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**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**

By

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ABSTRACT

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

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Physiological efficiency in regards to partitioning and remobilization is needed for improving the yields of bean (Phaseolus vulgaris L.) cultivars. Strains with a new architectural form, "architype," are higher yielding than accepted cultivars they are replacing. A study on C-assimilate partitioning, remobilization of carbohydrates and nitrogen, and abscission was undertaken to relate cultivars with differing plant architecture to seed filling parameters, and abscission, and to elucidate whether the yield advantage of the "architype" can be explained by efficiency in C-partitioning. Sugars, starch, and nitrogen were determined on plant tissues in two years. In 1979, three strains, and in 1980, nine strains were evaluated at different reproductive stages, at East Lansing, Michigan. Four architectural forms were studied. They were CIAT I "small bush" cultivars 'Seafarer,' 'Sanilac,' and 'Tuscola;' CIAT I "tall erect bush" breeding line C-14; CIAT II "classic II" cultivars 'Black Turtle Soup' and 'Nep-2;' and CIAT II "architype" breeding lines 61380, 61356 and 61618. Seed filling parameters were determined from cubic regressions. Abscission was evaluated by abscission collection receptacles. Ethylene evolved from reproductive structures was monitored.

Yield differences among the entries correlated with the length of the seed filling period. Dry matter remobilization from stems and pod walls,

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the most important sources of remobilizable reserves, was negatively associated with duration of the seed filling. Stem carbohydrates and nitrogen increased at mid-seed filling independently of entry. The highly significant interaction of entry x physiological stage for carbohydrates and nitrogen in stems and pod walls was due to differential late remobilization to the seeds. "Small bush" remobilized TNC from the stems after mid-seed filling. The "architype" remobilized carbohydrates but the "classic II" did not. A modified harvest index and the harvest nitrogen index were correlated with yield.

Fifty percent of the theoretical yield is lost by abscission and 61 percent of the total abscission was accounted by small pod dropping. Ethylene evolved from flowers of Sanilac and 61618 was associated with high rate of abscission. Competitive storage of TNC and Nitrogen in stems stimulated abscission in "small bush." Foliar abscission accounted for 70 percent of the foliar losses, and 80 percent of the foliar nitrogen was remobilized before abscission.

Starch status determined by IKI-starch score method allows for only gross separation among storing and non-storing entries. Yield superiority in the architype is based on extended filling period, high partitioning and remobilization of carbohydrates and nitrogen, large sink, and lower abscission rate. Remobilization could be the yield stabilizing mechanism. Selection for efficient partitioning and remobilization must be incorporated into breeding programs for yield improvement.

Note: This dissertation is presented as a series of five papers written in the style and format required by Crop Science and, the Journal of the American Society for Horticultural Science.

**To Giannina and Viviana,
my lovely daughters**

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INTRODUCTION

Over 45 percent of the world production of dry edible beans (Phaseolus vulgaris L.) is consumed in Latin America. Nevertheless, low yields of this crop are limiting the traditional role beans play as a staple food in the diets of poor and middle-income consumers of this region of the world.

Although bean yields of over 4000 kg.ha⁻¹ have been reported from experimental plots growing at the Centro Internacional de Agricultura Tropical (CIAT) in Colombia, the average bean yield in Latin America remains near 800 kg.ha⁻¹ (Temple and Song, 1980). A large reduction in the gap between yields experienced by farmers and yields possible must occur if the future of this crop is to succeed in meeting the nutritional needs of a burgeoning population.

Although increasing yield is imperative, this objective must be integrated with the genetic improvement of adaptation and resistance to stresses brought about by diseases, insects, and physical causes. The improvement of agronomic characters coupled with yield improvement could maximize the responses of the bean plant to available resources characteristic of subsistence production methods (Graham, 1978).

Plant breeders have had limited success in making important yield breakthroughs in dry beans. A few cultivars have been released recently that have improved disease resistance which allow greater yield potential to be expressed. In recent years breeders have been approaching the low yield problem by considering the development of plant ideotypes

(Donald, 1968). In dry beans an ideotype for production under monoculture has been proposed by Adams (1973). He speculated that productivity increases in dry beans could be obtained if an efficient allocation of assimilates into the economical sink of improved cultivars were developed by breeding. The bean ideotype was originally defined as a determinant plant with reduced number of branches, and an upright and narrow canopy with increased number of pod bearing nodes. Recently a new architectural form has been developed at the Michigan Agricultural Experiment Station (Adams, 1981) that approaches to a satisfactory degree the original ideotype and that has showed higher yields than standard cultivars.

The selection of cultivars with more effective partitioning of nitrogen and carbon assimilate from photosynthesis to the seed than older cultivars was thought to be the key factor for the improvement of yield in other grain crops, namely, rice (Oryza sativa L., Yoshida, 1972), peanuts (Arachis hypogea L., Duncan et al., 1972), and soybean (Glycine max Merr., Jeppsom et al., 1973).

Photosynthate partitioning is an important component of the yield equation and has been shown to be under genetic control in cereals (Donald and Hamblin, 1976), soybeans (Jeppsom et al., 1978) and sugarbeets (Snyder and Carlson, 1978). In beans, although variability for photosynthate partitioning has not been elucidated, Adams et al. (1978) showed genetic variation for starch accumulation during reproductive development. It has been postulated that genotypic variation in carbohydrate and nitrogen remobilization during periods of environmental stress when photosynthesis is adversely affected, may be related to maintenance of a high rate of seed filling and may buffer and stabilize

yields. Little is known concerning genetic variation of seed filling parameters (rate and duration) in this crop and the relationship of these parameters to patterns of assimilate partitioning among genotypes.

Reproductive abscission has been measured in cultivars of dry beans (Izquierdo and Hosfield, 1981) and could be important in reducing the yields. The availability of carbohydrate and nitrogen as well as hormones were suggested by Subhadrabandhu (1976) as regulating abscission and were important factors in influencing yield adjustment.

The primary objective of the present work was to study the relationship between photosynthate partitioning and remobilization and the seed filling process in P. vulgaris L. as well as controlling the level of reproductive and vegetative abscission. Specific objectives were to:

- 1) evaluate the effect of plant architecture on partitioning and seed filling,
- 2) elucidate the effect of total nonstructural carbohydrate and nitrogen status of the bean plant had on reproductive and vegetative abscission, and
- 3) characterize the relationship between remobilization and yield among contrasting plant architectures.

CHAPTER 1

APPLICABILITY OF IKI-STARCH SCORES AND CONTENT OF TOTAL SOLUBLE SOLIDS FOR EVALUATING CARBOHYDRATE PARTITIONING IN BEANS

ABSTRACT

In order to facilitate selection studies of carbon assimilate partitioning in strains of beans (Phaseolus vulgaris L.), a rapid and accurate means of estimating nonstructural carbohydrates is needed. The IKI-starch score technique and total soluble solids (TSS) content are two methods that could be used to evaluate a large number of cultivars and breeding lines. The purpose of this study was to assess the value of the two methods for carbohydrate partitioning studies by correlating subjective data with in vivo quantities of starch and sugars as determined in the laboratory. Correlations between IKI-starch scores and TSS content and quantitatively determined starch and water soluble sugars by HPLC were in moderate but not high agreement. Significant coefficients between in vivo starch and IKI-starch scores were obtained in roots ($r=0.51$), stems ($r=0.61$) and petioles ($r=0.77$). Total sugar determined by HPLC was significantly correlated ($r=0.42$) with TSS only in root tissue, while sucrose content was significantly correlated with TSS in roots ($r=0.41$) and stems ($r=0.44$). Glucose was found to be significantly correlated with TSS in petioles ($r=0.74$). Despite these findings, the IKI-starch score procedure was useful in discerning variability among three dry bean cultivars for their patterns of carbohydrate

partitioning during the reproductive growth period. The cultivars Black Turtle Soup and Nep-2 began remobilizing starch at late seed-filling while remobilization in the cultivar Tuscola was apparently triggered by the onset of seed-filling. Since the petioles store starch and the IKI-starch scores of this tissue correlated with in vivo starch more closely than scores from roots, stems and pod walls, the petiole is a useful organ for evaluating carbohydrate partitioning. Moreover, IKI-starch score evaluation in petioles is non-destructive in the sense that the whole plant need not be sacrificed.

Additional index words: Phaseolus vulgaris L., dry beans, seed-filling, High Performance Liquid Chromatography, quantitative sugar analysis, quantitative starch analysis.

INTRODUCTION

Most plants store, in one form or another, carbohydrate reserves which may or may not be used at later stages of development (1). In corn (Zea mays L.), the stalk can serve as a temporary storage site for sugars and other soluble solids before the ear becomes a dominant sink (4, 7). Adams et al. (1) reported genotypic differences for stored starch in stems and roots of dry edible beans (Phaseolus vulgaris L.). These researchers (1) suggested that starch remobilization from stem or root may be important to seed-filling and may buffer yield in bean plants against adverse circumstances of growth such as, for example, in a stress environment.

To facilitate selection and genetic studies of carbohydrate partitioning in dry beans, a rapid and accurate means of measuring water soluble carbohydrates (TNC) is needed. Several suitable analytical procedures

relying on colorimetric mensuration have been developed for carbohydrate analysis (sugars and starch) in a number of crops (9, 16, 17) and could be modified for beans. However, these methods are largely unsuited for analyzing a large number of samples. Experience has shown that the techniques require considerable skill, are time consuming and sensitive to slight variation in conditions.

