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The Relationship of Seed Filling to Yield among Dry Beans with Differing Architectural Forms[1]

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Abstract. **We compared 9 dry bean (*Phaseolus vulgaris* L.) strains characterized by the following architectures for seed filling, yield, and components of yield: small bush, tall erect bush, classic II, and architype. Small and tall erect bush are determinate in growth habit; classic II is indeterminate and produces a short vine. Architype is erect, contains 2–4 branches angled acutely upward, grows to about 75 cm, terminates in a short vine, and does not lodge at maturity. Seed dry weight vs. days after 50% flowering data were fit to a cubic polynomial to calculate the rate and duration of seed filling. Small bush produced the greatest pods/m^2 of the groups, but pod set was offset by a high percentage of shriveling and seed abortion. The architype outyielded the tall erect and small bush groups by 34 and 45%, respectively, which was due to a greater number of seeds/pod, seeds/m^2, and heavier seeds. The heavy seeds of the architype compared to the bush appeared to be due to a longer filling duration, because linear seed filling rates were similar. The architype filling duration was 11.3 days compared to 5.7 and 7.0 days for small and tall erect bush, respectively. The longer architype filling duration may be associated with its ability to prolong the duration of photosynthesis. The 17% yield increase of the architype over classic II was due to improved lodging resistance through a modification of the morphology by reducing branches and narrowing the plant canopy.**

Donald (9) suggested that yield in crop plants is a function of morphology and physiology. He concluded that breeders attempting to achieve superior yields should design and test model plants (ideotypes) on an architecural and physiological basis. Coyne (7) opined that sufficient information on the contribution and merits of many of the morphological and physiological components leading to yield is not available to develop a model which is likely to produce a high-yielding plant. He suggested that the most useful strategy now is to select parents with superior morphological and physiological traits associated with yield and to utilize these parents in breeding programs with other high-yielding germplasm.

In the search for high yield in seed crops, plant breeders have investigated the physiology of grain filling. Genetic differences exist among cultivars and breeding lines for both the rate and duration of grain filling in rice [*Oryza sativa* L., (14)], soybeans [*Glycine max*. L. (Merr.), (15)], maize [*Zea mays* L., (8, 10, 13)], barley [*Hordeum vulgare* L. (18)], wheat [*Triticum aestivum* L., (16, 20)], and cowpea [*Vigna unguiculata* L. (Walp.), (25)]. Several studies (8, 10, 15, 20, 24, 25) showed that the duration of grain filling was more closely related to yield than was the rate of filling. Other work (11, 14, 16, 20) indicated that the rate of seed filling was more closely related to cultivar differences in final grain weight.

Adams (2) proposed an ideotype for dry bean production under monoculture. He suggested that higher yields could be achieved if photosynthate were directed into the seeds more efficiently. The morphological model proposed (2) consisted of an erect, nonclimbing, single stem plant with 2 to 4 basal branches angled acutely upward giving the plant an overall narrow appearance in profile. The erect architecture was viewed as leading to a higher efficiency of carbon transport into the seed due, in part, to better light penetration and higher rates of net CO_2 fixation (2). The increased physiological efficiency was to be maintained over time by a stiff stem that prevents lodging.

Recently, high-yielding dry bean breeding lines that are erect and resist lodging have been developed in Michigan (3). Data collected during the past several years showed that some of these lines consistently outyielded the determinant small bush and indeterminant short vine cultivars currently grown commercially in Michigan (3, 23). Little information exists as to how these erect types achieved their superior yields.

Since plant morphology in crop plants can influence photosynthesis and carbon transport, it could also influence physiological behavior in varying degrees during the seed development period resulting in yield differences. The purpose of the present study was to compare strains of dry beans characterized by 4 distinct architectures for seed filling, yield, and their interrelationships.

Materials and Methods

Genetic materials and plant architecture. Nine strains of dry beans were used. They represented 4 separate architectures (Fig. 1) and were characterized by either a Type I or II growth habit of the classification of the International Center for Tropical Agriculture (CIAT), Cali, Colombia (6). Strains comprising the architectures were selected to represent a range in time to maturity, pattern of reproductive growth, and yield.

