New Genes, *stp* and *stp*^{hbw}, for Flower and Seedcoat Pattern in Common Bean

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Abstract. The inheritance of novel flower and seedcoat patterns was studied in three parental materials: PI 390775 and 'Springwater Half Runner' (SHR), which have patterned flower and seedcoat colors, and 5-593, a Florida dry bean breeding line with unpatterned purple flowers and seeds. Using crosses between 5-593 and the other two parents, an analysis of F₁, F₂, backcross F₂, and backcross F₃ data demonstrated that a single recessive allele in each of the patterned parents controlled flower and seedcoat pattern. Genetic tester stocks were used to demonstrate that the recessive gene for patterning in PI 390775 was nonallelic with *C*, *T*, and *Mar*, the three genes previously known to control seedcoat pattern in common bean. An allelism test between the recessive pattern genes from PI 390775 and SHR demonstrated that they were allelic and that the gene from SHR was dominant. The gene symbols *stp* (for the gene from PI 390775) and *stp*^{hbw} (for the dominant gene from SHR) are proposed, where *stp* stands for stippled seedcoat pattern and the superscript letters hbw stand for half banner white.

Prakken (1970) wrote a comprehensive, critical review of all previous work on the genetics of seedcoat colors of common bean (*Phaseolus vulgaris* L.), except for the red colors. He described two types of patterned seedcoats: the partly colored patterns that express only with the *t* gene and a very large allelic series of patterns that are controlled at the complex *C* locus. Prakken (1970) omitted reference to seedcoat patterns of the corona and margo types, but these have been described well recently by Bassett (1994a, 1995) and Leahey (1988). Bassett (1995) reported that the corona character of Lamprecht (1933) is controlled as a pleiotropic effect of the *v*^{lac} allele and is not controlled by an independent *Cor* locus.

During a visit to the plant introduction (PI) station at Pullman, Wash., in 1989, I saw a seed sample of PI 390775 on display. My intuitive judgment was that the seedcoat pattern of PI 390775 might be controlled by a gene other than the previously reported effects at *T* and *C* (Leahey, 1988; Prakken, 1970). Similarly, having obtained seed of 'Springwater Half Runner' I suspected that the inheritance of its unusual seedcoat pattern was not controlled by either *T* or *C*. The research reported herein describes inheritance studies done with two common bean materials: PI 390775 and 'Springwater Half Runner'.

Materials and Methods

The accession PI 390775 was selected for study based on its seedcoat appearance. It had an unusual seedcoat pattern that was not in the published literature, viz., it is covered with small colored dots (stippling) on a cartridge buff (beige) background. In some genetic backgrounds, the dotting coalesces to produce a fine marbling pattern (Fig. 1). The range of variation, observed in materials that have the stippled character in BC₁ to 5-593, is illustrated by the extremes of the range (Fig. 1). PI 390775 also has

Fig. 1. Drawings of seeds with the stippled pattern controlled by *stp*: upper seeds show the most extensive dark pattern color; lower seeds show the least extensive dark pattern color.

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Fig. 2. The flower on the left illustrates the color pattern controlled by *stp^{hbw}*; the flower on the right illustrates the color pattern controlled by *stp*.

Fig. 3. Drawings of seeds with the stippled pattern controlled by *stp^{hbw}*.

a unique flower color pattern. The banner petal is white except for a violet tip, and the wing petals are white except for a 2- to 3-mm violet border (Fig. 2, flower on right).

In 1989, 'Springwater Half Runner' (SHR) seeds were obtained from the Ferry Morse Seed Co. The seedcoat has a pattern similar to that of PI 390775 in that most of the seedcoat is stippled, but the stippling patterns are less variable than that of the PI (Fig. 3). The dark pattern color is solid in the hilum ring and corona region. The immediate micropyle area is stippled, but a solid dark pattern color surrounds the micropyle and continues over most of the micropyle end of the seed. The pattern is similar to many seed types with the margo (*mar*) character, except that the remainder is stippled instead of solidly colored in light pattern color. The flower color pattern has not been reported in the literature. The lower half of the banner petal is white or nearly white (Fig. 2).

