

# Yield stability of determinate and indeterminate dry bean cultivars\*

J. D. Kelly<sup>1</sup>, M. W. Adams<sup>1</sup> and G. V. Varner<sup>2</sup>

<sup>1</sup> Department of Crop and Soil Sciences, Michigan State University, E. Lansing, MI 48824, USA

<sup>2</sup> Dry Edible Bean Production Research Advisory Board, Saginaw, MI 48603, USA

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Summary. Yield stability of determinate and indeterminate dry bean (Phaseolus vulgaris L.) cultivars was compared using regression of genotypic performance on environmental means. Yields of 28 dry bean cultivars differing in plant growth habit and commercial class designation were obtained from 42 Michigan performance nurseries over the 6 year period 1980 to 1985. The determinate type I large-seeded kidney and cranberry bean cultivars had below-average seed yield and large mean square deviations from regression. Lower yielding determinate small-seeded navy cultivars had low deviation mean square values, while higher yielding determinate navy cultivars had correspondingly higher mean square deviations from regression. Although seed yield of cultivars with an indeterminate growth habit was greater than determinate cultivars, prostrate type III indeterminate cultivars had deviation mean square values equivalent to those of large-seeded determinate cultivars. The erect, short vine type II indeterminate cultivars (architypes) had greater than average seed yields and minimum deviations from regression. Compared with other plant types, the architype group showed a greater yield response to more productive environments, with regression coefficient values significantly greater than unity. These results indicate that the type II growth habit offers the breeder the best opportunity of obtaining greater seed yield without incurring loss of yield stability as occurs with the type I and type III growth habits. Since the dry bean cultivars utilized in this study represent two distinct centers of domestication, the regression analysis suggests that cultivars from the predominant genetic

\* Contributions from Michigan Bean Commission, Michigan Bean Shippers Assoc. and Michigan Agric. Exp. Sta., Michigan Agric. Exp. Sta. Journal Article No. 11986 center demonstrate more yield stability. A non-significant rank correlation coefficient between the combined and separate analyses for deviation mean square values of large-seeded cultivars implies that commercial dry bean classes should be compared separately based on center of domestication.

Key words: *Phaseolus vulgaris* L. – Gene pool – Growth habit – Centers of domestication – Architype

## Introduction

In times of surplus production and low market prices, growers are less interested in absolute yields from high inputs than in stable economic yields. Plant breeders sensitive to this concern should choose a strategy that permits selection for both enhanced yield stability and greater absolute yield over years and locations. Yield stability parameters as reported by Eberhart and Russell (1966) can be described by the regression of genotypic yield values upon an environmental index based on mean site performance of all cultivars. Regression techniques have permitted the separation of cultivars by genotype×environment (GE) interaction into two components. One component is that portion of the GE due to response in performance of cultivars to environments of varying levels of productivity and the second component is that portion of the GE due to unexplained deviations from regression. A stable cultivar is defined as having a regression coefficient equal to unity with minimum deviations from regression (Eberhart and Russell 1966). Plant breeders have attempted to use regression techniques to identify characteristics that enhance yield stability. These techniques have

identified both growth habit (Beaver et al. 1985) and maturity (Saeed and Francis 1983) as major traits which significantly affect yield stability parameters.

In dry beans (Phaseolus vulgaris L.), three distinct plant growth habits have been described by Singh (1982). According to this classification, type I refers to a determinate growth habit, while types II and III have indeterminate growth habits. The latter two types differ in the length of the indeterminate vine growth and branch angle, with type II exhibiting an upright short vine habit while type III has a longer vine with a prostrate growth habit. Beaver et al. (1985) demonstrated that determinate large-seeded dry bean cultivars produced lower yields and showed more significant deviations from regression compared to small-seeded indeterminate cultivars which possessed greater than average yields and exhibited minimum deviations from regression. Similarly, Beaver and Johnson (1981) found that indeterminate soybean (Glycine max (L) Merr.) cultivars of maturity group III have higher seed yield, average seed yield response to environments of varying levels of productivity, and minimum deviations from regression. Determinate cultivars of the same maturity group showed more significant deviations from regression, indicating that determinate types were less predictable in yield performance across diverse environments. Cooper (1976) suggested the need for breeding soybeans adapted to specific environments and has developed determinate soybean cultivars specifically for highly productive environments, although the same determinate cultivars have been shown to be prone to greater yield variation across diverse environments (Beaver and Johnson 1981).