Within Type I (determinate bush), 4 strains belonging to 2 architectural groups formed the basis for study. The navy bean 'Seafarer', 'Sanilac', and 'Tuscola' represented the small bush architecture (Fig. 1a), while the navy bean breeding line, C-14,

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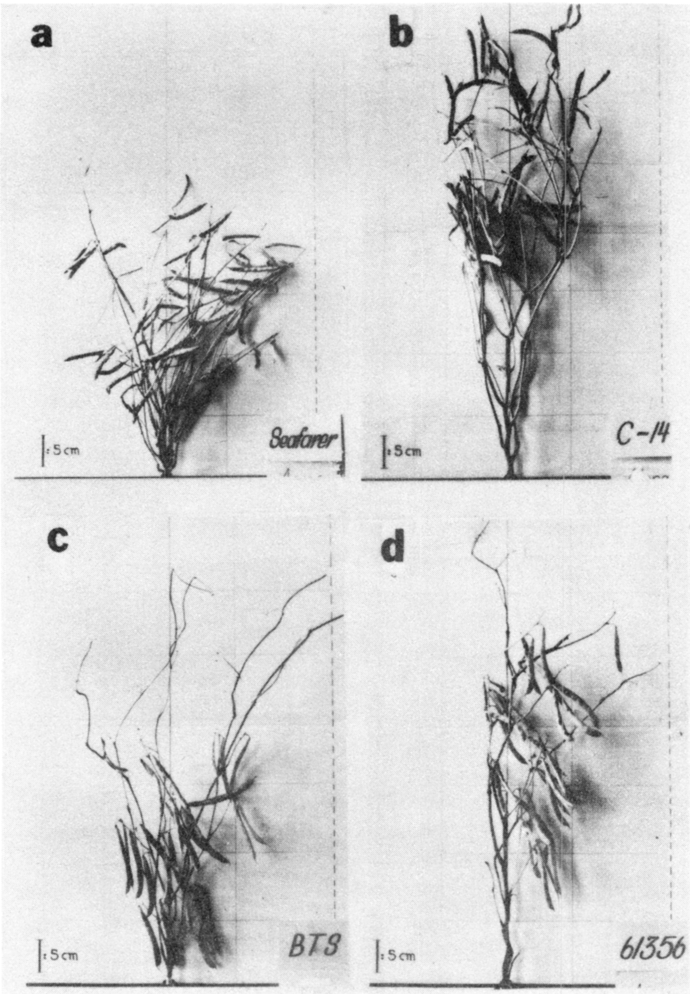

Fig. 1 Photographs of representative samples of architectures used in the experiment: a) small bush; b) tall erect bush; c) classic II; and d) architype. Photographs were taken just before harvesting; the vertical bar (I = 5cm) is a reference scale for comparing plant height and podding characteristics.

had a tall erect bush architecture (Fig. 1b). Small bush plants contain more than 4 branches, grow about 55 cm high, have a short erect canopy, and lodge at maturity. Tall erect bush plants are about 20 cm taller than the small bush and do not lodge at maturity.

The remaining 5 strains studied were characterized by 2 architectures and Type II growth habit (indeterminate, short vine). Two cultivars that were classic examples of Type II growth habit (6) formed the basis of the classic II architecture (Fig. 1c). These were 'Black Turtle Soup' ('BTS') and 'Nep-2', which are semi-erect plants that grow between 60–70 cm tall and lodge at maturity. The final architecture studied was characterized by a narrow profile, tall (75 cm), erect, and supported by 2–4 strong branches vertically oriented and separated from one another by an acute angle (15–25°). Plants with this architecture approximate Adams' model (2), are nonlodging at maturity, and are called architype (Fig. 1d). The architype was represented by 3 breeding lines of which two (61380 and 61356) were black-seeded and one (61618) was white-seeded.

