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Soybean pedigree analysis using map-based molecular markers: recombination during cultivar development

Abstract An analysis of the genome structure of soybean cultivars was conducted to determine if cultivars are composed of large regions of chromosomes inherited intact from one parent (indicative of minimal recombination) or if the chromosomes are a mixture of one parent's DNA interspersed with the DNA from the other parent (indicative of maximal recombination). Twenty-one single-cross-derived and 5 single-back-cross-derived soybean cultivars and their immediate parents (47 genotypes) were analyzed at 89 RFLP loci to determine the minimal number and distribution of recombination events detected. Cultivars derived from single-cross and single-backcross breeding programs showed an average of 5.2 and 8.0 recombination events per cultivar, respectively. A homogeneity Chi-square test based upon a Poisson distribution of recombination events across 13 linkage groups indicated that the number of recombinations observed among linkage groups was random for the single-cross cultivars, but not for the single-backcross-derived cultivars. A two-tailed t-test demonstrated that for some linkage groups, the number of recombinations per map unit exceeded the confidence interval developed from a t-distribution of recombinations standardized for map unit distance. Paired t-tests of the number of recombinations observed between linkage-group ends and the mid-portion of the linkage groups indicated that during the development of the cultivars analyzed in this study more recombinations were associated with the ends of linkage groups than with the middle region. Detailed analysis of each linkage group revealed that large portions of linkage groups D, F, and G were inherited intact from one parent in several cultivars. A portion of linkage group G, in contrast, showed more recombination events than expected, based on genetic distance. These analyses suggest that breeders may have selected against recombination events where agronomically favorable combinations of alleles are present in one parent, and for recombination in areas where agronomically favorable combinations of alleles are not present in either parent.

Key words Soybean · Cultivar development · Recombination · Molecular markers

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Introduction

Beginning in the early 1900s, recombination became recognized for its value in determining the genetic distance separating two or three characters. These distances were used to produce early linkage maps (Morgan 1911; Sturtevant 1913; Kwen 1923). It soon followed that recombination rates between characters showed variation between populations in species such as *Drosophila* (Bridges 1915), maize (Stadler 1925), and soybean (Pfeiffer and Vogt 1989). Studies in *Drosophila* (Chinnici 1971), wheat (Rao and Murty 1972), radish (Dayal 1976) and soybean (Pfeiffer and Vogt 1989) have shown that variation in recombination appears to be under polygenic control. Pfeiffer and Vogt (1989) and Pfeiffer (1993) analyzed F_2 soybean populations derived from crosses of 'AP12' and three 'Clark' near-isogenic lines. The recombination rates between *P1*, *R* and *Lnp2*,

and *Dt1* and *L1* were normally distributed among the F_2 progeny, and evidence of a single "major" gene affecting recombination was not observed. In contrast, Farcy et al. (1986) reported a single gene that acted to enhance recombination freqeuency in petunia.

The models for recombination have, until recently, remained relatively untested because the data needed for analysis was not available. The advent of restriction fragment length polymorphism (RFLP) and other DNA-based technologies may help alter this situation. The number of morphological loci contained in a known linkage group is usually limited. DNA-based loci, however, have been used to produce relatively saturated maps in many species (O'Brien 1993). Use of these DNA-based loci could provide some insight into the control and regulation of recombination.

Although it is generally believed that positive interference is the rule in eukaryotes (Bailey 1961) the results of Xu et al. (1995) indicate that recombination within the maize *a1* gene occurs predominantly within a 377-bp interval. The results of Sall and Nilsson (1994) using RFLP data generated from two barley mapping populations indicate that crossover distribution is random, both within and between chromosomes. However, these data were collected from randomly segregating populations. It is not known whether the breeding process, through the selection of individuals from segregating populations, selects individuals having undergone a minimal or maximal number of recombination events. In other words, it is not known whether breeders select for products of discrete recombination events or whether derived cultivars are a product of a thoroughly recombined genome. An analysis of the genomic structure of soybean cultivars derived from multiple breeding programs could determine if cultivars are composed of large regions of chromosomes inherited intact from one parent (indicative of minimal recombination), or if the chromosomes are a thorough mixture of DNA from both parents (indicative of maximal recombination).

The breeding process of an inbred species takes multiple generations, and each generation contains a meiotic event, which provides the opportunity for recombination. Take, for example, a cultivar derived from a single cross between two parents. The F_1 seed is allowed to self-pollinate and produce F_2 seed, which, in turn, is allowed to self-pollinate. This selfing process continues until the resulting progeny is essentially homozygous. Depending on the breeding strategy used, single plants are selected and advanced in one or more generations. In each generation of selfing, theoretically one-half of the heterozygous loci are fixed at one allele or the other. Therefore, in the F_6 generation, 96.87% of the loci that were heterozygous in the F_1 generation are now homozygous. This breeding strategy takes advantage of multiple meiotic events where recombination can alter the combination of alleles present.

