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**J.M. Lee · D. Grant · C.E. Vallejos · R.C. Shoemaker**

# Genome organization in dicots. II. Arabidopsis as a 'bridging species' to resolve genome evolution events among legumes

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**Abstract** Analysis of molecular linkage groups within the soybean (*Glycine max* L. Merr.) genome reveals many homologous regions, reflecting the ancient polyploidy of soybean. The fragmented arrangement of the duplicated regions suggests that extensive rearrangements, as well as additional duplications, have occurred since the initial polyploidization event. In this study we used comparisons between homoeologous regions in soybean, and the homologous regions in the related diploids *Phaseolus vulgaris* and *Vigna radiata*, to elucidate the evolutionary history of the three legume genomes. Our results show that there is not only conservation of large regions of the genomes but that these conserved linkage blocks are also represented twice in the soybean genome. To gain a better understanding of the process of genome evolution in dicots, molecular comparisons have been extended to another well-studied species, *Arabidopsis thaliana*. Interestingly, the conserved regions we identified in the legume species are also relatively conserved in Arabidopsis. Our results suggest that there is conservation of blocks of DNA between species as distantly related as legumes and brassicas, representing 90 million years of divergence. We also present evidence for an additional, presumably earlier, genome duplication in soybean. These duplicated regions were only recognized by using Arabidopsis as a 'bridging' species in the genome comparisons.

**Keywords** Soybean · Arabidopsis · *Phaseolus* · *Vigna* · Evolution · Paleopolyploid · Genome duplication

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J.M. Lee · D. Grant · R.C. Shoemaker (✉)
Department of Agronomy, Iowa State University, Ames, IA 50011, USA
e-mail: rcsshoe@iastate.edu
Tel.: +1-515-294-6233, Fax: +1-515-294-2299

D. Grant · R.C. Shoemaker
USDA-ARS Corn Insect and Crop Genetics Research Group, Iowa State University, Ames IA 50011, USA

C. Eduardo Vallejos
Horticultural Science Department and Plant Molecular and Cellular Biology Program, University of Florida, Gainesville, FL 32611, USA

*Present address:*
J.M. Lee, Center for Genomics and Bioinformatics, Karolinska Institutet, S17177 Stockholm, Sweden

## Introduction

The dynamic nature of plant genomes has made them an area of intense investigation. Recent research in plant genetics has revealed a great deal about genome duplications and polyploidization. Although relatively few stable polyploids exist in nature, both allo- and autopolyploidization events appear to have been common during the evolution of the plant kingdom (Lewis 1980). There appears to be a natural tendency for polyploid genomes to revert to a diploid state following polyploidization, a phenomenon termed diploidization (Stebbins 1966). Diploidization occurs at both the chromosomal and genic levels. In allopolyploids, genes such as *Ph1* in wheat have been identified which prevent the pairing of homoeologues during meiosis. This effectively allows the independent evolution of the genomes which contribute to diploidization (Riley and Chapman 1958; Gill et al. 1993). At the chromosomal level processes such as inversions and translocations convert the homoeologues into unique chromosomes, where only bivalents are formed at meiosis rather than potentially unstable quadrivalents. Interestingly, despite an often long history of such rearrangements, duplicate chromosomal regions resulting from ancient polyploidization events are still detectable in many plant species which seemingly behave as genetic diploids (Helentjaris et al. 1988; Whitkus et al. 1992; Shoemaker et al. 1996).

Selection may act during diploidization to keep certain complements of genes and/or DNA sequences together. Paterson et al. (1996) demonstrated that several segments of DNA ≤3 cM have remained co-linear in species separated by 130–200 million years of divergence.

These authors proposed that this might be the result of DNA being re-shuffled in relatively small conserved segments over long evolutionary periods. Evidence for the rearrangement of genomes by the movement of larger blocks of DNA has been shown in several lineages, including grasses (Moore et al. 1995) and brassicas (Kowalski et al. 1994; Lagercrantz 1998). The reason for DNA rearrangement in conserved blocks is unclear, although they may represent a genetic organization which confers a fitness advantage (Paterson et al. 1996).

Soybean has been suggested to be an ancient polyploid based on chromosome numbers (Lackey 1980; Bruneau et al. 1994), genome size (Arumuganathan and Earle 1991), and the identification of duplicate loci and homoeologous regions (Shoemaker et al. 1996). In addition, several pairs of genes with similar or identical function have been localized to chromosomal blocks which, based on common molecular markers, appear to be homoeologous (Zhu et al. 1994; Shoemaker et al. 1996). Surprisingly, we recently mapped a pair of duplicate function genes (*Pa*1 and *Pa*2) which condition appressed pubescence that do not fit this simple model of soybean genome evolution (Lee et al. 1999). The linkage groups containing these genes were investigated further in an attempt to determine if their organization and relationships could further elucidate the evolution of the soybean genome. This paper reports the results of our comparison of the genomic organization of soybean to that of two other legumes (*Phaseolus vulgaris* and *Vigna radiata*) and to the distantly related dicot *Arabidopsis thaliana*. The results of this study demonstrate the utility of using both closely and distantly related "bridging" species, with their independent evolutionary histories, in such studies.