Planting and harvesting procedures. The 9 entries were grown in 1980 at East Lansing, Mich. Seed was drilled into 8-row plots with a tractor-mounted air planter. Rows were 10-m-long and 47 cm apart. Plant spacing within rows was 7–8 cm. The arrangement was a randomized complete block design with 4 replications. Standard herbicide and fertilizer applications were used.

Mature plants were removed by hand from two, 2-m sections of adjacent rows (1.88 m^2) of individual plots and threshed by hand. Before threshing individual plants, the total number of pods and number of shriveled pods were recorded. Seed number per pod was determined from a 50-pod sample, and the average weight of 2, 100-seed samples was calculated. After threshing seeds, moisture content was analyzed and seeds weighed. Yields and 100-seed weights were adjusted to 16% moisture content.

The 50 pod samples consisted only of nonshriveled pods. After determining the number of seeds from this sample, seeds were separated into plump and shriveled or aborted seed. The total number of plump seeds per plot (1.88 m^2) was calculated.

Seed filling parameters. The second and seventh rows of each 8-row plot were subdivided into 7 segments, each 1 m long, with 5 plants separating each segment to serve as a guard. The 14 to 16 plants within each segment were the experimental units for sampling the seed-filling parameters.

Each experimental unit was observed each day to determine the date of anthesis (first open flower) in a plot. Sampling began on the day that 50% of the plants had 1 or more open flowers (50%F). Sampling was between 0800 and 0900 HR. Each segment was sampled only once. Five random plants were taken from one of the 1-m segments. All pods were then removed from the 4th, 5th, and 6th main stem nodes. The seeds were removed and dried in a forced air oven at 100°C for 1 hr followed by 70° for 36 hr.

The seed dry weights were plotted against the days after 50%F (DA 50%F). Sampling was every 4 days until physiological maturity (PM), the date at which about 90% of all pods had changed from green to pale yellow or brown.

The seed-filling parameters—rate and duration—were calculated by fitting curves to the data using equations appropriate for a first, second, and third degree polynomial (19). The curves were fit using the least squares regression technique with time (t) as DA 50%F and as the independent variable (x). The dependent variable (y) was the mean seed dry weight.

The linear seed-filling rate (LFR) was the linear regression, line of best fit, of the linear phase of seed growth. The LFR was expressed as mg/seed-day. First estimates of the time limits of the linear phase were obtained by superimposing a straight line over the linear phase of the curve resulting from fitting all data points to a cubic polynomial. After this was done, the coefficient of determination (R^2), and the F-statistic of the first degree polynomial were calculated for the linear period.

To reduce subjectivity in choosing the limits of the linear phase, the method of Sofield et al. (20) was used. Several data points in the middle of the linear phase of seed growth were selected, a least squares fit was determined, and an R^2 for a linear regression model was calculated (20). The number of data points was then progressively extended by taking additional points, at one end of the period and then at the other, and then including them one by one while refitting the curve and recalculating R^2. This was continued until inclusion of a new datum point did not change the magnitude of the F-value for the regression anaylsis of variance. Once this occurred, the datum point included was discarded and the penultimate datum point with all the other points was used to establish the growth rate. The linear filling duration (LFD) was then estimated by extrapolation of the line of best fit to its intersection with the ordinate (DA 50%F).

An estimate (prediction) of the maximum seed weight (Max W) that theoretically would be achieved should LFR and LFD be measured without error was calculated by setting the derivative of the cubic function f′(t), used to estimate the seed-filling

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Table 1. Pod and seeds per pod characteristics and seed weight and yield of 9 dry bean strains representing 4 architectures.

