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Towards an integrated linkage map of common bean. 4. Development of a core linkage map and alignment of RFLP maps

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Abstract Three RFLP maps, as well as several RAPD maps have been developed in common bean (*Phaseolus vulgaris* L.). In order to align these maps, a core linkage map was established in the recombinant inbred population BAT93 × Jalo EEP558 (BJ). This map has a total length of 1226 cM and comprises 563 markers, including some 120 RFLP and 430 RAPD markers, in addition to a few isozyme and phenotypic marker loci. Among the RFLPs mapped were markers from the University of California, Davis (established in the F_2 of the BJ cross), University of Paris-Orsay, and University of Florida maps. These shared markers allowed us to establish a correspondence between the linkage groups of these three RFLP linkage maps. In total, the general map location (i.e., the linkage group membership and approximate location within linkage groups) has been determined for some 1070 markers. Approaches to align this core map with other current or future maps are discussed.

Key words *Phaseolus vulgaris* L. · Core linkage map · RFLPs · RAPDs

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Introduction

Molecular markers have been used to tag genes of economic importance in many crop species. In common bean, for instance, these include (1) major genes for resistance to anthracnose (Adam-Blondon et al. 1994a, b; Young and Kelly 1997), bean common mosaic virus (Haley et al. 1994; Melotto et al. 1996; Johnson et al. 1997), common bacterial blight (Jung et al. 1997), rust (Miklas et al. 1993; Haley et al. 1993; Jung et al. 1996), and (Nodari et al. 1993a, b and (2) genes for morphological traits, many of them associated with the domestication syndrome (Koinange et al. 1996) and some already mapped in the classical linkage map of the common bean (Bassett 1991). Molecular markers have also been used to tag quantitative trait loci (QTLs) for resistance to common bacterial blight (Nodari et al. 1993b; Jung et al. 1996, 1997; Yu et al. 1998), bean golden mosaic virus (Urrea et al. 1996), and tolerance to drought stress (Schneider et al. 1997).

Molecular marker-based linkage maps in plant species have also been used to study genome evolution and the extent of synteny between related taxa (Ahn and Tanksley 1993; Paterson 1995; Boutin et al. 1995). In addition, linkage maps such as those of tomato, rice, and maize have been used to isolate genes of agronomic interest by map-based cloning (e.g., Martin et al. 1993;

Jones et al. 1994; Song et al. 1995; Doebley et al. 1997). These projects have been facilitated by the construction of high-density linkage maps in a single mapping population, by the joining of several linkage maps established in different populations, or a combination of both approaches as has been done in other plant species (Hauge et al. 1993; Lefebvre et al. 1995; Concibido et al. 1996; Qi et al. 1996; Wordragen et al. 1996).

Common bean (*Phaseolus vulgaris* L.; 2n = 2x = 22) is one the legume species with the smallest genomes (0.65 pg/haploid genome: Aramuganathan and Earle 1991). In recent years, several restriction fragment length polymorphism (RFLP)- and random amplified polymorphic DNA (RAPD)-based linkage maps have been published for common bean. RFLP-containing maps include those of the University of California, Davis (Nodari et al. 1993a; Gepts et al. 1993), the University of Florida (Vallejos et al. 1992; Boutin et al. 1995; Yu et al. 1998), and the University of Paris-Orsay (Adam-Blondon et al. 1994b) maps (henceforth, Davis, Florida, and Paris maps). The first two are based primarily on RFLPs revealed by probes from different *Pst*I and *Eco*RI-*Bam*HI genomic libraries, while the latter is based mainly on RAPD markers but also contains RFLP markers. RAPD maps include those reported by Jung et al. (1996, 1997) and Skroch et al. (1996). Altogether, the RFLP-based maps include 645 loci distributed along the estimated 1200 cM of the bean genome. If the RFLP maps could be joined, they would yield a map with an average of 1 marker every 2 cM. An even higher density could be achieved by incorporating the RAPD markers.

In the work reported here, we have established a linkage map in a recombinant inbred population (RI population) derived from the F_2 population in which the original Davis map was obtained. In addition to a subset of the RFLP markers mapped in the F_2, over 490 RAPD markers have also been mapped in this RI population. We have established the correspondence and co-linear orientation among linkage groups of the three common bean linkage maps containing RFLPs. This was achieved by reciprocal mapping of a sample of Davis and Paris clones in the Paris and Davis maps, respectively, and mapping of a sample of Florida clones on the Davis map. Thus, we have determined the general map location (i.e., the linkage group membership and approximate location within linkage groups) of some 470 RFLP and 570 RAPD markers in common bean, and some 40 biochemical and/or morphological markers.