Florida dry bean breeding line 5-593 was used as the recurrent parent in the study. The line has a determinate habit, purple flowers, and shiny black seedcoats. The seedcoat genotype of 5-

593 is *P[C r]DJGBVRk* (Bassett, 1994b; Prakken, 1970, 1972).

A program to develop genetic tester stocks, each with one or more recessive marker genes for seedcoat color or pattern backcrossed into the recurrent parent 5-593, was initiated in 1985. Details of the backcross procedure are described by Bassett (1994c). The tester stock, *t* BC₂ 5-593, has white flowers due to *t* (derived from 'Early Wax'), but self-colored black seeds due to having the genes in 5-593 that fully extend dark pattern color in the presence of *t* (Bassett and Blom, 1991). The tester stock, *c^u* BC₂ 5-593, was derived from 'Prakken 75' an all-recessive tester stock obtained from R. Prakken of the Netherlands (Bassett, 1994d). The tester stock, *mar* BC₁ 5-593, was derived from Lamprecht line V0553 (now PI 527753) and has dull, dark purple seeds (if grown in greenhouse) with a black hilum ring and nearly white corona (Bassett, 1994a). If the stock is grown in the field, the margo region is dark purple, but the remainder of the seedcoat is brown.

Crosses with PI 390775. The cross PI 390775 x 5-593 was made in 1989 and the F₂ progeny were grown in the field in 1991. All F₂ plants with indeterminate habit were rogued from the plot at the time the determinate segregants began flowering. Data were taken on flower and seedcoat color in the F₁ and for all determinate F₂ progeny. Selection was made in the F₂ for plants with the flower and seedcoat type of PI 390775 but the determinate habit of 5-593. Plants with the stippled seeds and patterned flower color were labeled STP plants.

An F₂ STP plant was progeny tested in the greenhouse and an F₃ progeny plant was used in the backcross F₃ STP x 5-593. The F₂ progeny were planted in the field in 1991. Data were taken on flower and seedcoat color and color pattern in the F₁ and F₂. Selection was made in the BC₁-F₂ for STP plants. Remnant BC₁-F₂ seed were planted in the greenhouse in 1993 and the BC₁-F₃ progenies were planted in the field in separate plots in 1994. The same type of data were taken as in the BC₁-F₂.

A single BC₁-F₂ STP plant was progeny tested in the greenhouse and a BC₁-F₃ STP progeny plant was selected for use in a series of test crosses for allelism: BC₁-F₃ STP x *c^u* BC₂ 5-593, *t* BC₂ 5-593 all black x BC₁-F₃ STP, and BC₁-F₃ STP x *mar* BC₁ 5-593. The F₂ of the first cross was planted in the field in 1992 and the F₂ of the latter two crosses were planted in the field in 1993. Data were taken on flower and seedcoat color and color pattern in the F₁ and F₂ progenies.

Crosses with SHR. In 1990, the cross SHR x 5-593 was made, and the F₂ was planted in the field in 1991. Data were taken on flower and seedcoat color and color pattern in the F₁ and F₂. Selection was made in the F₂ for plants with the flower and seedcoat color patterns of SHR, but having the determinate habit of 5-593.

An SHR-type F₂ selection was progeny tested in the greenhouse

Table 1. Segregation for flower and seedcoat pattern in the F₂ from the following crosses: 1) PI 390775 x 5-593 and 2) F₃ STP x 5-593.

Cross	Unpatterned flowers and seedcoats ^z	Patterned flowers and seedcoats ^y	χ^2 3:1	<i>P</i> value
1	57	9	4.546	0.033
2	105	27	1.455	0.22

^zFor cross no. 1, the flowers were bishops violet and the seedcoats were either black or unpatterned dark purple (the latter probably due to *P C J G b V*); for cross no. 2, the flowers were bishops violet and the seedcoats were black.