A similar need to broaden the genetic background and expand the yield potential of navy beans led Adams (1982) to propose a bean ideotype for high yield with a distinctly modified plant architecture referred to as an architype. One significant difference of the architype was its indeterminate plant habit as compared with the determinate habit of commercial (U.S.) navy bean cultivars. In addition to the different architectural features, the bean architypes are later-maturing, a characteristic which Saeed and Francis (1983) associated with increased yield stability in sorghum. The question raised by previous work is whether stability differences are due to variation in growth habit or to more fundamental genetic differences.

In dry beans, Gepts et al. (1986) have shown that two gene pools or centers of domestication exist and have classified bean cultivars into each center using different electrophoretic banding patterns of the major bean storage protein, phaseolin, as a genetic marker. Small-seeded navy and black cultivars fall into the Meso-American center while large-seeded kidney and cranberry beans are grouped in the Andean center. Interestingly, in crosses between cultivars from the two centers, numerous workers (Coyne 1965; Singh and Gutierrez 1984; van Rheenan 1979) have reported  $F_1$ sub-viability, lethality, and dwarfism resulting from genetically regulated zygotic incompatibility in hybrids. Ghaderi et al. (1982) used cluster analysis for seed yield to classify bean cultivars into sub-sets which coincided with commercial class designations. They also found that two clusters could possess almost identical mean yields yet vary in opposite directions over the same range of environments. The accumulated evidence indicates that bean germplasm from the Meso-American and Andean centers may not comprise a homogeneous gene pool in respect to yield performance across diverse environments.

One of the difficulties of using data from cultivar evaluation trials for stability analysis is that data sets vary in size and content as entries are added and eliminated. Pedersen et al. (1978) proposed the use of an area gene pool concept as a measure of the environmental index since entries grown in different years and locations will vary, but will be representative of a selected population gene pool. The choice of cultivars used as a measure of the environmental index for yield stability comparisons is critical to the conclusions drawn. The State of Michigan provides an ideal and model site for conducting stability experiments in dry beans. Michigan is a leading dry bean production area in North America, and the crop is grown in a belt of similar latitude that covers about 300 km. In this area, the macro and microclimates and edaphic factors are diverse.

This study compares yield stability parameters of determinate and indeterminate commercial dry bean cultivars grown across diverse locations and seasons in Michigan. The effect of center of domestication, plant type and maturity differences on the yield stability estimates are also considered.

#### Materials and methods

Data were obtained from 42 Michigan regional dry bean performance nurseries grown over a 6 year period from 1980 to 1985. The trials were conducted in the seven major dry bean production counties of Michigan in commercial fields following standard agronomic practices and recommended procedures for fertility and weed control. Randomized complete block designs with four replications were used at all locations. Experimental units consisted of two rows, each 6 m in length, but the standard row width of 70 cm varied occasionally from 70 to 75 cm, dependent on grower equipment. Seeding rate varied as per commercial recommendation from 16 seeds/m for small-seeded classes to 12 seeds/m for larger-seeded classes. A 5 m length of the experimental unit was harvested by hand at maturity and cleaned seed yields were adjusted to 18% moisture. No yield reductions were

Cultivar	Commercial seed class	Seed coat color	Hundred seed wt (g)	Growth <sup>a</sup> habit	Center of domestication
Seafarer	Navy	White	20	I	Meso-American
Midland	Navy	White	18	I	Meso-American
Wesland	Navy	White	20	I	Meso-American
Fleetwood	Navy	White	19	I	Meso-American
Laker	Navy	White	20	I	Meso-American
Bunsi	Navy	White	20	II	Meso-American
C-20	Navy	White	20	II	Meso-American
Swan Valley	Navy	White	19	II	Meso-American
Neptune	Navy	White	19	II	Meso-American
Aurora	Small White	White	16	II	Meso-American
Midnight	Black	Black	20	II	Meso-American
Domino	Black	Black	20	II	Meso-American
Black Magic	Black	Black	20	II	Meso-American
T-39	Black	Black	20	II	Meso-American
Black Beauty	Black	Black	20	II	Meso-American
Montcalm	Kidney	Dark Red	52	Ι	Andean
Charlevoix	Kidney	Dark Red	52	Ι	Andean
Isabella	Kidney	Light Red	52	Ι	Andean
Redkloud	Kidney	Light Red	52	Ι	Andean
Sacramento	Kidney	Light Red	52	I	Andean
Linden	Kidney	Light Red	53	I	Andean
Taylor Hort	Cranberry	Red Mottled	49	I	Andean
Cran-028	Cranberry	Red Mottled	45	I	Andean
Michicran	Cranberry	Red Mottled	50	III	Andean
Ouray	Pinto	Brown Mottled	40	Ι	Meso-American
Olathe	Pinto	Brown Mottled	40	Ш	Meso-American
Pindak	Pinto	Brown Mottled	39	III	Meso-American
Rufus	Red Mexican	Red	35	III	Meso-American