Materials and methods

Pre-existing linkage maps

Davis map

An F_2 generation of cross BAT93 × Jalo EEP558 was used as the mapping population for this map. *Eco*RI-*Bam*HI (clones numbered from D001 and D999) and *Pst*I (clones numbered from D1001 to D1862) genomic libraries were used as source of probes. This map consists of 194 RFLP marker loci, 20 of which were detected with Paris clones (clones labeled with P followed by a number, see below) (Nodari et al. 1992, 1993a).

Florida map

A backcross BC_1 (XR-235-1-1 × (XR-235-1-1 × Calima) was used as the mapping population. A *Pst*I library of size-selected genomic fragments was used as the source of probes. This map comprises 229 RFLP marker loci (Bng's), nine isozyme loci, nine seed protein loci, two RAPD marker loci, and one pigementation locus distributed among 11 linkage groups (A through K, Fig. 1) (Chase et al. 1991; Vallejos et al. 1992; Vallejos 1994).

Paris map

A backcross BC_1 (Ms8EO2 × Corel) was used as the mapping population. Probes were derived from an *Mbo*I bean genomic library (clones P1000 to P3050). This map comprises 51 RFLP marker loci, 11 of which were detected with *Pst*I clones developed at the University of California, Davis (see above). It also includes 100 RAPDs two sequence-characterized amplified regions (SCARs), and four morphological markers (Adam-Blondon et al. 1994b).

Construction of the core linkage map

Plant material

A recombinant inbred (RI) population of 75 lines was used as the mapping population for the core map. This RI population was derived from the BAT93 × Jalo EEP558 F_2 population used for the construction of the original Davis map, and was carried to the F_8 by single-seed descent. A randomly chosen subset of 72 lines was used for mapping RAPDs in Wisconsin.

Probes for RFLP analysis

A subset of 57 Davis genomic clones (D0000) and other markers separated by approximately 20 cM on the F_2 linkage map, 2 genomic clones from the Paris library (P0000), and 25 genomic clones from the Florida library (BNG000) were used for RFLP analysis. Southern hybridizations were performed according to the protocol of the Zetabind membrane manufacturer (AMF-CUNO) except that hybridizations were performed at 60°C using a 3 : 1 (v/v) solution of 10% SDS and 20 × SSPE. Sonicated salmon sperm DNA was added directly to each of the probes before denaturation by boiling. In addition to the random genomic clones from the three libraries, the clones of 16 biochemically characterized proteins were also used as probes. These clones included a cellulase (*Cel*; Tucker and Milligan 1991), chalcone isomerase (*ChI*; Mehdy and Lamb 1987), chalcone synthase (*ChS*; Ryder et al. 1987), chitinase (*Ch*; Hedrick et al. 1988), cinnamyl-alcohol dehydrogenase (*Cad*; Walter et al. 1988), a glycine-rich protein (*Grp1.8*; Keller et al. 1988), a heat-shock protein (*Hsp70*; Vidal et al. 1993), lipoxygenase (*Lox*; Meier et al. 1993), a hydroxyproline-rich glycoprotein (*Hrgp36*; Corbin et al. 1987), two pathogenesis-related proteins (*PvPR-1* and *PvPR-2*; Walter et al. 1990), two pectinesterases (*VPe-2* and *VPe-3*; Ebbelaar et al. 1996), a peroxidase (*Per*; M. Dron, unpublished results), a polygalacturonase-inhibiting protein (*Pgip*; Toubart et al. 1992), and a uricase (*Uri-3*; F. Sanchez, personal communication).