Architecture and strain	Pods: Total[z] (no./m²)	Pods: Shriveled[z] (%)	Pods: Non-shriveled[z] (no./m²)	Seed/pod: Total[z]	Seed/pod: Aborted[z] (%)	No. seed/m²[z]	100-seed wt.[z] (g)	Yield[z] (kg/ha)
Architype								
61380	320bcde	19.8bcd	254b	7.0ab	5.2ab	1728ab	18.1a	3477a
61356	286e	16.6cde	239b	6.4abc	3.4b	1493b	18.5a	3076ab
61618	313cde	18.5cde	255b	7.0ab	3.8ab	1736ab	16.5b	2949b
Mean	306	18.3	249	6.8	4.1	1652	17.7	3167
Classic II								
BTS	323bcde	15.8de	270ab	7.2a	4.8ab	1858ab	16.8b	2589bcd
Nep-2	358abc	9.2e	326a	6.8ab	5.0ab	2106a	15.3cd	2845b
Mean	341	12.5	298	7.0	4.9	1982	16.1	2717
Small Bush								
Seafarer	355abcd	27.0abc	258b	5.7c	4.8ab	1416b	17.5ab	2569bcd
Sanilac	412a	30.4a	287ab	5.9c	9.8a	1526b	14.9d	1823e
Tuscola	376ab	30.1ab	262b	5.8c	4.3ab	1515b	15.3cd	2162de
Mean	381	29.1	227	5.8	6.3	1486	15.9	2187
Tall Erect Bush								
C-14	295de	22.8abcd	227b	6.3bc	2.8b	1411b	16.8b	2366cd
Mean of experiment	338	21.1	264	6.4	4.5	1643	16.6	2701
LSD 5%[y]	59	10	67	0.7	6.4	498	1.1	480
CV (%)	11	21	14	8	9	17	5	13

[z]Mean separation within architectural forms and columns by Duncan's multiple range test, 5% level.
[y]Mean separation of architectural groups by Waller-Duncan's Bayesian LSD test.

parameters ($y = \beta_0 + \beta_1 x_1 + \ldots$), to zero and obtaining the corresponding root that maximized the cubic equation.

Results

The architype group outyielded the average of the small bush, tall erect bush, and classic II by 45, 34, and 17%, respectively (Table 1). This was significantly higher for the small and tall erect bush groups. The classic II group significantly outyielded the small but not the tall erect bush.

Each of the architype strains had higher yield than all others but differences were not always significant. Strain '61380' was significantly higher-yielding than strains of the other groups, while 61356 and 61618 were not significantly higher-yielding than 'BTS' and 'Nep-2' (classic II) and 'Seafarer' (small bush). The yields (Table 1) agree with statewide Michigan trials for similar strains (3, 23).

Pod numbers, seeds/pod, seeds/m², and 100-seed weights (Table 1) provided no clear explanation for the yield differences among the architectural groups, although trends were apparent. Architype strains had a significantly greater 100-seed weight than the other groups (except for the tall erect bush). Compared to the small bush, the architype group generally had more normally appearing seeds/pod in addition to heavier seeds (Table 1). The small bush cultivars tended to produce a greater number of pods/m² than did the architype strains, but increased pod production was generally offset by significantly more shriveled pods and increased but nonsignificant seed abortion. Most striking was the contrast between 'Sanilac' and 61356 (Table 1). 'Sanilac' produced a significantly greater number of pods/m² (412 vs. 286), while 61356 had a lower percentage of shriveled pods (16.6 vs. 30.4) and had less seed abortion (3.4 vs. 9.8%). Classic II had the largest number of nonshriveled pods and seeds/m². 'BTS' produced a few more nonshriveled pods than the experimental average (270 vs 227) and was similar to 'Nep-2' in the seeds/m² produced. The small yield increase of the tall erect bush over the small bush group (8%) could be due to slightly heavier seeds of C-14 (Table 1).

The LFR and LFD had good fit to a cubic polynomial equation (Fig. 2). This was found for rice by Jones et al. (14). The relatively high-yielding 'Seafarer' and low-yielding 'Sanilac' (Table 1) had a high and similar LFR (17.5 and 14.1 mg/seed/day) and a short and similar LFD (5 and 4 days). A homogeneity test indicated that linear regression coefficients for the LFR did not differ significantly within the architype, classic II, and small bush groups indicating no differences in LFR among strains within the same architectural group. However, a highly significant difference was detected for LFR between the architype and small bush groups indicating a dissimilarity in seed-filling rate.