 Table 1. Seed color and size characteristics, growth habit, and center of domestication of 28 dry bean cultivars representing seven commercial seed classes

<sup>a</sup> Growth habit I = determinate, II = indeterminate upright short vine, and III = indeterminate prostrate long vine, Singh (1982)

attributed to any major pathogenic problem at the 42 locations utilized in the study.

#### **Results and discussion**

A descriptive comparison of seed size, color, growth habit, and center of domestication of the 28 cultivars used in the study is presented in Table 1. The mean yield of entries at a location was used as an index of the productivity of that environment. Although the entries in the trials varied from year to year and location to location, they were considered to comprise groups which were representative of cultivars in seven major commercial seed classes. The same 28 cultivars represented a population gene pool within the testing area where cultivars are potentially competitive despite differences in yield performance and maturity.

In the statistical analyses, seed yield of individual entries was designated as the dependent variable (y) and the site mean seed yield as the independent variable (x). A simple linear regression analysis was used to estimate the regression coefficient (b), the coefficient of determination ( $r^2$ ) and the deviation mean square from regression ( $S_d^2$ ). Combined and separate stability analyses were performed on the two germplasm groups and the deviation mean square values of cultivars from each analysis were ranked and compared using Spearman's coefficient of rank correlation ( $r_s$ ). A stable cultivar in this study is defined as having a high mean seed yield, a regression coefficient not different from unity (b = 1) with minimum deviations from regression. The mean seed yield of the cultivars across locations and years ranged from 1,938 to 2,734 kg/ha with a grand mean of 2,380 kg/ha (Table 2). As a sub-group, the type II small-seeded cultivars had the highest yields, ranging from 2,131 to 2,734 kg/ha with a mean value of 2,487 kg/ha. The removal from the analysis of 'Aurora' and 'Bunsi', two type II cultivars which in plant structure resemble the determinate small-seeded cultivars, indicated that yields of the architypes as defined by Adams (1982) were high, ranging from 2,538 to 2,734 kg/ha. The larger-seeded type I group, represented by kidney and cranberry beans, comprised the lowest yielding cultivars, ranging from 1,938 to 2,455 kg/ha with a mean of 2,135 kg/ha, or 350 kg/ha less than the small-seeded group. The small-seeded type I navy beans ranged in yield from 2,004 to 2,530 kg/ha but in no case reached the yield potential of the architypes. The type III cultivars, represented by the pinto class, showed a range in yield from 2116 to