The relatively short history and the limited number of ancestral lines which have contributed to modern cultivars helps to make soybean an ideal system for pedigree analysis. Only 12 Plant Introductions account for over 88% of the germplasm present in modern cultivars (Specht and Williams 1984). Thus, the number of cultivars required for a pedigree analysis is not unmanageably large. The ability to follow chromosomal segments from parent to offspring has been demonstrated in soybean using RFLP markers (Shoemaker et al. 1992; Lorenzen et al. 1995). Thus, the potential exists to identify and evaluate regions of chromosomes that have undergone recombination events during the development of a soybean cultivar.

The purpose of the research described herein was to (1) estimate the amount of recombination within and among the linkage groups of 26 soybean cultivars and to determine whether the recombination can be explained by random chance, and (2) examine linkage groups in detail to identify chromosomal regions that are inherited as large linkage blocks, and regions with more recombination than expected, based on genetic distance.

Materials and methods

Selection of germplasm

Twenty-one cultivars derived from single-cross breeding programs and five cultivars derived from single-backcross breeding programs were selected for RFLP alalysis based on their commercial success. Their commercial success was measured by the number of acres on which they were planted. For example, in 1957, 'Harosoy', 'Hawkeye', 'Lee', and 'Clark' were planted on 55% of the soybean acreage in the United States. Two cultivars released by private companies in the 1980s and early 1990s were added to the study to include more modern germplasm. Additionally, one breeding line (N44-92) was included. The 26 different parental genotypes were also included to make a total of 47 soybean lines analyzed (Table 1).

RFLP probe analysis

DNA from the 47 soybean genotypes was digested with five restriction endonucleases, *DraI*, *EcoRI*, *EcoRV*, *HindIII* and *TaqI*. Eighty-two genomic DNA probes that detected 89 loci were screened against these genotypes using probe/enzyme combinations identical to those used in the preparation of the USDA-ARS:RFLP map (Shoemaker and Olson 1993). Only the mapped polymorphic fragment was scored in each cultivar. Extraction of DNA, restriction endonuclease digestions, electrophoresis, Southern transfer, and DNA hybridizations were performed as described previously (Keim et al. 1989).

RFLP allele assignment

The DNA fragments at each locus were given an allelic designation. The allele designations used in this analysis were consistent with those reported by Lorenzen et al. (1995). For graphical presentation, the RFLP alleles were coded with the "a" allele black, the "b" allele cross-hatch pattern, and the "c" allele vertical stripe pattern. Missing data were left blank (white). Graphical genotypes were created using SUPERGENE, a Macintosh software application (Boutin et al. 1995).

Detection and evaluation of recombination events

Not all RFLP loci were informative in each cultivar. An RFLP locus was defined as informative if a DNA fragment polymorphism defin-

Table 1 Cultivars and the parents from which they were derived are listed in ascending order according to the number of recombination events that were detected. The number of informative loci present in each cultivar is also listed

Cultivar	Female parent	Male parent	Number of recombinations	Number of informative loci
Single cross				
Century	Calland	Bonus	1	15
Evans	Merit	Harosoy	2	19
Hawkeye	Mukden	Richland	2	26
Corsoy	Harosoy	Capital	2	23
Blackhawk	Mukden	Richland	3	26
Adelphia	(Kent)	Adams	4	23
York	Dorman	Hood	3	38
Acme	Manitoba Brown	Mandarin Ottawa	5	30
Hark	Hawkeye	Harosoy	5	31
Hobbit	Williams	Ransom	5	35
FT1950	BSR201	A2943	6	24
Adams	Illini	Dunfield	6	22
A3127	Williams	Essex	6	27
Pagoda	Manitoba Brown	Mandarin Ottawa	6	31
N44-92	Haberlandt	Ogden	6	29
Lee	CNS	S100	7	39
A2943	A1265	A3127	7	38
B216	Corsoy	Wayne	8	47
Amsoy	Adams	Harosoy	8	38
Kent	Lincoln	Ogden	9	32
Merit	Blackhawk	Capital	10	39
Average			5.2	30.1
Single backcross				
Shelby	Lincoln(2)	Richland	6	29
Chippewa	Lincoln(2)	Richland	6	32
Clark	Lincoln(2)	Richland	7	31
Harosoy	Mandarin Ottawa(2)	AK Harrow	10	46
Ford	Lincoln(2)	Richland	11	32
Average			8.0	34.0

ing the locus was observed between the two parents. This polymorphism allowed a parental source to be assigned to a chromosomal region of the derived cultivar (Lorenzen et al. 1995; Boutin et al. 1995). Informative loci were coded to indicate which parent contributed the RFLP allele to the cultivar. If the parental source was different between two consecutive, informative RFLP loci, it was inferred that a recombination event had occurred between the two loci.

The number of detected recombination events was counted for each individual cultivar. The number of recombination events detected and the number of informative loci in cultivars derived from single-cross breeding programs were analyzed to determine if the distribution was normal (SAS 1989). The Shapiro-Wilk test was used to determine normality, with W = 0.97 or greater considered to be a normal distribution (SAS 1989).

