Inheritance of the Anasazi Pattern of Partly Colored Seedcoats in Common Bean

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ABSTRACT. Inheritance of Anasazi pattern of partly colored seedcoats in common bean (*Phaseolus vulgaris* L.) was studied in a genetic stock *t ana B V* Anasazi BC₃ 5-593, whose Anasazi pattern is derived from Plant Introduction (PI) 451802. Line 5-593 is a determinate, Florida dry bean breeding line (with small black seeds) used as the recurrent parent in the development of many genetic stocks. The F₂ from the cross *t ana B V* Anasazi BC₃ 5-593 × *tz virgarcus* BC₃ 5-593 segregated for two nonparental phenotypic classes and was consistent with the hypothesis that a single recessive gene, with tentative symbol *ana*, produces the Anasazi pattern with *t Z ana* and a new partly colored pattern Anabip with *tz ana*. Thus, the Anasazi factor is not an allele at the Z locus. Analysis of 57 random F₃ progenies from the cross *t ana B V* Anasazi BC₃ 5-593 × *tz virgarcus* BC₃ 5-593 supported a genetic model where: 1) with *t Z* the Anasazi phenotype is controlled by a single recessive gene *ana*, i.e., genotype *t Z ana*, 2) the Anabip phenotype has the genotype *tz ana*, and 3) *t Z/z ana* produces a restricted Anasazi pattern. The allelism test cross *t z ana* Anabip BC₃ 5-593 × *t z l^{ers}* white BC₃ 5-593 produced complementation in the F₂, demonstrating nonallelism of *Ana* (actually *Bip*) with the *L* locus. The allelism test cross *t z ana* Anabip BC₃ 5-593 × *tz bip* bipunctata BC₃ 5-593 failed to show complementation in F₁ and F₂, demonstrating allelism of *Ana* with the *Bip* locus. Using bulk segregant analysis, molecular markers linked in coupling to the *Ana* (OM9₂₀₀, 5.4 cM) and *Bip* (OJ17₇₀₀, 6.0 cM) genes were discovered. Allelism was also suggested by the result that the same linkage distance and recombination pattern were observed when the *Ana* marker was used to score the bipunctata population. We propose the gene symbol *bip^{ana}* for the recessive allele at the *Bip* locus that produces Anasazi pattern with genotype *t Z bip^{ana}* and the Anabip pattern with genotype *tz bip^{ana}*. Although *bip^{ana}* and *bip* are both recessive to *Bip*, their interactions with the Z locus are extraordinarily different. The pattern restrictive power of *bip^{ana}* expresses partly colored pattern with *t Z*, whereas *bip* requires *tz* to express partly colored pattern.

The genetics of partly colored seedcoats in common bean (*Phaseolus vulgaris*) was reviewed by Leakey (1988). A recessive gene (*t/t*) enables the various genes controlling specific patterns of partly colored seed to express, whereas *T/-* gives self-colored seed. The term self-colored describes a seed without partly colored pattern. When a bean genotype is *t/t*, numerous different color patterns are possible, where part of the seed has a nonwhite color and the remainder of the seed coat is pure white. The most extensive studies of the inheritance of partly colored patterns were conducted by Lamprecht (1934, 1940), Miyake et al. (1930), Prakken (1972), and Schreiber (1934, 1940). Numerous patterns were described in these papers, and inheritance of some of the patterns was reported.

The American Indians living in cliff dwellings (130 to ≈1300 A.D.) in the four corners area of the United States (now Colorado, Utah, Arizona, and New Mexico) were named by the Navajo tribe as Anasazi, which translates roughly as the ancient ones. The cliff dwellings in question are preserved at a number of sites, the most notable being Mesa Verde National Park. These pre-Columbian inhabitants of the four corners region grew beans with the Anasazi partly colored seed pattern (Kaplan, 1956; see his Fig. 1,

seed f). This partly colored pattern is now best known by its registered trade name, Anasazi (Fig. 1), which was created by the Adobe Milling Co., Dove Creek, Colo. The Anasazi market class of beans is presently grown at 2134 m elevation on the same land the Anasazi inhabited. This paper reports the inheritance of the Anasazi pattern of partly colored seedcoats.