## Material and methods

### Identification of homology and homoeology in legumes

Homologous and homoeologous regions within legumes were identified by comparing molecular genetic maps. Previously published maps for soybean (Cregan et al. 1999), *V. radiata* (Menancio-Hautea et al. 1993) and *P. vulgaris* (Vallejos et al. 2000) were used. Additional soybean RFLP probes were mapped in *P. vulgaris* during this study, using previously reported protocols (Vallejos et al. 1992).

### DNA sequencing

Plasmid DNA of RFLP clones was purified using the Wizard miniprep kit (Promega, Madison, Wisconsin). The sequence was generated from both ends of each genomic clone at the Iowa State University DNA Synthesis and Sequencing Facility (Ames, Iowa) using Universal Forward 21 M13 and Reverse M13-USB primers on an ABI 377 automated sequencer. Sequences were edited in Sequencher 3.1 where the 5′ vector sequence was trimmed off and the 3′ end was edited for quality. When an insert's end sequences overlapped, we combined them into a single contig and used that in the analysis.

### DNA sequence homology searches

The edited sequences were used for homology searches using BLAST programs (Altschul et al. 1990). Default parameter values were used for all homology searches. TBLASTX was used to compare DNA sequences from the RFLP probes which mapped to homologous legume linkage blocks to the *A. thaliana* DNA sequences contained in TAIR (http://arabidopsis.org) in June 2000. Only sequences with fewer than ten homologous sequences in *A. thaliana* and E values less than $10^{-5}$ were included in our analyses.

### Simulations

We used the algorithms reported by Grant et al. (2000) to test whether the intra- and inter-specific sequence-based synteny we detected was due to chance. At least 10,000 simulated genomes were analyzed in each test. Complete details of the simulations can be found at http://soybase.agron.iastate.edu/publication_data/Lee/synteny2.html.

## Results and discussion

Multiple homoeologous regions have been identified throughout the soybean genome (Shoemaker et al. 1996). In this report we focus on a subset which contained the duplicate-function genes *Pa*1 and *Pa*2. The most-parsimonious explanation for the presence of these two genes is that they are the result of the previously postulated whole-genome polyploidization event (Shoemaker et al. 1996). However, as shown in Fig. 1 A, while each gene is indeed located in one member of a pair of homoeologous regions, they are not in regions which are themselves obviously related (Lee et al. 1999). Additionally, two loci (*A162* and *A069*) stand out as being distant from their expected locations. While it is possible that these anomalous map locations reflect chromosomal rearrangements or duplication and insertion events after polyploidization, these results, in combination with the *Pa*1/*Pa*2 map locations, prompted us to study two different types of cross-species genomic comparisons to more-completely understand the evolutionary history of these chromosomes.

### Genome comparisons between legumes

The legumes *P. vulgaris* and *V. radiata* are closely related to each other and somewhat more distantly related to soybean (Boutin et al. 1995). Based on chromosome number (*P. vulgaris*: n=11; *V. radiata*: n=11; *G. max*: n=20) and a comparison of molecular maps, it has been suggested that soybean is an ancient tetraploid and that *P. vulgaris* and *V. radiata* are moresimilar to the ancestral diploid genome (Arumuganathan and Earle 1991; Boutin et al. 1995; Shoemaker et al. 1996). We have extended previous studies by using all available molecular loci to more completely delineate regions of homology between these legumes. Fig. 1B and C show the regions of synteny between soybean linkage groups B1 and H (burgundy loci) and the cognate linkage groups in *P. vulgaris* and *V. radiata*. These results are consistent with the model that the homoeologous chromosome blocks in soybean arose through an ancient whole-genome polyploidization event. We were not able to do a similar anal-