To assess the distribution of recombination events across chromosomes, we analyzed single-cross-derived cultivars and single-backcross-derived cultivars separately. A Chi-square test for homogeneity (Steel and Torrie 1980) was used to determine if the number of recombinations per linkage group was random when standardized for recombinations per informative marker.

A two-tailed t-test (Steel and Torrie 1980) was used to establish confidence intervals and to assess the distribution of the number of recombinations observed per linkage group when standardized for the number of recombinations per map unit.

To determine if recombinations were distributed randomly within

linkage groups we first separated the individual linkage groups into segments where the middle segment represented 50% of the genetic distance spanned by all informative markers for that group. Each end of the linkage group represented 25% of the informative genetic distance of the group (Fig. 1). A paired t-test (Steel and Torrie 1980) was then conducted to test if the number of recombinations differed between the mid-portions of the linkage groups and the end-portions. Recombinations were counted as follows. Each region of recombination residing solely within a segment was given a value of 1.0 for that segment. Each region of recombination possibly occurring in each of two segments was given a value of 0.5 for each segment in which it may have occurred, and each region of recombination possibly occurring in any of three segments was given a value of 0.33 for each segment.

Linkage blocks inherited intact from parent to offspring were identified by examining linkage groups to locate consecutive informative loci derived from the same parent. A minimum of 4 consecutive, informative loci derived from the same parent was required before classifying the region as a linkage block. Three consecutive informative loci derived from the same grandparent was required for a region to be considered a linkage block that was inherited for two generations. The number of consecutive markers required to identify linkage blocks, 4 for one generation, and 3 for two generations, was subjective. The criteria used by the authors was set to eliminate large "gaps" between markers where double recombination events would likely remain undetected.

Fig. 1 Linkage groups
evaluated for recombination
events among 21 single-cross-
derived and 5 single-backcross-
derived cultivars. Linkage
group designations are
according to Shoemaker and
Olson (1993). Probe
designations are shown to the
left of each linkage group and
map distances in centi Morgans
are shown to the *right* of
each linkage group. The *vertical
lines* to the *right* of each linkage
group indicate the region in
which a recombination took
place during the development of
one of the single-cross-derived
cultivars. The *length* of the
vertical lines depended upon
the specific combination of
informative markers for each
cultivar. The *dashed horizontal
lines* through each linkage
group indicate the separation
of the genetic distance covered
by informative markers into
two end-segments (25% distance
each, and a mid-segment
(50% distance)
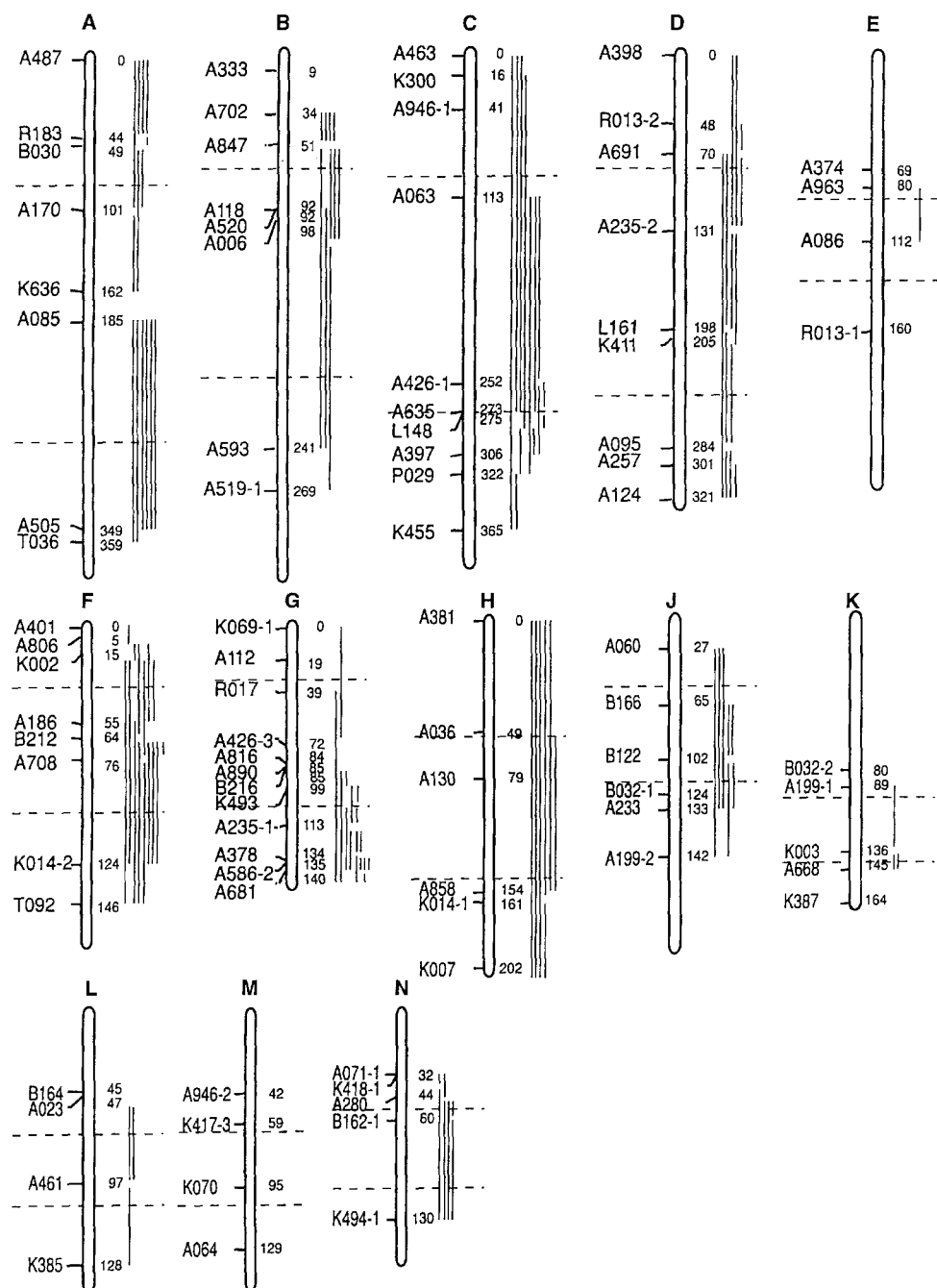
Results and discussion

