Tight Linkage between the *Fin* Locus for Plant Habit and the *Z* Locus for Partly Colored Seedcoat Patterns in Common Bean

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ABSTRACT. Linkage between the *Fin* locus controlling plant habit and the *Z* locus controlling partly colored seedcoats in common bean (*Phaseolus vulgaris* L.) was studied in the F_2 and F_3 progenies from the cross '*t virgarcus* BC₃ 5-593' (determinate habit, virgarcus pattern of partly colored seeds, *fin t z*) × 'Steuben Yellow Eye' (indeterminate habit, sellatus pattern of partly colored seeds, *Fin t z^{sel}*). The heterozygous genotype *z^{sel}/z* produces the piebald pattern of partly colored seeds, whereas *Fin* is completely dominant to *fin*. Selection was made in the F_2 for crossover phenotypes: indeterminate habit with virgarcus seeds or determinate habit with piebald seeds. Linkage calculations were based on crossover genotypes confirmed by F_3 progeny tests grown in the greenhouse. The recombination percentage between *Fin* and *Z* was 1.032 ± 0.33 map units. The gene symbol *z^{sel}* is proposed, where *t Z* gives the expansa partly colored seedcoat pattern, *t z^{sel}* gives sellatus, and *t z* gives virgarcus.

Partly colored seedcoats in common bean (*Phaseolus vulgaris* L.) depend on the genotype *t/t* for expression, where *T/-* gives self-colored (totally colored) seedcoats (Leakey, 1988). The genotype *t z* produces the virgarcus pattern (Fig. 1) of partly colored seedcoats (Lamprecht, 1940; Schreiber, 1940). The partly colored seedcoat pattern sellatus (saddle pattern, Fig. 2) was first reported by von Tschermak (1912), who used the gene symbol *Z₂* (*Z* for zonal) for the dominant allele expressing sellatus when homozygous. The heterozygous genotype *Z₂/z₂* produced a unique partly colored seedcoat pattern, piebald (Fig. 3), and *z₂/z₂* produced the virgarcus pattern (von Tschermak, 1912). In the comprehensive review of the genetics of partly colored seedcoats by Lamprecht

(1934), the *Z₁* locus of von Tschermak (1912) was recognized as a synonym for *T*. Consequently, Lamprecht (1934) proposed that the symbol *Z₁* be discontinued and that the subscript be dropped from the symbol *Z₂*. Subsequently, Schreiber (1940) demonstrated that the genotype *t Z* produces the expansa pattern (Fig. 4), whereas von Tschermak (1912) used the equivalent of *t Z* for sellatus. To avoid that ambiguity, I propose *z^{sel}* as a symbol for an allele at the *Z* locus that produces the sellatus pattern with *t*, where *z^{sel}* is a more pattern-limiting allele than *Z*. Thus, *t Z* produces expansa, *t z^{sel}* sellatus, and *t z* virgarcus, where the allelism at *Z* was established by von Tschermak (1912).

Schreiber (1940) described a group of seven partly colored phenotypes that with *t/t* are produced by the interaction of two

allele pairs, *Z/z* and *L/l*, viz., marginata (*Z/Z L/L*), expansa (*Z/Z l/l*), erasa (white seed produced by *z/z L/-*), restricta (*z/z l/l*), intermedia (*Z/z L/l*), laciniata (*Z/z L/L*), and ambigua (*Z/z l/l* or *Z/Z L/l*). The *L* allele either greatly restricts the area of colored seedcoat as with marginata, intermedia, and laciniata, or completely eliminates colored

Fig. 1. A ventral view (left seed) and a side view (right seed) of the virgarcus pattern of partly colored seedcoat.

Fig. 2. A ventral view (left seeds) and a side view (right seeds) of the sellatus pattern of partly colored seedcoat.

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Fig. 3. A side view (top and bottom seeds) of the piebald pattern of partly colored seedcoat.

seedcoat expression as with *erasa*.