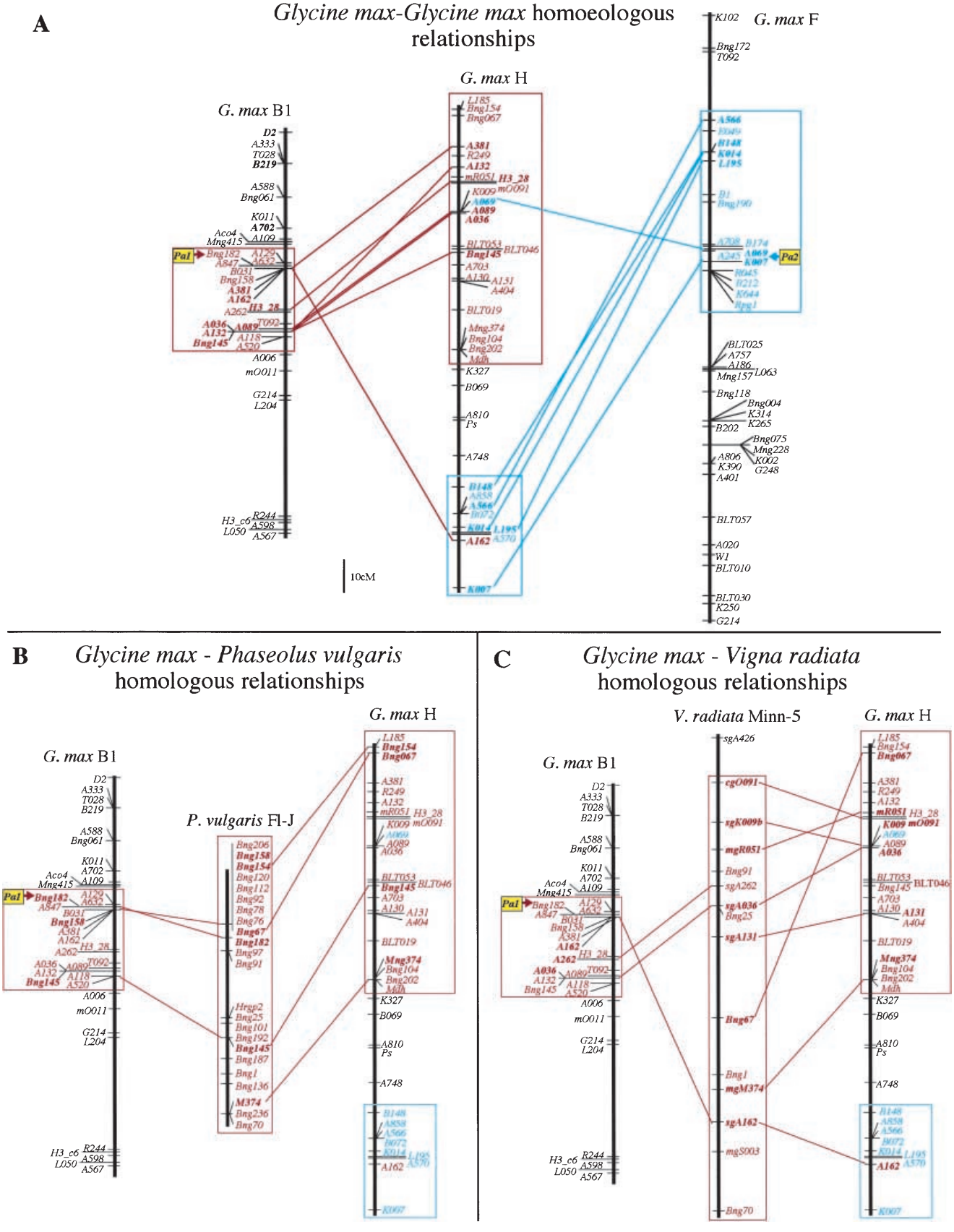



**Fig. 1A–C** Homologous and homoeologous relationships within legumes. **A** Homoeologous relationships within three linkage groups of *G. max*. **B** The corresponding homologous relationships between *G. max* and *P. vulgaris* and **C** *G. max* and *V. radiata* (the burgundy region). LG-F is shown in the inverted orientation compared to the one found in soybase (http://genome.cornell.edu/cgi-bin/WebAce/webace?db=soybase)