Observation of recombination events

Twenty-one soybean cultivars derived from single-cross breeding programs and 5 cultivars derived from single-backcross breeding programs were each analyzed at 89 RFLP loci distributed over 13 linkage groups (Table 1 and Fig. 1). Each cultivar contained a unique combination and distribution of informative RFLP loci. An RFLP locus was defined as informative if a DNA fragment polymorphism existed between the two parents.

The informative loci were coded to indicate which parent contributed the RFLP allele to the progeny cultivar. If the parental source differed between 2 consecutive, informative loci, it was inferred that a recombination event had occurred between the 2 loci.

The observed number of recombination events detected in cultivars derived from single-backcross breeding programs ranged from 6 in cvs 'Shelby' and 'Chippewa' to 11 in cv 'Ford', with an average of 8.0. The average number of informative loci among these cultivars was 34 (Table 1). The number of informative loci in cultivars derived from single-cross breeding programs ranged from 15 in cv 'Century' to 47 in cv 'B216', with an

average of 30.1 (Table 1). The distribution of the number of informative loci was normal, W = 0.98. The observed number of recombination events detected in cultivars derived from a single cross ranged from 1 in cv 'Century' to 10 in cv 'Merit', with an average of 5.2 (Table 1). The distribution of the number of observed recombination events was normal, W = 0.98.

The number of recombination events observed was positively correlated with the number of informative loci present in each cultivar. A regression of the number of recombination events on the number of informative loci resulted in an R^2 of 0.54, $P = 0.0001$. Thus, the number of detectable recombination events increased linearly as the number of informative loci increased. However, only 54% of the variation in the observed recombination events was explained by the number of informative loci. In addition to the number of informative loci, the distribution of informative loci along the linkage group may have affected the observed number of recombination events. Usually, informative markers were independently spaced "on average", but close linkage was observed between some informative loci. It is also possible that variation in the number of detected recombination events was affected by the quantitative nature of recombination, as described by Pfeiffer and Vogt (1989) and Pfeiffer (1993). A quantitative model is supported by the normal distribution of the number of observed recombination events.

Distribution of recombination events among linkage groups

The Chi-square test for homogeneity indicated that for the single-cross-derived cultivars, the number of recombinations per linkage group was not significantly different from that expected by random chance when the data were stadarized on the basis of recombinations per informative marker $\chi^2 = 14.07$). However, for both single-cross and single-backcross-derived cultivars the distribution of recombinations across some linkage groups exceeded the confidence interval when that distribution was developed from the number of recombinations standardized for recombinations per map unit (Table 2).

The Chi-square test for homogeneity using the single-backcross-derived cultivars also indicated that recombinations were not randomly distributed across linkage groups ($\chi^2 = 21.0$).