Surface (1916) reported that the *virgarcus* gene *z* was linked with the determinate habit gene *fin* in a cross between 'Improved Yellow Eye' (*sellatus*) and 'Old-Fashioned Yellow Eye' (*virgarcus*), but no calculation of recombination percentage was made for the fully classified F_2 population of 247 plants. This paper reports the results of an investigation of possible linkage between *Z* and *Fin*, based on the hypothesis of Surface (1916).

Materials and Methods

Seed of the dry bean variety 'Steuben Yellow Eye' (SYE) was obtained from S.J. Park, Harrow, Ontario, Canada. SYE has indeterminate habit and the *sellatus* pattern of partly colored seedcoats (*Fin t z^{sel}*). The genetic tester stock *t virgarcus* BC₃ 5-593 has determinate habit and the *virgarcus* pattern of partly colored seedcoats (*fin t z*). The development of *t*

virgarcus BC₃ 5-593 was described by Bassett (1996). In Fall 1994, the cross *t virgarcus* BC₃ 5-593 × SYE was made and the F_1 generation was grown in the greenhouse in Winter 1995. Data were taken on the seedcoat pattern of the resultant F_2 seed. The F_2 population was grown in the field in Spring 1995, with in-row plant spacing of 30 cm and rows 1.2 m apart. At maturity, the F_2 population was classified for plant habit (indeterminate or determinate) and seed pattern classes (*sellatus*, *piebald*, or *virgarcus*). Selection was made for plants that appeared to be members of the two recombinant classes: indeterminate habit with *virgarcus* seeds or determinate habit with either *piebald* or *sellatus* seeds.

In the Fall 1995 greenhouse generation, 12-plant F_3 progenies were grown from 7 selections for the recombinant class with determinate habit and *piebald* seeds, and 16-plant F_3 progenies were grown from 6 selections for the recombinant class with semi-vine habit and *virgarcus* seeds. Data were taken on plant habit and seedcoat pattern for each F_3 plant. Recombination percentage was calculated by the maximum likelihood method of Allard (1956).

Results and Discussion

The F_2 seed from the cross *t virgarcus* BC₃ 5-593 (*t z*) × SYE (*t z^{sel}*) had the *piebald* pattern of partly colored seedcoats, which is consistent with the expected genotype *t/t z^{sel}/z* (data not shown). A total of 962 F_2 plants was classified from the cross *t virgarcus* BC₃ 5-593 × SYE (Table 1). The observed segregation showed highly significant deviation with respect to the expected ratio of 3:6:3:1:2:1, which was due entirely to linkage (Table 1). The segregation at the *Fin* and *Z* loci was normal, i.e., fit the expected 3:1 ratio for each locus (Table 1). Of the six F_3 progenies of suspected recombinant F_2 plants with indeterminate habit and *virgarcus* seeds, only four were true breeding for *virgarcus* seedcoats, and those four also segregated for determinate habit (data not shown). Thus, each of those four F_2 selections carried the recombinant gamete with genotype *Fin t z*. The two F_2 selections for indeterminate habit and

virgarcus seeds that were not true breeding for *virgarcus* seeds were classification errors (really *z^{sel}/z*). Of the seven F_3 progenies of suspected recombinant F_2 plants with determinate habit and *piebald* seeds, only six segregated for plants with *sellatus* or *piebald* seed, and all six also segregated for plants with *virgarcus* seeds (data not shown). Thus, each of those six F_2 selections carried the recombinant gamete with genotype *fin t z^{sel}*. The seventh F_2 selection for determinate habit and *piebald* seeds that did not segregate for *virgarcus* was a classification error, i.e., it was not *piebald*. No F_2 plants were observed with the recombinant phenotype expressing determinate habit and *sellatus* seeds (Table 1). The classification of the F_2 for seedcoat pattern probably had a low

Fig. 4. A ventral view (left seeds) and a side view (right seeds) showing the range of variation of the white area for the *expansa* pattern of partly colored seedcoat. The middle pair of seeds shows the typical pattern.