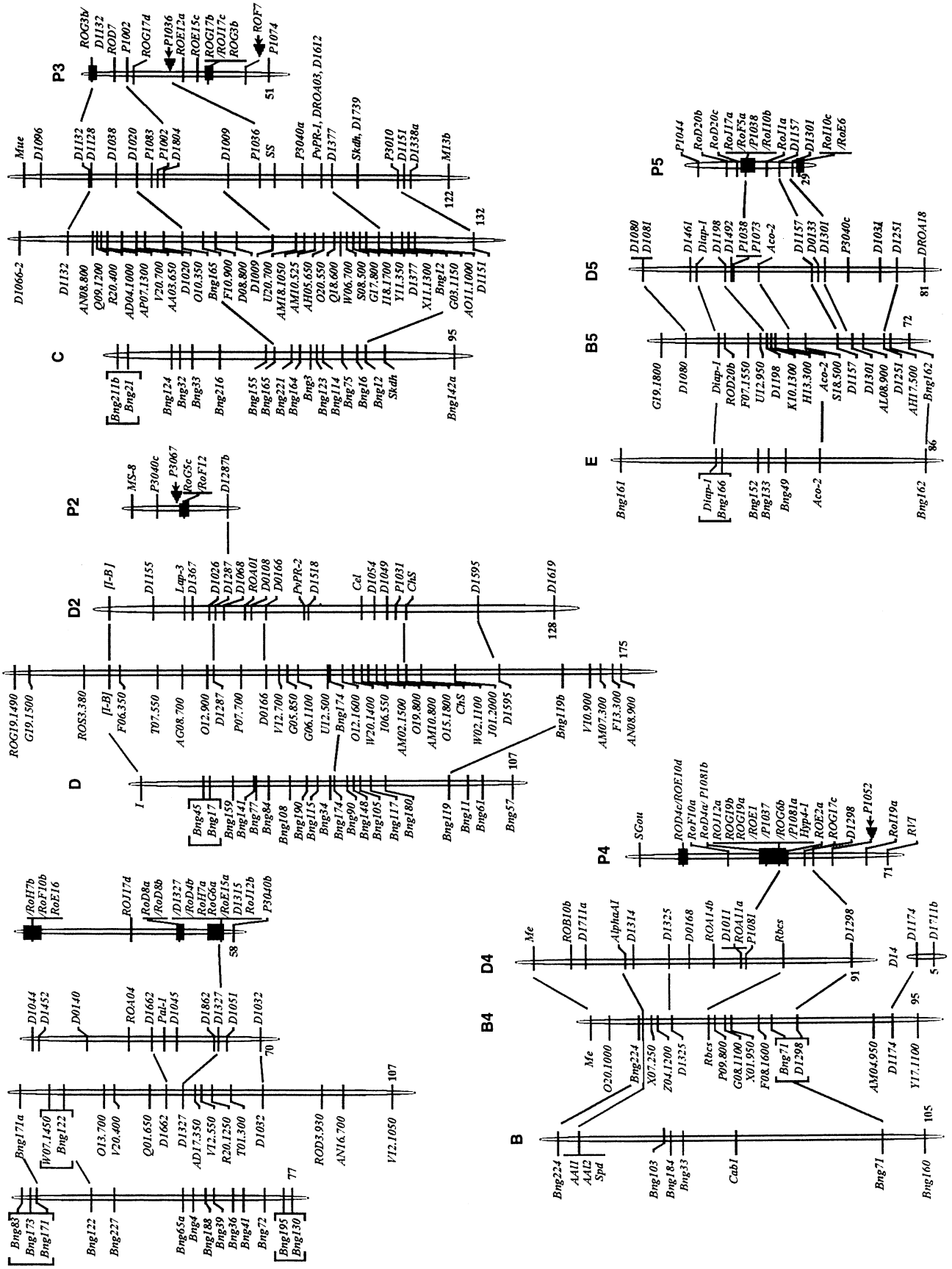
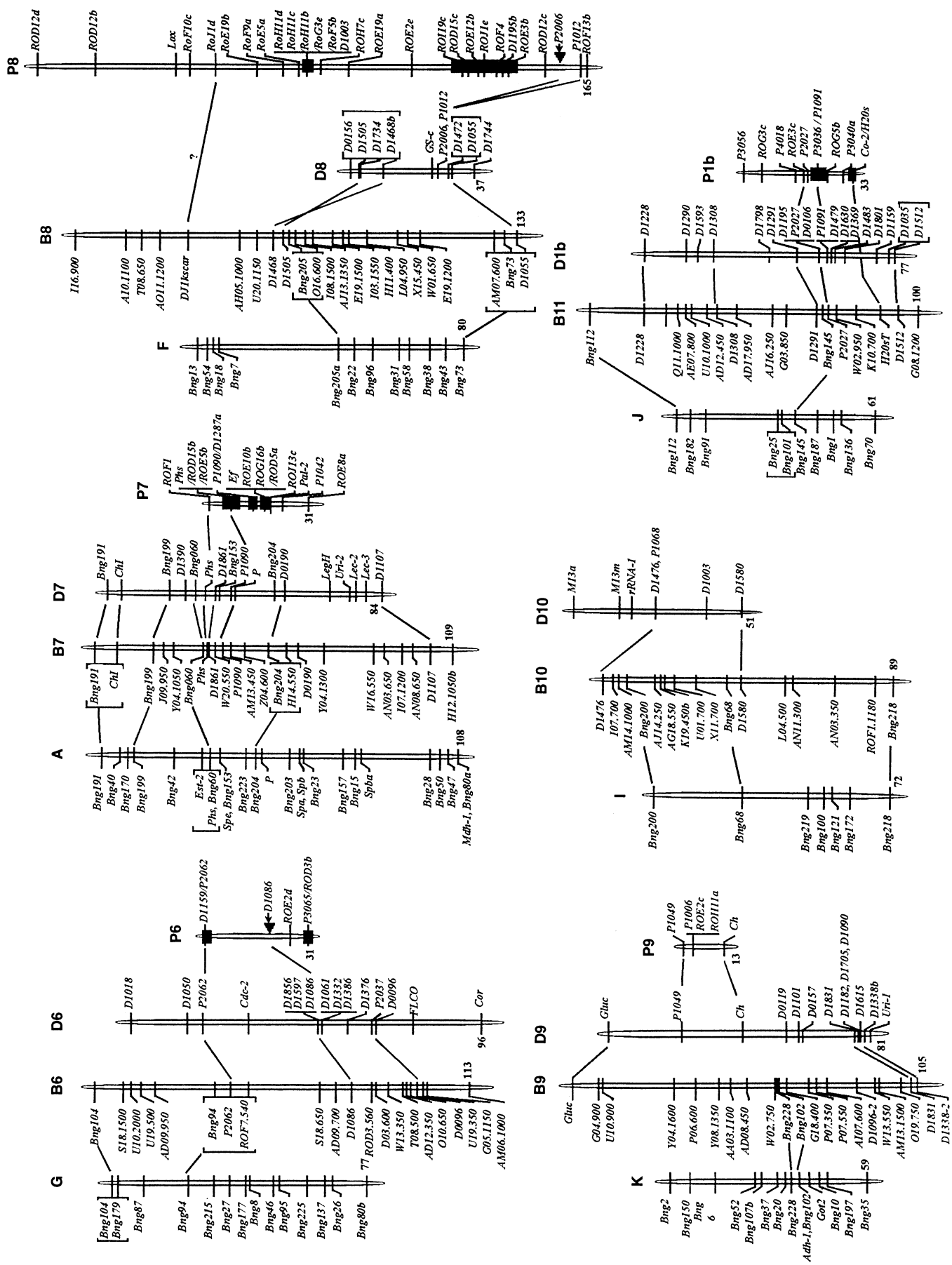