^yThe flowers had white banner petals with violet tips and white wing petals with 2- to 3-mm violet borders; the seedcoats had a stippled pattern in black dots on cartridge buff.

Table 2. Segregation for flower and seedcoat pattern in the F_3 progenies from 27 randomly selected F_2 parents from the cross F_3 STP x 5-593.^z

Genotype of F_2 parent	Unpatterned flowers and seedcoats ^y	Patterned flowers and seedcoats ^x	χ^2 3:1 ^w	P value
<i>Stp/Stp</i>	43			
<i>Stp/Stp</i>	48			
<i>Stp/Stp</i>	40			
<i>Stp/Stp</i>	46			
<i>Stp/Stp</i>	38			
<i>Stp/Stp</i>	44			
<i>Stp/Stp</i>	42			
<i>Stp/Stp</i>	49			
<i>Stp/Stp</i>	40			
<i>Stp/Stp</i>	41			
<i>Stp/stp</i>	33	11	0.00	1.00
<i>Stp/stp</i>	34	12	0.029	0.87
<i>Stp/stp</i>	34	10	0.121	0.73
<i>Stp/stp</i>	37	8	1.252	0.26
<i>Stp/stp</i>	29	15	1.939	0.16
<i>Stp/stp</i>	36	10	0.261	0.61
<i>Stp/stp</i>	30	9	0.077	0.78
<i>Stp/stp</i>	31	13	0.485	0.49
<i>Stp/stp</i>	30	16	2.348	0.13
<i>Stp/stp</i>	33	13	0.261	0.61
<i>Stp/stp</i>	34	17	1.889	0.29
Total	361	134	1.132	0.29
<i>stp/stp</i>		41		
<i>stp/stp</i>		34		
<i>stp/stp</i>		23		
<i>stp/stp</i>		21		
<i>stp/stp</i>		27		
<i>stp/stp</i>		25		

^zFor six true breeding STP parents, 11 segregating normal parents, and 10 true breeding normal parents, χ^2 (1:2:1) = 2.111, P = 0.35.

^yThe flowers were bishops violet and the seedcoats were black.

^xThe flowers had white banner petals with violet tips and white wing petals with 2- to 3-mm violet borders; the seedcoats had a stippled pattern in black dots on cartridge buff.

^wThe heterogeneity of χ^2 at 10 df is 7.53; P = 0.75 – 0.50.

and an SHR-type F_3 progeny plant was used in the backcross 5-593 x F_3 SHR. The F_2 was planted in the field in 1992. Data were taken on flower and seedcoat color and color pattern in the F_1 and F_2 . Selection was made in the BC_1 - F_2 from 5-593 x F_3 SHR for plants with the flower and seedcoat traits of SHR.

Remnant BC_1 - F_2 seed were planted in the greenhouse in 1993 and the BC_1 - F_3 progenies were planted in the field in separate plots in 1994. The same type of data were taken as with the BC_1 - F_2 .

A single BC_1 - F_3 SHR selection was progeny tested in the greenhouse in Fall 1992 and a selection for BC_1 - F_3 SHR was made. A final allelism test was made by crossing BC_1 - F_3 SHR x BC_1 - F_4 STP, the latter parent being a self progeny from the BC_1 - F_3 STP parent plant described above. The F_2 was planted in the field in 1993. Data were taken on flower and seedcoat color and color pattern in the F_1 and F_2 .

Results and Discussion

Crosses with PI 390775. The F_1 plants from the cross PI 390775 x 5-593 had bishops-violet flowers and unpatterned black seedcoats (data not shown). The F_2 segregated for indeterminate and

determinate plant habit. Among the determinate segregants it was noted that the patterned flowers and patterned seedcoats always cosegregated, but there was a significant deviation from the expected 3:1 segregation for unpatterned to patterned plants, respectively, due to a shortage of the latter (Table 1). Because further investigation supported a single gene hypothesis, other genetic models were not tested. The F_2 selection with patterned flowers and seeds was demonstrated to be true breeding for those traits in an F_3 progeny test grown in the greenhouse (12 plants). The hypothesis formulated was that a single recessive gene controls the seedcoat stippling and the flower color patterning. The patterning trait was given the label STP.

