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A RAPD-based Linkage Map of Peanut Based on a Backcross Population Between the Two Diploid Species *Arachis stenosperma* and *A. cardenasii*

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ABSTRACT

A molecular linkage map based on an interspecific diploid backcross population [*Arachis stenosperma* × (*A. stenosperma* × *A. cardenasii*)] was constructed utilizing RAPD and RFLP markers. One hundred sixty-seven RAPD loci and 39 RFLPs were mapped to 11 linkage groups, covering a total genetic length of 800 cM. Clusters of 2 to18 markers were observed in most linkage groups. Twenty seven percent of the markers showed segregation distortion and mapped to four regions. Thirty-nine RFLP markers shared with a previously published linkage map, based on an *A. stenosperma* × *A. cardenasii* F_2 population, and six RAPD markers were used to establish correspondence between maps and to compare recombination frequencies between common markers. A generalized reduction in the recombination fraction was observed in the backcross map compared to the F_2 map. All common markers mapped to the same linkage groups and mostly in the same order in both maps.

Key Words: Peanut, *Arachis hypogaea*, RFLPs, RAPDs, mapping, molecular markers.

The cultivated peanut (*Arachis hypogaea* L.) is a major crop in most tropical and subtropical areas of the world and provides a significant source of oil and protein to large segments of the populations of Asia, Africa and South America. In the U. S., peanut is a high-value cash crop of regional importance, with major production areas concentrated in the Southeast.

The genus *Arachis* is native to South America, with central Brazil postulated as the center of origin. The cultivated peanut and one other allotetraploid species (*Arachis monticola* Krapov. *et* Rig.) have been assigned to section *Arachis* along with at least 25 diploid species (Krapovickas and Gregory, 1994). Although large germplasm collections of both the cultivated and related wild species are available, peanut breeders have traditionally relied on crossing elite by elite germplasm for developing improved cultivars (Holbrook and Stalker, 2003). As a result, the germplasm base of peanut cultivars is extremely narrow and low levels of genetic variability at the molecular level have been shown by isozyme, Restriction Fragment Length Polymorphism (RFLP), Randomly Amplified Polymorphic DNA (RAPD), and Single Sequence Repeat (SSR) analyses (Patterson *et al.*, 2004). Conversely, abundant polymorphisms have been detected among related wild species in section *Arachis* with these same marker types (Stalker and Mozingo, 2001), representing a valuable source of desirable traits not available in the cultivated gene pool.

Molecular markers offer plant geneticists and breeders a set of genetic tools that are abundant, non-deleterious and reliable. Marker systems have

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been successfully used over the last several decades to construct genetic maps, assess genetic diversity, and locate genes of interest. The advent of the RAPD assay (Williams *et al.*, 1990) provided an efficient method to detect DNA polymorphisms and generate a large number of molecular markers for genomic applications. RAPD markers for mapping and analysis of genetic diversity have been reported for a wide variety of plants including tobacco (*Nicotiana* spp.) (Lin *et al.*, 2001), plantain (*Musa* spp.) (Ude *et al.*, 2003), potato (*Solanum tuberosum* L.) (Sun *et al.*, 2003) and barley (*Hordeum vulgare*) (Fernandez *et al.*, 2002).

Genetic maps are normally constructed from a single segregating population, but it is expected that some of the information can be applied to other crosses or species. In peanut, two low density genetic maps have been published by utilizing variation in *Arachis* species, including one from diploids (Halward *et al.*, 1993) and the second from tetraploid crosses with *A. hypogaea* (Burow *et al.*, 2001). In the case of polyploid species such as peanut, it is often more efficient to construct initial maps in diploid relatives. Since the genomes of diploid and closely related polyploid species should be similar, one can predict the positions of loci in polyploids based on diploid maps and then search for markers associated with single gene or quantitative trait loci (QTLs) with DNA clones that are most likely to be spaced at regular intervals throughout the polyploid's genome. This strategy can save considerable time and resources versus making *de novo* maps in polyploids. The approach has been employed in wheat (Guyomarc'h *et al.*, 2002; Gill *et al.*, 1991), alfalfa (Echt *et al.*, 1993; Brummer *et al.*, 1993), and oat (Yu and Wise, 2000).