Cultivar	Days to maturity	Seed yield (kg/ha)	b±s <sub>b</sub>	s <sub>d</sub> <sup>2</sup>	r²
Seafarer	85	2,004	$0.93 \pm 0.082$	56,537	0.79
Midland	89	2,168	$1.01 \pm 0.077$	46,897	0.84
Wesland	94	2,336	$1.03 \pm 0.098$	68,256	0.79
Fleetwood	97	2,530	$0.84 \pm 0.102$	88,261	0.66
Laker	104	2,494	$1.00 \pm 0.128$	121,670	0.67
Bunsi	95	2,472	$0.85 \pm 0.120$	102,998	0.62
C-20	98	2,734	$1.06 \pm 0.096$	74,181	0.78
Swan Valley	105	2,538	$1.27 \pm 0.103 *$	76,073	0.83
Neptune	102	2,572	$1.35 \pm 0.105 **$	62,224	0.89
Aurora	93	2,131	0.69±0.082**	53,899	0.68
Midnight	97	2,717	1.18±0.078*	56,964	0.86
Domino	97	2,695	$1.20 \pm 0.071 **$	45,632	0.89
Black Magic	97	2,729	1.27±0.074**	29,461	0.94
T-39	93	2,598	$1.07 \pm 0.090$	62,546	0.81
Black Beauty	100	2,593	$1.25 \pm 0.115 *$	75,787	0.84
Montcalm	96	2,095	$0.82 \pm 0.114$	114,527	0.60
Charlevoix	96	2,184	$0.96 \pm 0.106$	99,652	0.71
Isabella	86	2,148	$0.87 \pm 0.202$	211,549	0.46
Redkloud	88	1,990	$0.94 \pm 0.183$	212,024	0.48
Sacramento	84	1,938	$0.78 \pm 0.185$	271,535	0.36
Linden	105	2,165	$0.79 \pm 0.211$	211,847	0.39
Taylor Hort	85	2,136	$1.02 \pm 0.135$	142,291	0.66
Cran-028	99	2,445	$0.76 \pm 0.193$	152,005	0.48
Michicran	99	2,199	$0.88 \pm 0.115$	113,569	0.62
Ouray	85	2,116	$0.84 \pm 0.143$	100,064	0.60
Olathe	88	2,537	$0.99 \pm 0.121$	114,152	0.69
Pindak	90	2,734	$1.23 \pm 0.116$	84,265	0.82
Rufus	97	2,638	$0.93 \pm 0.216$	270,596	0.42
Mean		2,380			

**Table 2.** Days to maturity, seed yield, regression coefficient (b) and standard error  $(s_b)$ , deviation mean square  $(s_d^2)$  and coefficient of determination  $(r^2)$  of 28 dry bean cultivars from 42 trials conducted in Michigan during 1980–1985

\*. \*\* Significantly different from b = 1.0, at the 0.05 and 0.01 levels, respectively

2,734 kg/ha with a mean of 2,527 kg/ha. These data support the suggestion that the indeterminate growth habit offers the best potential for developing high yielding bean cultivars.

There is, however, a confounding effect between yield and maturity (Table 2). The later maturing beans were more often indeterminate and the correlation between yield and days to maturity was highly significant (r=0.48, P < 0.01). Caution must therefore be exercised in selection for high yield to avoid indirect selection of later maturing cultivars, which are at risk of crop loss because of frost in northern latitudes. This problem can be avoided through selection for both greater yield per se and greater yield per unit time. The highest yielding cultivars, 'C-20' and 'Pindak', produced among the greatest yields per unit time, ranging from 27.9 to 30.4 kg/ha/day. The lowest yielding cultivar, 'Sacramento', had an average yield per unit time of 23.1 kg/ha/day, whereas a later maturing cultivar, 'Linden', produced the lowest yield per unit time of 20.6 kg/ha/day.

The regression coefficients (b) of the combined data varied from 0.69 to 1.35 with the small-seeded type I navy cultivars approaching a value of unity. The type II small-seeded cultivars, excepting Aurora and Bunsi, had b values of  $\geq 1.0$ , indicating a positive yield response to more productive environments, in agreement with previous work (Beaver et al. 1985). The type II cultivars, 'Aurora' and 'Bunsi', which were identified as not typical of the type II architype group, had b values significantly < 1.0, indicating lower yield response to more productive environments. These two cultivars resembled the small-seeded determinate group in yield and stability parameters. The regression coefficients for the large-seeded cultivars were generally less than, but not significantly different from, unity.

There was greater than a 9-fold difference in magnitude of the mean square deviations from regression  $(S_d^2)$  values for the cultivar 'Black Magic' and the kidney bean cultivar, 'Sacramento'. As a group, the largeseeded type I kidney and cranberry cultivars displayed the largest  $S_d^2$  values. This finding was in agreement with Beaver et al. (1985) who showed large deviation mean squares for determinate large-seeded cultivars of the 'Pompadour' class grown in the Dominican Republic. The marked similarity in performance of these cultivars across diverse environments is consistent with the hypothesis of their similar origin (Gepts et al. 1986). Improvement of yield and yield stability within this group appears limited by the lack of genetic variability both for response to favorable environments and for associated stability traits such as indeterminacy.