Fig. 1 See page 851 for legend


P8
B8
D8
F
B11
D1b
P1b
J
P7
A
B7
D7
P6
D6
B6
G
D10
B10
I
P9
D9
B9
K

RAPD markers

Using random primers from Operon Technologies (Alameda, Calif.), we mapped 489 RAPD marker loci in the RI population. Data for 60 of these markers were obtained at Davis and for the other 429 at Wisconsin. At Davis, the RAPDs were amplified in a 96-well Twinblock thermocycler (Ericomp) programmed for 1 cycle of 2 min at 94°C; 3 cycles of 1 min at 94°C, 1 min at 35°C and 2 min at 72°C; 32 cycles of 10 s at 94°C, 30 s at 35°C, and 1 min at 72°C; followed by a 5-min extension at 72°C. Polymerase chain reaction (PCR) amplifications were conducted in a 25-µl reaction volume containing 50 m*M* KCl, 10 m*M* TRIS-HCl, 0.1% Triton X-100, pH 9.0, 2 m*M* $MgCl_2$, 100 µ*M* dNTPs, 0.4 µ*M* primer, 20 ng total genomic DNA, and 1 U *Taq* DNA polymerase. Amplification products were separated on 1.5% agarose gels in 1 × TAE buffer (0.04 *M* TRIS-acetate, 0.001 *M* EDTA). Loci corresponding to clear and segregating bands for each primer were named as follows: R(APD)O(peron) followed by the primer serial name, a period, and the size of the band in basepairs (bp): e.g., *ROS3.380*. Amplification of RAPD markers at Wisconsin was accomplished with either an Idaho Technology Air Thermal Cycler under conditions described by Skroch and Nienhuis (1995) or an MJ Research PTC-100 thermal cycler as described by Johns et al. (1997). RAPD marker loci were named as above.

Sequence-characterized-amplified regions, SCARs

The segregation of four SCARs was monitored in the RI family. These SCARs were developed by the Paris group and were derived from bands produced by Operon primers F3, J1, and H20 (Adam-Blondon 1994; Adam-Blondon et al. 1994a). Cycling conditions were 1 cycle of 2 min at 94°C; 40 cycles of 1 min at 94°C, 1 min at 60°C, and 2 min at 72°C; followed by 5 min at 72°C. For F3, only 30 cycles of amplification were used, and for J1k and H20 the annealing temperature was raised to 65°C. Products from amplification with the H20 SCAR were digested with *Taq*I in order to detect polymorphism.

