A Brief Review of the Genetics of Partly Colored Seed Coats in Common Bean

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All the partly colored seed coat patterns discussed in this review have their names, genotypes, and random amplified polymorphic DNA (RAPD) markers listed in Table 1, and the patterns are illustrated (graphic layout by Rachel Stevens) on the last two pages of the review. The seed coat patterns controlled by the *C* and *Stp* genes are not discussed in this paper.

Partly colored seed coat patterns are expressed only with the genotype t/t, the recessive genotype at Emerson=s (1) T locus for Totally colored seeds. Today, these seeds are now usually referred to as self-colored seeds. The t/t genotype has a pleiotropic effect leading to white flowers and is epistatic to the V gene for purple flowers (1). The colored area of the seed coat can have any of the many hues possible for common bean (2), except for white, which is always the color of the non-colored area. Four additional genes control the size and shape of the colored seed coat pattern: zonal (Z), bipunctata (Bip), limiter (L), and the J gene. A third allele at T, viz., $t^{\rm cf}$, permits the expression of partly colored seed coats without changing the flower color to white (3). But in otherwise equivalent genetic backgrounds, the restriction of colored area patterns due to $t^{\text{cf}}/t^{\text{cf}}$ is not as severe as with t/t (Bassett, unpublished data). For example, $t^{\text{cf}} z l^{+}$ produces patterns ranging from self-colored to one similar to expansa (Fig. 1 without the fibula arcs), whereas $t z l^+$ produces the more restricted virgarcus pattern (Fig.4). Similarly, $t^{cf} z l^{ers}$ and another unidentified gene produce the two points pattern (Fig. 2) (Bassett, unpublished data), whereas $t z l^{ers}$ produces a white seed. With genotype $t Z Bip J l^{+}$ the seed coat can be either selfcolored (4) or have the expansa pattern (5), which is the same as the minimus pattern (6, see Fig. 10 in that article). A newly discovered dominant acting gene, Fibula arcs (Fib), also affects patterning. With genotype $t Z Bip J l^+ Fib$ the seed coat has the expansa with fibula arcs pattern (Fig. 1), where Fib expresses the fibula arcs pattern and restricts slightly more the expansa pattern (Bassett, unpublished data).

The Z locus discovered by von Tschermak (7) controls several seed coat patterns reported in that article: virgarcus ($t z Bip J l^+$) (Fig. 4), piebald ($t z^{sel}/z Bip J l^+$) (Fig. 5), and sellatus ($t z^{sel} Bip J l^+$) (Fig. 6). Lamprecht (8) removed the subscript 2 from von Tschermak=s Z_2 locus symbol to re-designate it Z, and Bassett (9) assigned Z to the allele giving no pattern restriction and z^{sel} to the sellatus pattern allele. The genotype $t Z/z Bip J l^+$ has the highly variable seed coat pattern ambigua (Fig. 3), which was discovered by Schreiber (5). The degree of instability of Z/z ambigua pattern declines greatly with increasing homozygosity of the entire genome.

The inheritance of the bipunctata pattern with genotype $t z bip J l^+$ (Fig. 9) was reported simultaneously by Lamprecht (6) and Schreiber (5) and confirmed by Bassett (10). A third allele at Bip, viz., bip^{ana} , controls the Anasazi seed coat pattern (Fig. 7) with genotype $t Z bip^{ana} J l^+$ (11). The genotype $t Z bip^{ana} J l^+$ produces the Anabip pattern (Fig. 8), which is nearly as restricted as bipunctata (Fig. 9) (11).

The J locus was discovered to have interactions with t by Bassett (12, 13), where genotype $t Z Bip j l^+$ expresses the marginata pattern (Fig. 10). The same marginata pattern can also be expressed by the genotype t Z L, according to Schreiber (5). Genotype $t Z Bip j l^+$ expresses white seed coat (14), as does $t Z Bip J l^{ers}$ (15); and when those two genotypes are crossed, the F_1 and F_2 progeny express only white seed coats (Bassett, unpublished data). Those

allelism test results give strong support to the hypothesis that J and L are allelic; but unlike the data demonstrating that the z and d (former symbol for the hilum ring factor) alleles are one and the same (14), the j and $l^{\rm ers}$ alleles cannot be identical. For example, t Z Bip j expresses marginata (12, 13), whereas the $t Z Bip l^{\rm ers}$ genotype expresses self-colored or expansa (15). Much additional research is needed to establish the details of a possible allelic series including J (same as l^+), j, L (j^L ?), and $l^{\rm ers}$ ($j^{\rm ers}$?), where the J symbol has precedence over L. Similarly, much additional research is needed to explore the hypothesis that the fibula arcs factor Fib can transform $t Z bip^{\rm ana} fib$ Anasazi into $t Z bip^{\rm ana} Fib$ marginata and transform t Z Bip J fib virgarcus into t Z Bip J Fib arcus (almost indistinguishable from weak virgarcus, Fig. 11) (Bassett, unpublished data).

The mutual independence of the genes T, Z, and Bip has been established repeatedly in previous literature cited above, e.g., (4, 5). Also, the independence of the genes T, Z and L has been established (5). Recently, the Bip locus was demonstrated to be independent of the L locus by means of the test cross t z bip (bipunctata) x $t z t^{ers}$ (white seed), which segregated in the F_2 for the virgarcus class, the expected class demonstrating non-allelism (Bassett, unpublished data). Therefore, there are at least four independent genes controlling expression of partly colored seed coat patterns, viz., T, Z, Bip, and D (Table 1).

