

F₁ hybrid weakness in the common bean

Differential geographic origin suggests two gene pools in cultivated bean germplasm

ABSTRACT: The geographic origin of cultivars involved in F₁ hybrid weakness was established using phaseolin type, as determined by one-dimensional SDS/PAGE. In all cases investigated, F₁ weakness arose in crosses between an 'S' phaseolin, small-seeded parent of Middle American origin and a 'T' or a 'C' phaseolin, large-seeded parent of Andean origin. The appearance of F₁ hybrid weakness reflects the geographical isolation of common bean cultivars of the two regions and points to the existence of two separate gene pools in cultivated common bean germplasm.

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ELECTROPHORETIC ANALYSIS of phaseolin, the major seed storage protein of the common bean (*Phaseolus vulgaris* L.), revealed a wide range of variability for this protein among wild-growing genotypes⁹. In Middle America, wild beans exhibited the 'S' phaseolin type—previously described among cultivated beans—as well as the highly diverse 'M' phaseolin class. Colombian wild beans exhibited both the diverse 'CH' phaseolin class and the 'B' phaseolin type. In Peru and Argentina, wild beans exhibited only the 'T' phaseolin pattern. Six phaseolin patterns were found among cultivated common bean genotypes: 'A', 'B', 'C', 'H', 'S', and 'T'^{3,9,13,14}. There was a correspondence between the geographical distribution of phaseolin types in wild and cultivated genotypes. In addition, 'S' and 'B' phaseolin cultivars tended to have smaller seed than 'A', 'C', 'H', and 'T' phaseolin cultivars⁹.

These findings have led to the hypothesis of multiple domestications of cultivated common beans along the distribution area of its wild relative. In Middle America, domestication gave rise to small-seeded, 'S' phaseolin cultivars; in Colombia to small-seeded, 'B' phaseolin cultivars; and in the southern Andes (Peru and Argentina) to large-seeded, 'T' (and possibly 'A', 'C', and 'H') cultivars⁹. World-wide dissemination patterns of common bean cultivars were determined using phaseolin type as a marker⁹.

The existence of a trait such as phaseolin type allows us to distinguish between Middle

American and Andean wild or cultivated beans and to trace the origin of common bean cultivars back to either of these regions. The objective of the present study was to determine whether any geographical pattern, as determined by phaseolin type, could be detected among the cases of F₁ hybrid weakness that have been reported previously in the literature.

Materials and Methods

Seed used for the analysis of phaseolin and for the measurement of seed sizes were kindly supplied by R. Hannan (Western Regional Plant Introduction Station, USDA, Pullman, Washington, USA) and Drs. R. Hidalgo H. and S.P. Singh (Centro Internacional de Agricultura Tropical, Cali, Colombia).

One-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE) of phaseolin and measurement of seed sizes were performed as described by Gepts⁹.

Results

Phaseolin type analysis

A survey of the literature provided several examples of crosses leading to F₁ hybrid weakness. For some of these cases we were able to obtain the parental genotypes involved in the crosses and to analyze their phaseolin by one-dimensional SDS/PAGE. We provide here a short summary of each of the cases of

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F₁ hybrid inviability studied. Phaseolin types of the parental genotypes are shown in Tables I and II.

First case: Coyne⁵: The cross PI209806 ('Yelloweye'; Kenya) × 'Great Northern' (GN) Nebraska No. 1 (USA) gave rise to 'crippled' plants in the F₂ and F₃ generations. Segregation data suggested that the 'crippled' trait was controlled by two complementary recessive genes.

Our analysis of the seed proteins indicates that PI209806 has a 'T' phaseolin type and GN Nebraska No. 1 an 'S' phaseolin (Table I).