Allozymes and agronomic markers

Isozyme analyses were conducted as described before (Singh et al. 1991). Five loci were mapped: aconitase (*Aco-2*), diaphorase (*Diap-1*), malic enzyme (*Me*), rubisco small subunit (*Rbcs*), and shikimate dehydrogenase (*Skdh*). Evaluation of resistance to Bean Common Mosaic Virus (BCMV) conditioned by the *I* gene was performed as described by Nodari et al. (1993a) for the core map and by Zimmerman and Vallejos (1992) for the Florida map.

Segregation and linkage analyses

Goodness-of-fit tests for 1:1 segregation ratios and independence tests were performed on a random subset of 599 markers in a Microsoft Excel spreadsheet on a PC-compatible computer. The linkage map for the BAT93 × Jalo EEP558 RI population was constructed using the Macintosh version of MAPMAKER 2.0 (Lander et al. 1987). Initially, pairwise LOD scores were used to select a small number of markers (up to 6) that could be ordered (tested using the 'COMPARE' command) with a LOD score difference between the most probable and the second most probable order of at least 3.0. Additional markers were added using the 'TRY' command. All markers were included that could be placed with a LOD difference greater than 2.0 between the most likely and second most likely interval for that marker. Map distances were expressed in Kosambi (1944) units.

Markers were placed in an order based on the precision of marker placement and whether the marker was used for mapping in more than one population. Thus, markers that could be placed with the greatest statistical precision were placed first. However, markers that had been mapped in more than one population were given priority for mapping. All RFLP markers that were used in more than one population were placed on this core map.

Results

The strategy to develop a coordinated linkage map of common bean relied on two approaches. First, we developed a linkage map in a recombinant inbred population derived from the F_2 population in which the original Davis linkage map (Nodari et al. 1993a) had been established. This was accomplished by mapping a sample of the RFLP markers already mapped in the F_2 generation and adding RAPD markers to this map to increase its saturation. Second, clones from the Paris and Florida maps were mapped in the F_2 or RI populations of BAT93 × Jalo EEP558 or in the Paris BC population. For most linkage groups, at least 2 common markers were analyzed to determine the relative orientation of the linkage groups in the respective maps.

Development of a linkage map in the BAT93 × Jalo EEP558 recombinant inbred population

A linkage map had already been established in the F_2 generation of the BAT93 × Jalo EEP558 cross (Nodari et al. 1993a). Forty-five anonymous RFLP markers previously mapped in this F_2 population were mapped in the BAT93 × Jalo EEP558 RI population and used to align linkage groups between the F_2 and RI maps. Additional loci included 31 RFLP markers for genes of known function, 7 and 36 anonymous RFLP markers from the Paris and Florida maps, respectively, a total of 489 RAPDs (429 from Wisconsin and 60 from Davis), and 12 other markers (four SCARs, seven seed proteins and isozymes, and one disease resistance gene, *I*). Hence, the segregation of a total of 620 marker loci was assayed in the RI population.

Fig. 1 Alignment of RFLP-containing linkage maps of common bean. For each of the 11 linkage groups, four maps are presented, from *left to right*, the Florida map (Vallejos et al. 1992), the core map (current work), the Davis map (Nodari et al. 1993a; Gepts et al. 1993), and the Paris map (Adam-Blondon et al. 1994b). For the core map, only the framework markers are shown. For the other maps, all markers are shown as originally published, except for the Florida map where only one representative marker is shown. Groups of markers that are *bracketed* on the Florida and core maps or near *thicker bars* on the Paris map are sets of markers that were not ordered with LOD > 2.0. *Lines* unite shared markers between the different maps. *Numbers* at the *bottom* of each linkage group indicate the cumulative mapping distance in Kosambi centiMorgans for that linkage group. For explanations on symbols, see Materials and methods and the original references (Vallejos et al. 1992; Gepts et al. 1993; Adam-Blondon et al. 1994b)

Table 1 Transmission of alleles in recombinant inbred population BAT93 × Jalo EEP558 depending on parental origin and marker type

