somes with interstitial bands. In chromosomes with excessive contraction the bands fuse together and only a few bands are actually detected. The SAT chromosome is easy to identify because of the presence of the secondary constriction and also because of the large terminal band on the long arm of the chromosome.

The distinctive C-banding pattern of ssp. *caerulea* chromosomes enabled us to develop a standard karyotype that may be helpful in studying cytogenetic and evolutionary relationships among species of *Medicago*. The differences we observed in the banding patterns of these two subspecies makes it possible to identify parental chromosomes in the hybrid.

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Genetic Marker Transmission in Early Generation Common × Tepary Bean Hybrids

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A set of BC_1F_2 populations derived from common bean × tepary bean interspecific hybrids was examined for isozyme segregation within 12 different enzyme systems. The BC_1F_1 parents of the BC_1F_2 populations, as inferred from the BC_1F_2 progeny data, were found to be heterozygous for approximately half of the marker loci examined, in agreement with transmission genetic theory predictions. In contrast, segregation ratios for isozyme loci in the BC_1F_2 families deviated significantly from expected Mendelian ratios in approximately 50% of the cases, due to a severe deficiency of individuals homozygous for the tepary allele, as well as having a deficiency of heterozygotes in some cases. Using data from a diagnostic pair of linked isozyme loci, evidence of intergenomic recombination at levels equal to or greater than that encountered in intraspecific crosses was detected in one BC_1F_2 family.

The tepary bean (*Phaseolus acutifolius* A. Gray) has been reported to exhibit a greater tolerance to heat, drought, and salinity than common bean (*P. vulgaris* L.) and to possess certain insect and bacterial resistances that are of interest to common bean breeders (Miklas et al. 1994; Omwega et al. 1989; Pratt and Nabhan 1988; Thomas et al. 1983). Unfortunately when hybridization is undertaken to introgress tepary bean genes into common bean, serious obstacles are encountered. F_1 hybrids are effectively self-sterile, and early generation backcross plants also frequently exhibit significant sterility problems (Mejia-Jimenez et al. 1994; Parker and Michaels 1986; Thomas and Waines 1984). Additional backcrossing increases fertility, but this poses a dilemma to breeders because further backcrossing to common bean will continue to eliminate the tepary bean genome.

While the infertility of early generation tepary × common bean hybrids poses a formidable barrier to interspecific gene transfer, segregation distortion, that is, the preferential elimination of genetic materials from one parent in hybrid plants, can compound the difficulties caused by low fertility because it will reduce opportunities for introgressive recombination. Segregation distortion is frequently encountered in plant interspecific hybrids (Zamir and Tadmor 1986) and has been reported in hybrid derivatives of *P. vulgaris* and *P. coccineus* (Guo et al. 1994; Ibrahim and Coyne 1975; Manshardt and Bassett 1984; Wall 1968).

Previous studies have examined populations derived from common bean × tepary bean crosses for the presence of tepary bean genes (Haghighi and Ascher 1988; Mejia-Jimenez et al. 1994; Parker and Michaels 1986; Pratt and Gordon 1994). These studies examined few simply inherited marker genes and sometimes included morphological characters for which neither the genetic basis nor possible pleiotropic effects are known. This has made it difficult to quantify the introgression of the tepary bean genome in common × tepary bean hybrids, and to date no studies have empirically examined the transmission genetics of common × tepary bean hybrids.

The objectives of this study were to use a set of defined isozyme genes to quantify the transmission of the tepary bean genome in the first segregating generations obtained from common × tepary bean crosses and to search for evidence of intergenomic recombination in this material.

Materials and Methods

Six BC_1F_2 populations were obtained from common × tepary BC_1F_1 hybrids repre-

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Table 1. Observed segregation for isozyme loci in BC_1F_2 populations derived from *Phaseolus vulgaris* × *P. acutifolius* crosses