Materials and Methods

A set of genetic stocks was developed, each of which has a different genotype (one or more recessive alleles) for seedcoat color or pattern substituted into a genetic background that has dominant genes at all the other loci affecting seedcoat color or pattern. The backcross method was used to create those stocks, using the Florida dry bean breeding line 5-593 as the recurrent

Fig. 1. The left seed (ventral view); Anasazi partly colored seedcoat pattern. The right two seeds (side views); Anasazi pattern.

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Fig. 2. The left seed (ventral view); virgarcus partly colored seedcoat pattern. The right seed (side view); virgarcus pattern.

Fig. 3. The left seed (ventral view); bipunctata partly colored seedcoat pattern. The right seed (side view); bipunctata pattern.

seed size, and shiny black seeds with the seedcoat genotype *T P [Cr]DJGBVRk* (Bassett, 1994, 1996a; Bassett and Blom, 1991; Prakken, 1970).

PI 451802 has indeterminate plant habit and the Anasazi pattern (Fig. 1) of partly colored seedcoats, where the colored area is red, probably due to the red kidney gene *rk*. There is a groove in the seedcoat surface at the border of the colored and noncolored zones, but there is no difference in the color of the red area and the border line groove. The genetic tester stock *t V* self-colored BC₂ 5-593 has black seeds and was developed by backcrossing the *t* allele from 'Early Wax' snap bean into 5-593 (Bassett and Blom, 1991).

In Fall 1989, the cross PI 451802 x 5-593 was made and the F₁ was grown in the greenhouse in Winter 1990. The F₂ was grown in the field in Spring 1990, and selection was made for compact determinate habit and seeds with the Anasazi partly colored pattern in black and white. The F₃ progeny, grown in the greenhouse in 1990, segregated for plants having seeds with Anasazi pattern (Fig. 1), pale greenish yellow color (due to genotype *g b v*), and the circumlineatus character (Prakken, 1972). The border between the pale greenish yellow and white areas was marked with a narrow orange line that followed a groove in the seedcoat surface. This character, named circumlineatus, is controlled by the single recessive gene *cl* (Prakken, 1972). Even small dots of color were entirely circumscribed with the orange border line and groove. Plants with seeds showing the pale greenish yellow color and circumlineatus character were progeny tested in the field in 1991, and a true breeding F₄ with 30 plants was selected. The progeny derived by self-pollination of that selection was designated F₅ *t v* circumlineatus Anasazi.

In Fall 1991, the cross F₅ *t v* circumlineatus Anasazi x *t V* self-colored BC₂ 5-593 was made in the greenhouse and the F₂ seeds were produced in Winter 1992. In Spring 1993, F₃ progeny tests

were made using 24 randomly selected F₂ parents (produced in Winter 1993 greenhouse) from the cross F₅ *t v* circumlineatus Anasazi x *t V* self-colored BC₂ 5-593. Selection was made for segregants with Anasazi pattern in black and white seedcoat color, which were designated *t ana B V* BC₁-F₃ 5-593. The tentative gene symbol *ana* denotes the recessive factor (data presented below) controlling Anasazi pattern, but whether the *ana* locus is new or *ana* is a new allele at a previously reported locus controlling partly colored seedcoat patterns has not been established. In Fall 1993, the cross *t ana B V* BC₁-F₃ 5-593 x 5-593 was made, and the F₂ progeny were field planted in Spring 1994. Selection was made for segregants with Anasazi pattern in black and white seedcoat color, which were designated *t ana B V* BC₂ 5-593. In Fall 1994, the cross *t ana B V* BC₂ 5-593 x 5-593 was made, and the F₂ was field planted in Spring 1995. Selection was made for a segregant with Anasazi pattern in black and white seedcoat color, which was designated *t ana B V* Anasazi BC₃ 5-593.