Distribution of recombination events within linkage groups

We were able to test the hypothesis that recombinations are randomly distributed within a linkage group by separating the linkage groups into end- and mid-portions, each representing 50% of the genetic distance covered by informative markers. The paired t-test in-

Table 2 Recombination values lstandardized for recombination/length of linkage groups in single-cross and single-backcross cultivars. Values shown for each linkage group are recombinations per centiMorgan

Linkage group	Cultivar	
	Single cross	Single backcross
A	0.042	0.022
B	0.038	0.012
C	0.033	0.011
D	0.040	0.031
E	0.011	0.000
F	0.096	0.014
G	0.100	0.043
H	0.035	0.010
J	0.061	0.000
K	0.036	0.000
L	0.036	0.000
M	0.000	0.000
N	0.071	0.041
Mean	0.046	0.014
CI[a]	$0.028 < \mu < 0.064$	$0.005 < \mu < 0.023$
CI[b]	$0.021 < \mu < 0.071$	$0.001 < \mu < 0.027$

[a] CI, Confidence interval at $\alpha = 0.05$ level
[b] CI, Confidence interval at $\alpha = 0.01$ level

Table 3 Estimated minimum number of recombinations for middle- and end-regions of 13 soybean linkage groups estimated from 21 single-cross-derived cultivars

Linkage group	Number of recombinations		
	End region (Y_1)	Middle region (Y_2)	Difference $(Y_1 - Y_2)$
A	8.50	5.50	3.00
B	7.16	2.83	4.33
C	8.34	5.67	2.67
D	7.66	5.33	2.33
E	0.50	0.50	0.00
F	8.50	6.17	2.33
G	11.50	4.00	7.50
H	5.00	2.00	3.00
J	3.00	6.00	-3.00
K	1.50	1.50	0.00
L	1.50	1.50	0.00
M	0.00	0.00	0.00
N	5.00	2.00	3.00
Mean	5.24	3.31	1.93[a]

[a] Observed t-value $= 2.69 > t (12, 0.05) = 2.18$

dicated a significant difference in the number of recombinations observed between linkage group segments (Table 3). The ends of the linkage groups contained more recombinations (5.24 average) than did the mid-portions of the groups (3.31 average).

It is not possible to unequivocally say that soybean breeders have selected cultivars with recombined regions. Also, because no correlation between the molecular genetic map and the physical organization of the chromosomes exists for soybean, it is not possible to say

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that these findings relate to the occurrence of more recombinations at the end of chromosomes. However, a direct 1:1 correlation between chiasmata and recombination nodules has been reported for tomato (Herickhoff et al. 1993), and high chiasmata density has been associated with increased recombination in the subtelomeric regions of human chromosomes (Chandley and Mitchel 1988). In the tetraploid wheat B-genome, genetic recombination was absent in all proximal chromosome arm regions and increased exponentially with the distance from the centromere (Lukaszewski and Curtis 1993). Yu and Peterson (1973) demonstrated through the use of chromosome interchanges that the rate of intragenic recombination in the *wx* locus of maize increased with an increasing distance from the centromere. Although the position of centromeres relative to the soybean molecular genetic map is not known, the data from this study suggest that during the development of commercially successful cultivars, central regions of chromosomes undergo less recombination than distal regions.

Inheritance of large linkage blocks

Manly linkage groups contained 4 or more informative markers. It is difficult to use statistical analysis on informative loci that are not separated by equal distances, but these linkage groups can still provide valuable information by lending a more accurate assessment of the potential origin of the chromosome segments in a particular cultivar.

Each of the 26 cultivars derived from hybridization programs was analyzed at 13 linkage groups. A total of 338 linkage groups were analyzed. Of these 338 linkage groups 71 had 4 or more informative loci. Of the 71 linkage groups 30 (42%) had 4 to 9 consecutive, informative loci derived from the same parent (Table 4). The size of regions that appeared to be inherited intact from parent to offspring ranged from 74 cM to 372 cM, with an average of 184 cM. Fig. 2 shows 5 cultivars where it seems that an entire linkage group was inherited intact from one parent. The most striking example was linkage group C in cv 'Lee'. Nine consecutive informative loci which spanned 372 cM were all derived from the ancestral cultivar 'S100'.

These linkage blocks were not all randomly scattered across the genome. Three linkage groups contained regions which were inherited intact during the independent development of more than 1 cultivar. First, linkage group D contained a region 170 cM in length that was inherited as a linkage block in 4 separately derived cultivars (Fig. 3). This linkage block included more than half of the 321 cM present on the linkage group. Second, linkage group F contained a region 130 cM in length that was inherited as a linkage block in 5 separately derived cultivars (Fig. 4). The 130-cM linkage block represented a substantial portion of linkage group F (146 cM total length) (Fig. 4). Finally, linkage group G

Table 4 Cultivars which contain a large linkage block inherited from one parent. Regions on linkage groups were considered to be large linkage blocks if a minimum of 4 consecutive, informative loci were derived from the same parent

Cultivar	Linkage group	Number of consecutive markers	Number of CentiMorgans in block
Lee	C	9	372
Kent	G	7	100
Hobbit	F	6	165
York	G	6	113
Shelby	C	5	259
Clark	C	5	259
B216	D	5	120
Hawkeye	D	5	250
B216	F	5	130
Hark	F	5	130
York	A	4	259
Harosoy	A	4	306
Merit	A	4	142
Amsoy	A	4	142
Corsoy	A	4	300
Hawkeye	A	4	197
Ford	B	4	235
Chippewa	B	4	325
Chippewa	C	4	162
Merit	C	4	162
N44-92	C	4	90
Hobbit	C	4	306
Chippewa	D	4	205
Blackhawk	D	4	170
York	F	4	130
Acme	F	4	124
Adelphia	F	4	74
B216	G	4	94
A2943	G	4	134
Lee	H	4	153