The F_1 plants from the backcross F_3 STP x 5-593 had bishops-violet flowers and black seeds without any pattern in either organ. The BC_1 - F_2 segregated for only two phenotypic classes, unpatterned flowers and seeds or patterned flowers and seeds, and a satisfactory goodness of fit to a 3:1 segregation ratio was observed for the classes, respectively (Table 1). Thus, there was further support that a single locus controls patterning in flowers and seedcoats.

To critically test the single-gene hypothesis, an F_3 progeny test was conducted. The F_3 progeny of all the stippled F_2 parents were true breeding. Segregating F_3 progenies from unpatterned F_2 parents fit a 3:1 ratio of unpatterned to stippled, respectively (Table 2). There was a 1:2:1 ratio for true-breeding stippled progenies, segregating progenies, and true-breeding unpatterned progenies, respectively (Table 2). Thus, I have conclusively demonstrated that a single gene (tentatively given the symbol *stp*) controls the STP trait, but it is possible that the STP locus is an unreported allele at the *C*, *T*, or *Mar* loci, which have been previously shown to control seedcoat pattern (Leakey, 1988; Prakken, 1970).

A single BC_1 - F_2 STP selection was true breeding for the STP trait in a BC_1 - F_3 progeny test (12 plants). Three allelism tests were conducted with a single BC_1 - F_3 STP progeny plant. The F_1 plants from the cross BC_1 - F_3 STP x c^u BC_2 5-593 had unpatterned bishops-violet flowers and black seeds with very tiny cartridge buff flecks typical of C/c^u ; i.e., the phenotype was nonallelic (data not shown). The gene symbol *stp* was tentatively adopted for the locus controlling the stippled seedcoat phenotype. The hypothesis of nonallelism was confirmed in the F_2 , in which independent segregation at *C* and *Stp* was observed: 151 *C Stp*, 59 *C stp*, 45 c^u *Stp*, 13 c^u *stp* (χ^2 for 9:3:3:1 = 2.912, P = 0.41). The F_1 plants from the allelism test cross t BC_2 5-593 all black x BC_1 - F_3 STP had unpatterned bishops violet flowers and self-colored black seeds (data not shown), a nonallelic phenotype. The hypothesis of nonallelism was confirmed in the F_2 , in which independent segregation at *T* and *Stp* was observed: 171 *T Stp*, 53 *T stp*, 38 *t Stp*, 13 *t stp* (χ^2 for 9:3:3:1 = 6.348, P = 0.10). The F_1 plants from the allelism test cross BC_1 - F_3 STP x *mar* BC_1 5-593 had unpatterned bishops-violet flowers and unpatterned black seeds, a nonallelic

Table 3. Segregation for flower and seedcoat pattern in the F_2 from two crosses: 1) 'Springwater Half Runner' (SHR) x 5-593 and 2) F_3 SHR x 5-593.

Cross	Unpatterned flowers and seedcoats ^z	Patterned flowers and seedcoats ^y	χ^2 3:1	P value
1	90	29	0.025	0.87
2	105	27	1.455	0.23

^zThe flowers were bishops violet and the seedcoats were black.

^yThe flowers were bishops violet except that the lower half of the banner petal was white, and the seedcoats had the largely stippled pattern of the SHR parent.