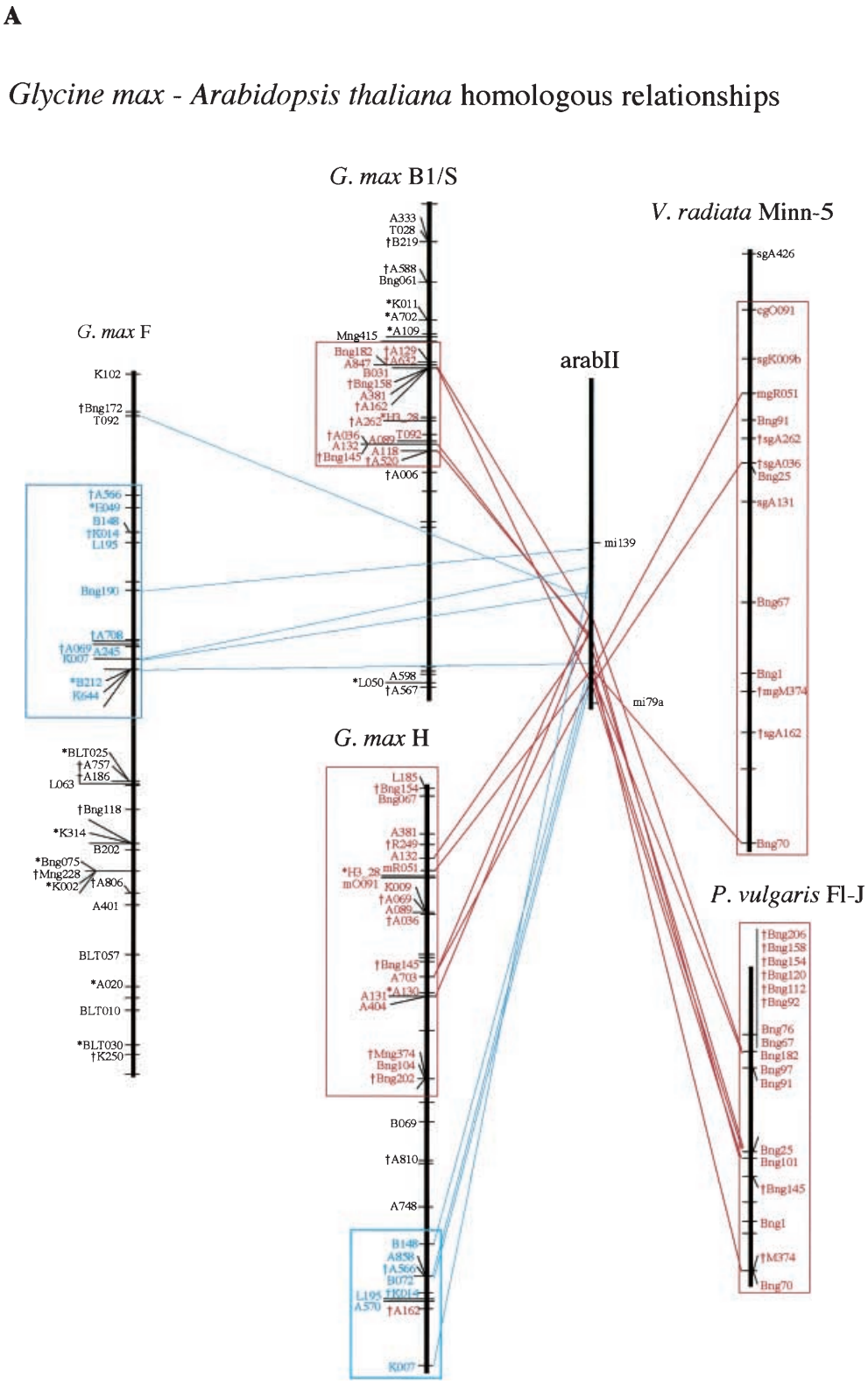
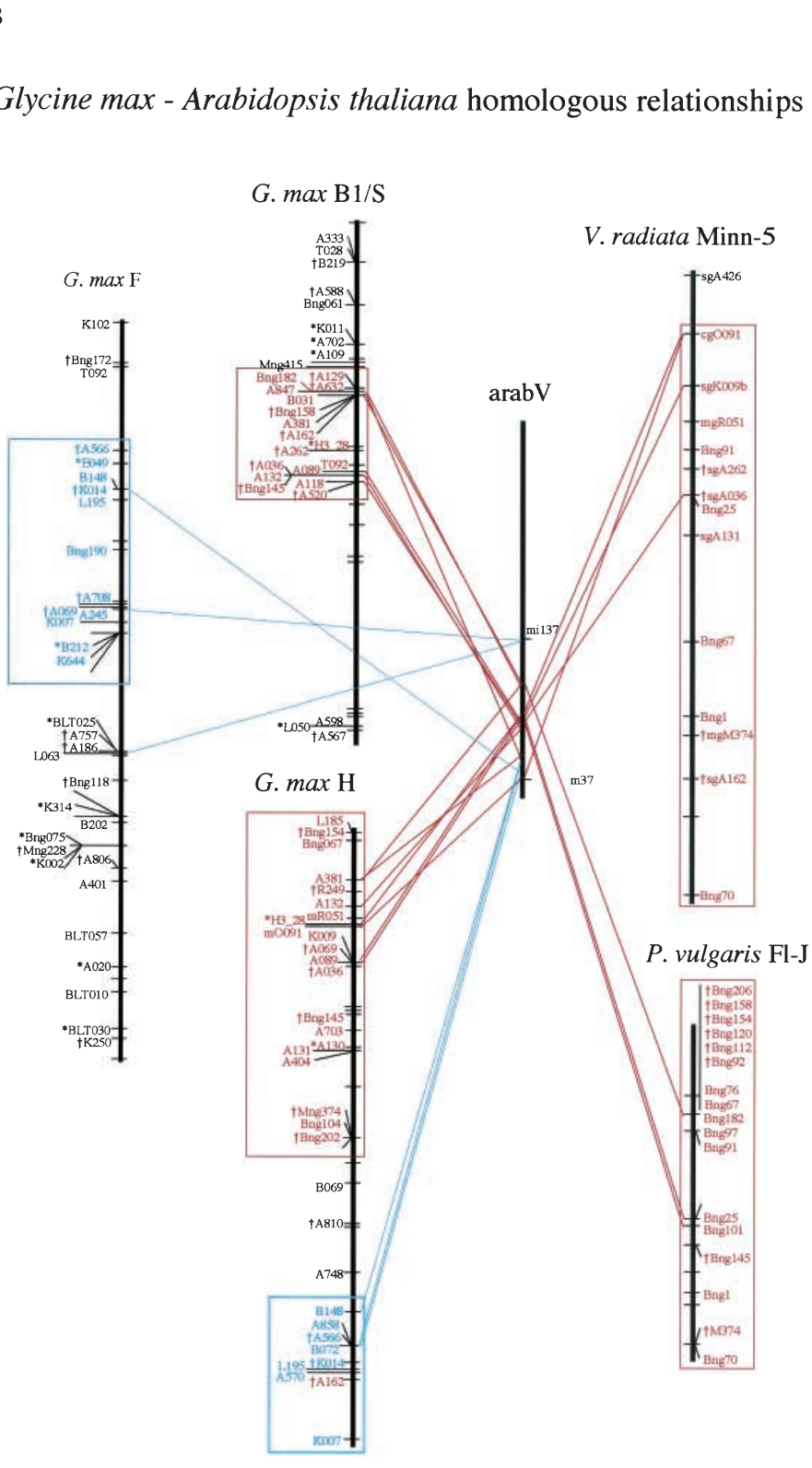