Fig. 2 Five cultivars that seem to have inherited an entire linkage group from one parent. *Letters* to the *left* of the linkage group indicate the parental source of the linkage segment
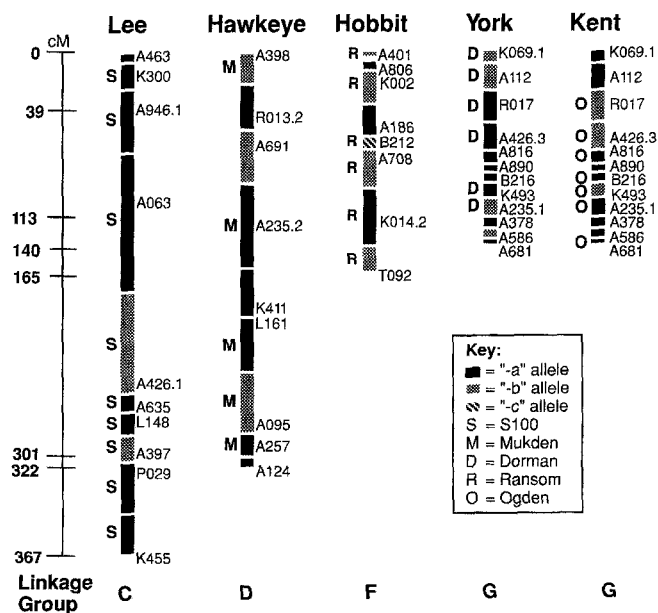
Fig. 3 Linkage group D is shown for 4 cultivars. Regions of the linkage group contained in the *box* indicate linkage blocks that are common among the cultivars. Characters to the *left* of the linkage group indicate the parental source of that allele
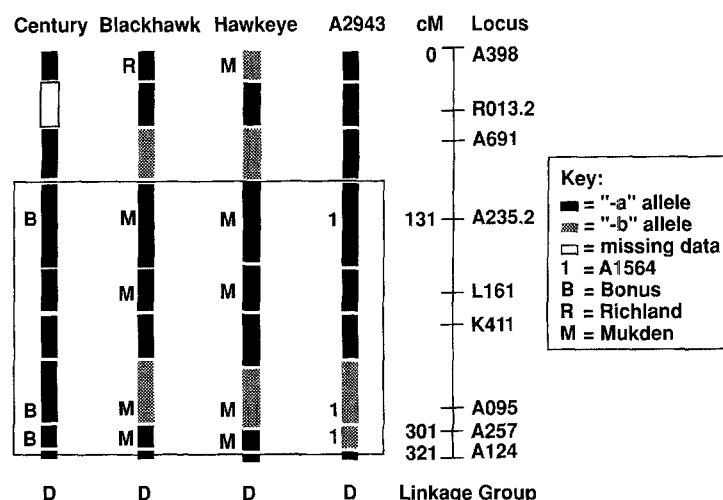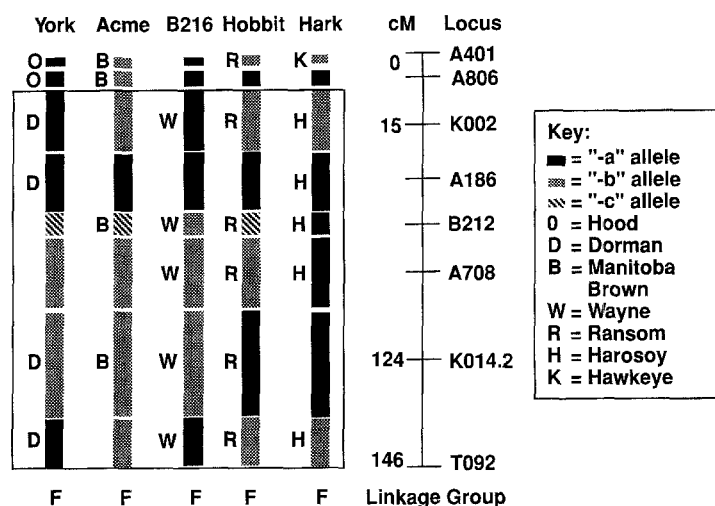

Century Blackhawk Hawkeye A2943 cM Locus

Key:
■ = "-a" allele
▨ = "-b" allele
□ = missing data
1 = A1564
B = Bonus
R = Richland
M = Mukden

D   D   D   D   Linkage Group

Fig. 4 Linkage group F is shown for 5 cultivars. Regions of the linkage group contained in the *box* indicate linkage blocks that are common among all of the cultivars. Characters to the *left* of the linkage group indicate the parental source of that allele

York Acme B216 Hobbit Hark cM Locus

Key:
■ = "-a" allele
▨ = "-b" allele
▨ = "-c" allele
0 = Hood
D = Dorman
B = Manitoba
    Brown
W = Wayne
R = Ransom
H = Harosoy
K = Hawkeye

F   F   F   F   F   Linkage Group

contained a region 113 cM in length that was inherited as a linkage block in 5 seperately derived cultivars (Fig. 5). The total length of linkage group "G" is 140 cM (Fig. 5).