Recently, individual sugars and starch have been separated and quantified from tissues of dry beans by High Performance Liquid Chromatography (HPLC) (11). Although HPLC provides for rapid and excellent quantitative determinations of sugars, it has certain practical and methodological limitations. The chief disadvantages of using HPLC for routine analyses are high initial cost of instrumentation, and maintenance costs associated with periodic replacement of degenerated columns.

Previously, carbohydrate partitioning in beans was studied (1) using the principle that addition of triiodic ion to starch yields a brilliant blue complex (12, 13) due to the strong affinity amylose has for iodine. The method consisted of treating freshly cut tissue with several drops of an iodine-potassium iodide indicator solution (IKI) and visually ranking the color development (IKI-starch score) against facsimiles sketched on a color chart. Although the IKI-starch score method was rapid and varying degrees of color development were observed among cultivars in stems and roots, no evaluation of the method's accuracy was made comparing the subjectively determined scores with quantitative analysis of starch from the same materials. To support the basis for their work, Adams et al. (1) relied on a correlation ($r=0.85$, 18df) between IKI-starch scores and in vivo starch determined in a separate study (3).

Water soluble sugars (WSS), one of the components of TNC, can be estimated collectively in plant tissues from the total soluble solids content (TSS). Refractometer determinations of TSS have been used routinely by researchers as an indication of dry matter and sugar content in a number of crops (5, 6, 7, 14, 15). In carrots, correlation coefficients of 0.79 and 0.84 between TSS content and WSS justify using these terms interchangeably (6). Campbell and Hume (5) took refractometer readings above and below the ear on 1072 corn internode samples representing a wide range of genotypes and plant densities. The correlation coefficient in this study was 0.54 and highly significant. When refractometer readings were corrected for tissue moisture content the correlation was improved considerably ($r=0.93$).

Methods for studying carbohydrate partitioning among strains of common bean needs to be rapid, reproducible, accurate, and inexpensive. The present study was conducted to evaluate the IKI-starch score technique and refractometric determined TSS content as acceptable methods. Specific objectives were to: 1) determine TNC status of stems, roots, petioles, and pod walls during the reproductive growth period, 2) correlate IKI-starch scores and TSS content from the respective tissues with values obtained from quantitative determinations by HPLC, and 3) evaluate the utility of using IKI-starch scores and TSS content for comparing bean genotypes.

MATERIALS AND METHODS

Three dry bean cultivars, 'Tuscola' (TUSC; determinate), 'Nep-2' (N-2; semi-determinate), and 'Black Turtle Soup' (BTS; semi-indeterminate) were used in the experiment. Since the cultivars differed in

growth habit, flowering pattern, and yield, it was assumed, a priori, they might also differ in carbohydrate partitioning.

The cultivars were grown in three-row plots in a nursery at East Lansing, Michigan in 1979. Rows were 50 cm apart with plants spaced 6 cm apart. Four replications were used. Plants were harvested for carbohydrate evaluations during the reproductive growth period. Sampling began at first flowering which was chosen as that date when 50 percent of the plants in a plot had at least one open flower (50 percent F). Sampling continued approximately every four days (DA 50 percent F) to physiological maturity (PM) and involved a total of 12 sampling dates. Physiological maturity was taken as the date at which approximately 90 percent of all pods had changed color visually from normal green to pale yellow or brown.

At each sampling date, five random but representative plants were removed from the middle row of the plot. Just prior to removing plants, approximately a one-meter segment was marked at random in each replication and plants were taken from this part of the row. This procedure was followed to eliminate any competitive effects on the next sampling date that might be caused by removing plants. Each plant was immediately dissected into roots, stems, and petioles. Pod wall tissue was sampled and evaluated beginning at sampling No. 5 (16 DA 50 percent F) and continuing until sampling No. 11 (40 DA 50 percent F). This period corresponded to the time when pods had elongated to a point they could be reasonably evaluated until they had senesced to the point where readings obtained could no longer be considered valid. Roots and stems were sectioned according to Adams et al. (1) and petioles and pods were

taken from plants at the same nodal position as the stem cut was made. Pods were cut transversely at the middle-third region.

Immediately after sectioning, three or four drops of an IKI indicator solution, made by dissolving 0.3 g iodine and 1.5 g potassium iodide in 100 ml water, were applied to the freshly cut section of each tissue. The amount of starch was rated on a 5-point subjective scale; 1 (least) to 5 (most). A color photograph containing a series of IKI-stained cross sections of each respective tissue evaluated and taken from bean strains with varying amounts of stored starch was used for scoring (Figure 1).

The WSS content of each tissue was estimated from TSS measured using a Kikuchi, 0 to 25 percent Brix, temperature corrected, hand held refractometer. The refractometer was calibrated using sucrose standard solutions ranging from 0.01 to 10.0 percent. The standard curve obtained showed a linear response of the TSS readings (Y) over the sucrose range (X) evaluated. The equation for a linear fit to 24 data points was $Y = -0.368 + 1.083X$ and the correlation coefficient (r) between the values was 0.998 and highly significant.

The TSS content was determined on parts of tissue immediately behind or in front of the cut where IKI-starch was evaluated. One or two drops of juice were expressed from each tissue with a pliers and placed directly on the prism surface.

Immediately following the IKI-starch score and TSS evaluation, remnants of each respective tissue from each cultivar were bulked and frozen at 0–3°C for several days and dried. Drying was effected by using either a convection oven (100°C for one hour and 65°C for 72 hours) or freeze dryer (Virtis, Freeze Mobile II Model). After drying, tissue was ground in a Wiley mill to pass through a 40 mesh screen,

collected in glass bottles, capped, and stored at -10°C until analyzed. Ground tissues from two replications and seven sampling dates were extracted for laboratory determinations of WSS and starch. Heat drying and freeze drying at -60°C for 48 hours had no significant effect on the levels of WSS and starch determined by HPLC. Lack of significant differences between the two methods of drying agrees with results reported by Smith (16).

The extraction of WSS from tissue was completed using essentially the method of Black and Bagley (2) for defatted soybean meal except we washed the residue remaining after centrifugation (pellet) once. This procedure saved approximately one hour per sample during extraction and did not significantly affect the results. Sugars were separated from the extracts by HPLC by the procedure of Lester et al. (11). Starch content was determined on each tissue by analyzing a 200 mg sample of the dried pellet fraction and following a modification of the procedure of Dekker and Richards (8). A soluble starch solution was prepared by suspending 200 mg of oven-dried pellet in five ml of a 0.5N sodium hydroxide solution for one hour. Starch solubilization proceeded by constantly agitating the suspension for one hour in a water bath maintained at 35°C . After solubilization, the solution was neutralized by adding approximately five ml of a 0.5N acetic acid solution. The solubilized starch was exhaustively hydrolyzed to glucose using an enzyme cocktail made by combining one ml of amyloglucosidase (obtained from Rhizopus spp. mold), 0.5 ml α -amylase (Type 11-A), and 0.2 ml β -amylase (Type 1-B). The enzymes were obtained from the Sigma Chemical Company, St. Louis, Missouri. Incubation of the enzymes in the

starch solution was carried out for 30 minutes by shaking in a water bath maintained at 30°C and for 30 minutes at 55°C. The glucose liberated from starch digestion was determined quantitatively by HPLC (11).

Plot means were calculated for the three methods of carbohydrate determinations. Analyses of variance were performed on data for each cultivar and sampling date both separately and combined. Means were separated using the Duncan Multiple Range Test (DMRT) procedure. Simple correlation coefficients were calculated between IKI-starch scores and TSS content and starch and WSS determined quantitatively by HPLC.

RESULTS AND DISCUSSION

The IKI-starch score of a tissue and its corresponding starch content determined quantitatively by HPLC showed agreement as indicated by significant or highly significant correlations (Table 1). However, the coefficient values were not of sufficient magnitude to allow the substitution of IKI-starch scores for actual quantitative levels of starch in bean tissue. At best, the IKI-starch scores must be used in a semi-quantitative sense only. No improvement in the correlations could be made by normalizing the IKI-starch score data by transformation (Table 1). However, recalculation of the coefficients after data points with significant residuals ($\pm 2\sigma$) were eliminated from the regression equation greatly improved the correlations for stem and petioles (Table 2). Further inspection of Tables 1 and 2 shows that IKI-starch scores from petioles reflected the most accurate ($r=0.77$ and 0.85) and root scores the least accurate ($r=0.51$ and 0.49) estimates of starch content, respectively. Although not in agreement with the stem and root correlation ($r=0.85$)

used by Adams et al. (1) as supporting evidence for their work, correlations obtained from the present study are supported by findings from a separate experiment conducted in 1980 (data not shown). In the 1980 study, correlations were determined on nine dry bean strains (including N-2, BTS, and TUSC) with four replications and four physiological stages. Analyses of these data revealed significant correlations for roots, stems, and petioles of 0.49, 0.66, and 0.65, respectively. Recalculation of the correlations after eliminating data points with significant residuals from the regression improved the respective 1980 determined coefficients to 0.53, 0.72, and 0.79.

The lack of good agreement in the present study between subjective measurements and starch quantitatively determined in the laboratory could be due to misclassification of IKI-starch scores falling into the intermediate classes brought about by a lack of consistency in ascribing a particular score to a particular pattern and intensity of color development. The LSD values presented in Figure 1a, b, d support the suggestion that some misclassification of data occurred.