Halward *et al.* (1993) constructed an RFLP map in peanut from an F_2 population derived from an interspecific cross between the two diploid species (*A. stenosperma* Krapov. and W.C. Gregory and *A. cardenasii* Krapov. and W.C. Gregory). Due to the dominant nature of RAPD markers and, to take advantage of the speed with which large numbers of polymorphic markers can be identified, a RAPD map utilizing a backcross population derived from the same interspecific cross [*A. stenosperma* × (*A. stenosperma* × *A. cardenasii*)] was constructed. By establishing linkage relationships with common RFLP markers, or bridge markers, RAPD markers could then be positioned on the peanut core RFLP map. A comparison with the previous map (Halward *et al.*, 1993) is based on a common set of probes and RAPD primers mapped in both studies.

Materials and Methods

Plant Material. A backcross population of 44 plants derived from the cross [*A. stenosperma* × (*A. stenosperma* × *A. cardenasii*)] represented the mapping population (referred to as the BC population). A single F_1 plant was used as a male parent and backcross seeds were obtained by hand emasculation and controlled pollination. Plants were grown and maintained in greenhouse facilities at North Carolina State Univ., Raleigh, NC.

RFLP Analyses. Forty-one RFLP probes of known map position (Halward *et al.*, 1993) were selected to provide coverage of all linkage groups and used to screen the BC population. They also provided anchor points to compare the BC and F_2 maps. DNA isolation, digestion, Southern blotting and hybridization procedures were completed as described by Kochert *et al.* (1991).

RAPD Analyses. DNA isolation, reaction mixtures, PCR amplification conditions and DNA size fractionation were performed as described by Garcia *et al.* (1995). To construct a RAPD map, a total of 428 10-base random primers were screened against the F_1 and the recurrent parent (*A. stenosperma*). DNA bands present in the F_1 and absent in *A. stenosperma* correspond to heterozygous loci and should segregate in a 1:1 ratio in the BC population. These polymorphic bands are *A. cardenasii*-specific (nonrecurrent parent) and were scored in the population. To be certain that polymorphic bands would correspond to heterozygous loci, and would be amplified with enough intensity to be reliably scored in the BC population (also in heterozygous state), the F_1 was used during the screening step rather than the nonrecurrent parent. One hundred fifty-six primers were selected based on the size and intensity of the RAPD polymorphisms amplified. Segregating RAPD markers were identified by the manufacturer's primer code (Operon primers as A–Z, each from 1 to 20, and University of British Columbia primers as UBC 100–200, 500–600) corresponding to a particular 10-base sequence, followed by a slash and a number indicating the fragment size in base pairs. Likewise a group of framework RAPD markers was mapped in the F_2 mapping population to provide additional anchor points to help align both maps.

Segregation and Linkage Analysis. A χ^2 test (P = 0.05) with Yates correction factor was performed to test the null hypothesis of 1:1 segregation for all markers. Markers deviating significantly from the expected 1:1 segregation were excluded from the initial grouping and later added to the framework map as accessory markers. Linkage analysis was performed using MAPMAKER (Lander *et al.*,
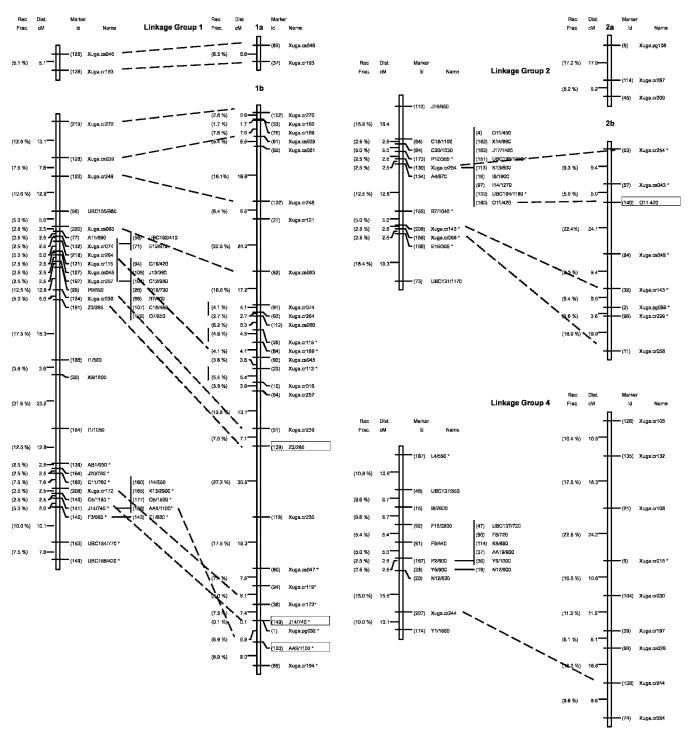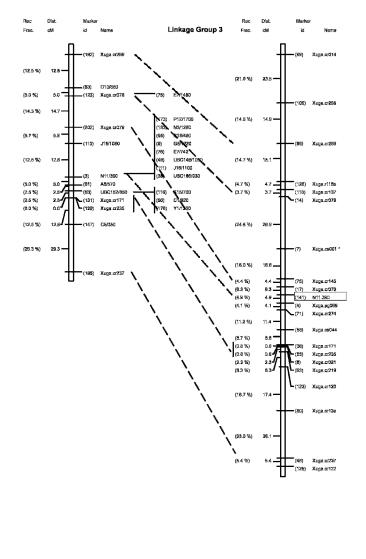
Fig. 1. Genetic linkage maps of peanut: on left is the molecular map based in an interspecific backcross population [*Arachis stenosperma* × (*A. stenosperma* × *A. cardenasii*)]; on right is the RFLP map based on an F$_2$ population derived from the same interspecific cross. Cosegregating marker loci are listed to the right of the linkage group. Loci with distorted segregation ratios from the expected 1:1 are denoted with a (.) to the right of the marker designation. Linkage groups were identified from 1 to 11 according to Halward *et al.* (1993) based on a common set of RFLP markers, and not based on their relative size. Map distances are presented in centimorgans (Kosambi function) to the left of the linkage groups. Boxed markers represent RAPD markers segregating in a 3:1 ratio in the F$_2$ population. Linkage groups arbitrarily numbered 9 to 11 have not been associated with the core RFLP map.