	Linkage group											
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	Total
Jalo EEP558 vs. BAT93												
Jalo EEP558 allele	674	590	1041	295	609	522	418	520	410	302	768	6327
BAT93 allele	397	777	788	388	557	602	581	559	418	373	714	6299
χ^2 (1:1)	71.64[a]	25.58	35.00	3.58	2.32	5.69	26.6	1.41	0.08	7.47	1.97	0.06
Allele in excess	J[b]	B	J	–	–	B	B	–	–	B	–	–
RFLP vs. RAPD[c]												
χ^2 (1:1)	15.25[a]	4.27	8.89	0.16	4.93	1.16	0.69	0.61	2.64	0.13	0.03	0.22
Distorted marker class	RFLP	RFLP	RFLP	–	RFLP	–	–	–	–	–	–	–

[a] χ^2 ($P = 0.05$; $1df$) = 3.84
[b] B, BAT93; J, Jalo EEP558
[c] Analyses for RAPDs conducted on 48 randomly chosen lines

There was no preferential transmission of maternal and paternal alleles when considering all loci in the aggregate as a nearly equal number of BAT93 and Jalo EEP558 alleles were counted in the RI population ($\chi^2 = 0.22$; Table 1). Nevertheless, 105 of 599 marker loci (18%) showed a distorted segregation as determined by goodness-of-fit test for a 1:1 ratio at $P = 0.05$. Fifty-six loci showed an excess of Jalo EEP558 alleles, whereas 49 loci showed an excess of BAT93 alleles. Jalo EEP558 alleles were preferentially transmitted on linkage groups B1 and B3 (Table 1). On linkage group B1, the locus with the highest distortion level favoring the Jalo EEP558 allele was *D1662* ($P < 0.001$), whereas neighboring loci such as *D1327* showed only a significant distortion ($P < 0.05$). On linkage group B3, no loci showed distortion levels above $P = 0.05$. BAT93 alleles were preferentially transmitted on linkage groups B2, B6, B7, and B10 (Table 1). On linkage group B2, a region encompassing loci *U12.500* and *O12.1600* showed highly significant distortion ($P < 0.01$) favoring the BAT93 allele. On linkage groups B6 and B7, loci *AM06.1000* and *D1107*, respectively, showed a very highly significant distortion ($P < 0.001$) towards the BAT93 allele. On linkage group B10, none of the individual loci showed a significant distortion.

A comparison of transmission of RFLP and RAPD markers revealed that in 4 linkage groups RFLP markers as a category showed distorted segregation. In no case did RAPDs as a marker class show distortion, although individual RAPD markers did show distorted segregation. One possible explanation for this increased segregation distortion observed for RFLPs compared to RAPDs is that the RFLP probes were selected because they represent single-copy sequences (Nodari et al. 1992; Vallejos et al. 1992). Hence, they could represent, or be tightly linked to, expressed genes which would be subject to viability and fertility selection during the generation advance until the F_8.

The resulting map consists of 563 markers, 240 of which are placed unequivocally as framework markers (Fig. 1) and 323 are placed in intervals (see links to individual linkage group maps in http://agronomy.ucdavis.edu/gepts/geptslab2.htm). Fifty-seven markers remain unassigned to a linkage group. Eleven linkage groups were identified that are shared among the Davis, Florida, and Paris maps (Table 2). Linkage group D1 originally identified by Nodari et al. (1993a) has been split into two linkage groups, B1 and B11, in the interval marked by loci *D1032* and *D1228*. Nodari et al. (1993a) had joined these 2 linkage groups based on a LOD score larger than 3.0 in this interval although the map distance was approximately 40 cM. Data from the BAT93 × Jalo EEP558 RI population, as well as from the alignment with other maps (see below), did not confirm this linkage. Linkage group D14, identified in the F_2 generation of the BAT93 × Jalo EEP558 cross, has been attached to linkage group B4 through the mapping of RAPD marker *AM04.950* (Fig. 1). Linkage groups D11 and D15 remain unattached to the larger, core linkage groups. The length of the core map is around 1226 cM, which is an increase of approximately 275 cM with respect to the map in the F_2. This increase in map length can be attributed to map expansion due to a higher marker density, to additional coverage of the genome provided by newly mapped markers (linkage groups B1, B2, B8, and B10), and to the joining of linkage groups (D4 with D14). The current map length corresponds closely to the predicted map length for the BJ population (Gepts et al. 1993).