It is tempting to speculate, however, that the lack of correspondence between IKI values and in vivo starch may have been due to differences in starch quality among cultivars. Starch in plants may consist of both amylose and amylopectin; the ratio of one form to the other may vary among cultivars. Should stored starch consisting of significant amounts of amylopectin (weakly detectable with IKI solution) be peculiar to a cultivar, IKI-starch score readings would be lower when compared to a cultivar with the same level of total starch but with starch stored primarily in the form of amylose.

Further work is needed to corroborate this suggestion but supporting evidence comes from the fact that of the 24 significant residuals noted for roots, stems, and petioles, when these tissues were considered simultaneously, the cultivar BTS accounted for more than half (Table 2). Furthermore, 11 residuals were attributable to both BTS and N-2 in data corresponding to 40 DA 50 percent F and PM samplings. Starch was present in both cultivars at these periods but not appreciably discernible using the IKI starch indicator solution.

The second method of examining carbohydrate partitioning in beans was to plot TSS percentage in roots, stems, and petioles of the three cultivars throughout the reproductive growth period. Correlation coefficients (Table 1) indicated that TSS percentage and total WSS as determined by HPLC were significantly related only in root tissue. However, TSS and sucrose content were correlated in roots and stems, although the coefficients were not large. In the petioles, TSS was correlated with glucose content. It was interesting but not surprising to find glucose as the predominant WSS in petioles. The petiole is an organ adjacent to a major photosynthetic source (leaf); hence, the glucose found probably reflected photosynthate produced shortly before (current) sampling occurred. Although the glucose detected conceivably could have arisen from sucrose hydrolysis by invertase, it was unlikely because samples were frozen almost immediately after sap was expressed for TSS determination. Moreover, fructose was not detected in sugar separation by HPLC. If sucrose hydrolysis had occurred, both fructose and glucose would have been detected.

Table 3 shows that quantitatively determined starch (measured as glucose) and WSS were determined by HPLC with a high degree of accuracy.

Significant differences detected for sampling dates (DA 50 percent F) and cultivars agreed with similar differences detected (data not shown) for IKI-starch score and TSS. Only one significant interaction was noted (DA 50 percent F x cultivar) but does not detract from the usefulness of HPLC for quantitative analysis of carbohydrates in bean tissues. Variability among field replications was low compared to the experimental error and good reproducibility was obtained between duplicate injections of samples on the HPLC.

The IKI-starch score method has been used as an indicator of the presence or absence of starch in tissues of common bean and to identify strains that remobilize starch during the reproductive growth period (1, 10). Despite the shortcomings of the procedure, we support its use to evaluate starch reserves in different storage sites of the plant provided the investigator establishes a reference for his material by making quantitative determinations of starch on the same tissues. In other words, the IKI-starch scores representing the highest and lowest categories determined on a particular hedonic scale should correlate to a high degree with the highest and lowest levels, respectively of starch content in vivo. Once a reference is established, the main concern to the investigator would be to accurately classify the IKI-starch scores falling into intermediate categories. Comparing IKI-starch scores with a quantitatively determined reference for starch quantity could also improve the method's usefulness as a quantitative tool. Since the relationship between IKI-starch score and a quantitatively determined starch reference will vary depending on genotype and environment, the investigator should establish a reference as circumstances warrant.

Once the investigator is satisfied as to the utility of the IKI-starch score method under his set of conditions, he might wish to know when to begin sampling plants for starch accumulation. On the basis of the present study, the IKI-starch score procedure was useful in discerning differences among cultivars for reserve carbohydrate during the seed-filling period (Figure 2). The beginning of seed fill was determined on a seed fresh weight basis in a separate experiment as 17, 20, and 26 DA 50 percent F, for BTS, TUSC, and N-2, respectively. Based on IKI-starch scores the cultivars N-2 and BTS apparently began remobilizing starch in roots during late seed-filling which corresponded to approximately 30 DA 50 percent F (Figure 2a). The IKI-starch score pattern in roots and pod walls of TUSC (Figure 2a, d) indicated that remobilization in these tissues was triggered by the onset of seed-filling. Beginning seed-filling also appeared to initiate starch remobilization in petioles of N-2 and BTS while sharp remobilization occurred in this tissue at mid seed-filling for TUSC (Figure 2c). Appreciable starch remobilization was noticeable at late seed-filling for stem tissue of the three cultivars (Figure 2b).

Although Table 3 indicates that TSS percentage is significantly correlated in several tissues with either total WSS or sucrose content, the magnitude of the coefficients do not justify using TSS percentage and sugars interchangeably. Correlation coefficients between TSS content and sugar content in crops where refractometer readings are used routinely are generally greater than 0.75 (5, 6, 15, 16). We suggest, however, that at specific points in the life cycle cultivar differences for carbon assimilation could be ascertained by reading TSS percentages of the petioles. In addition, refractometer readings taken at the petiole

coupled with IKI-starch scores of the same tissue could provide the researcher with insight as to carbon assimilate partitioning. It should be pointed out that the IKI-starch score and TSS percentage evaluation of a petiole provides a non-destructive measurement in the sense that the whole plant can be sub-sampled at several nodes and need not be sacrificed. Saving the plant is not possible when evaluations take place on roots and stems.

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Table 1. Simple correlation coefficients between IKI-starch scores and total soluble solids (TSS) with starch and water soluble sugars (WSS) determined quantitatively by HPLC in three tissues of beans

Correlation [†]	Correlation coefficient		
	Root	Stem	Petiole
Starch (mg/g) and IKI-starch scores	.51*	.61*	.77**
Starch (mg/g) and log IKI-starch score	.48*	.59**	.69**
Total sugar (mg/g) and TSS	.42*	.11	-.06
Total sugar (mg/g) and log TSS	.43*	.11	-.15
Sucrose (mg/g) and TSS	.41*	.44*	.10
Sucrose (mg/g) and log TSS	.42*	.36	.07
Glucose (mg/g) and TSS	.28	.31	.74**
Glucose (mg/g) and log TSS	.18	.22	.68**
Sucrose (mg/g) and total sugar (mg/g)	.84**	.85**	.08
Glucose (mg/g) and total sugar (mg/g)	.42*	.23	.76**
Starch (mg/g) and sucrose (mg/g)	.29	-.16	.10
Starch (mg/g) and glucose (mg/g)	.17	-.11	-.02

*, ** Significant at the 0.05 and 0.01 level of probability, respectively. Data averaged over three cultivars (BTS, N-2, and TUSC) and seven sampling dates during the reproductive growth period. Degrees of freedom = 21 for each tissue.

[†]Carbohydrates expressed on a dry weight basis.

Table 2. Correlations in roots, stems, and petioles between IKI-starch scores and in vivo starch determined by HPLC of three dry bean cultivars after deletion of data points with significant residuals from the regression equation

Tissue	No. of Observations	Correlation Coefficient	No. of data points with significant ($\pm 2\sigma$) residuals			
			Cultivar			
			BTS	TUSC	N-2	Total
Root	73	0.49*	5	4	2	11
Stem	77	0.69**	3	1	3	7
Petiole	78	0.85**	5	1	0	6

, * Significant at the 0.05 and 0.01 level of probability, respectively.

Table 3. Mean squares from the analysis of variance of quantitatively determined TNC (mg/g) by HPLC from root tissue of three dry bean cultivars.

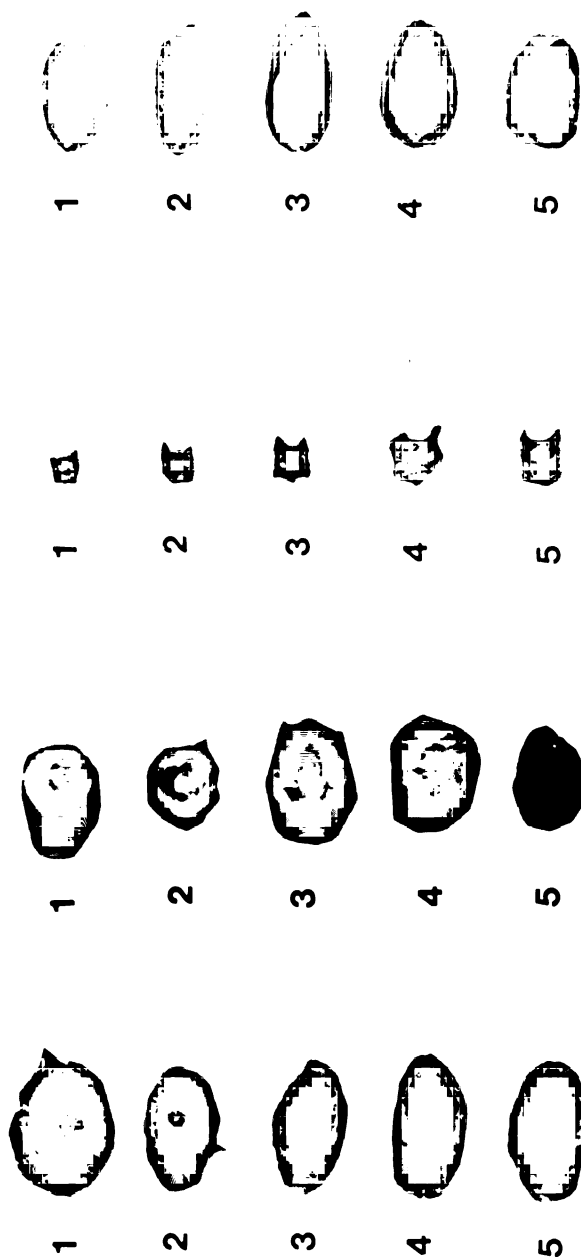
Source	d.f.	Carbohydrate			
		Total sugar	Sucrose	Glucose	Starch
Replications	1	11.09	19.3	59.9	13.8
Days after 50% flowering					
(DA 50%F)	6	4,071**	1,978**	563*	313**
Error a	6	271	133	68	13.2
Genotype (G)	2	1,162*	1,238**	21.9	702**
DA 50%F x G	12	340.6	384	328**	185
Error b	14	285	156	81.9	115
Injection (I)	1	71.3	16.0	3.2	1.9
DA 50%F x I	6	39.3	24.7	6.8	25.4
G x I	2	81.2	58.1	35.4	27.8
DA 50%F x G x I	12	126	53.9	17.5	25.2
Error c	21	61.9	25.1	32.2	24.9
Total	83	--	--	--	--

*, ** Significant at the 0.05 and 0.01 level of probability, respectively.
Data taken from two replications and seven sampling dates.

