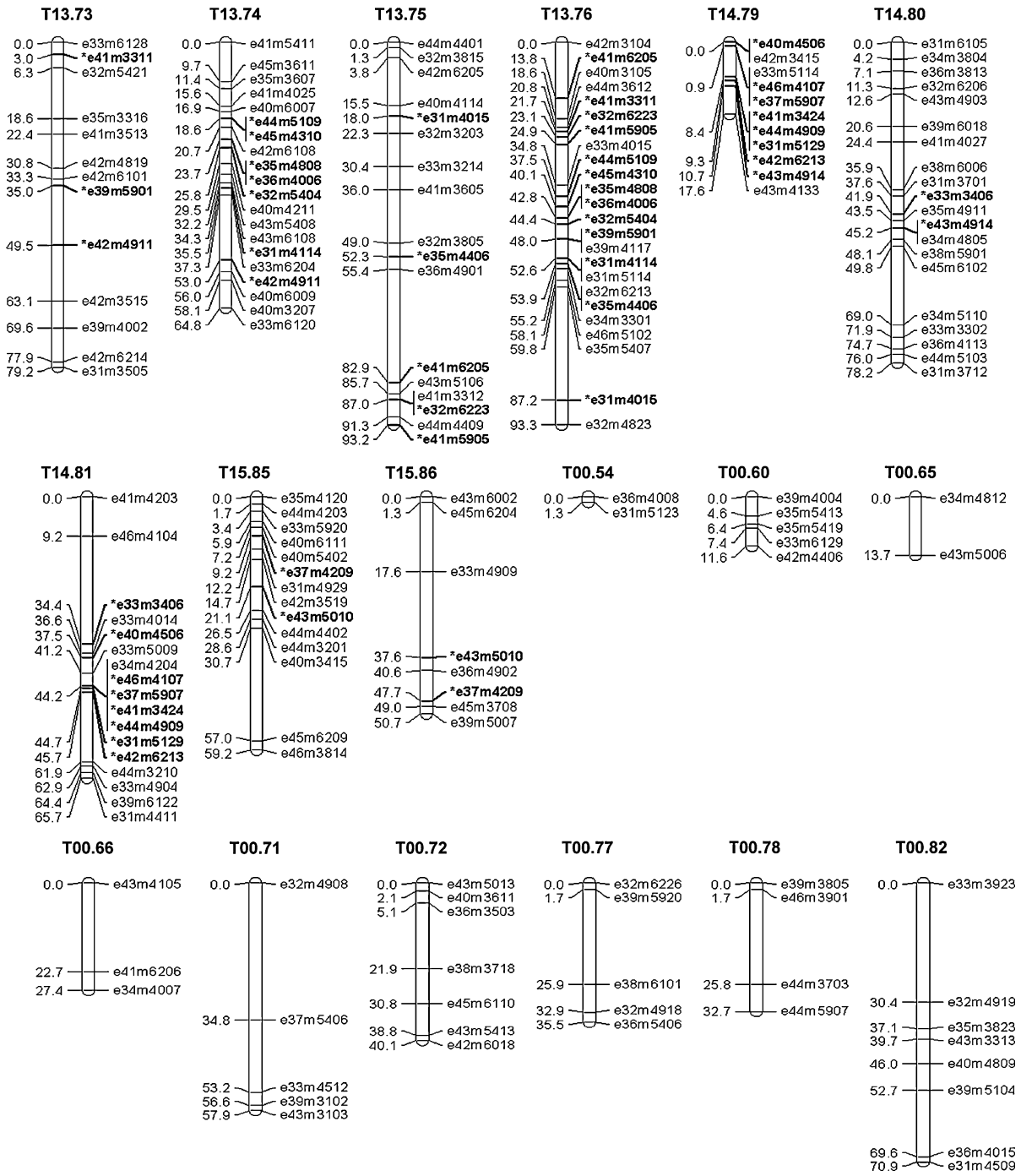

Fig. 2 continued

et al. 1992). In fact, in our applied breeding program we have observed strong linkages of some traits in the sweetpotato phenotypes in several different populations, e.g., flesh and skin color of the storage root (Yencho, personal observations). Therefore, in those regions with suppressed recombination, a higher number of recombination events may be needed for a fine resolution and detailed mapping.