Seed-filling data, rather than taken on a daily basis, were recorded every 4 days after 50%F so the precise time at which seeds reached their maximum weight could not be determined. Nevertheless, there was good agreement between actual seed weight at harvest (Table 1) and seed weight predicted using a cubic polynomial (Max W, Table 2).

A strain's predicted seed weight (except for 61618) was overestimated compared to its observed seed weight. The average overestimation was 9%. This was probably due to estimating Max W from data taken on pods from the 4th to 6th nodes while harvest seed weights were from a random sample of bulked seed taken from all pods of the entire plant. Evidently pods at the 4th to 6th nodes produced seed more uniform in weight than

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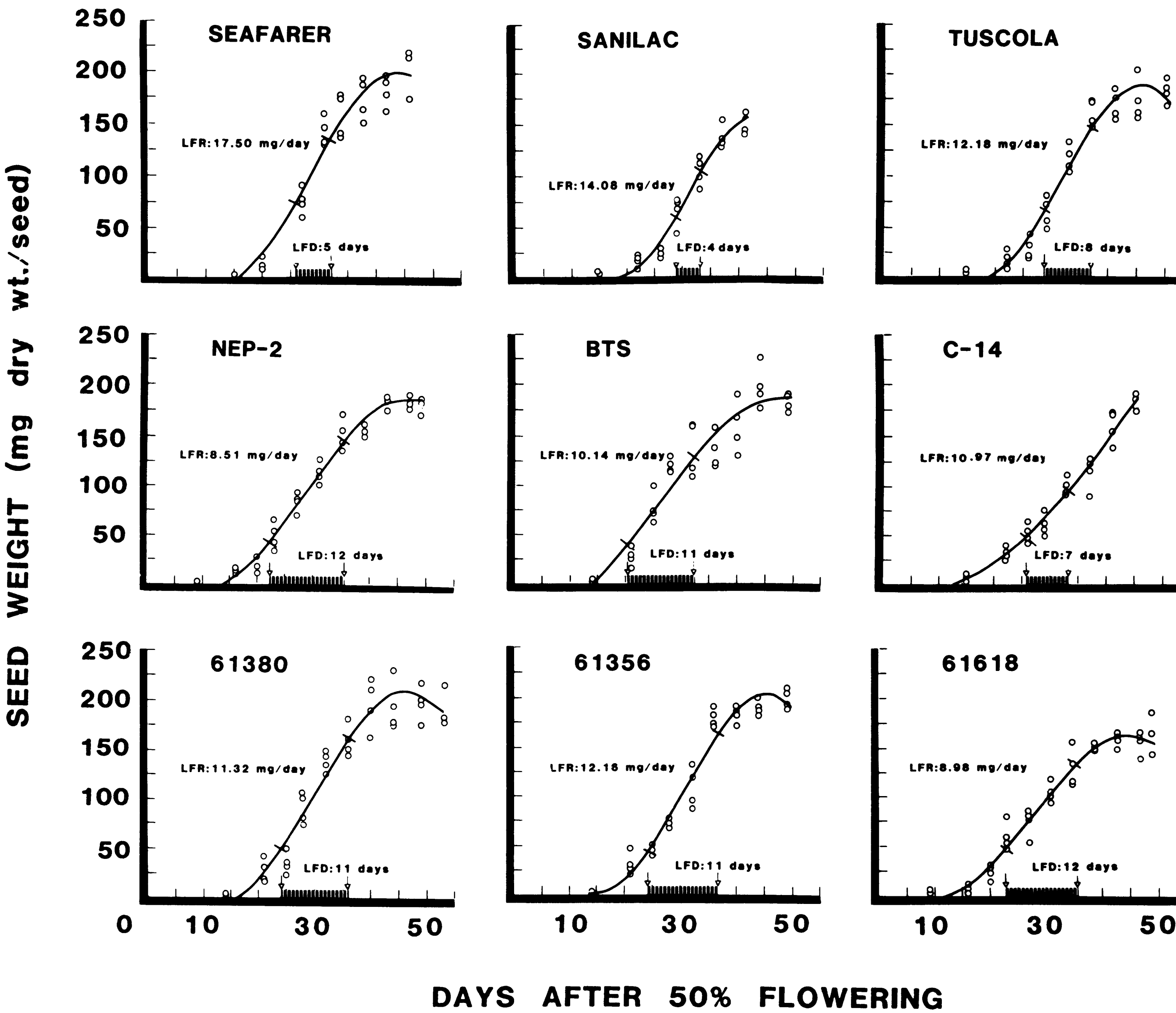