Figure 1. Photograph showing hedonic scale of color development from low (1-score) to high (5-score) used to classify roots, stems, petioles, and pod walls of beans for IKI-starch score

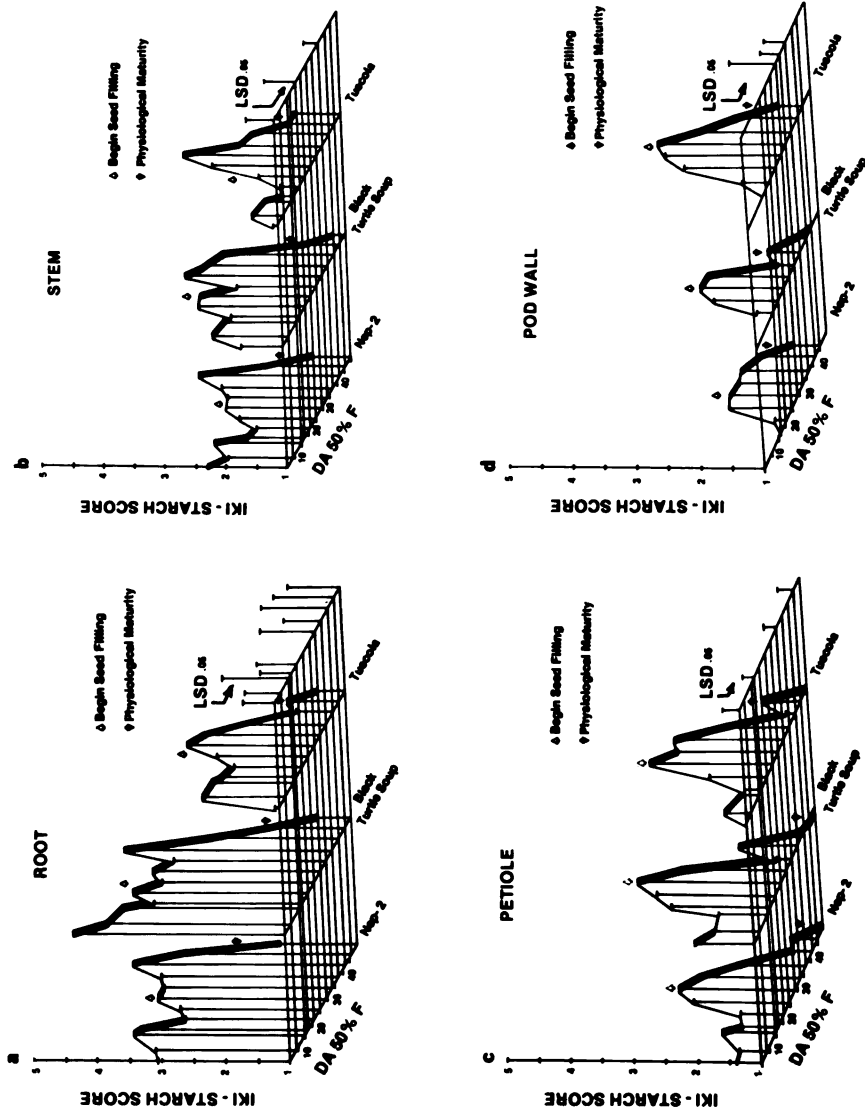
IKI-STARCH SCORE

ROOT STEM PETIOLE POD WALL



2/3/10

Figure 2. Pattern of IKI-starch scores found in four tissues (a = root, b = stem, c = petiole, and d = pod wall) of three dry bean cultivars (Nep-2, BTS, and Tuscola) during the reproductive growth period in 1979



CHAPTER 2

RELATIONSHIP OF SEED FILLING AND DRY MATTER REMOBILIZATION TO YIELD DIFFERENCES AMONG BEAN PLANTS WITH DIFFERING ARCHITECTURES

ABSTRACT

The development of a new dry bean (Phaseolus vulgaris L.) cultivar with increased yield must be viewed in context with a more efficient allocation of assimilates to the developing seed than in presently grown varieties. The purpose of this paper is to evaluate the physiological parameters affecting seed filling and their relationship to yield through the remobilization of dry matter from temporary storage sites among dry bean entries with differing plant morphology. Significant differences in yield among the entries were more associated with the length of the seed filling period than with the rate of growth. A new architectural form: architype and the cultivars Nep-2 and Black Turtle Soup (Growth Habit II) extended more than two-fold the duration of the filling period when compared with standard bush cultivars grown extensively in northern states in the United States. Dry matter remobilization from stem and pod walls, the most important sources of remobilizable dry matter, was negatively and significantly correlated with the duration of the seed fill. A very high dry matter remobilization factor (RF) characterized the standard bush form which filled the seed at the highest rates during the shortest period. A high dependence in remobilization for this architectural form is proposed as the mechanism for obtaining

relative low yields. On the other hand, the high yield potential of the archetype lines 61380 and 61356 was characterized by a long filling period and associated high dry matter remobilization.

Additional index words: Phaseolus vulgaris L., linear filling rate, linear filling period, remobilization factor, archetype, growth habit.

INTRODUCTION

Low crop productivity is limiting the traditional role of dry edible beans (Phaseolus vulgaris L.) as a staple food in the diet of a rapidly expanding population of Latin America. This region consumes 45 percent of the world production (6). Increased productivity must be viewed in context with the genetic improvement for resistance to agronomic constraints, stabilization of yield and to maximize responses to environmental resources available for this crop (18).

It has been postulated that productivity increases in dry beans could be obtained if allocation of assimilates into the seeds (economical sink) of new cultivars was more efficient than in older cultivars (4). The selection of cultivars with more effective partitioning of nitrogen and products of current photosynthesis to the seed was thought to be the key factor for the improvement of yield in other grain crops, namely rice (Oryza sativa L., 37), peanut (Arachis hypogaea L., 12), and soybean (Glycine max L., Merrill, 21).

There is evidence which suggests that partitioning in dry beans is under genetic control. Differences in starch accumulation among several dry bean cultivars were detected (3). Timing of starch reallocation in relation to the initiation of grain filling has been studied by Izquierdo et al. (22) who showed differences in the responses among

several tissues. From this work the stems and pod walls were shown to be important sites for the temporary storage of nonstructural carbohydrates. Moreover, there was variability among the cultivars in their ability to accumulate and reallocate starch from vascular tissues. Evidence suggests that storage of reserve carbohydrate during the reproductive growth period may play a role in the rate and duration of seed filling and to buffer strains during periods of stress. However, the significance of the accumulation and reallocation of starch and their effects on yield by some bean strains during the reproductive period remain to be established for this crop.

In search for crop plants with superior yields, plant breeders have studied the physiology of the grain filling rate and duration. In general, results in rice (25), soybean (26), corn (Zea mays L., 10, 13, 24), barley (Hordeum vulgare L., 31), wheat (Triticum aestivum L., 28, 32) and cowpea [Vigna unguiculata L. (Walp.), 36] indicated that genetic differences existed among cultivars and breeding lines for both the rate and duration of grain filling. Several studies (10, 13, 26, 28, 33, 35, 37) in grain crops showed that the duration of grain filling was more closely related to yield than the filling rate. However, Nass and Reiser (28), Egli and Legget (14) and Jones et al. (25) concluded that the length of the grain filling period was not important in determining the yield, and more precisely, filling rate, was more accountable for differences in final weight than filling duration in rice (25) and in wheat (32).

In dry beans as well as for other legumes, the yield of seed is taken as the product of the number of seeds per unit area and the seed size. Since no mechanical impediment occurs in beans to limit seed

growth as in rice (25), seed size simply is the rate of seed dry matter accumulation integrated over time.

Seed filling in common bean is sustained largely by current photosynthesis and possibly the remobilization of stored assimilates (8). Keeping these facts in mind, the present study was conducted to determine: i) the parameters that characterize the physiology of seed filling; ii) the effect of rate and duration of the grain filling on yield, and iii) the variability among dry bean growth habits.

MATERIALS AND METHODS

Genetic Materials and Plant Architecture

Nine strains of dry beans were used as entries in this study. The entries represented four distinct architectural forms (Figure 1) and two growth habits type I and II according to the classification of the International Center for Tropical Agriculture, Cali, Colombia (6). The architectural forms were selected on the basis of their differences in time to maturity, reproductive growth pattern, and yield.