1987). All pairs of linked markers were first assigned to linkage groups using the "GROUP" command with a LOD ≥ 4.0 and recombination fraction θ = 0.30. Co-segregating markers (no recombination among markers within a linkage group) were detected from 2-point linkage data. Framework maps were constructed using only one from each set of cosegregating markers. "1st

Fig. 1. Continued.

ORDER" and "COMPARE" commands in MAP-MAKER were used to identify the most probable marker order within a linkage group. After establishing a framework map, the data were scanned for double cross-overs. If double cross-overs were observed adjacent to a single locus, primary data was rechecked for potential scoring errors. Additional markers were added to the framework map using the "TRY" command. Map distances in centimorgans (cM) between markers were calculated from recombination frequencies using Kosambi's mapping function (Kosambi, 1944).

Results

Primer Screening and Map Construction. Thirty-one of the 428 primers screened (7.2%) did not produce visible amplification, 145 (34%) did not detect polymorphisms between *A. stenosperma* and *A. cardenasii*, and 252 primers (58.8%) detected at least one polymorphic fragment. A total of 340 polymorphic bands, averaging nearly 1.35 polymorphic bands/primer were observed. From the 252 polymorphic primers, 156 were selected to screen the BC population. One hundred seven primers, identifying a total of 178 polymorphic loci,

Linkage Group 7

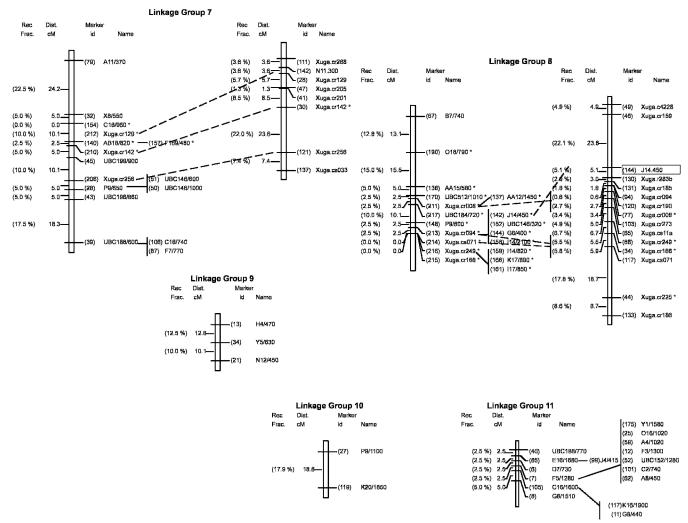| Rec Frac.	Dist. cM	Marker id	Name
		(79)	A11/370
(22.5 %)	24.2		
(5.0 %)	5.0	(32)	X8/550
(0.0 %)	0.0	(154)	C18/960 *
(10.0 %)	10.1	(212)	Xuga.cr129 *
(2.5 %)	2.5	(140)	AB16/820 * — (157) F16/480 *
(5.0 %)	5.0	(210)	Xuga.cr142 *
		(45)	UBC199/900
(10.0 %)	10.1		
		(206)	Xuga.cr256 — (51) UBC146/600
(5.0 %)	5.0	(28)	P9/650 — (50) UBC146/1000
(5.0 %)	5.0	(43)	UBC196/860
(17.5 %)	18.3		
		(39)	UBC188/600 — (106) C16/740 (87) F7/770