Fig.2 Seed filling of 9 dry bean strains. The LFR is the linear filling rate and is delineated by slashed lines intersecting the growth curves of each strain; the LFD is the duration of linear filling and is delineated by a hatched bar.

pods of the other canopy layers. Despite the 9% overestimation, the overall correlation between Max W and observed seed weight was 0.882 and highly significant ($P < 1\%$).

The predicted seed weight (Table 2) at the end of the LFD accounted for between 37.7 ('Sanilac') to 72.1% (61356) of a strain's observed seed weight (Table 1). Two patterns emerged when comparing the architectural groups for the proportion of their final seed weight due to the LFD. The architype and classic II groups were high and similar (68.6 and 66.4%, respectively) and the small and tall erect bush groups were low and similar (48.5 and 46.1%, respectively).

The LFD was significantly and positively correlated with yield and with seeds/pods, seeds/m^2, and seed weight (Table 3). The LFR was negatively correlated with seeds/pod, seeds/m^2, and yield. The correlation was only significant for seeds/pod (Table 3). No significant correlation existed between either the LFR and LFD and pods/m^2.

Discussion

Architype 61380 and 61356 had the highest yields and heaviest seed of the strains studied (Table 1). Moreover, the correlation between the number of normally appearing seeds/pod and seed weight for these 2 strains were nonsignificant and positive ($r = 0.35$). The positiveness of this correlation suggested that for these strains seed weight within a pod was not adversely affected by the number of seeds/pod. This does not agree with Adams' (1) demonstration of yield component compensation in the small bush group. Developing bean seeds compete for available photosynthate, nutrients, and water. Competition is greatest within a phytomeric unit [leaf, leaf axil, and adjoining reproductive

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Table 2. Seed-filling rates, duration of seed filling, predicted seed weight, and percentages of seed weights accounted for by the linear phase of filling for 9 dry bean strains.

Architecture and strain	Filling rate[z] (mg/seed-day) Linear (LFR)	Filling period[z] (days) Linear (LFD)	Effective (EFD)	Predicted seed wt.[z] (mg/seed) Maximum (Max W)	By linear filling	% of maximum predicted seed wt (Max W) due to linear filling	% of observed size due to linear filling[y]
Architype							
61380	11.3	11.0	16.0	208.9	124.5	59.5	68.7
61356	12.2	11.0	15.0	202.6	133.7	65.9	72.1
61618	9.0	12.0	18.0	162.1	107.7	66.4	65.0
Mean	10.8	11.3	16.3	191.2	122.0	63.9	68.6
Classic II							
BTS	10.1	11.0	17.0	184.7	111.5	60.3	66.2
Nep-2	8.5	12.0	18.0	185.8	102.1	59.5	66.6
Mean	9.3	11.5	17.5	185.3	106.8	60.1	66.4
Small Bush							
Seafarer	17.5	5.0	10.0	196.9	87.5	44.4	50.0
Sanilac	14.1	4.0	11.0	153.8	56.3	36.5	37.7
Tuscola	12.2	8.0	13.0	189.1	97.4	51.4	57.7
Mean	14.6	5.7	11.3	179.9	80.4	44.1	48.5
Tall Erect Bush							
C-14	11.0	7.0	15.0	190.0	76.7	40.4	46.1
Mean of experiment	11.8	9.0	15.0	185.9	99.7	53.8	58.9