Within CIAT type I (determinate bush), entries with form A and B architectures could be identified. Form A is a small bush plant containing more than four branches and characterized by a short and non-erect canopy. Form A plants lodge at maturity (Figure 1a). Examples of entries belonging to form A were the cultivars 'Seafarer,' 'Sanilac,' and 'Tuscola.' These entries also belong to the navy commercial class and represent a large proportion of the dry beans grown in the USA (2). Strains belonging to architectural form B are erect bush plants, approaching 75 cm in height and resisting lodging at maturity. The navy bean breeding line, C-14, used in this study is a characteristic form B (Figure 1b).

The type II growth habit (indeterminate, semi-vine) contained architectural forms C and D. Form C, "classic type II," is characterized by semi-erect plants which lodge at maturity. The cultivars 'Black Turtle Soup' (BTS) and the white seeded 'Nep-2' are examples of the form C (Figure 1c). Nearly all black dry edible beans growing in the USA are of the Black Turtle type (2). Plants fitting the description of form D are characterized by a narrow profile, tall (75 cm), erect, and supported by two to four strong branches vertically oriented and separated from one another by an acute angle (15-25°). Plants with this architecture are non-lodging at maturity and are referred to as archetypes (Figure 1d). The black seeded breeding lines 61380 and 61356 and the white seeded breeding line 61618 are considered archetypes.

Planting and Final Harvesting Procedures

The nine entries were grown in 1980 at East Lansing, Michigan. Seed was precision drilled into eight row plots with a tractor mounted air planter. Rows were 10 m in length and spaced 47 cm apart. Within row spacing was 7-8 cm giving between 14 and 16 plant per meter of row. Plots were arranged in a randomized complete block with four replications. Standard practices for herbicide and fertilizer application were used.

In late September, mature plants were removed by hand from two, 2-m sections of row (1.88 m^2) of individual plots and threshed by hand. Just prior to threshing, data were recorded on individual plants for the total number of pods produced and the number of shriveled pods comprising the total number. In addition, seed number per pod was determined from a 50 pod sample, and one hundred seed weight was calculated as the average of two, 100-seed samples. After threshing, seeds were

analyzed for moisture content and weighed for yield (g) per plot.

Yields were adjusted to 16 percent moisture content.

When taking the 50 pod sample, only non-shriveled pods were used. In determining the number of seeds from this sample, seeds were separated into plump or otherwise normally appearing seed and shriveled or aborted seed. The total number of plump seeds per unit land area (1.88 m^2) was calculated according to the following equation: $[(\text{total number of pods}/\text{m}^2) - (\text{percent of shriveled pods}) \times (\text{total number of seeds/pod}) - (\text{percent of aborted seeds})]$.

Seed Filling Parameters

For this phase of the study, the second and seventh rows of each eight row plot were subdivided into seven segments each 1 m long. Five plants separated each segment and acted as a guard. These procedures permitted the entry growing in each segment to be bordered on either side and at each end by itself. The 14 to 16 plants growing within each of the seven segments of each row were considered the experimental units and all sampling was done on plants comprising these units.

The experimental units were observed closely each day to determine the date of anthesis (A) defined here as the date when the first open flower was noticed in a plot. After flowering began, observations were made to determine the date when 50 percent of the plants in a plot (experimental unit) had at least one open flower (50 percent F). When 50 percent F was reached for a plot, sampling began. The procedure followed was to take five plants at random from one of the 1-m segments and remove all pods formed at the fourth, fifth, and sixth nodes of the main stem. Pods were measured for length (mm) and opened with a razor blade to remove seeds. The seeds and empty pods were dried in a

forced air oven at 100°C for one hour followed by 70°C for 36 hours. Sampling was performed between 0800 and 0900 on each sampling date and once a segment (experimental unit) was sampled, it was no longer used and another of the remaining segments was chosen at random for the next sampling date. Sampling was carried out every four days until physiological maturity (PM) occurred. Physiological maturity was taken as the date at which approximately 90 percent of all pods had changed color perceptively from normal green to pale yellow or brown.

After they were dried, the weights for pods (g) and seeds (mg) were determined. The data for pod length, pod dry weight, and seed dry weight were plotted concomitantly against the number of days after 50 percent F (DA 50 percent F) at which the respective samples were taken. When exponential increments in the mean pod length and the mean seed weight were reached, the period of middle-pod elongation (MPE) and middle-seed filling (MSF) were established for each of the nine entries.

The seed filling parameters--rate and duration--were calculated by fitting the data to a third degree polynomial using the least squares regression technique with time (t) as days after 50 percent F as the independent variable (x). The polynomial model used was of the form, $y = \beta_0 + \beta_1x + \beta_2x^2 + \beta_3x^3$. The definition of y was dependent on the variable calculated and was defined as the mean pod length ($\text{mm} \cdot \text{pod}^{-1}$), or mean pod dry weight ($\text{g} \cdot \text{pod}^{-1}$) or mean seed dry weight ($\text{mg} \cdot \text{seed}^{-1}$), respectively. The partial regression coefficients were: β_0 = the y intercept, and $\beta_1, \beta_2, \beta_3$ were equal to the constants for each order of the three terms used in the polynomial equation.

The linear seed filling rate (LFR) was calculated using the linear regression coefficient determined from the line of best fit to the data

points during the linear phase of seed growth. First estimates of the limits of the duration of the linear phase were obtained by super-imposing a straight line over the linear phase of the curve corresponding to the cubic polynomial. After this was done, and by using linear regression, the regression coefficient (rate) defined as $b = \text{mg} \cdot \text{seed}^{-1} \cdot \text{day}^{-1}$, the coefficient of determination (R^2), and the F-statistic of the first degree polynomial were calculated for the linear period.

In order to reduce subjectivity in choosing the limits of the linear phase, a method proposed by Sofield et al. (32) was used to obtain this parameter. First, data points in the middle region of the linear phase of seed growth were selected, a least squares fit determined, and a determination coefficient calculated (32). This middle region was then progressively extended by taking additional points, first at one end of the period and then the other, and adding them one by one while refitting the curve and recalculating the determination coefficient. This procedure was continued until the inclusion of a new data point had no effect on changing the magnitude of the F-value from the regression analysis of variance. Once this occurred, the data point included was discarded and the penultimate data point used to establish the growth rate. The linear filling period was then estimated by extrapolation of the line of best fit to its intersection with the ordinate (DA 50 percent F).

An estimate of the maximum seed weight (Max W) was calculated by setting the first derivative of the cubic function $f'(t)$, used to estimate the seed filling parameters ($y = \beta_0 + \beta_1 x_1 + \dots$), to zero and obtaining the corresponding root that maximized the cubic equation. Extrapolation of Max W to its intersection with the x-axis (DA 50 percent F) gave an estimation of the total filling duration (TFD). The mean seed filling rate

($\overline{FR}$) was then estimated by the Max W/TFD ratio. The maximum filling rate (MFR) was estimated by equating the second derivative $f''(t)$ to zero and obtaining the value of t that maximized $f'(t)$. The effective seed filling period was estimated by dividing the observed seed size at PM by the LFR (10, 36).

Dry Matter Partitioning

To study the partitioning of dry matter in various organs of the bean plant, a 1-m segment of plants was removed from one of the four center rows of each eight row plot at each of the four physiological stages (A, MPE, MSF, and PM). Five random plants were used as sub-samples and separated into tap roots, stems (including the raceme peduncles), petioles and leaf blades. Roots and stems were sectioned according to Adams et al. (3). Petioles were taken from the point of attachment to the stem to the point where the leaf branched into trifoliate. The leaf blades consisted of the trifoliate lamella. At MSF, pods were prominent and were sampled here and at PM. When pods were sampled, all of these structures were removed from plants (leaving the pedicel attached to the racemes). Pods were opened longitudinally separating them into pod wall tissues (PW) and seeds (G). All plant parts were frozen at -19°C until they were heat dried according to procedures described above. After drying, plant parts were weighed and the data averaged over the five plant sub-sample. Since the sub-sample was considered to be representative of the plants growing in the one meter from which they were removed and the one meter segment was representative of the plot, data were expressed as $\text{g} \cdot \text{m}^{-2}$. From the data a dry matter remobilization factor (DRF) was calculated. The DRF is similar to

the proportioning factor described by Gallagher (16). The DRF is defined as changes in dry weight of a plant component divided by changes in dry weight of either pods or seeds (16). When it is assumed that no losses of carbon are occurring because of respiration and abscission, the theoretical maximum expression of DRF is -1.

RESULTS

The highest yields noted were produced by the architypes and yield differences over the small bush form were significant. These results are in agreement with data from statewide performance trials (1, 34). The yield advantage noted for the architypes (70 percent over the small bush type) were principally due to a larger number of seeds per pod and a larger seed size (Table 1). On the other hand, the small bush cultivars Seafarer, Sanilac and Tuscola, produced a larger number of total pods per square meter which was due to an increased sink production (flowers $\cdot m^{-2}$). However, the superiority in pod set of the three navy cultivars was negatively affected by a higher percentage of pod shriveling and seed abortion than in the other architectural forms. In this regard when the seed yields were adjusted to account only for normal seeds, the yield superiority of the architypes had greatly increased (Table 1). The significant yield difference noted for the architypes over BTS (classic II) was due to heavier seeds. The breeding line, C-14 (tall erect bush), produced a higher yield than the average of the small bush cultivars but this difference was non-significant. Except for pod shrivel and the adjusted seed number per square meter, all yield data had low coefficients of variability (CV) (Table 1) indicating a satisfactory degree of experimental consistency.