Rec Frac.	Dist. cM	Marker id	Name
(3.6 %)	3.6	(111)	Xuga.cr288
(3.6 %)	3.6	(142)	N11.300
(5.7 %)	5.7	(28)	Xuga.cr129
(1.3 %)	1.3	(47)	Xuga.cr205
(8.5 %)	8.5	(41)	Xuga.cr201
		(30)	Xuga.cr142 *
(22.0 %)	23.6	(121)	Xuga.cr256
(7.4 %)	7.4	(137)	Xuga.cs033

Linkage Group 8

Rec Frac.	Dist. cM	Marker id	Name
		(67)	B7/740
(12.8 %)	13.1		
		(190)	O18/790 *
(15.0 %)	15.5		
(5.0 %)	5.0	(138)	AA15/580 *
(2.5 %)	2.5	(170)	UBC512/1010 * — (137) AA12/1450 *
(2.5 %)	2.5	(211)	Xuga.cr008 *
(10.0 %)	10.1	(217)	UBC184/720 * — (142) J14/450 *
(2.5 %)	2.5	(148)	P9/800 * — (152) UBC146/320 *
(2.5 %)	2.5	(213)	Xuga.cr094 * — (144) G6/400 *
(0.0 %)	0.0	(214)	Xuga.cs071 — (158) I17/100
(0.0 %)	0.0	(216)	Xuga.cr249 * — (159) I14/820 *
		(215)	Xuga.cr168 — (166) K17/890 * (161) I17/850 *

Rec Frac.	Dist. cM	Marker id	Name
(4.9 %)	4.9	(49)	Xuga.c4228
		(46)	Xuga.cr159
(22.1 %)	23.8		
(5.1 %)	5.1	(144)	J14.450
(2.6 %)	3.0	(130)	Xuga.r283b
(1.8 %)	1.8	(131)	Xuga.cr185
(0.6 %)	0.6	(94)	Xuga.cr094
(2.7 %)	2.7	(120)	Xuga.cr190
(3.4 %)	3.4	(103)	Xuga.cr008 *
(4.9 %)	5.0	(103)	Xuga.cr273
(6.7 %)	6.7	(65)	Xuga.cs11a
(5.5 %)	5.5	(68)	Xuga.cr249 *
(5.8 %)	5.9	(34)	Xuga.cr168 *
		(117)	Xuga.cs071
(17.8 %)	18.7		
		(44)	Xuga.cr225 *
(8.6 %)	8.7	(133)	Xuga.cr186

Linkage Group 9

Rec Frac.	Dist. cM	Marker id	Name
		(13)	H4/470
(12.5 %)	12.8		
		(34)	Y5/630
(10.0 %)	10.1	(21)	N12/450

Linkage Group 10

Rec Frac.	Dist. cM	Marker id	Name
		(27)	P9/1100
(17.9 %)	18.8		
		(119)	K20/1850

Linkage Group 11

Rec Frac.	Dist. cM	Marker id	Name
(2.5 %)	2.5	(40)	UBC188/770
(2.5 %)	2.5	(85)	E18/1660 — (99) J4/415
(2.5 %)	2.5	(6)	D7/730
(2.5 %)	2.5	(7)	F5/1280
(5.0 %)	5.0	(105)	C16/1600
		(8)	G8/1510

(175) Y1/1580
(25) O16/1020
(58) A4/1020
(12) F3/1300
(52) UBC152/1280
(101) C2/740
(62) A8/450
(117) K16/1900
(11) G8/440

Fig. 1. Continued.

were reliably scored and used for mapping (1.7 mapped markers/selected primer and 0.42 mapped markers/any arbitrary primer).

At a LOD = 4.0, the map consisted of 206 markers that coalesced into 11 linkage groups. The number of mapped loci for each linkage group ranged from two to 40, comprising genetic distances of 2.5–29.3 cM (Fig. 1). Mapped markers include 167 RAPD markers, 34 *Arachis* root-specific cDNA clones and five *Arachis* shoot-specific cDNA clones. Twelve RAPD markers and two of the root-specific cDNA clones could not be assigned to any linkage group at the statistical stringency used, thus their linkage association was not determined.