Considering our markers resolved into 90 and 86 linkage groups for 'Beauregard' and 'Tanzania', respectively, we believe that our data is of good quality, since the actual number of chromosomes is 90. Size differences and number of markers of the chromosomes in the genetic linkage map might not be due exclusively to marker clustering, but to the physical size differences of the chromosomes in sweetpotato. Cytological studies have shown that sweetpotato has very small chromosomes, which vary in size by several fold (Sinha and Sharma 1992). Also, in other species, a high correlation was observed between the chromosome's physical size and the number of markers per chromosome (Castiglioni et al 1999; Tanksley et al. 1992). Nevertheless, the distribution of markers can vary within regions of the chromosomes with regions also showing low density of markers, which are presumed to be regions with high levels of recombination, or regions with low numbers of genes (Lindahl 1991; Tanksley et al. 1992). Approximately 18% of the single-dose makers in our maps were separated by more than 15 cM, however we cannot speculate on the physical meaning of this observation, as map distance is only based on the percentage of recombination between the markers, and may not reflect the true physical proximity of the markers.

The total length of our maps was approximately 1500 cM larger than those obtained by Kriegner et al (2003). Of special interest is the length of the common parental map, 'Tanzania'. Size differences could be simply explained by the better coverage of our map, since our framework map comprises 947 single-dose markers, which is more than twice the amount of markers mapped by Kriegner et al. (2003) or the maps reported by Mwanga et al. (2002). Also, the difference in the interval distance, which affects the overall map length, could be explained in part by the higher divergence of the parental clones used to construct our maps. The higher heterogeneity between 'Beauregard' and 'Tanzania' can probably cause some reduction in the recombination frequencies in those chromosomal regions with more divergent sequences (Schnable et al. 1998; Opperman et al. 2004; Chetelat et al. 2000), thus decreasing the distance between markers in certain regions of our maps.

Based on flow cytometry estimations of the nuclear genome size of sweetpotato, the haploid DNA content is between 1.55 and 2.25 pg/C nuclei or between 1515 and 2200 Mbp (Kriegner 2001; Ozias-Okins and Jarret 1994). Considering the length of our maps, we hypothesize that the typical average distance between markers should be approximately 300 Kbp. However, it is important to note that this value can vary tremendously depending on the specific chromosomal region due to the differences in recombination frequencies between markers along the map and more research is required to validate this assertion.

The percentage of simplex markers to non-simplex markers for the data from both parents was in agreement with the expected ratio for an autohexaploid (75% simplex and 25% non-simplex), supporting the hypothesis that the genome of cultivated sweetpotatoes is primarily autopolyploid. Similar findings have been reported by Ukoskit and Thompson (1997) using RAPDs, and Kriegner et al. (2003) using AFLPs. This proportion is assessed by considering only duplex and triplex markers, as they are the only informative multidose markers when dealing with dominant markers, given that a greater dosage would yield monomorphic bands. A similar criterion based on the comparison between expected and observed proportion of single- to multiple-dose markers was used to evaluate ploidy type in *Saccharum spontaneum* (da Silva and Sorrells 1996).

Duplex markers generally aligned to two different linkage groups and by complementing alignments, 103 homologous connections were observed in 'Beauregard' and 99 in 'Tanzania'. The connected linkage groups were assumed to be putative homologs, and by inference if one element of a pair was homologous to a third linkage group, then its pairing group was assumed also to be homologous to the third group. Some homologous groups were connected by several duplex markers. For example, groups B11.62 and B11.66 were connected by 17 duplex markers and groups B12.68 and B12.71 were connected by 14 duplex markers in the 'Beauregard' map. Similarly, in the 'Tanzania' map, groups T05.25–T05.27 and T08.44–T08.47 were connected each by 8 duplex markers, while groups T14.79–T14.81 were connected by seven duplex markers.