Pedigree	Genotype[a]	*Aco-1*	*Aco-2*	*Adh-1*	*Adh-2*	*Fdh-1*	*Gpi-c1*	*Gpi-c2*	*Idh-x*	*Lap-1*	*Mdh-2*	*Skd-1*	*Acp-1*	*Pgm-1*	*Idh-3*
		Number of individuals													
(ICA Pijao × PI319443) × ICA Pijao															
Population 1	V	30	30	30	30	6	5		7		25				
	A	0	0	0	0	2	7		9		1				
	VA	0	0	0	0	16	6		14		4				
	χ^2	—	—	—	—	4.0	2.4		0.4		54.4**				
Population 2	V	13	31	20	26		7	20		11	31	30			
	A	7	0	1	0		9	0		0	0	0			
	VA	8	0	9	4		15	11		7	0	0			
	χ^2	7.7*	—	28.8**	61.2**		0.3	28.4**		14.3**	—	—			
(NB585 × PI 319443) × NB585															
Population 3	V	29	19	24	21	29	28	29	14		29				
	A	0	4	0	0	0	0	0	0		0				
	VA	0	5	5	4	0	1	0	0		0				
	χ^2	—	27.6**	52.2**	42.0**	—	79.2**	—	—		—				
Population 4	V	8	3				2	7	3		4	6			
	A	0	0				1	0	0		0	0			
	VA	0	3				5	1	3		4	0			
	χ^2	—	3.0				0.8	16.8**	3.0		4.0	—			
(Linden × PI319443) × Linden															
Population 5	V	8	8	8	8		4	8	4		5	5			
	A	0	0	0	0		0	0	0		0	0			
	VA	0	0	0	0		4	0	4		3	0			
	χ^2	—	—	—	—		4 0		4.0		6.8*	—			
(NB585 × G40035) × L571															
Population 6	V	25	9	25		5	5	25	5	25	9	17	25	8	10
	A	0	0	0		7	7	0	7	0	8	0	0	5	4
	VA	0	16	0		13	13	0	13	0	8	8	0	12	11
	χ^2	—	8.4*	—		0.4	0.4	—	0.4	—	3.3	26.4**	—	0.8	3.3

[a] V, A, VA = homozygous for *P. vulgaris* allele, homozygous for *P. acutifolius* allele, and heterozygotes, respectively.
*, ** significant at 5% and 0.1%, respectively.

senting four different pedigrees. The BC_1F_1 hybrids were originally obtained by backcrossing interspecific F_1 plants to common bean, with the recurrent parent serving as the pollen donor (Federici and Waines 1989; Stockinger and Waines 1986). In all cases, plants used to produce the F_1 and BC_1F_1 generations were derived from lines grown several generations in the greenhouse to enforce inbreeding and ensure homozygosity across loci. The BC_1F_2 populations varied in size from 1 to over 200, which reflects the range of fertility generally encountered in such BC_1F_1 plants.

Random samples of up to 31 individuals from the BC_1F_2 populations were assayed for isozyme polymorphisms using starch-gel electrophoresis. Seed and leaf tissue were used for the analysis, and samples were prepared and electrophoresis conducted as previously described (Garvin et al. 1989). Stains for aconitase (ACO), alcohol dehydrogenase (ADH), formate dehydrogenase (FDH), glucosephosphate isomerase (GPI), isocitrate dehydrogenase (IDH), phosphoglucomutase (PGM), and shikimate dehydrogenase (SKD) were obtained from Garvin et al (1989). Malate dehydrogenase (MDH) and acid phosphatase (ACP) were stained essentially as described by Vallejos (1983), while leucine aminopeptidase (LAP) was stained following the procedure of Wall (1968). ADH, FDH, IDH, and LAP were scored in seed tissue, while the other enzymes were scored either in seeds or leaves, since both tissues gave identical results. Selfed progeny from the original parents of the F_1 hybrids were included as controls on the gels.

Gel interpretations and genetic nomenclature for most of the isozyme loci are based on previous studies of isozyme polymorphisms in *Phaseolus* (Garvin et al. 1989; Garvin and Weeden 1994; Koenig and Gepts 1989; Schinkel and Gepts 1989). Isozyme segregation ratios were tested for goodness-of-fit to monogenic segregation ratios with the chi-square statistic. Further, both BC_1F_1 and BC_1F_2 genotype data were examined for evidence of intergenomic recombination by deducing the gametic composition of individuals for *Gpi-c1* and *Fdh*, isozyme loci previously shown to be moderately linked (12 cM) in tepary bean (Garvin and Weeden 1994).

Results

Within the enzyme systems analyzed, isozyme polymorphisms differentiating common and tepary bean alleles were detected at 14 different isozyme loci. Owing to the lack of appropriate plant tissue at the time of the analysis or poor resolution of polymorphisms on gels, there are some missing data. Despite this, the data obtained provide valuable information on patterns of segregation in common × tepary bean interspecific hybrids.

With the data from the BC_1F_2 populations (Table 1) serving as a progeny test, it was possible to infer isozyme genotypes of the BC_1F_1 parents. In all six of these BC_1F_1 individuals, tepary bean alleles were present at multiple loci, and the proportion of heterozygous loci ranged from approximately 33–70% in the different plants.

Segregation ratios for isozyme loci segregating in BC_1F_2 families were found to deviate significantly from Mendelian expectations in approximately half of the cases (Table 1). Loci exhibiting segregation distortion possessed a deficiency of individuals homozygous for the tepary allele in every instance, and a deficiency of heterozygotes was also frequently observed (Table 1). In two cases the sizes of the BC_1F_2 population were too small to allow concrete conclusions about segregation distortion to be drawn, even though

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the statistical tests indicated that the segregation ratios do not differ from a 1:2:1 ratio. Thus the 50% incidence of segregation distortion observed across loci is likely to be a conservative underestimate.