A reduction in genetic recombination compared to the F_2 map was observed in all linkage groups except for group #7. The recombination fractions between identical pairs of linked markers in the F_2 population studied by Halward *et al.* (1993) and in the BC population studied here were compared to determine whether levels of recombination observed in both mapping populations were similar. Based on two-point analysis, only five of 35 intervals (14.3%) located throughout the genome were larger in the BC map than in the F_2 map (Table 1). This suggests that recombination in the F_2 population exceeds that of the BC population in most regions. A more compact map, covering 800 cM (average interval 8.1 cM) was established as compared to the 1400 cM covered by the F_2 map. The 39 previously mapped mapped probes and the six RAPD markers (mapped in the F_2 population) were located on the same linkage groups and mostly in the same order in both populations (Fig. 1).

Ninety-four of the 206 mapped markers (45.6%) co-segregated into 15 clusters of different sizes in almost all linkage groups and, in most cases towards the center of the group. Clusters are formed by markers with no observed recombination. This uneven distribution of markers

Table 1. Interval size (cM) between markers common to both F$_2$ and backcross linkage maps of *Arachis stenosperma* $\times$ *A. cardenasii*.

Interval	Linkage group[a] no.	F$_2$	BC
		------------------------------------- cM -------------------------------------	
Xuga.cs046-Xuga.cr193	1	6.6	5.1
Xuga.cr270-Xuga.cs039	1	11.9	13.1
Xuga.c039-Xuga.cr246	1	22.1	7.6
Xuga.cr246-Xuga.cs063	1	30.7	17.9
Xuga.cs063-Xuga.cs074	1	17.2	5.0
Xuga.cs074-Xuga.cr264	1	4.1	2.5
Xuga.cr264-Xuga.cr115	1	9.0	5.0
Xuga.cr115-Xuga.cs045	1	8.9	2.5
Xuga.cs045-Xuga.cr257	1	12.9	2.5
Xuga.cr257-Xuga.cr239	1	13.1	15.3
Xuga.cr239-Z3/265	1	7.1	5.0
Z3/265-*Xuga.cr172*	1	64.4	70.5
Xuga.cr172-J14/740	1	7.4	5.0
J14/740-AA9/1100	1	7.0	0
Xuga.cr254-O11/420	2	15.3	0
O11/420-*Xuga.cr143*	2	33.5	20.3
Xuga.cr143-Xuga.cr058	2	32	2.5
Xuga.cr266-Xuga.cr078	3	23.5	17.8
Xuga.cr078-Xuga.cr079	3	47.9	14.7
Xuga.cr079-N11/390	3	6.3	18.6
N11/390-*Xuga.cr171*	3	29.2	10.0
Xuga.cr171-Xuga.cr235	3	0.8	0
Xuga.cr235-Xuga.cr237	3	54.9	42.1
Xuga.cr111-Xuga.cr029	5	22.7	40.7
C5/530-*Xuga.cr140*	5	41.6	28.4
Xuga.cr140-Xuga.cr027	5	15.4	0
Xuga.cr277-Xuga.cr090	6	53.9	47.1
Xuga.cr090-Xuga.cr073	6	28.3	20.5
Xuga.cr073-Xuga.cr116	6	6.5	12.5
Xuga.cr129-Xuga.cr142	7	15.5	12.6
Xuga.cr142-Xuga.cr256	7	23.6	15.1
J14/450-*Xuga.cr094*	8	9.9	0
Xuga.cr094-Xuga.cr008	8	3.3	10.1
Xuga.cr008-Xuga.cr249	8	8.4	2.5
Xuga.cr249-Xuga.cs071	8	18.1	2.5

[a]These markers were ordered using all the available markers. Only markers common to the F$_2$ map are listed in the table, therefore, if markers are separated by more than 30 cM it means that other markers (not listed in this table) map between them.

suggests that the frequency of recombination varies greatly from one region to another on the same chromosome. Only five RFLP markers (12.8%) were found in clusters of two or more as compared to 47% of the mapped RAPD markers (Fig. 1). The resolution was limited in several regions due to the small sample size evaluated. For example, in linkage group #5, three clones (*Xuga.cr027, Xuga.cr140* and *Xuga.cr029*) cosegregated in the BC map but mapped to opposite ends of the linkage group in the F$_2$ map (Fig.1). Originally, linkage group #5 in the F$_2$ map was reported as two subgroups (5a and 5b) (Halward *et al.*, 1993) due to the loose linkage observed between *Xuga.cr177* and *Xuga.cs035*. The RAPD marker C5/530 mapped between the two RFLP clones and the two subgroups were joined without map expansion.