Alignment of the Davis, Paris, and Florida maps

A total of 20 RFLP markers were analyzed jointly between the Davis F_2 and the Paris BC segregating populations. Twenty RFLP probes from Paris were mapped in the Davis F_2 population, 11 probes from Davis were mapped in the Paris BC population, and

Table 2 Correspondence among linkage groups of common bean RFLP maps and the classical map

Core (RI population) (present work)	Davis (F_2) (Nodari et al. 1993a)	Florida (F_2) (Vallejos et al. 1992)	Paris (BC) (Adam-Blondon et al. 1994)	Classical map (various populations) (Bassett 1991)
B1	D1[a]	H	P1	IV
B2	D2	D	P2	III, VI
B3	D3	C	P3	
B4	D4	B	P4	XII
B5	D5	E	P5	
B6	D6	G	P6	
B7	D7	A	P7	X, XIII
B8	D8	F	P8	
B9	D9	K	P9	
B10	D10	I		
B11		J	P12	
			P10	
	D11[b]		P11	
	D12-D15[b–d]			

[a] Linkage group D1 has been split into linkage groups B1 and B11
[b] Linkage groups D11 and D15 remain unlinked
[c] Linkage groups D12 and D13 have been attached to linkage groups B6 and B7, respectively (Gepts et al. 1993)
[d] Linkage group D14 has been attached to linkage group B4 (present work)

two cDNA probes of clones of known function were mapped in both populations. Based on these markers, we were able to align 10 of 11 linkage groups (Table 2). With the exception of linkage group pairs D2 and P2 and B11 and P12, which have only 1 common marker, and linkage groups D8 and P8 where two Paris probes map on the same locus in the Davis map, we were also able to co-orient the linkage groups. The Paris map has 1 additional linkage group (P10) with few markers for which no correspondence has as yet been established with the Davis linkage groups.

The segregation of 36 RFLP loci from the Florida map was assayed in the BAT93 × Jalo EEP558 RI population. One marker (*Bng70*) remained unlinked, and the segregation data of the other 35 markers were combined with those of previously shared markers including *I* (on Davis linkage group D2 and Florida linkage group D), *Skdh* (D3 and C), *αAI* (D4 and B), *Diap-1* and *Aco-2* (D5 and E), and *Phs* and *P* (D7 and A). The 42 shared markers (RFLPs, allozymes, seed proteins and the disease resistance gene *I*) between the Davis and Florida maps allowed us to align all linkage groups (Fig. 1). With the exception of linkage group B9, all linkage groups could also be oriented with respect to each other. On linkage group B9, the 2 markers assayed – *Bng102* and *Bng228* – were mapped at a LOD threshold greater than 2.0 in both the core map and the Florida map. However, their close linkage suggests caution in the determination of the respective orientation of the linkage groups. Mapping of some Florida clones allowed us to map traits that had been mapped in other populations. Thus, markers *Bng171*, *Bng173*, and *Bng122*, which mapped on linkage group B1, are linked to a gene conferring partial resistance to the cyst nematode in soybean (SCN) (Concibido et al. 1996; Danesh et al. 1998). Whether a nematode resistance gene also maps to this region in common bean constitutes an interesting comparative mapping experiment that remains to be performed. Markers *Bng102* and *Bng228*, located on linkage group B9, are linked to the nuclear male fetility restorer gene *Fr* of common bean (He et al. 1995).

Discussion

Development of the core map and alignment of maps

One of our goals in using a recombinant inbred population to establish a map was to provide a permanent segregating population in which segregation data can be accumulated. The BAT93 × Jalo EEP558 population is an ideal population for this purpose. The two parents exhibit a high level of polymorphism. Hybridization with over 80% of the *Pst*I random genomic clones showed polymorphism after digestion of parental genomic DNA with at least one of three restriction enzymes (*Eco*RI, *Eco*RV, and *Hin*dIII) (Nodari et al. 1992). Such a high level of polymorphism ensures that additional clones will be easily mapped in this population in the future. This population also segregates for the interaction between the common bean host and several microrganisms, including a viral pathogen (BCMV, bean common mosaic virus), a bacterial pathogen (*Xanthomonas campestris*, agent of common bacterial blight), fungal pathogens (*Uromyces phaseoli*, agent of rust; *Phaeoisariopsis griseola*, agent of angular leafspot; and *Colletotrichum lindemuthianum*, agent of anthracnose), and *Rhizobium* symbionts (Nodari et al. 1992, 1993b).

Comparative mapping depends on the ability to detect and map unique sequences. Most RFLP probes used here are single-copy number probes (Nodari et al. 1992; Vallejos et al. 1992). Occasionally these probes will recognize low-copy number multigene families. These families can cluster to the same complex locus as shown by the mapping of the phaseolin multigene family (*Phs*) on linkage group B7. Alternatively, these multigene families can be dispersed in the genome. When different members of multigene families are scored, this may result in discrepancies in location between different maps, as illustrated, among other examples, by the lectin (*Lec*) family, which maps on linkage groups B4 and B7, and the phenylalanine ammonialyase (*Pal*), which maps on linkage groups B1 and B7. Such discrepancies obviously cast a note of caution on comparative mapping experiments.