Data points for seed dry weight of the nine entries were well fitted by the cubic model with the smallest R^2 calculated showing a good fit (0.908) to the polynomial equation used (Table 2). The same model produced highly significant regressions and the smallest R^2 equal to 0.952 for data on seed fresh weight sampled every four days for the cultivars Nep-2, BTS and Tuscola, grown in 1979. Jones et al. (24) suggested that a cubic polynomial was useful in estimating seed filling parameters in rice. Moreover, since data in the present studies were taken at only four day intervals after 50 percent F, the time at which seeds reached their maximum weight could not be determined precisely.

Entries differed for the predicted linear filling rate (LFR) and linear filling period (LFP), respectively. Archetypes had a longer LFP with a lower LFR, while the small bush types had a shorter LFP and a higher LFR. Plants of both classic type II and the tall erect type I had intermediate values. A test of the homogeneity of the linear regression coefficients (=LFR) was not significant within the architectural types (archetype and small bush) but was highly significant between them (data not shown).

Predicting seed weight using a cubic polynomial can either overestimate or underestimate the seed weight at PM. The predicted seed size (Table 2) at the end of the linear growth phase explained 37.7 to 72.1 percent of the observed seed size at maturity. Max W overestimated observed size by nine percent. This was probably due to estimation of Max W from data taken from pods at the fourth and sixth nodes while the final seed weight at harvest came from a random threshed and bulked sample of seed over the entire plant. Evidently, the fourth and sixth node pods produced seeds with a more uniform weight than in pods harvested over the entire

plant. However, the correlation between Max W and actual seed weight was 0.882 and highly significant. This supports the usefulness of a cubic polynomial model for estimating Max W in spite of the four day spaced sampling method. Table 3 shows that the seed filling rate parameters (LFR, Max FR and $\overline{FR}$) were negatively and in most case nonsignificantly related to yield or to the components of yield. Only LFR was significantly and negatively correlated with a yield component (seed number per pod). On the other hand, Table 4 shows that the filling duration parameters (TFP, EFP and LFP) were positively correlated to yield and the yield components seed size, seeds/pod and seeds/m². Non-shriveled pod/m² was negatively but nonsignificantly correlated with yield, although sink number (seed/m²) was positively correlated with yield after correction for pod shriveling and seed abortion (Table 4). Seed size was positively correlated with yield and negatively with pod/m².

Table 5 shows the data pooled over genotypes for dry weight of roots, stems, petioles, leaf blades, pod walls, and seed at the A, MPE, MSF and PM stages of development. The analysis of variance revealed (data not shown) that the interaction of genotype x stage was significant for all the plant components except for pod wall. The interaction was due to the fact that the dry weights of the organs of the small bush and tall erect bush cultivars were significantly decreased at PM while classic II and architype maintained higher weights than those of the bush forms, possibly indicating losses due to remobilization to seed at late seed filling in the navies. Significant dry matter losses were observed in the stem, petiole and leaf blade from MSF to PM (Table 5). Over 80 percent of the losses in the dry weight of petiole and leaf blades were due to foliar abscission determined using the abscission collection receptacle (ACR)

described by Izquierdo and Hosfield (21). In view of this finding, the remobilization of dry matter to seed from petioles and leaf blade appear to be non-important.

Losses in dry matter were observed in the pod wall and in the stems. This suggests that pod walls and stems both may be important as storage sites for photosynthate which can be remobilized to seeds during late reproductive growth. The calculated remobilization factor (DRF) for pod walls indicated an equal or superior remobilization than from the stems. The DRF in the root was positive, indicating no net remobilization occurred from this organ (Table 5).

Changes in dry weight in stems and pod walls were associated with genotypes (Tables 6 and 7). A negative change in stem dry weight was found in 61356 and BTS at MSF, however, 61356 continued to remobilize dry matter from the stem until PM. All entries showed a negative change in stem dry weights at PM. Seafarer and Sanilac were the highest remobilizers, reallocating 56.1 and 45.3 g.m^{-2} of dry matter from stems during the mid-seed filling to physiological maturity, respectively, Nep-2 did not show changes in stem dry weights and had the lowest remobilization factor (RF=0.2 percent). However, 61356 (architype) and Seafarer had a stem DRF of 36.5 and 26.1 percent respectively (Table 6).

The lack of remobilization of dry matter to seed was associated in the case of Nep-2 with a positive RF of pod wall to seed (Table 7). The breeding line 61356 and Sanilac produced RFs of 61.6 and 53.5 percent, respectively. By MSF, most of the entries continued allocating dry matter into the stems as revealed by the stem to pod remobilization factor (Table 7) but, during late seed filling remobilization was directed from stems to pods in all entries. The highest pod wall dry matter to seed

remobilization factor was calculated for Sanilac. Although this navy bean cultivar had a higher rate of seed filling than Nep-2 (Figure 2), Nep-2 was compensated for its apparent yield disadvantage by a three-fold longer LFP than Sanilac. Nep-2 had a 60 percent less rapid LFR but produced significantly more yield than Sanilac.

Figure 3 shows the scattering of the entries for the RF from pod walls and stems in relation to the LFP. A highly significant negative correlation ($r = -0.764$, $n=36$) was found.

DISCUSSION

Implicit in our sampling is the assumption that growth analysis and estimates of seed filling parameters represent pod populations sampled at the same physiological age. There is a normal overlapping of seed filling rates due to a normal overlap of pod sizes and ages due to the interval of flowering. Under these conditions one must exercise a degree of caution to insure sample homogeneity. In our case, since pod samples were collected between the fourth and sixth nodes of plants, pods are assumed to represent the middle-canopy population of pods with respect to both chronological and physiological age. In contrast to our sampling method, Egli and Legget (14) and Wien and Ackah (36) tagged pods of field growing soybean and cowpea plants respectively. Pod tagging led to homogeneous samples, as day to day variation in pod development was virtually eliminated (14, 36). However, in our case pod tagging resulted in a negative response of pod and seed growth. Tagging bean pods produced pods that had an appearance similar to if they had been "strangled." Apparently, the pressure created by a tag to the peduncle of the pod affected the mobilization of assimilate and possibly nutrients and water

into seeds. These observations agree with other pod tagging work from this laboratory (Izquierdo, 1981, unpublished).

The results of the study herein shows that variation in filling rate and filling duration existed among the nine entries with the architypes and classic II having lower filling rates and longer filling durations (periods) than the small bush forms (Table 2). It should be noted that the filling duration parameters for an entry were more related to yield than the filling rate (Table 3). This finding is in agreement with results reported for other grain crops (10, 15, 21, 36).

Seeds compete with each other within the pod for available assimilate, nutrients, and water. Also developmental competition within a phytomeric unit (4) involving a synchrony of adjustment between source and sink was shown to occur in P. vulgaris (33). Oliker et al. (29) applied the adjustment (33) to seed growth analysis in relation to metabolic processes in beans. The negative correlation between MFR and $\overline{FR}$ and the significant negative correlation between LFR and number of seeds/pod (Table 3) agree with their work (33, 29).

Extending the duration of seed filling should provide more available photosynthate, water, and nutrients to the seed which in turn will produce heavier seeds per pod. Under this physiological regime and in the absence of or low expression of yield component compensation higher yields should be achieved. This idea has been proposed as breeding strategy for increasing soybean productivity (17). In our case, the architypes with their large seeds (architypes lines 61380 and 61356) produced the highest yields (Table 1) although the correlation between 100-seed weight and number of normal seed per pod was only 0.35 (Table 4).

This low, but positive, correlation between these two yield components is not in agreement with results by Adams (5) who showed yield component compensation in P. vulgaris L. The archetypes with their high number of seed/pod and heavy seeds could apparently overcome the limitations imposed by the usual negative correlations between yield components (5). Bennett et al. (7) proposed an ideotype as a model to overcome yield component compensation and increase yield. Their concept was one that showed a sharp reduction in branching yet keeping a high number of productive nodes per branch. In addition, this plant would have a narrow profile (1). The archetypes approached Adams' ideal (1, 4, 7).

Final seed yields were more associated with the entries themselves than with architectural forms. For example, Nep-2, Seafarer and 61356 were no different in yield according to the Duncan Multiple Range test although these entries differed in architectural form. On the other hand, remobilization of dry matter from stem and pod walls clearly separated classic II from small and tall erect bush forms (Tables 6, 7, Figure 2).

Apparently as breeders selected plants for the archetype growth form, they fortuitously selected for physiological aspects related to sink development, or the archetypes consisted of a genetically integrated genic complex such that when the architecture is produced it is inseparable from those aspects of their physiology leading to high yield.

Archetypes ranged from low to high DRF (Figure 3). A low stem remobilization factor characterized the archetype 61618 (Table 6) suggesting a lack of reallocation of carbohydrates late in the growing season. A low remobilization factor also suggests competition for dry matter accumulation by storage sites (Table 7) during the early seed filling period with the

stem to pods remobilization factor for all the strains. An extreme case of competitive allocation into storage organs was demonstrated by Nep-2 (Tables 6 and 7) including a positive pod wall to seed remobilization factor at late seed filling, indicative of a lack of remobilization of assimilates from this temporary storage site.

Lower yields characteristic of the small bushes compared to the archetypes could have been due to a more rapid remobilization over a shorter duration. This rapid and early remobilization could result in an early and irreversible self-destruction that effectively terminated any possibility of high yield. This becomes apparent when comparing archetypes with Nep-2 (classic II). Both entries reallocated less dry matter to the seed (Tables 6 and 7), but produced the highest yield among the architectural forms through a combination of lower filling rates and longer filling duration (Figure 2). The lack of reallocation in some archetypes 61618 and Nep-2, suggested a lack of a need to remobilize stored carbohydrate because assimilate demand by the sink (seeds) was being satisfied by currently produced photosynthesis. The idea invoked by Adams (3) for dry beans that some plants reallocate stored starch during time of stress to satisfy sink demand was not apparent for the archetypes or Nep-2. In this regard, reallocation was not seen either because stresses were not of a magnitude during the growing season to elicit a need for reallocation or because current photosynthesis was sufficient to satisfy sink demand.