**Fig. 2** Syntenic relationship between homologous regions of *G. max*, *P. vulgaris* and *V. radiata*, and a 25-cM region on Chromosome II (**A**) and Chromosome V (**B**) in *A. thaliana*. These relationships demonstrate duplication in the *A. thaliana* genome

ysis of soybean linkage groups F and H (blue loci) as these molecular markers have not yet been mapped in the other legumes.

Pairwise comparisons between these legumes, while always showing significant synteny, often failed to reveal the complete regions of putative ancestral homology. This is the result of (1) not all RFLP probes being tested in all three species, and (2) the relatively low level of RFLP polymorphism in legumes and, thus, our inability to map more than a subset of the loci

**Fig. 2**




associated with each RFLP probe. However, by using data from all three pairwise comparisons we were able to recognize the probable size and structure of the ancestral legume chromosomes. Thus, the homologous blocks we show in Fig. 1 are often larger than would be seen by comparing any two species alone.

It is clear from Fig. 1 that each of these chromosomes has undergone rearrangement since the time of their last common ancestor. Several differences in the homologues

are evident between these legumes, although, at least for the chromosomes shown in Fig. 1, *P. vulgaris* appears to be less rearranged relative to soybean than is *V. radiata*. The homoeologues in soybean have also evolved separately. For example, only the central part of the putative ancestral chromosome (the burgundy loci on LG-H) is found on LG-B1, suggesting that the current location of this chromosomal block is due to a translocation after the most-recent polyploidization event. It is likely that once all of the map locations for these molecular markers are known in soybean it will be possible to identify the remaining part of this ancestral chromosome.

## Legume-Arabidopsis homologies

Synteny between Arabidopsis and soybean has been previously reported (Grant et al. 2000). In order to further assess the extent of conservation between legumes and *A. thaliana*, and to gain further insight into the evolution of the soybean genome, DNA sequences from RFLP markers that defined a set of legume homoeologous/homologous regions were compared to the *A. thaliana* sequences (TAIR, http://arabidopsis.org). We found evidence for conservation of the same blocks of DNA in *A. thaliana* as were detected in the legume lineage.