Second case: Shii et al.^{19,20}: 'Crippled' plants developed in the F₁ of the Cuilapa 72 (Guatemala) × Bolivia 6 (Bolivia) cross. The F₁ plants were characterized by retarded growth, chlorosis of the trifoliolate leaves, the formation of adventitious roots on the hypocotyl, and reduced root growth. The intensity of the phenotypic aberrations was increased at higher temperatures. Genetic analysis of the F₂ and BC progenies revealed that the trait is under the control of two complementary loci (*DL*₁ and *DL*₂), the severity of the abnormalities being dependent on the allelic dosage. No reciprocal differences were observed. Grafting experiments indicated that *DL*₁ (derived from Cuilapa 72) and *DL*₂ (derived from Bolivia 6) control a root and a shoot factor, respectively. Alleviation of reduced root growth by exogenous cytokinins might indicate that *DL*₁ and *DL*₂ affect the hormonal metabolism.

One-dimensional SDS/PAGE showed Cuilapa 72 and Bolivia 6 to have an 'S' and a 'T' phaseolin, respectively (Table I).

Third case: York and Dickson²⁵: Reciprocal crosses between PI165435 (Mexico) on one hand and 'Maestro' or 'Spartan Arrow' (USA) on the other hand gave rise to 'crippled' F₁ plants characterized by chlorotic primary leaves, the absence of trifoliolate leaves, degeneration of the tap root, and development of adventitious roots on the stem just above the soil line. Genetic analysis of the F₂ and BC generations of the 'Maestro' × PI165435 cross showed that the 'cripple' character resulted from the interaction of two dominant genes.

PI165435 showed an 'S' phaseolin, 'Maestro' a 'T' phaseolin, and 'Spartan-Arrow' a 'C' phaseolin (Table I).

Fourth case: Osborn and Bliss (pers. comm.): F₁ plants of the cross between Bush Blue Lake (BBL) 274 and Rosinha 6-1 (Brazil) were characterized by the absence of roots.

Analysis of the seed proteins showed that BBL 274 has a 'T' phaseolin and Rosinha 6-1 an 'S' phaseolin (Table I).

Fifth case: Provvidenti and Schroeder¹⁶: These authors described three abnormalities—seedling wilt, leaf rolling, and apical chloro-

sis—in the progeny of the 'Red Kidney' × 'Black Turtle' cross. Seedling wilt and leaf rolling were conditioned by two complementary recessive genes.

Although it was not possible to determine the phaseolin type of the original genotypes used in their study, kidney beans generally have a 'T' phaseolin type and small black beans (e.g. 'Black Turtle') have an 'S' phaseolin⁴.

Sixth case: Singh²¹, Singh and Gutierrez²²: At the Centro Internacional de Agricultura Tropical, Cali, Colombia, some of the crosses between small and medium or large seeded cultivars yielded hybrid dwarfs, similar to the ones described by Shii et al.²⁰

The phaseolin type of the parental genotypes involved in the crosses producing hybrid dwarfism was determined by one-dimensional SDS/PAGE. In all cases, the small-seeded parent had an 'S' phaseolin and the large seeded parent a 'T' or a 'C' phaseolin (Table II).

Seed size analysis

Seed of the genotypes with a 'T' or a 'C' phaseolin type were significantly larger than seed of genotypes with an 'S' phaseolin type. No differences in seed size were observed be-

tween 'T' and 'C' phaseolin cultivars (Table III).

Discussion

The results reported here indicate that without exception the observed cases of F₁ hybrid weakness arose in crosses between small-seeded cultivars having an 'S' phaseolin on the one hand, and large-seeded cultivars with a 'T' or 'C' phaseolin type on the other hand. Because these two types of cultivars were hypothesized to have originated in Middle America and the Andes, respectively, the occurrence of these cases of F₁ hybrid weakness may actually reflect a differential geographic distribution of the weakness-inducing genes.

Within Middle America or the Andes, this F₁ hybrid weakness seems to have been selected against since no cases were observed in crosses where both parents had an 'S' or 'T' or 'C' phaseolin or where both parents were either small- or large-seeded. The appearance of F₁ hybrid weakness may be seen as a consequence of the geographical isolation between the cultivars of middle America and the Andes.