Higher rates of photosynthesis in Seafarer (small bush) than in Nep-2 (classic II) were observed by Burga (8) and agree with other work (20, 27, 30). An increase in rate of photosynthesis during pod filling of dry beans (30) could indicate a feedback control of the sink

on the source (35). This can best be seen by observing the high LFR of the small bush forms during their short filling period. On the other hand, although it is not possible to discount completely the role of photosynthesis as a major contributor to seed filling during the late seed filling period, reallocation was apparently related to dry weight change in the seed indicating an effective reallocation of carbohydrates from stems and pod walls of small bush forms during seed filling.

The archetype approaches the ideotype (4) of non-climbing (determinate and semi-determinate) and non-vine producing forms in dry beans for use under monoculture. These architectural forms overcome some of the difficulties such as lodging and pod contamination by soil due to fruiting nodes being close to the ground associated with architectural forms A and C. In addition to a yield superiority compared with older architectural forms, the archetype 61618 has shown stability for yield generally not associated with dry beans grown throughout Michigan, a major dry bean production area in North America (Gadheri, 1981, personal comm.). Increased stability could be due to an apparent effect brought about by reallocation of C-assimilates but only under conditions of stress. The archetype 61618 associated a long filling period with low remobilization and 61380 produced the highest yield by a long filling and high RF (Figure 3). In achieving their superior yields compared to other dry bean forms, the archetypes appear to have combined a longer filling period duration with a larger sink size. The longer filling period was apparently associated with this architectural form's ability to satisfy sink demand by prolonging the duration of photosynthesis. Archetypes retain photosynthetically active leaves much later in the growing season than small bush and tall erect bush entries.

The yield advantages of the archetype not only appear to be related to improvement in lodging resistance but modification of the morphology mainly through branch reduction and narrowing the plant canopy has resulted in a plant capable of being directly harvested by combining, thus reducing seed losses associated with pulling, windrowing, and then combining as is the present practice.

The evidence from the present work is sufficient to allow us to speculate that an extended seed filling period and the ability to sustain seed filling through remobilization of reserves from storage sites optimizes and stabilizes yields in dry beans. Further research is needed under stress conditions to corroborate this theory.

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Table 1. Total and non-shriveled pods, percentage of shriveled pods, yield components and yield of nine dry bean entries grown in 1980

Architectural form and strain	Pods		Seed.pod ⁻¹						Yield, 16% moist kg
			Non- shriveled m ⁻²		Aborted seed Effective†		Seed.m ⁻²	Weight of 100 seeds g	
	Total.m ⁻²	Shriveled %	No.	%	No.	%			
Architype	No.	%	No.	%	No.	%	No.		
61380	320 bcde [‡]	19.8 bcd	254 b	7.0 ab	5.2 ab	6.7 ab	1728 ab	18.1 a	3577 a
61356	286 e	16.6 cde	239 b	6.4 abc	3.4 b	6.2 ab	1493 b	18.5 a	3076 ab
61618	313 cde	18.5 cde	255 b	7.0 ab	3.8 ab	6.7 ab	1736 ab	16.5 b	2949 b
Classic II									
BTS	323 bcde	15.8 de	270 ab	7.2 a	4.8 ab	6.8 a	1858 ab	16.8 b	2589 bcd
Nep-2	358 abc	9.2 e	326 a	6.8 ab	5.0 ab	6.4 ab	2106 a	15.3 cd	2845 b
Small bush									
Seafarer	355 abcd	27.0 abc	258 b	5.7 c	4.8 ab	5.4 c	1416 b	17.5 ab	2569 bcd
Sanilac	412 a	30.4 a	287 ab	5.9 c	9.8 a	5.3 c	1526 b	14.9 d	1823 e
Tuscola	376 ab	30.1 ab	262 b	5.8 c	4.3 ab	5.5 bc	1515 b	15.3 cd	2162 de
Tall erect bush									
C-14	295 de	22.8 abcd	227 b	6.3 bc	2.8 b	6.1 abc	1411 b	16.8 b	2366 cd
Mean	338	21.1	264	6.4	4.5	6.2	1643	16.6	2701

[†]Effective seed.pod⁻¹ = total seed.pod⁻¹ - percent aborted seed.

[‡]Mean separation in columns by Duncan's multiple range test, five percent level.

Table 2. Predicted seed filling rates, durations and sizes, and their multiple correlation coefficients calculated from data fitted to a cubic polynomial model for each entry of nine field grown dry bean cultivars

Architectural Form and Strain	Filling Rate			Filling Period			Predicted Seed Size			R ²
	Maximum (MFR)	Mean (FR)	Linear (LFR)	Total (TFD)	Effective (EFD)	Linear (LFD)	Maximum (Max W)	By Linear Filling	% of Max W due to Linear Filling	% of Observed [†] Size due to Linear Filling
	—mg. seed ⁻¹ .day ⁻¹				— days			— mg. seed ⁻¹		
Archetype										
61380	9.57	4.50	11.32	46	16	11	208.9	124.5	59.5	68.7
61356	10.02	4.46	12.16	45	15	11	202.6	133.7	65.9	72.1
61618	7.10	3.61	8.98	45	18	12	162.1	107.7	66.4	65.0
Classic II										
BTS	7.60	3.94	10.14	47	17	11	184.7	111.5	60.3	66.2
Nep-2	8.17	4.07	8.51	46	18	12	185.8	102.1	59.9	66.6
Small bush										
Seafarer	9.73	4.50	17.50	43	10	5	196.9	87.5	44.4	50.0
Sanilac	9.89	3.64	14.08	42	11	4	153.8	56.3	36.5	37.7
Tuscola	10.01	4.13	12.18	42	13	8	189.1	97.4	51.4	57.7
Tall erect bush										
C-14	6.80	4.12	10.97	46	15	7	190.0	76.7	40.4	46.1
Mean	8.76	4.10	11.76	45	15	9	185.9	99.7	53.8	58.9

[†]Seed weight at harvest.

Table 3. Simple correlation coefficients between seed filling parameters and yield components, and yield of nine dry bean strains grown in 1980

Seed Filling Parameters	Component of Yield				Yield
	Pod.m ⁻²	Seed.Pod ⁻¹	Seed.m ⁻²	100 Seed Weight	
Maximum Filling Rate	.068	-.581	-.342	.082	.056
Mean Filling Rate	-.327	-.064	-.254	.399	.495
Linear Filling Rate	.038	-.725*	-.448	.563	-.243
Total Filling Period	-.222	.773**	.365	.363	.520
Effective Filling Period	.095	.930**	.698*	.594	.604*
Linear Filling Period	.117	.912**	.705*	.611*	.744*

Table 4. Simple correlation coefficients among pod characteristics, yield components, and seed abortion and yield of nine dry bean strains grown in 1980

Characteristic	Characteristic						
	Non-shriveled			Normal			100-seed weight
	Total pod.m^{-2}	Pod shriveled pod.m^{-2}	Seed. pod^{-1}	Aborted Seed. pod^{-1}	Seed. pod^{-1}	Seed. m^{-2}	
	No.	%	No.	%	No.	No.	g
Pod shrivel (%)	.456**						
Non-shriveled pod.m^{-2} (No.)	.636**	-.394*					
Seed. pod^{-1} (No.)	-.596**	-.750**	.090				
Aborted seed. pod^{-1} (%)	.814**	.352*	.533	-.274			
Normal seed. pod^{-1} (No.)	-.646**	-.728**	-.032	.715**	.055		
Seed. m^{-2} (No.)	.035	-.805**	.737**	.715**	.055	.648**	
100-seed weight (g)	-.799**	-.200	-.653**	.297	-.578**	.355	-.235
Yield (kg.ha^{-1})	-.646**	-.599**	-.150	.672**	-.460*	.694**	.373*
							.732**

Table 5. Plant organ dry weight and their percentage of the total plant dry weight, and remobilization factor (RF) for nine dry bean strains at four stages during reproductive growth

Plant Organ	Stages							
	Anthesis (A)		Mid-pod elongation (MPE)		Mid-seed filling (MSF)		Physiol. maturity (PM)	Remobilization Factor
	g.m^{-2}	%	g.m^{-2}	%	g.m^{-2}	%	g.m^{-2}	%
Pod	-	-	37.33 c	8.39	324.53 b	44.76	487.19 a	62.96
Seed	-	-	-	-	132.50 b	18.27	334.90 a	43.28
Pod Wall	-	-	-	-	190.26 a	26.24	152.80 a	19.74
Leaf Blade	148.04 ab [†]	56.83	188.20 a	42.31	149.27 ab	20.58	77.84 b	10.05
Petiole	32.79 b	12.58	42.83 a	9.62	41.03 a	5.65	21.70 c	2.80
Stem	63.09 c	24.22	150.83 b	33.90	182.43 a	25.16	156.62 b	20.24
Root	16.14 b	6.19	29.53 a	6.63	28.34 a	3.90	29.92	3.86
								+.007

[†] Mean separation in rows by Duncan's multiple range test, five percent level.