The fact that RFLP linkage maps constructed with diverse genotypes, including both Andean and Mesoamerican representatives, can be easily aligned demonstrates that no major rearrangements have occurred in the common bean genome. This observation is in agreement with that made by Skroch et al. (1996) which is based on a comparison of RAPD marker-based maps of the common bean. The extensive colinearity observed among RFLP maps of common bean (present results), between common bean and mungbean (Boutin et al. 1995), and between mungbean and cowpea (Fatokun et al. 1992) suggests extensive synteny within the Phaseolinae subtribe of the Phaseoleae tribe. This synteny, however, does not extend to the same level to other members of the Phaseoleae such as soybean. However, smaller syntenic intervals between Phaseolinae species, on one hand, and soybean on the other, more distantly related legumes may still be of interest, particularly if they include genes of agronomic interest. The lower levels of synteny observed in legumes compared to grasses does not appear to be related to differences in the relative age of divergence within these families (Crepet and Feldman 1991; Herendeen et al. 1992; Herendeen and Crane 1995).

Integrations with other RAPD maps have been initiated. Skroch et al. (1996) described a strategy and preliminary results for using the RAPD map constructed in the BAT93 × Jalo EEP558 RI population to align the RAPD maps of Jung et al. (1996, 1997). Hence, the RFLP maps described here could also be aligned with these other RAPD maps. Alignments with other maps could be established using PCR-based markers. SCAR markers have been located on linkage groups 2 (near *I*, Melotto et al. 1996), 6 (near *bc-3*, Johnson et al. 1997), 8 and 10 (*Jlks* and *Jlds*, respectively; Adam-Blondon 1994), and 11 (*H20s* and *F3s*, Adam-Blondon et al. 1994a). In addition, clones with known sequences have been mapped on linkage groups 1 (*Pal-1*), 2 (*PvPR-2*, *PGIP*, *Cel*, *ChS* and *ChS-2*, *Vpe-2*, and *Uri-3*), 3 (*PGRP1.8-3*, *PvPR-1*, and *SS*), 4 (*Lec-Arl-αAI*, *Hrgp4-1*, and *Cab-1*), 5 (*Lox-1*), 6 (*Hsp70*, *Cdc-2*), 7 (*ChI*, *Ef*, *Lec-2* and *Lec-3*, *LegH*, *Per*, *Phs*, *Uri-2*), 8 (*GS-c* and *Lox-2*), 9 (*Gluc*, *Ch*, *Cad*), and 10 (*Vpe-3*) as shown in Fig. 2. Based on published sequences for these genes, PCR primers can be designed so that polymorphisms between parents of the different mapping populations can be detected, either directly or after restriction digestion.

Utilization of aligned linkage maps

One of the primary uses of our aligned RFLP maps is to provide increased marker density in selected genomic regions. Such increases in marker density can be used to identify closely linked polymorphic markers for indirect selection or for map-based cloning. We have used this approach to increase the density of markers around the phaseolin locus (*Phs*) on linkage group D7. Originally, only 5 markers were identified around this locus (Nodari et al. 1993a) with an average map distance of 11 cM per interval. By analyzing the segregation of Florida (Bng) markers and 1 Paris marker mapping to this same region, we were able to increase the density to 3 cM per interval. In particular, we were able to physically link 2 markers (*D1861* and *Bng060*) to the *Phs* locus on a 1.9-Mb *Not*I restriction fragment (Llaca and Gepts 1996). Recent comparative mapping among common bean, mungbean, and soybean (Boutin et al. 1995) and between mungbean and cowpea (Fatokun et al. 1992) provides additional opportunities to increase the density of markers in the *Phs* region. For example, linkage group B7 corresponds to linkage group 4 of the mung bean map, and the phaseolin region may map to linkage group O of soybean (Boutin et al. 1995).

In conclusion, our map alignment efforts have allowed us to determine the approximate, relative location of over 1060 markers, corresponding to approximately 190 RFLP markers on the Davis F_2 map, 489 RAPD markers on the core map, 240 markers on the Florida map, and 160 markers on the Paris map. Using the maps published here and on the Davis web site (http://agronomy.ucdavis.edu/gepts/mapdata 2.htm), geneticists and breeders can choose a set of markers for their region of interest and determine a more precise order of markers for that region in their own mapping populations.

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