The predominantly two-allele nature of soybean RFLP loci made it difficult to follow alleles for more than one generation. Even with this limitation, we were able to detect 6 linkage groups with linkage blocks containing 3 consecutive informative loci, including linkage group G mentioned above, that could be followed for two generations. The lengths of these linkage blocks ranged from 74 cM contributed from 'Ogden'→'Kent'→'Adelphia', to 300 cM contributed by 'Mandarin' 'Ottawa'→'Harosoy'→'Corsoy' (Table 4). Many additional linkage blocks inherited intact for two generations were detected by relaxing the detection criteria to 2 consecutive, informative loci. Thus, it appears that large regions of chromosomes often times remained intact during the process of cultivar development. These could represent regions where favorable combinations of alleles are present and se-

lected for or regions where recombination has been suppressed. These two explanations are not necessarily mutually exclusive. Kimura (1956) and Nei (1967, 1968) have proposed that natural selection can affect rates of recombination, ultimately leading to the closer linkage of favorable alleles. Thus, it follows that a breeder selecting for agronomic traits will select for regions where favorable combinations of alleles existed in the parents, and against regions where recombination events have broken up these favorable combinations. Additionally, the influence of genetic control must not be overlooked. The linkage blocks present on linkage groups D, F, and G may have been under genetic control that suppressed recombination in these regions.

Multiple recombination events

The existence of large linkage blocks inherited from the same parent was demonstrated in this study. Linkage groups also were analyzed to detect the opposite phe-

Fig. 5 Linkage group G is shsown for 5 cultivars. Regions of the linkage group contained in the *box* indicate linkage blocks that are common among all of the cultivars. Informative loci do not extend to the top of the linkage group in all of the cultivars. Therefore, the linkage block may be limited to the central portion of the linkage group. Characters to the *left* of the linkage group indicate the parental source of that allele
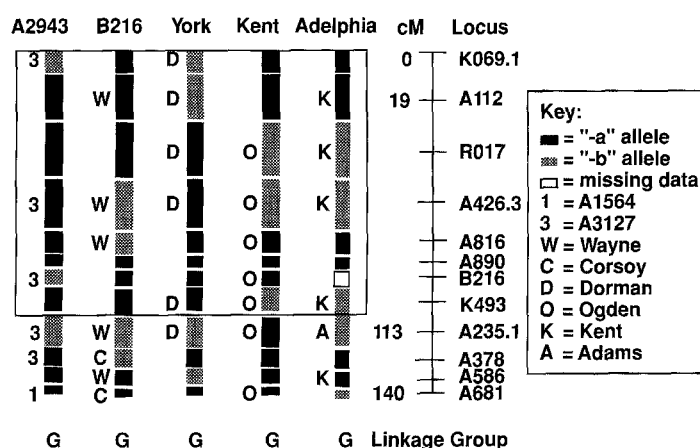
nomenon, namely multiple recombination events located on the same linkage group. Among the 338 linkage groups analyzed (26 cultivars × 13 linkage groups), 6 linkage groups contained 3 or more recombination events (Table 5). One striking example was linkage group G in cv 'B216', where 3 recombination events were detected in a 27 cM region. An additional 20 linkage groups (located among the 26 cultivars) contained 2 recombination events.

The presence of multiple recombination events on a linkage group suggests that either breeders selected for recombination events with favorable alleles or that re-

Table 5 Linkage groups which have undergone three or more recombination events. The number of recombinations observed exceed the Confidence Interval for $P < 0.01$ (Table 2), for the reported centimorgan distances

| Cultivar	Linkage group	Number of centiMorgans	Number of recombination events
B216	G	27	3
FT1950	G	60	3
Merit	F	131	3
Clark	D	301	3
Ford	D	301	4
Chippewa	A	367	3

combination was "enhanced" in these regions. Again, the two explanations are not necessarily mutually exclusive. The selection for combinations of alleles that were not present in parental germplasm would likewise select for recombination in that region. The possibility also exists that enhanced recombination in particular regions is under genetic control.