Sixteen legume DNA sequences from RFLP probes mapping to the burgundy colored regions in Fig. 1 showed significant homology ($E \leq 10^{-5}$) to Arabidopsis sequences in a 25-cM region near the bottom of chromosome II (arabII) (Fig. 2A, burgundy). This represents about 30% of the legume sequences analyzed. This subset includes loci which had not been directly shown to be homologous in the legumes, although an ancestral relationship could be inferred from the genetic maps. The legume sequences which showed ten or more sequence homologies to Arabidopsis (marked with * in Fig. 2) were not included in this count or subsequent analyses. Approximately 38% of the legume sequences (marked with † in Fig. 2) had no detectable homologues in Arabidopsis. We also observed a very similar pattern of legume-Arabidopsis homology covering about 25 cM of arabV (Fig. 2B, burgundy). Although some of the RFLP probe sequences show homology to regions in addition to those on arabII and arabV, there were no other cases of clustering found.

Detection of multiple homologues in the Arabidopsis genome is not surprising. Using the BLASTing strategy employed here, comparisons of soybean and Arabidopsis (Grant et al. 2000) and tomato and Arabidopsis (Ku et al. 2000) uncovered a similar network of synteny and suggested that the Arabidopsis genome may have undergone multiple rounds of duplication.

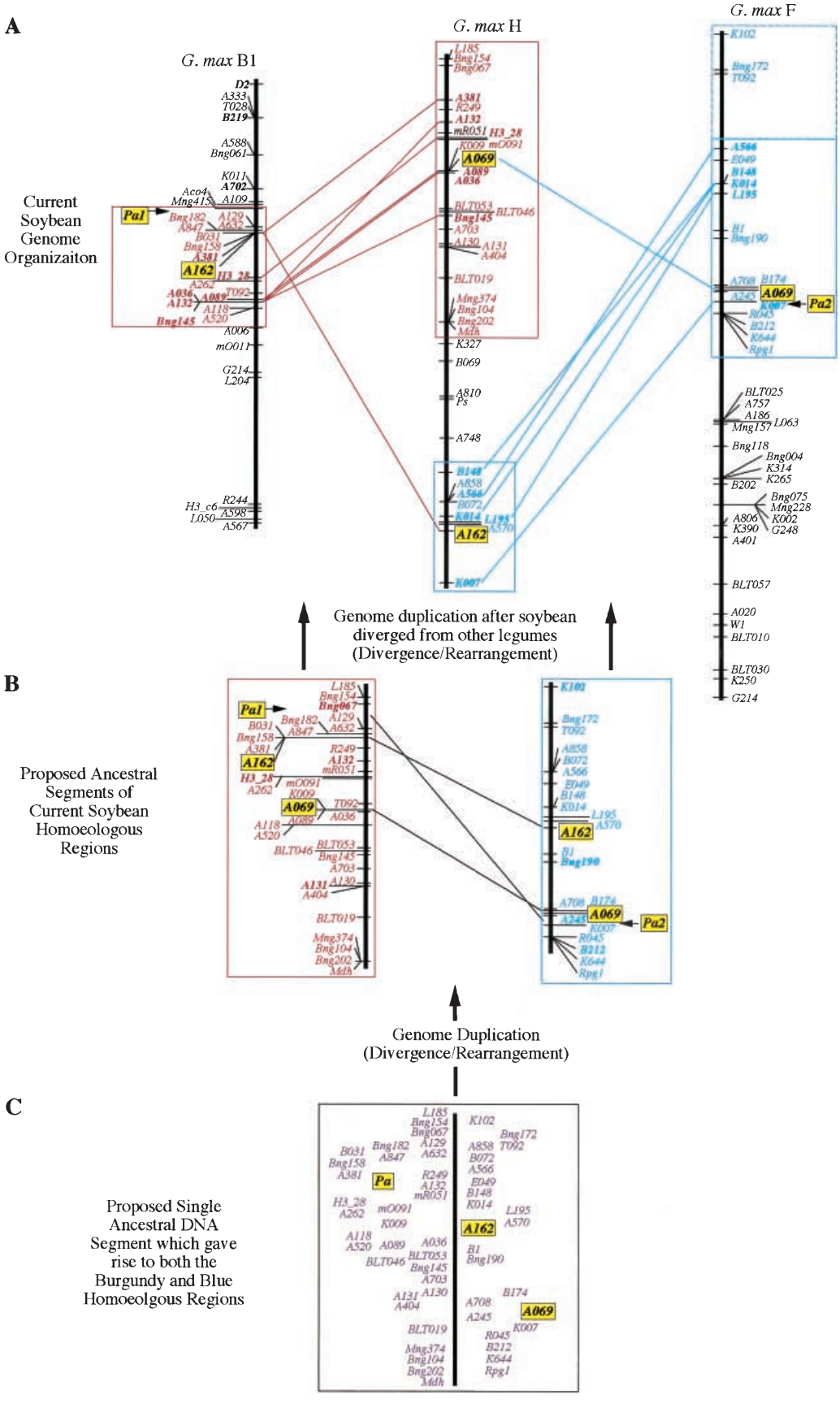
We used simulations similar to those reported by Grant et al. 2000 to assess the probability that the patterns of sequence homology we observed might be simply due to chance (i.e., the result of making many sequence comparisons to a limited number of possible targets). In 20,000 simulated genomes where the number and genetic linkage of the homologous sequences in Arabidopsis, but not the map order, was considered, a result equivalent to that shown in Fig. 2 was never observed. Therefore, the probability that our observations occurred by chance is $<5\times10^{-5}$.