Formal linkage analysis was not conducted with the BC_1F_2 data because of the high levels of segregation distortion and small population sizes. However, in two of the BC_1F_2 populations in which *Gpi-c1* and *Fdh* were jointly segregating, evidence of intergenomic recombination was found. In population 1 (Table 1), 7 of 15 individuals for which joint *Gpi-c1* and *Fdh* scores were available were derived from recombinant gametes. Of the 30 gametes that contributed to these individuals, eight were recombinant, which equates to a recombination frequency of 27%. In population 3, *Fdh* was not segregating, while *Gpi-c1* was (Table 1), indicating that the maternal gamete contributed to the BC_1F_1 individual by the original F_1 plant was recombinant. In contrast, no recombination was detected between *Gpi-c1* and *Fdh* in population 6.

Discussion

The presence of tepary bean characters in common × tepary bean hybrid material representing various generations has been assessed in previous studies, with indications that that some tepary bean genetic material is maintained in BC_1 and later generations (Haghighi and Ascher 1988; Mejia-Jimenez et al. 1994; Parker and Michaels 1986; Pratt and Gordon 1994). However, the type of data collected in these studies was not amenable for use in quantifying tepary bean genome transmission in hybrid material. To our knowledge, the results presented in this study are the first attempt to quantify the fate of the tepary bean genome in common × tepary bean backcross hybrids by examining Mendelian segregation at a series of codominant genetic markers and testing the results against expectations of transmission genetic theory.

Our results suggest different patterns of tepary bean genome transmission in two contrasting generations. In the BC_1F_1 generation, regions of the tepary bean genome tagged by the marker loci are, on average, transmitted at expected proportions in plants representing different pedigrees. These results are in contrast to the results of Waines et al. (1988), who found no tepary bean alleles at three isozyme loci in a small number of BC_1F_1 plants. Such contrasting results may relate to specific pedigree-based differences in the retention or elimination of the tepary bean genome.

In contrast to the apparently normal transmission of the tepary bean genome to the BC_1F_1, selfing of BC_1F_1 plants results in widespread deviations from Mendelian segregation in the derivative populations, with a significant degree of tepary bean genome elimination evident. A previous study reported similar severe segregation distortion for a diaphorase gene in a common × tepary bean BC_1 population (Pratt and Gordon 1994). Such segregation distortion has also been found to occur upon selfing *P. vulgaris* × *P. coccineus* F_1 hybrids (Guo et al. 1994), as well as in some intraspecific *P. vulgaris* hybrids (Koenig and Gepts 1989).

The contrast between the BC_1F_2 versus the BC_1F_1 generation with respect to the transmission of tepary bean genes might reflect a differential transmission of the tepary bean genome through the egg and pollen. Gametic selection has been suggested to cause an underrepresentation of some *P. coccineus* genes in crosses to *P. vulgaris* (Guo et al. 1994). The production of the BC_1F_1 generation measures transmission of the tepary bean genome through the egg, whereas tepary bean genes are transmitted via either gamete to the BC_1F_2 generation. As such, our results may indicate that the tepary bean genome is transmitted normally through the egg but not the pollen. Such differential gametic transmission has previously been reported in *P. vulgaris* × *P. coccineus* hybrids (Wall 1968). The underrepresentation of tepary bean alleles could also represent the outcome of postzygotic elimination of genotypes possessing deleterious intergenomic combinations, and might also provide an explanation for the embryo abortion often observed in this interspecific cross.

Rabakoarihanta et al. (1980) suggested that crossing over between common and tepary bean chromosomes could occur for the majority of the chromosomes, based on the formation of bivalents during meiosis in hybrids. The presence of tepary bean bacterial blight resistance in elite bean lines also implies that intergenomic recombination does occur (Scott and Michaels 1992). In this study we provide data on the magnitude of intergenomic recombination between the common bean and tepary bean genomes. Interestingly, recombination between *Gpi-c1* and *Fdh* in one BC_1F_2 population was higher than that found in intraspecific tepary bean crosses (Garvin and Weeden 1994), whereas in another population of roughly equal size, no recombination was detected. Since these populations were derived from different pedigrees, there could be a genetic basis to the observed recombinational differences.