[z]Calculated from data fit to a cubic model polynomial for each of the 9 dry bean strains used in the study.
[y]Observed size = seed wt at harvest.

structures (2)]. With competition among seeds within pods and among pods at different canopy levels, seed filling is adjusted via a balance of the competition between source and sink (17, 22). When source becomes limiting, seed filling is disrupted. The last seeds to develop within a pod are penalized in size (weight) and may abort. The negative correlation (−0.725) between LFR and seeds/pod (Table 3) suggested that this sequence of events occurred. However, in the architype's case, source was not limiting to the point it restricted seed development. This is further shown by the fact that the architype had nearly a 2-fold greater LFD (Table 2), 11% fewer shriveled pods, and 35% fewer aborted seed than the small bush (Table 1). Thus, the architype (at least 61380 and 61356) appeared to have overcome developmental and physiological limitations that lead to yield component compensation in beans.

Seed yields of the 9 strains were not perfectly associated with their architectural form (Table 1). For example, 61356, 'Nep-2', and 'Seafarer' (all relatively high yielding) were not significantly different in yield (Table 1) yet each belonged to a different architectural group. Similarly, C-14, 'Tuscola', and 'BTS' were alike in yield but were different architecturally. Nevertheless, the yield trends are in harmony with data from statewide performance trials (23) which suggested that a "yield barrier" breakthrough was made in navy and 'BTS' classes of beans by changing the morphology to an erect and narrow profile architecture. Architype strains outyielded commercially grown cultivars characterized by nonerect architectures during the past several years in Michigan (3, 23).

Adams (2) predicted that a greater yield in dry beans could be achieved by structurally improving the plant. Structural features are important becase they are related to or have an influence on physiological function (2). Breeding for the dry bean ideotype (2) should also overcome yield component compensation (2, 5). In achieving the goal of high-yielding dry beans, Adams (3) selected on a morphological basis via the architype route. Although selection criteria included a narrow profile, erectness, and higher yield, indirect selection for physiological aspects related to sink development obviously occurred. Alternatively,

Table 3. Simple correlation coefficients between seed-filling parameters and yield, and components of yield for 9 dry bean strains.

Seed-filling parameters	Correlation coefficient (r) Yield	Component of yield Pod/m^2	Seed/pod	Seed/m^2	100-seed wt.
Linear filling rate (LFR)	−.243	.038	−.725*	−.448	.563
Linear filling duration (LFD)	.744*	.117	.912**	.705*	.611*
Effective filling duration (EFD)	.604*	.095	.930**	.698*	.594

*,**Statistically significant at the 5% (*) and 1% (**) level of probability.

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the architype could consist of an integrated genic complex such that when the architecture is produced, it is inseparable from those aspects of its physiology leading to high yield. For example the architype, compared to the bush groups, appeared to have achieved their higher relative yields through a longer filling duration leading to a larger sink size. It is possible that the architype's filling period was closely associated with the ability of this group to satisfy sink demand by prolonging the duration of photosynthesis. Our experience indicates that the architype retains green leaves that are presumably photosynthetically active much later in the growing season than do small and tall erect bush strains. Also, a supply of carbohydrate to sustain seed filling could have come from the remobilization of reserves from storage sites (12). Remobilization of stored carbohydrates during the seed filling period has been observed in dry beans and variability has been observed among small bush and classic II strains (4).

Since seed weight/m^2 and seed filling rate and duration were similar for the architype and classic II (Tables 1, 2), the higher yield of the architype was most likely related to improved lodging resistance brought about mainly through branch reduction and narrowing of the canopy. Architype strains have stood for several weeks after maturity with little or no plant breakdown compared to the other architectural groups. Stoffella et al. (21) suggested that an erect plant type could reduce harvesting losses and increase physiological yields.