The two Arabidopsis regions shown in Fig. 2 are not identical. However, based on their shared homologies with legume chromosomes, it is apparent that they are homoeologues. These results lead to two conclusions. First, the homologous chromosomal blocks we identified in legumes apparently predate the evolutionary split between brassicas and legumes. Second, this region, and possibly the entire proto-Arabidopsis genome, has been duplicated during evolution.

## Evidence for earlier duplication in soybean

Two RFLP markers (*A069* and *A162*) and a pair of duplicated genes (*Pa*1, *Pa*2) mapped to unexpected locations based on the homoeologous relationships in soybean (Fig. 1A). Interestingly, *Pa*1 and one map location each of *A069* and *A162*, are in one pair of homoeologous regions while *Pa*2 and a second map location of *A069* and *A162* are in another pair of homoeologous regions (Fig. 3A; burgundy colored regions and blue colored regions, respectively). These locations suggested a possible evolutionary relationship between the two pairs of homoeologous regions. In particular, an earlier duplication involving the region investigated might explain why the functional duplicated genes were not located in directly homoeologous regions. As an aid to understanding these results we compared the legume RFLP sequences shown in blue in Fig. 1 to Arabidopsis. Fig. 2 shows that they were homologous to Arabidopsis sequences in the same regions as were the ones described above, confirm-

**Fig. 3A–C** A paleooctoploid model of genome evolution leading to the current organization of the soybean genome. This model invokes two rounds of polyploidization each followed by diploidization events. **A** The current genome organization in soybean showing homoeologous regions. The block on LG-F includes a *dotted box* representing soybean sequences not detected in the blue homoeologous regions from comparisons within legumes, but inferred through comparisons to *A. thaliana*. **B** Ancestral regions of homoeologous groups identified in **A**. The ancestral regions represent a composite of the markers that were most likely present in the immediate ancestor to modern soybean. Some markers mapping to one region in soybean, but not in the homoeologous group, may be present but not mapped for lack of polymorphisms. It is possible that the DNA sequences have been eliminated or recently attained in one of the homoeologous regions during diploidization. The ancestral blue and burgundy regions were compared for similarity and found to be homoeologous. They have three markers in common (*Pa*, *A069* and *A162*), and at least three sequences detected with a TBLASTX search to *A. thaliana* are descended from a common region (shown in bold). Additional segmental duplications of sequences occurred independently in each region following duplication. The common markers are connected by *solid lines*. **C** The ancestral regions are most likely descended from a common ancestor. *Purple* is used to signify it as an ancestor of the blue and burgundy regions. The duplicate loci in A and B are only present once in **C** for clarity. *Pa* is used to identify the ancestral gene of *Pa*1 and *Pa*2


A
G. max B1
G. max H
G. max F
Current Soybean Genome Organizaiton
Pa1
Pa2
A162
A069
Genome duplication after soybean diverged from other legumes (Divergence/Rearrangement)
B
Proposed Ancestral Segments of Current Soybean Homoeologous Regions
Genome Duplication (Divergence/Rearrangement)
C
Proposed Single Ancestral DNA Segment which gave rise to both the Burgundy and Blue Homoeolgous Regions
Pa

ing that the four chromosomal blocks in soybean are evolutionarily related.

These surprising results suggest that the current soybean genome may be the result of two polyploidization events: the one previously identified by duplicate RFLP loci and a presumably much earlier one reported here. The latter had not been previously recognized, presumably because of a combination of the subsequent diploidization events and the low RFLP polymorphism in soybean. This earlier duplication is hinted at by the "misplaced" RFLP loci (*A162* and *A069*) and the duplicate function genes *Pa*1 and *Pa*2 indicated in Fig. 1. However, the use of Arabidopsis as a bridging species allowed us to unambiguously recognize the earlier duplication and shows the value of this multi-species approach to studying genome evolution.