Certain yield stability parameters within the determinate growth habit appeared to be associated with low-yielding small-seeded cultivars. Cultivars 'Midland' and 'Seafarer' had low S<sup>2</sup><sub>d</sub> values and below average yields. Higher yielding determinate cultivars such as 'Fleetwood' and 'Laker' were later in maturity and had large  $S_d^2$  values. In general, the architype navy and black bean cultivars had considerably below-average  $S_d^2$ values coupled with above-average mean seed yields. The cultivar 'Black Magic' had the lowest  $S_d^2$  value and one of the highest mean yields of 2,729 kg/ha. The type III cultivars had large  $S_d^2$  values, indicating less stability for this growth habit. These cultivars were developed for semi-arid production areas where indeterminate growth is needed to produce high yields. The upright architecture of the type II growth habit would not be particularly advantageous in those regions since weather and disease losses related to plant type are minimal. A non-significant correlation (r=0.19) was found between maturity and deviation mean square values, which is in agreement with previous research on dry beans (Beaver et al. 1985). These data indicate that the type II architypes afford the best opportunity of combining high yield with yield stability.

The coefficient of determination  $(r^2)$  ranged from 36% to 94%, indicating that much of the variation in entry performance could be attributed to site mean performance. In wheat, Pedersen et al. (1978) interpreted  $r^2$  values of  $\geq 53\%$  as evidence that limited additions and deletions to the gene pool over years and locations did not affect the strong relationship between site mean yield and genotypic mean yield. If one is to assume that similar additions and/or deletions did not significantly alter the response of the gene pool, then the r<sup>2</sup> values of 36% to 42% obtained in this study raised the question of whether the regional gene pool selected is an appropriate measure of the environmental index for certain cultivars. To investigate this point further, separate regression analyses were performed on each of two data subsets representing cultivars from the two centers of domestication. The 15 small-seeded cultivars represented 56% of the values used in the complete data set, whereas the nine-cultivar largeseeded group represented only 30% of the total data set. Using deviation from regression as a basic measure of stability,  $S_d^2$  values were ranked for the two analyses where a higher ranking indicated a lower  $S_d^2$  value (Tables 3 and 4). The rank correlation value of  $r_s = 0.85$  $(P \le 0.01)$  was highly significant for the small-seeded cultivars (Table 3) of the Meso-American center whereas the  $r_s = 0.1$  for the large-seeded Andean center (Table 4) was not significant. These results suggest that the origins and genetic backgrounds of the two seed size groups are sufficiently different that they should be recognized as distinct gene pools and data analyzed separately. In an analysis where small-seeded cultivars dominate the gene pool in terms of numbers evaluated and analyzed, other distinct cultivars will appear different, if not inferior, for stability parameters such as the coefficient of determination (r<sup>2</sup>). The mean square deviation from regression values and r<sup>2</sup> values are valid measures of cultivar predictability of performance over environments only when the environmental index has been determined largely by performance of cultivars from a common genetic background. In dry beans, where distinct seed classes are found in different centers of domestication, caution is recommended in grouping different seed classes into a single gene pool for analysis because the proportion of individuals from

**Table 3.** Regression coefficient (b) and standard error (s<sub>b</sub>), deviation mean square (s<sub>d</sub><sup>2</sup>), coefficient of determination ( $r^2$ ) and stability ranking of 15 small-seeded dry bean cultivars from 42 trials conducted in Michigan during 1980–1985

Cultivar	$b\pm s_b$	s <sub>d</sub> <sup>2</sup>	r <sup>2</sup>	Stability* ranking	
				c	s
Seafarer	$0.85 \pm 0.078$	60,015	0.77	6	11
Midland	$0.92 \pm 0.069$	45,700	0.85	3	6
Wesland	$0.95 \pm 0.079$	59,195	0.82	9	10
Fleetwood	0.83±0.081*	64,177	0.75	13	13
Laker	$1.00 \pm 0.094$	78,573	0.79	15	14
Bunsi	$0.82 \pm 0.098$	82,639	0.69	14	15
C-20	$1.01 \pm 0.078$	56,115	0.84	10	9
Swan Valley	1.17±0.084*	61,660	0.87	12	12
Neptune	1.28±0.077**	39,257	0.93	7	3
Aurora	0.66±0.067**	42,889	0.75	4	5
Midnight	$1.09 \pm 0.068$	50,363	0.87	5	7
Domino	$1.10 \pm 0.057$	35,279	0.91	2	2
Black Magic	1.14±0.055*	20,763	0.96	1	1
T-39	$1.02 \pm 0.067$	41,798	0.87	8	4
Black Beauty	$1.17 \pm 0.088$	53,486	0.88	11	8