While backcrossing appears to permit the normal transmission of the tepary bean genome in common × tepary bean hybrids, selfing appears to result in strong selection against it. However, it may be possible to counteract the effects of this segregation distortion and its deleterious effect on opportunities for recombination by maintaining specific tepary bean chromosome segments during backcrossing through selection of marker loci tagging the desired intervals at each backcross generation. Alternative strategies for recovering fertile hybrids without the cost of concomitant elimination of the tepary bean genome, as occurs during repeated backcrossing, should also be considered. One such approach that holds promise is congruity backcrossing (Haghighi and Ascher 1988), which can increase the fertility of early generation interspecific hybrids.

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Inheritance of a Gene Conditioning Blotchy Root Color in Table Beet (*Beta vulgaris* L.)

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The primary pigments in red beet are the betalains, which include the red-violet betacyanins and the yellow betaxanthins. The recent adoption of betalain pigments from red beet as an alternative to synthetic food dyes has heightened interest in genetic modification of pigment production. Dominant alleles at two tightly linked loci (*R* and *Y*) condition production of betalain pigment in the beet plant, however several alleles at the *R* locus influence pigment amount and distribution. In addition, recurrent selection for pigment concentration has been effective at increasing pigment concentration, suggesting other modifying genes play an important role in betalain synthesis. A mutant phenotype, characterized by irregular sectors of blotchy red and white root color, was observed in a breeding line in the beet breeding nursery at the University of Wisconsin-Madison. The blotchy mutant plant was used in crosses with nonblotchy inbred lines to characterize its inheritance. Chi-square goodness-of-fit tests of segregation data in backcross and F_2 generations for several genetic backgrounds did not deviate from the hypothesis that a single recessive gene controls the blotchy phenotype. We propose the symbol *bl* to describe the genetic control of this blotchy phenotype.

Red beet (*Beta vulgaris* subsp. *vulgaris*) is an important vegetable crop in Europe and parts of Asia and the United States. It was selected originally for its use as a leafy vegetable in the Mediterranean region, then later for use as a fresh or stored root (Campbell 1976). European herbals clearly point toward distinct uses for the leaf portion, which was the primary form of the vegetable at that time, and the swollen red hypocotyl and root, which is the common form of the vegetable today (Pink 1993). In the 18th century the use of beet root was expanded to include animal feed and the fodder beet was developed. By the 19th century the fodder beet became an important component of European agriculture and was the progenitor of the sugar beet (Pink 1993).

The primary pigments in red beet are the betalains, which are unique to the Caryophyllales. Betalain pigment is derived from betalamic acid following the cleavage of L-DOPA between the 4- and 5- positions (Clement et al. 1992; Fischer and Dreiding 1972; Impelizzeri and Piatelli 1972). The cleavage of L-DOPA results in two intermediates, 4,5-secodopa and cyclodopa glucoside. The former intermediate is converted into betalamic acid, which in turn condenses with cyclodopa glucoside to form the red-violet betacyanins (BC) and the yellow betaxanthins (BX). These differ by conjugation of a substituted aromatic nucleus to the 1,7-diazaheptamethinium chromophore, which is present in BC.

Table 1. Genotypes at the *R* and *Y* loci affecting color phenotypes in table beet

Genotype	Phenotype
R-Y-	Red roots, hypocotyls, petioles
rrY-	Yellow roots, hypocotyls, petioles
R-yy	White roots and red hypocotyls
R^*R^*Y-	Red hypocotyls
rryy	White roots and yellow hypocotyls
R^tR^tY-	Striped petioles
R^tR^tyy	Striped petioles
R^t-Y^r	Red roots and green leaves
rrY^r	Yellow roots and green leaves
R^t-Y^r-	Red roots and striped petioles
R^pR^p	Pink roots, hypocotyls, and petioles

Descriptions in Wolyn and Gabelman (1989).

The presence of dominant alleles at two tightly linked loci (*R* and *Y*) condition production of betalain pigment in the beet plant (Keller 1936). Wolyn and Gabelman (1989) demonstrated that three alleles at the *R* locus determine the ratio of betacyanin to betaxanthin in the beet root and shoot. They observed incomplete dominance for pigment ratio in R'_ and R'_ genotypes, and suggested *R* might be a structural locus coding for an enzyme directly affecting BC production. Color patterning in the beet plant is affected by these *R* locus alleles and alleles at the *Y* locus (Table 1). Red roots are observed only when dominant alleles at the *R* and *Y* loci are present, while white roots are conditioned by recessive alleles at the *Y* locus. A *yyrr* genotype produces no BC and BX only in the hypocotyls. R^tR^tY_ and R^tR^tyy genotypes condition red and white striped petioles and striped roots. In these plants xylem and phloem tissue in both root and shoot are present in concentric alternating bands of white and red, respectively, and the resulting root cross section has a targetlike appearance.

In addition to these simply inherited genes controlling pigment synthesis, additional modifying genes likely play an important role in betalain accumulation because populations of beet plants carrying

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