Table 1. Segregation for plant habit and partly colored seedcoat patterns in the F_2 from the cross t virgarcus BC_3 5-593 ($fin\ t\ z$) $\times$ Steuben Yellow Eye ($Fin\ t\ z^{sel}$), where $t\ z^{sel}/z$ produces a distinctive heterozygous seedcoat pattern (Fig. 3).^z

Indeterminate habit			Determinate habit		
Sellatus	Piebald	Virgarcus	Sellatus	Piebald	Virgarcus
$Fin/-$ z^{sel}/z^{sel}	$Fin/-$ z^{sel}/z	$Fin/-$ z/z	fin/fin z^{sel}/z^{sel}	fin/fin z^{sel}/z	fin/fin z/z
231	485	4	0	6	236

^zThe coupling phase linkage between the Fin and Z loci was calculated to be 1.032 ± 0.33 using the maximum likelihood method of Allard (1956) and the expected segregation ratio of 3:6:3:1:2:1 for the six classes above (taken left to right). Only those F_2 selections for recombinant phenotype that were confirmed in F_3 progeny tests are listed in the table. Combining the z^{sel}/z^{sel} and z^{sel}/z classes, the data for the genotypes $Fin/-\ z^{sel}/-$, $Fin/-\ z/z$, $fin/fin\ z^{sel}/-$, and $fin/fin\ z/z$ are 716, 4, 6, and 236, respectively; and the orthogonal contrasts of Mather (1957) for the 9:3:3:1 ratio are $\chi^2_{Fin} (3:1) = 0.0125$, $P = 0.911$; $\chi^2_Z (3:1) = 0.0014$, $P = 0.970$; and $\chi^2_L = 912.0005$, $P < 0.001$.

error rate generally, except for plants suspected of having recombinant phenotypes. The three classification errors described above were due to selecting a few dubious "border line" plants in an effort to not miss any true recombinants. This "over reaching" approach was taken knowing that all selection errors would be detected in F_3 progeny tests.

The recombination percentage for the Z and Fin loci was calculated to be 1.032 ± 0.33 (Table 1). The surprisingly tight linkage of ≈ 1 cM was obtained from only 962 F_2 plants because one of the loci, Z , reveals all the heterozygotes phenotypically. Thus, about half of the information that would have been obtained by complete F_3 testing of each F_2 parent was obtained visually in the F_2 without the need for an F_3 . F_4 stocks with $fin\ t\ z^{sel}$ (sellatus seed on a determinate habit) have been backcrossed to 5-593 to initiate a program to develop a $fin\ t\ z^{sel}$ sellatus BC_3 5-593 genetic stock. There are no reports in the literature about the interactions of z^{sel} with Z or with various alleles at L .

The work of von Tschermak (1912) established the hypothesis that a single locus, his Z_2 , controls both the sellatus and virgarcus patterns of partly colored seedcoats. The work reported above confirms the hypothesis of von Tschermak (1912), but I use the symbol Z (without the subscript 2) as proposed by Lamprecht (1934) for the same locus. Lamprecht's (1934) final synthesis was that $t\ Z$ produces the sellatus pattern, using the revised gene symbols. In the absence of pattern-restricting genes at other loci, Schreiber (1940) demonstrated that $t\ Z$ produces the expansa pattern, which was confirmed by Bassett (1996). I propose the gene symbol z^{sel} for the allele from 'Steuben Yellow Eye', which produces the sellatus pattern, to avoid the ambiguity in the literature cited above.

In the absence of pattern restrictions produced by genes at loci other than T and Z , there are three known homozygotes for partly colored seedcoats (Schreiber, 1940), viz., $t/t\ Z/Z$ gives the most extensively colored pattern, expansa, $t/t\ z^{sel}/z^{sel}$ gives the intermediate pattern extension, sellatus, and $t/t\ z/z$ gives the least extensive pattern, virgarcus.

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