Distorted Loci. Fifty-four loci (26.2%) showed segregation distortion (a = 0.05), as is common in interspecific crosses. Eleven were RFLP (28%) and 43 (26%) were RAPD loci, suggesting that there is no prevalence of distortion with either type of marker. About one third of the distorted loci (three RFLPs and 13 RAPDs) showed an excess of the *A. stenosperma* alleles and all but one mapped to linkage group #2. The remaining 38 distorted loci (eight RFLPs and 30 RAPDs) showed an excess of *A. cardenasii* alleles and mapped to linkage groups #7, #8, and the distal end of #1.

Discussion

One of the primary uses of a genetic linkage map is to locate markers linked to genes of interest that can be either a single gene or a quantitatively inherited character. Because of the relatively low efficiency in mapping RAPDs in F_2 populations due to the dominant nature of the markers, a BC population was utilized to construct a genetic linkage map of peanut. The BC map now comprises 206 markers (167 RAPDs and 39 RFLPs) distributed into 11 linkage groups.

The ratio of mapped markers per selected primer (equaling 1.7) is about half of that reported in *Eucalyptus* (Grattapaglia and Sederoff, 1994) and lettuce (Kesseli *et al.*, 1994) interspecific crosses. This contrast in efficiency is probably due to differences in genomic complexity and genome size and because only polymorphic bands with an intensity score of 2 or 3 (according to Grattapaglia and Sederoff, 1994) were mapped.

A major feature of the peanut map is reduced genetic recombination, resulting in less genome coverage (800 cM) and higher clustering of markers than the F_2 RFLP map of the same species (Halward *et al.*, 1993). This higher marker density towards the middle of linkage groups could correspond to centromeric areas which are rich in repetitive DNA, thus providing a better target for RAPD markers as compared to RFLP probes (Williams *et al.*, 1993). Reduced levels of meiotic recombination in areas surrounding the centromere also could have caused markers to cluster in these regions even though they are physically well separated. These factors, combined with the limited resolution of our mapping population with only 44 meioses, are the likely reasons for the excessive clustering and reduced recombination observed in the BC map. Hauge *et al.* (1993) made similar observations in *Arabidopsis* spp. when comparing their map with that from Reiter *et al.* (1992) based on a larger population size. Marker clustering was also observed by Kesseli *et al.* (1994) in lettuce, and by Grattapaglia and Sederoff (1994) in *Eucalyptus* spp.

Twenty-six percent of the loci mapped in the BC population exhibited skewed segregation ratios. This percentage was comparable to the 25% observed by Halward *et al.* (1993) in the peanut F_2 map. This is higher than that observed by Kesseli *et al.* (1994), and Grattapaglia and Sederoff (1994) in lettuce, and *Eucalyptus*, respectively; but lower than that found by Brummer *et al.* (1993) in alfalfa. Distorted segregation of markers has also been reported for *Lotus japonicus* (Regel) K. Larsen, a model legume species (Sandal *et al.*, 2002). The observed skewed linkage groups most likely represent real associations among loci since a chromosomal segment showing distorted segregation also will cause skewed segregation ratios in neighboring segments. The large linkage block at the distal end of linkage group #1 could really map to a different area of the genome; however, because *Xuga.cr172*, J14/740 and AA9/1100 map in the same position in the F_2 map, it was concluded as being part of linkage group #1.

Probes that showed skewed segregation in the F_2 population were also distorted in the BC population and could be mapped to the same linkage groups. Although it has been suggested that backcrosses are less sensitive to skewing than F_2 populations because recombination measurements are limited to alleles coming from only one parent (Causse *et al.* 1994), the results with peanut showed no significant difference in the amount of distortion found in either type of mapping populations or between the RAPD and RFLP markers. The results for peanut also suggest that the cause of the distortion is not relevant to the size of the segregating population. Similar findings were reported in a common bean intraspecific F_2 mapping population (Adam-Blondon *et al.*, 1994).

The information provided by the BC map along with that provided by the F_2 map can greatly aid in the identification and placement of markers linked to genes of agronomic interest into the peanut RFLP core map. Moreover, since both types of markers are known to target different areas of the genome, combining the information provided by both maps will increase the genome coverage of the current diploid peanut RFLP map.

Acknowledgments

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