Table 4. Segregation for flower and seedcoat pattern in the F₃ progenies from 32 randomly selected F₂ parents from the cross F₃ SHR x 5-593.²

Genotype of F ₂ parent	Unpatterned flowers and seedcoats ^y	Patterned flowers and seedcoats ^x	χ^2 3:1 ^w	P value
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	47			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	42			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	48			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	45			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	44			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	45			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	43			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	48			
<i>Stp</i> ^{hbw} / <i>Stp</i> ^{hbw}	45			
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	34	10	0.121	0.73
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	33	13	0.261	0.61
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	36	10	0.261	0.61
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	31	16	2.05	0.15
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	37	9	0.725	0.40
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	38	9	0.858	0.35
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	36	11	0.064	0.80
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	30	19	4.959	0.03
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	36	10	0.261	0.61
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	33	12	0.067	0.80
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	33	10	0.07	0.79
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	32	12	0.121	0.73
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	32	13	0.363	0.55
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	42	7	3.00	0.08
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	38	9	0.858	0.35
<i>Stp</i> ^{hbw} / <i>stp</i> ^{hbw}	39	18	1.316	0.25
Total	560	188	0.007	0.93
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		25		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		27		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		26		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		28		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		27		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		28		
<i>stp</i> ^{hbw} / <i>stp</i> ^{hbw}		27		

²For 7 true breeding SHR parents, 16 segregating normal parents, and 9 true breeding normal parents, the χ^2 (1:2:1) = 0.250, P = 0.88.

^yThe flowers were bishops violet and the seedcoats were black.

^xThe flowers had white banner petals with violet tips and white wing petals with 2- to 3-mm violet borders; the seedcoats had a stippled pattern in black dots on cartridge buff.

^wThe heterogeneity of χ^2 at 15 df is 15.348; P = 0.50 – 0.25.

phenotype. The hypothesis of nonallelism was confirmed in the F₂, in which independent segregation at *Mar* and *Stp* was observed, although a disturbed segregation occurred. The observed data were 187 *Mar Stp*, 91 *Mar stp*, 79 *mar Stp*, 38 *mar stp* (χ^2 for 9:3:3:1 = 16.954, P = 0.001. Using the orthogonal contrasts of Mather (1957), χ^2_{Mar} = 4.497, P = 0.034; χ^2_{Stp} = 12.355, P < 0.001; χ^2_L = 0.102, P = 0.75. The disturbance was due to an excess of the margo and stippled segregants, but no explanation for the highly significant deviation from expected is apparent. On the basis of the above allelism tests, it is clear that the STP character is not controlled by a new allele at any of the three known genes for seedcoat patterning, viz., *C*, *T*, or *Mar*. Thus, it is proposed that the gene symbol *stp* be formally given to the recessive allele at a new locus for stippled seedcoat pattern in common bean, now identified in PI 390775.

Crosses with SHR. The F₁ plants from the cross 5-593 x SHR had unpatterned purple (bishops violet) flowers and unpatterned

black seeds (data not shown). In the F₂ progeny, patterned flowers and patterned seedcoats always cosegregated (Table 3). The data fit to a 3:1 segregation ratio for the parental phenotypes of 5-593 and SHR, respectively, with respect to flowers and seedcoats (Table 3), and it was hypothesized that a single recessive gene controls the stippled seedcoats and patterned flowers. The combination of flower and seedcoat traits was given the label SHR. The F₂ selection for SHR flower and seedcoat type was true breeding in the greenhouse F₃ progeny test (10 plants).

The F₁ plants from the backcross 5-593 x F₃ SHR had unpatterned bishops violet flowers and unpatterned black seeds (data not shown). The BC₁-F₂ segregated for only two phenotypic classes, unpatterned flowers and seeds or patterned flowers and seeds, and the data fit to a 3:1 segregation ratio was observed for the classes, respectively (Table 3). Those data further supported the hypothesis that a single locus controls flower and seedcoat pattern.

To test the single gene hypothesis critically, an F₃ progeny test was conducted, and the gene symbol *stp*^{hbw} was tentatively given to the SHR locus (Table 4). The F₃ progeny of all F₂ parents with SHR pattern in flowers and seedcoats were true breeding. Segregating F₃ progenies from the unpatterned F₂ parents fit a 3:1 ratio of plants with patterned flowers and seeds to plants with unpatterned flowers and seeds, respectively (Table 4). The F₃ progenies segregated for a 1:2:1 ratio of true breeding SHR progenies, segregating progenies, and true breeding unpatterned progenies, respectively (Table 4). Thus, I have conclusively demonstrated that a single gene controls the SHR trait, but it is not known whether there is an allelic relationship with a previously published gene. Because there was a certain similarity between the *stp* marker from PI 390775 and the marker gene in the SHR parent, an allelism test was conducted.