The phenotypic expression of F₁ hybrid weakness, as described by the different authors, seemed to differ according to the cross

Table I. Phaseolin types and seed sizes of parental genotypes involved in F₁ hybrid weakness

Source	Genotype (country of origin)	Phaseolin type	Seed size (mm)		
			length	height	width
Coyne ⁵	PI209806 (Kenya)	'T'	12.5	7.7	6.5
	GN Nebraska No. 1 (USA)	'S'	12.3	7.6	5.2
Shii et al. ¹⁹	Cuilapa 72 (Guatemala)	'S'	10.4	6.5	4.2
	Bolivia 6 (Bolivia)	'T'	13.9	6.8	4.8
York and Dickson ²⁵	PI165435 (Mexico)	'S'	9.1	6.0	5.6
	'Maestro' (USA)	'T'	13.1	5.7	4.8
	'Spartan Arrow' (USA)	'C'	14.4	6.2	4.7
Osborn and Bliss (pers. comm.)	BBL 274 (USA)	'T'	12.8	5.8	5.6
	Rosinha 6-1	'S'	8.6	5.9	3.7
Singh ²¹	BAT332*	'S'	9.3	6.0	4.4
	BAT1061*	'S'	8.5	5.4	4.5
	'Carioca' (Brazil)	'S'	10.2	6.5	4.9
	G153 (Turkey)	'C'	12.5	9.0	6.7
	G568 (Turkey)	'T', 'C'	12.8	9.7	6.8
	G623 (Turkey)	'C'	13.5	9.3	6.6
	G5066 (Brazil)	'T'	11.3	7.5	5.4
	G5129 (Brazil)	'T'	15.3	8.1	5.5
	G7148 (Brazil)	'S'	9.9	6.1	4.5
	G7613 (Spain)	'T'	16.8	8.3	5.7
G7633 (France)	'T'	11.6	8.3	6.3	
Linea 23 ¹	'T'	14.0	7.3	5.0	
'Tortolas Diana' (Chile)	'C'	11.2	8.2	6.6	

*Breeding line of the Centro Internacional de Agricultura Tropical, Cali, Colombia

¹Breeding line of the Instituto Colombiano Agropecuario, Palmira, Valle, Colombia

This may be due to the existence of different physiological or biochemical mechanisms (and genes) leading to F₁ hybrid weakness or to the same mechanism (or genes) being expressed in different genetic backgrounds or environments. In the absence of any data from diallel crosses, we cannot at present decide between these two possibilities.

In only one case has the general biochemical lesion (hormone metabolism) been investigated²⁰. The fact that some crosses between 'S' and 'T' or 'C' phaseolin cultivars produce normal F₁ hybrids makes it unlikely that phaseolin genes are involved in the expression of F₁ hybrid weakness. The same observation can be made regarding seed size. It is possi-

ble, however, that the genes determining F₁ hybrid weakness are genetically linked to the phaseolin or any seed-size loci.

In cases where the genetic control was investigated, F₁ hybrid weakness was always controlled by two complementary genes—dominant or recessive. Other examples of F₁ hybrid weakness have been identified in *Oryza* and *Triticum*. Oka¹⁵ found that hybrid inviability arising in intervarietal *O. sativa* crosses was under the control of two complementary dominant or recessive genes. In *Triticum aestivum*, hybrid necrosis is controlled by two complementary genes—*Ne*₁ and *Ne*₂—and grass clump dwarfness by three complementary dominant genes—*D*₁, *D*₂, and *D*₃. In the two types of hybrid weakness the genes involved had different geographic distributions²⁶.

As suggested by Levin¹², there is no evidence that complementary genes involved in hybrid inviability or weakness evolved specifically to reduce introgressive hybridization. They may be genes performing essential functions in the growth and development of nonhybrid plants and only incidentally lead to F₁ hybrid weakness in *P. vulgaris*. This may be indicative of incipient geographical speciation within this species. Further divergence on an evolutionary time scale may lead to more widespread isolation barriers that are genetically and physiologically more complex.

The occurrence of F₁ hybrid weakness in crosses involving Andean and Middle American cultivars is evidence for the geographical isolation between the cultivars of these two regions. This isolation in turn could have led, on an evolutionary time scale, to genetic divergence and the establishment of an Andean and a Middle American gene pool. A gene pool is defined here as a set of genotypes characterized by similar allele frequencies and allele associations, with these sets usually displaying a geographic distribution pattern.