Development of the genetic stocks *t z* virgarcus BC₃ 5-593 (Fig. 2) and *t z bip* bipunctata BC₃ 5-593 (Fig. 3) was described previously (Bassett, 1996b). The development of the white seedcoat genetic stock *t z l^{ers}* white BC₃ 5-593 was described elsewhere (Bassett, 1997).

In Fall 1995, the cross *t ana B V* Anasazi BC₃ 5-593 x *t z* virgarcus BC₃ 5-593 was made, and the F₂ was field planted in Spring 1996. Data were recorded on seedcoat pattern in the F₁ and F₂. In Fall 1996, remnant F₂ seed of the cross *t ana B V* Anasazi BC₃ 5-593 x *t z* virgarcus BC₃ 5-593 was used to produce F₃ seed from 57 random F₂ plants. The F₃ seed was planted in the field in Spring 1997, and data were recorded on seedcoat pattern in F₂ and F₃. Selection was made in F₃ for a true breeding plot with seedcoat pattern Anabip (Fig. 4), which has the genotype and designation *t z ana* Anabip BC₃ 5-593.

In Fall 1997, two additional allelism test crosses were made, viz., *t z ana* Anabip BC₃ 5-593 x *t z l^{ers}* white BC₃ 5-593 and *t z ana* Anabip BC₃ 5-593 x *t z bip* bipunctata BC₃ 5-593. The F₂ generation from both crosses was planted in the field in Spring 1998, and data were taken on seedcoat pattern in F₁ and F₂.

Bulk segregant analysis was performed to isolate markers linked to the genes *Ana* and *Bip*. For *Bip*, an F₂ population of 38 plants from the cross *t z bip* bipunctata BC₃ 5-593 x *t z Bip* virgarcus BC₃ 5-593 was grown in the greenhouse, and the seedcoat phenotype of the progeny was classified. For *Ana*, an F₂ population of 72 plants from the cross *t ana B V* BC₃ 5-593 x *t z* virgarcus BC₃ 5-593 was grown

in the greenhouse, and the seedcoat phenotype was classified. DNA isolation, randomly amplified polymorphic DNA (RAPD) identification, and linkage analysis were performed as described in Brady et al. (1998). For the *Ana* experiment, the *Ana* bulk consisted of DNA from F₂ plants with self-colored seed, and the *ana* bulk consisted of DNA from F₂ plants with Anasazi seedcoat pattern. For the *Bip* experiment, the *Bip* bulk consisted of DNA from F₂ plants with the virgarcus seedcoat pattern, and the *bip* bulk consisted of DNA from F₂ plants with bipunctata seedcoat pattern.

Fig. 4. Ventral view of the Anabip partly colored seedcoat pattern.

Table 1. Segregation for partly colored seedcoat patterns in the F₂ from the cross *t ana B V* Anasazi BC₃ 5-593 (Z) × *t z virgarcus* BC₃ 5-593 (*Ana*).

Combined ^z Z/- <i>Ana</i> /-	Anasazi Z/- <i>ana/ana</i>	Virgarcus z/z <i>Ana</i> /-	Anabip z/z <i>ana/ana</i>	χ^2 9:3:3:1	<i>P</i>
96	34	33	7	1.420	0.70

^zCombined refers to the phenotypic classes self-colored, expansa, and ambigua. The expansa pattern is mostly colored, but has a small white region on the dorsal side near the micropyle end of the seed. The ambigua pattern is mostly colored, but the extent of the colored zone varies greatly from ≈50% (mostly on the ventral side and skewed to the raphe end of the seed) to ≈75% or more.