Linkage group G appeared to contain a 56 cM region that was particularly prone to recombination events (Fig. 6). Nineteen recombination events were observed among 15 cultivars in this 56 cM region (Fig. 5). The 4 sister cultivars 'Clark', 'Chippewa', 'Ford', and 'Shelby' were derived from the cross 'Lincoln^2', × 'Richland'. The development of these 4 cultivars was independent except that 'Clark' and 'Shelby' trace to a single S3 plant after the backcross (Carter et al. 1993). Each of the cultivars contained a recombination event in the same 1 cM region on linkage group G (Fig. 5). In each instance the RFLP allele, A890-b, was contributed by 'Lincoln', and allele B216-a, located 1 cM away, was contributed by 'Richland'. This suggests that a recombination in this region, for this particular cross, brought together a favorable combination of alleles. Alternately,

Fig. 6 Linkage group G is shown for 15 cultivars. *Arrows* indicate regions where a recombination event was observed. Characters to the *left* of the linkage group indicate the parental source of that allele
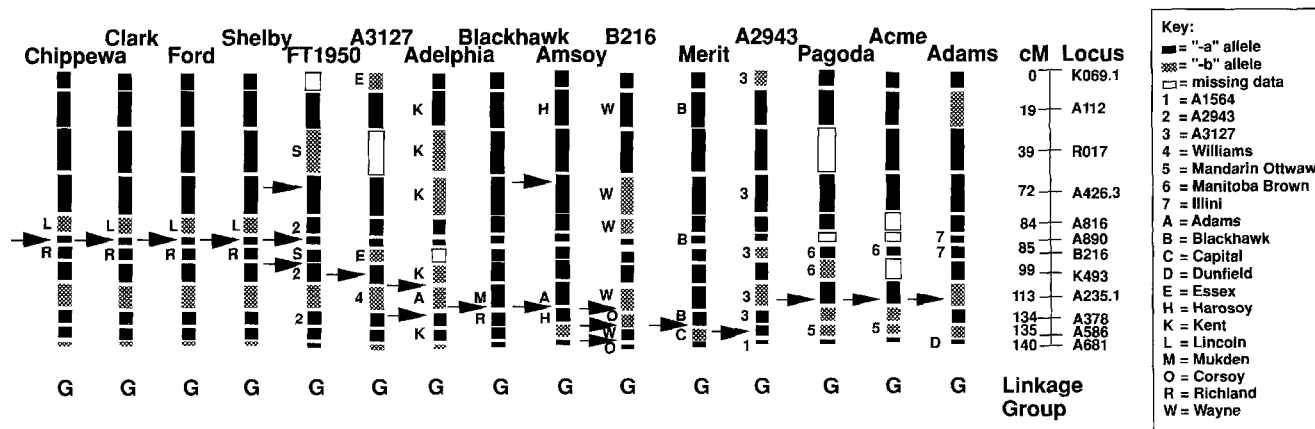
this region may have been under genetic control, representing a genetic recombination 'hot-spot', and that this combination of alleles was conducive to enhancing recombination at this location. Unfortunately, 'Lincoln' and 'Richland' were monomorphic at the remaining 10 loci on linkage group G, and therefore it remains unknown whether this recombination event resulted in the derivation of one-half of the linkage group from 'Lincoln' and one-half from 'Richland' or if a smaller region was introgressed from one parent. 'FT1950' also contained a recombination event in this same, 1 cM, region (Fig. 6).

Summary

The ends of linkage groups underwent more recombination during cultivar development than the middle regions of the linkage groups. Observation of the distribution of recombination events which occurred during the development of these cultivars potentially may provide evidence of selection in specific genomic regions. Large genomic regions which have not undergone recombination potentially contain favorable combinations of alleles, while regions that have undergone recombination events have potentially brought together favorable combinations of alleles. When analyzing chromosomal regions in detail, we often observed evidence for both minimizing and maximizing recombination on different linkage groups of the same cultivar. For example, cv 'Ford' has a 235 cM region on linkage group B apparently inherited intact from 'Lincoln', while linkage group D showed 4 recombination events. Evidence for maximal and minimal recombination was also seen on the same linkage group within a cultivar or between cultivars. Cultivar 'B216' has a region on linkage group G where 80 cM appeared to be inherited intact from 'Wayne', while the adjacent 27 cM of the linkage group showed 3 recombination events. Additionally, linkage group F showed 3 recombination events in cv 'Merit', while for 5 other cultivars a large region of this chromosome was inherited as a linkage block. Three linkage groups, D, F, and G contained large linkage blocks inherited intact during the independent development of 4, 5 and 5 cultivars, respectively. Linkage group G also contained a region where multiple cultivars showed recombination events in the same 1 cM interval.

This retrospective analysis of recombination during soybean cultivar development has begun the process of identifying potentially favorable combinations of alleles located on the same linkage group (linkage blocks) as well as regions where favorable combinations of alleles may not yet have been fixed by breeders (multiple recombination events). Alternatively, the linkage blocks and the regions with multiple recombination events that were identified could be genomic regions under cross-specific genetic control that enhances or suppresses recombination, irrespective of the allelic combinations which are present. Ultimately, it will be necessary to know the chromosomal locations of many more agronomically important genes in order to distinguish between recombination events under the influence of breeder selections and recombination events under genetic control.

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