Preliminary indications point to the existence of two such gene pools. Cultivars of Middle American and Andean origin are characterized by different growth habits^{7,8}, isozyme variants¹, and environmental adaptations¹⁰. The dominant *I* gene for bean common mosaic virus resistance⁶ was found originally only among land races of Middle American origin, although subsequently it has been introduced by breeding into cultivars of Andean origin (S. Temple, pers. comm.).

Coevolution between the common bean plant and associated organisms such as pathogens, pests, and *Rhizobium phaseoli*, may have led to analogous gene pools in these organisms and to specific interactions with common bean gene pools. Stavely^{23,24} observed that 'red kidney' beans and snap beans,

Table II. Phaseolin types of parents involved in F₁ hybrid weakness cases observed at the Centro Internacional de Agricultura Tropical, Cali, Colombia

Parent A		Parent B	
Identification	phaseolin	Identification	phaseolin
'Carioca (Brazil) (small seeded)	'S'	G7623 (Turkey)	'C'
		G5066 (Brazil)	'T'
		G7633 (France)	'T'
G623 (Turkey) (large seeded)	'C'	'Tortolas Diana' (Chile) (all large seeded)	'C'
		'Carioca' (Brazil)	'S'
		G7148 (Brazil)	'S'
		BAT332*	'S'
		BAT1061* (all small seeded)	'S'
BAT332* (small seeded)	'S'	G153 (Turkey)	'C'
		G568 (Turkey)	'T', 'C'
		G623 (Turkey)	'C'
		G5066 (Brazil)	'T'
		G5129 (Brazil)	'T'
		G7613 (Spain)	'T'
		G7633 (France)	'T'
		Linea 23†	'T'
		'Tortolas Diana' (Chile) (all large seeded)	'C'

* Breeding line of the Centro Internacional de Agricultura Tropical

† Breeding line of the Instituto Colombiano Agropecuario, Palmira, Valle, Colombia

Table III. Statistical analysis of seed dimensions in relation to phaseolin types for cultivars involved in F₁ hybrid weakness

1. Analysis of variance	Seed dimension			
	length	height	width	
H ₀ : No differences in seed size between cultivars with different phaseolin type				
F value†	13.63***	5.74*	7.60**	
***P < 0.001; **P < 0.01; *P < 0.05; †df = 2, 18				
2. Duncan's multiple range test‡	Seed size (mm)			
Phaseolin type	No. lines	length	height	width
'T'	9	13.5‡	7.3‡§	5.5‡
'C'	4	12.9‡	8.2‡	6.2‡
'S'	8	9.8‡	6.3‡	4.4‡

‡Within each column, values followed by the same symbol are not significantly different at the P = 0.05 level

both large seeded types whose origins have been traced back to the Andes on the basis of their phaseolin types, had similar reactions to a set of 20 races of common bean rust (*Uromyces phaseoli* (Reben) Wint). The pathogen and the host may therefore have different genes for virulence and resistance, respectively, in Middle America and in the Andes. It might be worthwhile investigating whether a combination of genes for resistance from the two regions is more stable than a combination of genes from the same region.

Coevolution also might be operating in the *P. vulgaris*-*R. phaseoli* symbiosis. Differences between cultivars in the ability to fix nitrogen have been observed^{11,18}, and this trait can be genetically improved². Likewise, differences between strains in N₂ fixation ability and cultivar × strain interactions have been observed¹⁷. It is possible that *R. phaseoli* also exhibits an Andean and a Middle American gene pool.

The existence of coevolution between *P. vulgaris* and *R. phaseoli* might have consequences for common bean breeding and production. Knowledge of coevolutionary relationships may allow us to better match the host and *rhizobium* genotypes to achieve maximum levels of N₂ fixation. One or the other regions may have produced host-*rhizobium* combinations adapted to stress conditions, such as low pH or high soil temperatures that are quite prevalent in the tropics. Identification of favorable combinations might lead to new common bean production systems with higher and more stable yields.

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