Literature Cited

1. Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. Crop Sci. 7:505–510.
2. Adams, M. W. 1973. Plant architecture and physiological efficiency in the field bean. Seminar on potential of field bean and other food legumes in Latin America. Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia, p. 266–278.
3. Adams, M. W. 1981. Update: new bean architype. Michigan Dry Bean Dig. 5(2):12–13.
4. Adams, M. W., J. V. Wiersma, and J. Salazar. 1978. Differences in starch accumulation among dry bean cultivars. Crop Sci. 18:155–157.
5. Bennett, J. P., M. W. Adams, and C. Burga. 1977. Pod yield component variation and intercorrelation in *Phaseolus vulgaris* L. as affected by planting density. Crop Sci. 17:73–75.
6. Centro Internacional de Agricultura Tropical (CIAT). 1967. Annu. Rpt., Cali, Colombia.
7. Coyne, D. P. 1980. Modification of plant architecture and crop yield by breeding. HortScience 15:244–247.
8. Daynard, T. B., J. W. Tanner, and W. G. Duncan. 1971. Duration of the grain filling period and its relation to grain yield in corn *Zea mays* L. Crop Sci. 11:45–48.
9. Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385–403.
10. Duncan, W. G. 1980. "Maize", p. 23–50. In: L. T. Evans (ed.). Crop physiology: some case histories. Cambridge Univ. Press, England.
11. Egli, D. B. and J. E. Leggett. 1976. Rate of dry matter accumulation in soybean seeds with varying source-sink ratios. Agron. J. 68:371–374.
12. Izquierdo, J. A. 1981. The effect of accumulation and remobilization of carbon assimilate and nitrogen on abscission, seed development, and yield of common bean (*Phaseolus vulgaris* L.) with differing architectural forms. PhD Thesis, Michigan State Univ., East Lansing.
13. Johnson, D. R. and J. W. Tanner. 1972. Calculation of the rate and duration of grain filling in corn (*Zea mays* L.). Crop Sci. 12:485–486.
14. Jones, D. B., M. L. Peterson, and S. Geng. 1979. Association between grain filling rate and duration and yield components in rice. Crop Sci. 19:641–644.
15. Kaplan, S. L. and H. R. Koller. 1974. Variation among soybean cultivars in seed growth rate during the linear phase of seed growth. Crop Sci. 14:613–614.
16. Nass, H. G. and B. Reiser. 1975. Grain filling period and grain yield relationship in spring wheat. Can. J. Plant Sci. 55:673–678.
17. Oliker, M., A. Poljakoff-Mayber, and A. M. Mayer. 1978. Changes in weight, nitrogen accumulation, respiration and photosynthesis during growth and development of seeds and pods of *Phaseolus vulgaris*. Amer. J. Bot. 65:366–371.
18. Rasmusson, D. C., I. McLean, and T. L. Tew. 1979. Vegetative and grain filling periods of growth in barley. Crop Sci. 19:5–9.
19. Snedecor, G. W. 1956. Statistical methods. Iowa State Univ. Press, Ames.
20. Sofield, I., L. T. Evans, M. G. Cook, and I. F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Austral. J. Plant Physiol. 4:785–797.
21. Stoffella, P. J., R. T. Sandsted, R. W. Zobel, and W. L. Hymes. 1979. Root characteristics of black beans. I. Relationship of root size to lodging and seed yield. Crop Sci. 19:823–826.
22. Tanaka, A. and K. Fujita. 1979. Growth, photosynthesis and yield components in relation to grain yield of the field bean. J. Fac. Agr. Hokkaido Univ. 59:145–237.
23. Varner, G. V. 1981. Research report. Mich. Dry Bean Dig. 5(2):27–29.
24. Wardlaw, I. F. 1980. Translocation and source-sink relationships, p. 297–339. In: P. S. Carlson (ed.). The biology of crop productivity. Academic Press, New York.
25. Wien, H. C. and E. E. Ackah. 1978. Pod development period in cowpeas: varietal differences as related to seed characters and environmental effects. Crop Sci. 18:791–794.

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