The F₁ plants from the cross BC₁-F₃ SHR x BC₁-F₄ STP had the flower and seedcoat pattern of the SHR parent, which is an allelic interaction between the recessive marker gene in SHR and the *stp* gene from PI 390775 (data not shown). Thus, it appears that the allele in the SHR parent is dominant. The F₂ from the allelism test segregated for only two phenotypic classes: either the flower and seedcoat pattern of the SHR parent or the flower and seedcoat pattern of PI 390775 (Table 5). The data fit to a 3:1 segregation ratio for the two classes, respectively (Table 5). Thus, the results presented above have confirmed that the marker genes for flower and seedcoat pattern in the SHR parent and PI 390775 are allelic and that the allele from SHR is dominant. For the dominant allele, the gene symbol *stp*^{hbw} is proposed, where the superscript letters hbw stand for half banner white. The new gene symbol was based on flower color differences, which are more obvious than the differences in seedcoat patterns. Thus, the gene symbol based on flower, rather than seedcoat, patterns was deemed more appropriate.

Table 5. Segregation for flower and seedcoat pattern in the F₂ from the cross BC₁-F₃ SHR x BC₁-F₄ STP.

SHR flower and seedcoat pattern ^z	PI 390775 flower and seedcoat pattern ^y	χ^2 3:1	P value
285	107	1.102	0.29

^zPurple flowers, except that the lower half of the banner petal is white, and largely stippled seedcoats, except for a wide black corona and a black region around the micropile end of the seed.

^yWhite flowers, except for a violet banner petal tip (1–2 mm) and a violet border on the wing petals (2–3 mm), and densely stippled (fine marbling?) over most of the seedcoat, except for black regions on either side of the micropile.

Literature Cited

- Bassett, M.J. 1994a. The margo (*mar*) seedcoat character and the *t mar* interaction in common bean. J. Hered. 85:404–407.
- Bassett, M.J. 1994b. The genotype for seedcoat color of breeding line 5-593. Annu. Rpt. Bean Improv. Coop. 37:244–245.
- Bassett, M.J. 1994c. The *griseoalbus* (gray-white) seedcoat color is controlled by an allele (*p^{gr}*) at the *P* locus in common bean. HortScience 29:1178–1179.
- Bassett, M.J. 1994d. Tight linkage of purple pod character and the complex *C* locus in common bean. J. Hered. 85:288–290.
- Bassett, M.J. 1995. The dark corona character in seedcoats of common bean cosegregates with the pink flower allele *v^{lae}*. J. Amer. Soc. Hort. Sci. 120:520–522.
- Bassett, M.J. and A. Blom. 1991. A new genotype for white seedcoat discovered in ‘Early Wax’ snap bean. J. Amer. Soc. Hort. Sci. 116:131–136.
- Lamprecht, H. 1933. Zur Genetik von *Phaseolus vulgaris*. VI. Vierter Beitrag zur Vererbung der Testafarbe. Hereditas 17:249–316.
- Leakey, C.L.A. 1988. Genotypic and phenotypic markers in common bean, p. 245–327. In: P. Gepts (ed.). Genetic resources of *Phaseolus* beans. Kluwer Academic Press, Boston.
- Mather, K. 1957. The measurement of linkage in heredity. 2nd ed. Wiley, New York.
- Prakken, R. 1970. Inheritance of colour in *Phaseolus vulgaris* L. II. Critical review. Meded. Landbouwhogeschool Wageningen 70-23:1–38.
- Prakken, R. 1972. Inheritance of colours in *Phaseolus vulgaris* L. III. On genes for red seedcoat colour and a general synthesis. Meded. Landbouwhogeschool Wageningen 72-29:1–82.