A similar situation was observed for triple dose markers. Each triplex marker aligned to 3 or 2 linkage groups, and by inference the connected groups were considered homologous (e.g., groups T02.08–T02.09–T02.10, T03.14–T03.15, and T05.27–T05.28). No markers aligned to more groups than their dosage

number, suggesting that the data is reliable. The fairly large numbers of duplex markers allowed us to almost completely identify all 15 homologous groups in 'Beauregard' and 'Tanzania'. However, there were six linkage groups of 'Beauregard' that remained ungrouped due to lack of bridging connections between these linkage groups and those already assigned to a homologous group. In general, the assumption for homology detection using multiple-dose markers is that homologous segments are only present on homologous chromosomes, and therefore there is an absence of duplication of the chromosomal region in non-homologous chromosomes (da Silva et al. 1995; Ripol et al. 1999).

According to Ripol et al. (1999) approximately 200 duplex markers would be needed to guarantee the identification of complete homologous groups in an octaploid species containing 64 chromosomes. Thus, increasing the number of duplex marker in our case may have helped to arrange our unassigned chromosomes into one of the 15 homologous groups. A similar case was observed in 'Tanzania' with 11 linkage groups that could not be assigned to any of the homologous groups. In 'Tanzania', we were able to assign 75 out of the 86 linkage groups into 15 homologous groups, with eight complete homologous groups (i.e., containing six linkage groups each), and six incomplete homologous groups (i.e., containing 2, 3, 4 or 5 linkage groups). In 'Beauregard', we were able to assign into homologous groups 84 out of the 90 linkage groups, resulting into 11 complete homologous groups (i.e., each containing 6 linkage groups) and 4 incomplete homologous groups, which were only missing 1 or 2 chromosomes.

Similar to Kriegner et al. (2003), our results support the proposed autopolyploid nature of sweetpotato. Our observation of distorted segregation in some markers of different dosages in this study suggests that some preferential pairing occurs in sweetpotato. However, strict allopolyploidy can be ruled out due to the observed segregation ratios of the markers and the proportion of simplex to multiple-dose markers. This conclusion is also supported by earlier observations of meiotic pairing in sweetpotato chromosomes, where bivalent as well as multivalent associations including hexavalents were observed (Magoon et al. 1970). These results are also in agreement with findings of Ukoskit and Thompson (1997) who, based on the ratio between single-dose and multiple-dose RAPD markers, concluded that sweetpotatoes were most likely autopolyploids. Given the observation that irregular pairing during meiosis can occur in polyploids, it is possible that some of the homologous chromosomes in sweetpotato may not recombine in a given generation. Thus, we believe that this may have reduced our ability to identify all homologous linkage groups in our map.

To the best of our knowledge, the sweetpotato genetic maps described herein represent the most comprehensive genetic mapping resource available for sweetpotato. These maps will provide a valuable tool to the sweetpotato research community for conducting genetic analysis in this species and for future studies of the inheritance of economically important traits via analyses of quantitative trait loci (QTL). Currently, this mapping population is maintained in-vitro and in the greenhouse by the NC State Sweetpotato Breeding and Genetics Program, and it is available to the sweetpotato research community for research and breeding purposes. In many other crop species, genetic mapping populations have been used to identify economically important genes. This is especially true for small grains and cereals (Becker et al. 1995; Cregan et al. 1999; Harushima et al. 1998; Yu and Wise 2000; Zwart et al. 2005), maize (Castiglioni et al. 1999), tomato (Broun and Tanksley 1996; Tanksley et al. 1992), potato (Costanzo et al. 2005; Gebhardt et al. 1989; Ghislain et al. 2001; Li et al. 2005; Milbourne et al. 1998), and other species where diploid relatives exist (Dugo et al. 2005; Qu and Hancock 1997; Sargent et al. 2004). For sweetpotato, the construction of a dense molecular genetic map is the first step needed for more detailed studies on the mode of inheritance of this species, which is as of yet unclear (Kriegner et al. 2003), and possibly provide new opportunities for accelerating the introgression of economically important traits into breeding lines by providing important information on trait inheritance, and where feasible and appropriate through the incorporation of MAS.

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