<sup>\*. \*\*</sup> Significantly different from b = 1.0, at the 0.05 and 0.01 levels, respectively

<sup>&</sup>lt;sup>a</sup> Ranking of  $s_d^2$  values from lowest (1) to highest (15) for two data sets; c=complete data set from Table 2; s=small seeded data set from Table 3 above

**Table 4.** Regression coefficient (b) and standard error  $(s_b)$ , deviation mean square  $(s_d^2)$ , coefficient of determination  $(r^2)$  and stability ranking of 9 large-seeded, determinate dry bean cultivars from 42 trials conducted in Michigan during 1980–1985

Cultivar	$b\pm s_b$	s <sup>2</sup> d	r²	Stability* ranking	
				с	1
Montcalm	$0.94 \pm 0.071$	46,742	0.84	3	2
Charlevoix	$0.96 \pm 0.101$	92,357	0.73	1	5
Isabella	$1.10 \pm 0.111$	71,418	0.82	6	4
Redkloud	$1.13 \pm 0.085$	57,291	0.86	8	3
Sacramento	$1.10 \pm 0.121$	116,999	0.72	9	6
Linden	$0.78 \pm 0.192$	199,068	0.43	7	9
Tavlor Hort	1.14±0.073*	45,294	0.89	4	1
Cran-028	$0.72 \pm 0.180$	150,938	0.48	5	7
Ouray	$0.76 \pm 0.197$	151,795	0.39	2	8

\* Significantly different from b = 1.0, at the 0.05 level

<sup>a</sup> Ranking of  $s_d^2$  values from lowest (1) to highest (9) for two data sets; c=complete data set from Table 2; l=large seeded data from Table 4 above

one pool may lead to overestimation of the other pool's stability parameters. Stability parameters of the largeseeded kidney and cranberry group improved when these cultivars were analyzed separately as compared to when they were analyzed with all other seed classes. However, separate analyses did not change the conclusion that determinate, large-seeded cultivars were inherently less stable. The data present a strong argument for the development of indeterminate cultivars with a type II architecture in large-seeded classes for the improvement of yield potential and stability across a diverse production area.

### References

- Adams MW (1982) Plant architecture and yield breeding in *Phaseolus vulgaris.* Iowa State J Res 56:225-254
- Beaver JS, Johnson RR (1981) Yield stability of determinate and indeterminate soybeans adapted to the Northern United States. Crop Sci 21:449–454
- Beaver JS, Paniagua CV, Coyne DP, Freytag GF (1985) Yield stability of dry bean cultivars in the Dominican Republic. Crop Sci 25:923-926
- Cooper RL (1976) Modifying morphological and physiological characteristics of soybeans to maximize yields. In: Hill LD (ed) World Soybean Research. Interstate Printers and Publ Inc, pp 230-236
- Coyne DP (1965) A genetic study of 'crippled' morphology resembling virus symptoms in *Phaseolus vulgaris* L. J Hered 56:162–176
- Eberhart SA, Russell WA (1966) Stability parameters for comparing varieties. Crop Sci 6:36-40
- Gepts P, Osborn TC, Rashka K, Bliss FA (1986) Phaseolin protein variability in wild forms and landraces of common bean, *Phaseolus vulgaris* L.: evidence for multiple centers of domestication. Econ Bot 40:451-468
- Ghaderi A, Adams MW, Saettler AW (1982) Environmental response patterns in commercial classes of common bean (*Phaseolus vulgaris* L.). Theor Appl Genet 63: 17–22
- Pederson AR, Everson EH, Grafius JE (1978) The gene pool concept as a basis for cultivar selection and recommendation. Crop Sci 18:883-886
- Saeed M, Francis CA (1983) Yield stability in relation to maturity in grain sorghum. Crop Sci 23:683-687
- Singh SP (1982) A key for identification of different growth habits of *Phaseolus vulgaris* L. Annu Rep Bean Improv Coop, New York 25:92–95
- Singh SP, Gutierrez JA (1984) Geographical distribution of the  $DL_1$  and  $DL_2$  genes causing hybrid dwarfism in *Phaseolus* vulgaris L., their association with seed size, and their significance to breeding. Euphytica 33:337–345
- Van Rheenen HA (1979) A sub-lethal combination of two dominant factors in *Phaseolus vulgaris* L. Annu Rep Bean Improv Coop, New York 22:67–69