The development of RAPD markers for genes controlling partly colored seed coat patterns has added important support to test-cross evidence for a number of discoveries. Examples are, 1) establishing t^{cf} as a new allele at T(3), 2) confirming the allelism of z and d(14), and 3) establishing bip^{ana} as a new allele at Bip(11). RAPD markers for T were achieved first (16) and applied to the t^{cf} discovery (3). Next, a RAPD marker for Z was applied to the establishment of allelism of d and d and

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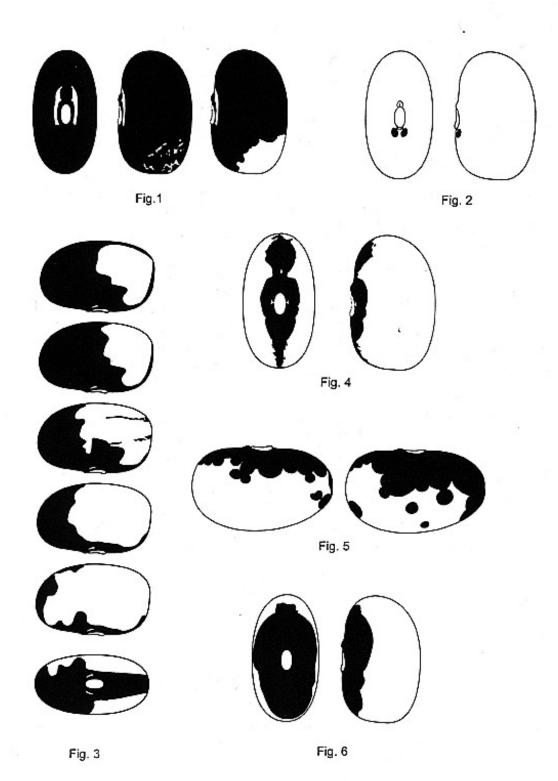
<u>Table 1</u>. Names and genotypes of partly colored seed coat patterns and RAPD markers for three of the four principal genes involved in pattern expression..

	RAPD markers	Ref.	Linkage		Partly colored patterns		
Gene symbol			cM	Phase	Genotype	Name	Figures ^a
T	OAM13 ₁₃₅₀	15	2.5	R	t Z Bip fib	Self-colored	
	OAM19 ₄₀₀	15	1.4	R	t Z Bip Fib	Expansa with fibula arcs	1
					$t^{\text{cf}} z l^{\text{ers}} ?^{\text{b}}$	Two points	2
Z	OAM10 ₅₆₀	13	1.4	C	t Z/z Bip	Ambigua	3
					t z Bip	Virgarcus	4
					$t z^{\rm sel}/z Bip$	Piebald	5
					$t z^{\rm sel} Bip$	Sellatus	6
Bip	OM9 ₂₀₀	10	5.4	C	t Z bip ^{ana}	Anasazi	7
					t z bip ^{ana}	Anabip	8
	OJ17 ₇₀₀	10	6.0	C	t z bip	Bipunctata	9
$J(l^+?)$					tZj (or tZL)	Marginata	10
					$t z l^+/l^{\rm ers}$	Weak virgarcus (Arcus)	11
					t z J/j	See footnote c	
					$t z j$ (or $t z l^{ers}$)	White	
					TZj	Margo	12
					Tzj	Margo Ad@	13

^aThe figures appear on the following two pages.

^bAn unidentified gene controls the expression of two points pattern on the otherwise white seed produced by t z l^{ers}.

^cThe pattern produced by t z J/j is different and not illustrated and may be described as Aweak bipunctata,@ i.e., an otherwise white seed having two tiny, pale gray dots, one at the raphe and the other at the micropyle. Schreiber (5) described the expression of $t z I^+/L$ as white, but that genotype (derived from his >Thuringia= source) grown at Gainesville expressed the Aweak bipunctata@ pattern of t z J/j (Bassett, unpublished data).



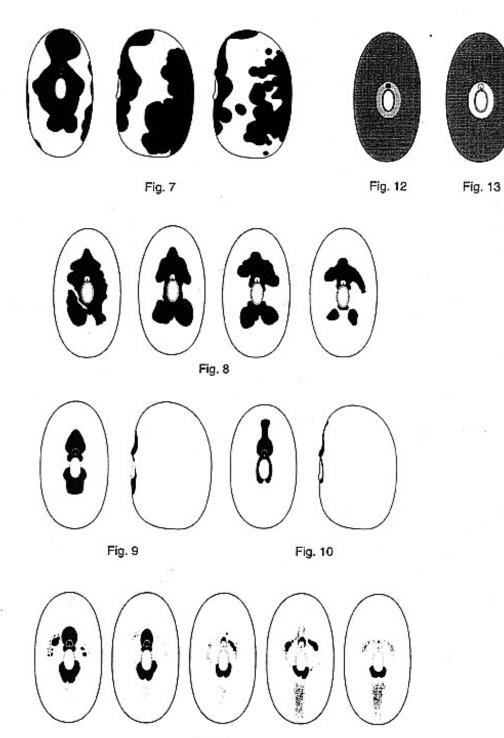


Fig. 11