Results and Discussion

Previous observations made during development of the *t ana B V* Anasazi BC₃ 5-593 genetic stock showed that a single recessive gene in addition to *t* was sufficient to transform self-colored or expansa seedcoats to the Anasazi pattern (data not presented), but the locus of the Anasazi factor was unknown. The cross *t ana B V* Anasazi BC₃ 5-593 (Z) × *t z virgarcus* BC₃ 5-593 (*Ana*) was an allelism test to determine whether the *Ana* locus is the same as the *Z* locus. The F₁ plants had seed coats with the expansa pattern (data not presented). The F₂ from the above cross segregated for two nonparental phenotypic classes (Table 1). The four phenotypic classes fit a 9:3:3:1 segregation ratio for the combined class (self-colored, expansa, and ambigua), Anasazi, virgarcus, and Anabip phenotypes, respectively. The expansa and ambigua patterns are described (Table 1, footnote z). The genetic hypothesis is that the Anasazi parent carries *Z*, and the virgarcus parent carries *Ana*; thus, clear two-locus segregation was observed (Table 1). A new partly colored seedcoat pattern with the hypothetical genotype *t z ana* was observed and named Anabip (Fig. 4). Clearly, the Anasazi factor is not an allele at the *Z* locus.

An F₃ progeny test was performed, using remnant F₂ seed of the cross *t ana B V* Anasazi BC₃ 5-593 (Z) × *t z virgarcus* BC₃ 5-593 (*Ana*), to provide an independent test for the hypothesis that the Anasazi factor is a single recessive allele and for the hypothetical genotype for the Anabip class. Results of the F₃ progeny test are presented in Table 2. Either the expected segregation or the expected true breeding progeny was observed for each of the nine expected genotypes from the F₂, and the frequencies of F₃ progenies falling into each of the nine genetic segregation classes gave a satisfactory fit to the expected 1:2:1:2:4:2:1:2:1 ratio

(Table 2). The three genotypes segregating at the *Ana* locus in Table 2 each gave a satisfactory fit to the expected segregation for 3 non-Anasazi to 1 Anasazi or Anabip. Thus, the hypotheses that a single recessive gene controls Anasazi and that the *t z ana* genotype expresses the Anabip pattern are supported. The genotype *t/t Z/z ana/ana* gave a more restricted Anasazi pattern, termed weak Anasazi, than *t/t Z/Z ana/ana* (Table 2). The variability within each class (Anasazi or weak Anasazi) is too great for error-free classification in F₂, but with progeny testing the truly restrictive effect of the heterozygote *Z/z* becomes apparent.

A test cross, viz., *t z ana* Anabip BC₃ 5-593 × *t z l^{ers}* white BC₃ 5-593, was made to determine whether the *Ana* factor is an allele at the *L* locus. The F₁ plants had seedcoats with the weak virgarcus pattern (illustrated previously by Bassett, 1997; data not presented). Because the *l⁺/l^{ers}* genotype is completely epistatic to all genotypes at *Z* and *Ana*, one must examine the F₂ for evidence of complementation. The F₂ segregated for the nonparental class, virgarcus, which is expected as evidence of complementation (Table 3). Although the frequency of virgarcus segregants was lower than expected, the presence of this class is firm evidence of nonallelism between the *Ana* locus and the *L* locus. The expected ratio of the three classes was 9 weak virgarcus and Anabip, 3 virgarcus, and 4 pure white, respectively. Possibly the *t z l^{ers}* white BC₃ 5-593 parent carries the dominant fibula arcs factor, which restricts virgarcus to arcs, a pattern similar to virgarcus (Bassett, unpublished data). Thus, only 1/16 of the F₂ would be virgarcus.

A test cross, *t z ana* Anabip BC₃ 5-593 × *t z bip* bipunctata BC₃ 5-593, was made to determine whether the *Ana* factor is an allele at the *Bip* locus. The F₁ plants had seedcoats with a pattern very close to the Anabip parent, but slightly more restricted; hence, it was named near Anabip (data not presented). The F₂ segregated

Table 2. Segregation for partly colored seedcoat patterns in F₃ progenies of 57 randomly selected F₂ progeny from the cross *t ana B V* Anasazi BC₃ 5-593 (Z) × *t z virgarcus* BC₃ 5-593 (*Ana*).