Figure 3 shows a model for the evolution of the soybean genome that accounts for our results. We propose that the proto-soybean genome contained in a single chromosome (Fig. 3C) the loci which today are located in three distinct linkage groups (Fig. 3A). There were then two genome duplications, each followed by diploidization, which resulted in the modern soybean genome.

Because of a lack of mapped common loci from the blue homoeologous regions (Fig. 1) in *P. vulgaris* and *V. radiata*, our data do not allow us to deduce the relative order of the earlier duplication and the diversification of the legumes, although chromosome numbers suggest that it preceded the legume radiation. Unfortunately, such an ancient event would most likely be as hard to detect in *P. vulgaris* and *V. radiata* as it was in soybean. An analysis of one of the diploid legumes similar to the one presented here should establish whether the first genome duplication preceded the legume radiation and possibly reveal whether it preceded the legume-brassica split.

It is possible that one or both of the duplication events we describe was the result of a segmental duplication rather than a whole-genome polyploidization. However, as shown in Fig. 1, the homoeologues in soybean essentially correspond to whole chromosomes in the related legumes, suggesting that the most-recent duplication covered the entire genome. Data supporting or refuting the model that the earlier duplication similarly included the whole genome are not currently available, although, if this duplication was constrained to only the regions shown in Fig. 1, then at a minimum it involved a whole chromosome.

## Conclusions

Based on the presence of numerous homoeologous chromosome blocks, soybean is considered to be an ancient tetraploid whose genome has been diploidized since the duplication event (Shoemaker et al. 1996). However, the duplicated functional genes *Pa*1 and *Pa*2 do not map to directly homoeologous regions as would be expected if they were generated by a single polyploidization event (Lee et al. 1999). To determine the origins of these genes we analyzed the genomic regions surrounding them and compared these regions to their homologues in other species.

Significant homologies between these regions and the chromosomes of other legumes were identified. The homologous/homoeologous blocks we report between soybean and other legumes are larger than those previously found (Boutin et al. 1995) and frequently encompass large segments of linkage groups. In each case the duplicated chromosomal blocks in *G. max* are homologous to a single block in the diploid legumes *P. vulgaris* and *V. radiata*. The simplest model to explain these results is a whole-genome polyploidization event which occurred after the soybean lineage split from that of the other legumes. Due to the low level of RFLP polymorphism present in legumes, no single comparison was sufficient to completely delineate the ancestral proto-legume chromosome. However, combining all of the interspecific comparisons for a given region suggests that *P. vulgaris* and *V. radiata* most likely have gene complements that are similar to that of the ancestral genome.

We extended our study to determine whether the conserved blocks detected in legumes have remained intact from a time prior to the divergence of legumes and brassicas, approximately 90 million years ago (Gandolfo et al. 1998). Comparisons of soybean genomic-clone sequence data to the *A. thaliana* genome database provided evidence for significant genomic conservation between legumes and *A. thaliana*. In addition to the homology between soybean and Arabidopsis, we found two large homoeologous regions on chromosomes II and V in Arabidopsis. Similar results have been reported by Grant et al. (2000) and Ku et al. (2000) for other chromosomal regions, and more recently Blanc et al. (2000) presented results consistent with a complete genome duplication event during the evolution of Arabidopsis. Based on these data it is not possible to decide whether the earlier duplication in soybean is the same as the one observed in Arabidopsis or if the two lineages have independently gone through polyploidization events. What is clear is that the last genome duplication event in the soybean lineage occurred after the legume-brassica split and after the divergence of the legumes.

Genome evolution by rearrangement of large chromosomal blocks was also reported in other species (Kowalski et al. 1994; Moore et al. 1995; Lagercrantz 1998). Our results suggest that the shuffling of relatively large chromosomal blocks has also been common during the evolution of the legumes. Surprisingly, these same blocks seem to have been maintained in separate lineages over the 90 million years since the legume-brassica split. The occurrence of this phenomenon in several lineages suggests a selective advantage in the retention of certain cassettes of genes or DNA sequences in a genome. It is interesting to note that these chromosomal blocks, while maintained as a unit over long evolutionary times, have not retained exactly the same gene order, as shown by the similar but not identical genetic maps of both homoeologous and homologous regions in the spe-

cies studied. Any model to explain this aspect of genome evolution must reconcile the apparent selective advantage of maintaining these chromosomal blocks while allowing frequent rearrangements within the blocks.

Our detection of ancient duplication and possibly polyploidization events by using *A. thaliana* as a bridging species demonstrates how this can be a powerful technique for the investigation of plant genomes for evidence of paleopolyploidy and/or for identification of multiple rounds of paleopolyploidy not only within the legume family but also in other lineages.

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