F ₂ plant phenotype ^z	Genetic hypothesis	No. of F ₃ progenies ^y	Self-c/exp/amb ^z Z/- <i>Ana</i> /-	Anasazi Z/- <i>ana/ana</i>	Virgarcus z/z <i>Ana</i> /-	Anabip z/z <i>ana/ana</i>	χ^2 (ratio tested)	<i>P</i> value
Self-colored	Z/Z <i>Ana/Ana</i>	6	268					
Self-colored	Z/Z <i>ana/ana</i>	2	72	22			0.128 (3:1)	0.72
Anasazi	Z/Z <i>ana/ana</i>	4		142				
Self-c/exp ^z	Z/z <i>Ana/Ana</i>	11	358		131		0.835 (3:1)	0.36
Exp/amb ^z	Z/z <i>Ana/ana</i>	19	447	159	174	43	4.587 (9:3:3:1)	0.21
Weak Anasazi ^x	Z/z <i>ana/ana</i>	8		209		64	0.353 (3:1)	0.55
Virgarcus	z/z <i>Ana/Ana</i>	3			103			
Virgarcus	z/z <i>Ana/ana</i>	3			70	15	2.451 (3:1)	0.12
Anabip	z/z <i>ana/ana</i>	1				35		

^zSelf-c = self-colored, exp = expansa, amb = ambigua. The self-c/exp name, for example, indicates that both self-colored and expansa progeny were observed; similarly for self-c/exp/amb. The orthogonal contrasts of Mather (1957) for the data gave $\chi^2_Z = 0.820$, $P = 0.37$; $\chi^2_{Ana} = 0.091$, $P = 0.76$; and $\chi^2_L = 3.676$, $P = 0.06$.

^yFor the data 6, 2, 4, 11, 19, 8, 3, 3, 1 the χ^2 (1:2:1:2:4:2:1:2:1) = 13.526, $P = 0.10$.

^xThe term weak means that the Anasazi pattern was more restricted than normal, i.e., the colored zone pattern was entirely, or nearly so, absent from the dorsal side of the seed.

Table 3. Segregation for partly colored seedcoat patterns in the F₂ from the cross *t z ana* Anabip BC₃ 5-593 x *t z l^{ers}* white BC₃ 5-593.

Weak virgarcus ^{z,y} and Anabip ^x <i>l⁺/l^{ers}</i> -/- <i>z</i>				
<i>l⁺/l⁺</i> Ana/ <i>ana</i> ^y	Pure white <i>l^{ers}/l^{ers}</i> -/-	Virgarcus <i>l⁺/l⁺</i> Ana/ <i>Ana</i>	χ^2 12:3:1 ^w	<i>P</i>
163	43	18	1.316	0.52

^zThe genotype *t z l⁺/l^{ers}* is epistatic to the genotypes at the *Ana* locus.

^yThe genotype *t z Ana/ana* is expected to produce virgarcus pattern, but the parent *t z l^{ers}* white BC₃ 5-593 probably carries the fibula arcs factor, which restricts virgarcus to arcus (similar to weak virgarcus) (Bassett, unpublished data).

^xThe genotype *t z l⁺ ana* produces the Anabip pattern.

^wFor the data, 181 other and 43 pure white, the χ^2 (13:3) = 0.029, *P* = 0.86.

Table 4. Segregation for partly colored seedcoat patterns in the F₂ from the cross *t z ana* (*bip^{ana}*) Anabip BC₃ 5-593 x *t z bip* bipunctata BC₃ 5-593.

Anabip ^z <i>bip^{ana}</i> -/-	Bipunctata <i>bip/bip</i>	χ^2 3:1	<i>P</i>
229	62	2.118	0.15

^zThe Anabip class includes segregants with the near Anabip pattern of the F₁ plants (F₂ seed) from the above cross. The genetic hypothesis is that *ana* is an allele at the *Bip* locus, which is given the symbol *bip^{ana}*.

for only two unambiguous phenotypic classes, which correspond to the parental phenotypes and fit a ratio of 3 Anabip (or near Anabip) to 1 bipunctata, respectively. The near Anabip and true Anabip were combined and were clearly distinguishable from the bipunctata segregants (Table 4). The absence of complementation, i.e., the failure of virgarcus segregants to appear in the F₂, gives strong support for the hypothesis of allelism between the *Ana* locus and the *Bip* locus. We propose the gene symbol *bip^{ana}* for the recessive allele at *Bip*, which with *t Z* can convert self-colored or expansa to Anasazi pattern. The *bip^{ana}* allele is strongly, but not completely, dominant to *bip*, i.e., the near Anabip (*bip^{ana}/bip*) pattern is nearly identical to the Anabip (*bip^{ana}/bip^{ana}*) pattern, not a midparent intermediate between

Anabip and bipunctata (*bip/bip*). Thus, the dominance order is *Bip* > *bip^{ana}* > *bip*.

The pattern restricting power of *bip^{ana}* is greater than that of *bip*. With *t Z*, the *bip^{ana}* allele can restrict expansa to Anasazi, whereas the weaker *bip* allele has no expression with *t Z*. The genotypes *t Z bip* and *t Z Bip* both produce expansa pattern. The *bip* allele relies on the boost from *z* to convert virgarcus (*t z Bip*) to bipunctata (*t z bip*).

The hypothesis of allelism between the *Bip* and *Ana* loci

was supported further by molecular marker data. Bulk segregant analysis and subsequent genetic characterization of two populations identified RAPD markers linked to *bip^{ana}* and *bip*. For the *bip* analysis, the segregating population fit the expected 3 virgarcus : 1 bipunctata ratio (*P* = 0.58). Our bulk-segregant analysis revealed a molecular marker (OJ17₇₀₀, Fig. 5A) linked in coupling to *Bip* at a Kosambi (1944) distance of 6.0 cM (2/38 recombinants). The segregation of the Anasazi population fit the expected 9 self-colored : 3 virgarcus : 3 Anasazi : 1 Anabip ratio (*P* = 0.99). Analysis of this population identified the marker OM9₂₀₀ linked in coupling to *Ana* (*Bip*) at a Kosambi distance of 5.4 cM (4/72 recombinants). Fig. 5B shows the polymorphic band in the population segregating for *bip*.

Because the genetic evidence suggested an allelic relationship between the Anasazi and bipunctata phenotypes, we wished to see if our molecular markers would support this conclusion. We applied our markers by analyzing each population with the complementary marker. When the population segregating for the Anasazi pattern was scored with the marker linked to *Bip* (OJ17₇₀₀), the same recombination pattern between seedcoat phenotype and this second marker was observed. Likewise, the same molecular pattern was observed when the bipunctata population was screened with the *Ana* (*Bip*) marker (OM9₂₀₀). (See Fig. 5A and B for comparison). This allowed us to make two conclusions. First, the analysis of the two independent populations allows us to conclude that the two markers cosegregate. Furthermore, the fact that each phenotype is linked at the same distance to two independently derived markers provides further substantiation of the close (or allelic) genetic relationship between the Anasazi and bipunctata phenotypes.

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Fig. 5. Molecular markers linked to the Anasazi and bipunctata phenotypes. (A) segregation of the OJ17₇₀₀ RAPD marker linked in coupling to *Bip*. The phenotypes associated with each lane are bipunctata (1, 4, 5), and virgarcus (2, 3, 6, 7, 8, 9, 10). Lane 2 represents a recombinant F₂ plant. (B) segregation of the OM9₂₀₀ RAPD marker linked in coupling to *Ana* (*Bip*). The same F₂ plants were scored as in Fig. 5A.