Table 6. Stem and seed dry weight (W), dry weight change (Δ) and stem(s) to seed (g) dry matter remobilization factor (RF) of nine dry bean cultivars at four stages of the reproductive development

Architectural form and strain	Reproductive stages									
	1		2		3		4		Δg (4-3)	Remobilization factor†
	(Anthesis) Ws_1	(Mid-pod elongation) Ws_2	(Anthesis) Ws_1	(Mid-pod elongation) Ws_2	(Mid-seed filling) Ws_3	(Mid-seed filling) Ws_3	(Physiological maturity) Ws_4	(Physiological maturity) Ws_4		
Archetype										
61380	61.49	155.48	93.99	163.93	120.28	7.45	139.75	326.08	-23.18	-0.1126
61356	53.62	148.44	94.82	134.57	148.65	-13.87	104.76	230.22	-29.81	-0.3654
61618	71.42	158.17	86.74	187.16	172.46	28.98	177.22	467.08	-9.93	-0.0337
Classic II										
BTS	48.24	151.75	103.51	143.27	131.88	-8.48	128.98	349.27	-14.28	-0.0657
Nep-2	59.00	204.76	145.75	204.55	200.00	-0.21	204.14	383.02	-0.41	-0.0022
Small bush										
Seafarer	76.81	143.27	66.45	248.86	199.17	105.59	192.75	414.07	-56.10	-0.2610
Sanilac	68.11	136.64	68.53	228.57	86.54	91.92	183.22	346.79	-45.34	-0.1742
Tuscola	63.35	107.66	44.30	178.88	90.47	71.22	156.10	313.04	-22.77	-0.1023
Tall erect bush										
C-14	65.63	150.31	84.67	153.00	42.23	2.69	122.15	186.33	-30.84	-0.2140

LSD .05 for stem weight strain x stage interaction = 57.5, CV percent stem weight = 23.9

$$\dagger \Delta S_{(4-3)} / \Delta g_{(4-3)}$$

Table 7. Remobilization factors from stem to pods (RF_{st-pd}) and pod wall to seeds (RF_{pw-g}) calculated at early and late seed filling for nine dry bean strains grown in 1980

Strain	Seed filling [†]		
	Early	Late	
	(RF_{st-pd})	(RF_{st-pd})	(RF_{pw-g})
61380	+ .037	- .106	- .146
61356	- .059	- .929	- .616
61618	+ .083	- .042	- .193
BTS	+ .026	- .073	- .108
Nep-2	- .0006	- .002	+ .271
Seafarer	+ .222	- .317	- .165
Sanilac	+ .241	- .373	- .535
Tuscola	+ .247	- .139	- .276
C-14	+ .018	- .269	- .271

[†]Early seed filling = mid-pod elongation to mid-seed filling; late seed filling = mid-seed filling to physiological maturity.

Figure 1. Architectural plant forms; a) small bush, b) tall erect bush, c) classic II, and d) architype. Photographs were taken viewing down the row after all leaves were completely abscised from the plants

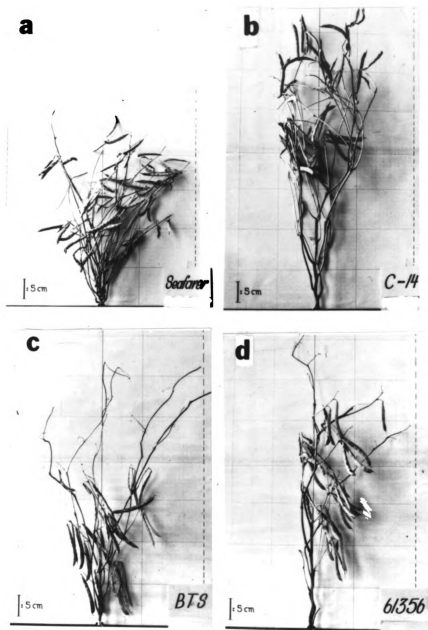


Figure 2. Seed growth curves showing predicted linear filling parameters and actual data points, stem and seed dry weights, and stem to seed remobilization factors for two dry bean cultivars sampled at four physiological stages during reproductive development. The parameters, LFR, LFP, A, MPE, MSF, PM and $\Delta s / \Delta g$ are linear filling rate ($\text{mg} \cdot \text{seed}^{-1} \cdot \text{day}^{-1}$), linear filling period (days), anthesis, mid-pod elongation, mid-seed filling and stem to seed remobilization factor, respectively. Arrows indicate maximum values for pod length

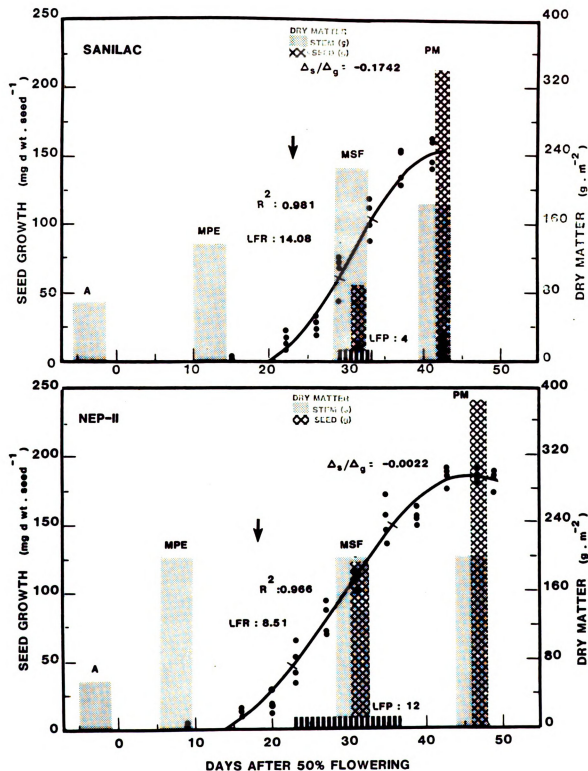
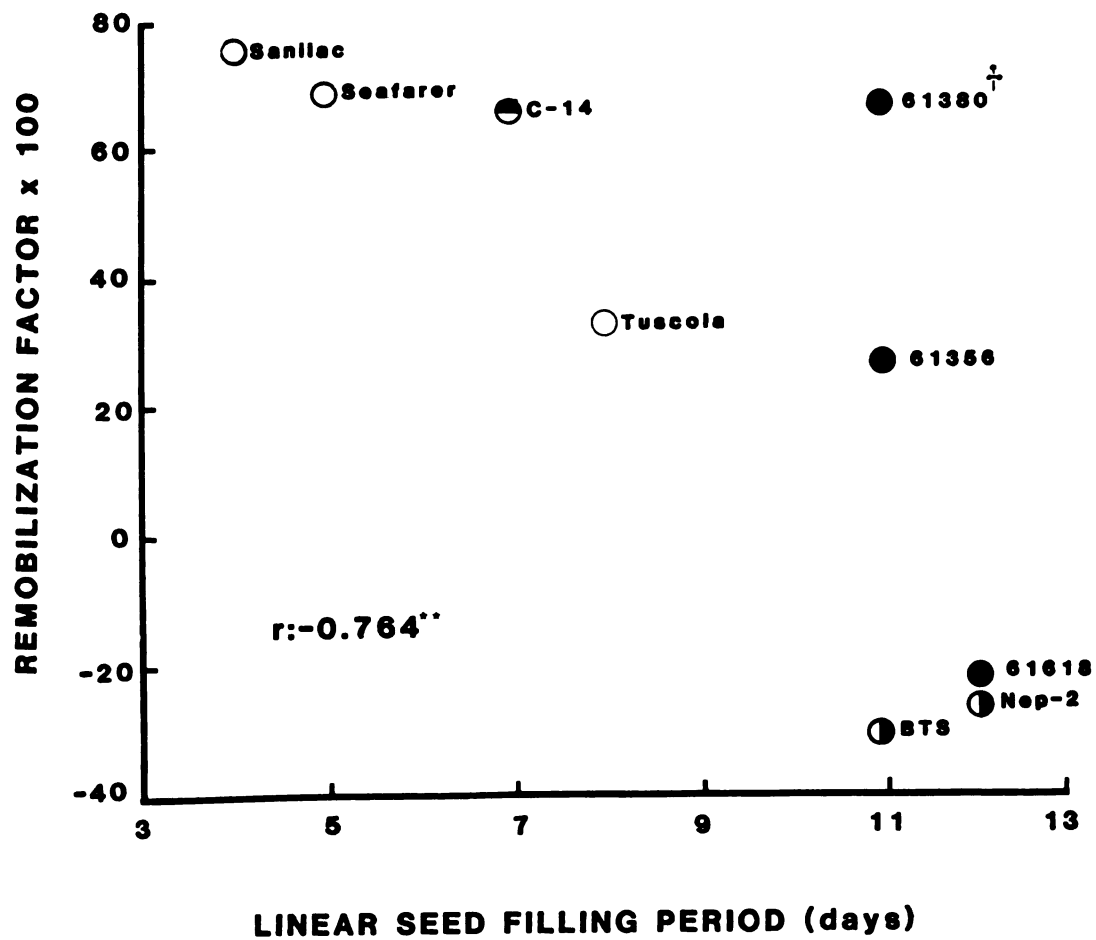


Figure 3. Dry matter remobilization factor for stems and pod walls and their relationship to the duration (length) of the linear seed filling of nine dry bean entries characterized by four architectural forms; O = small bush, ● = tall erect bush, ① = classic II, and ● = archetype.

†Data point excluded from the correlation analysis.

**Significant to the one percent level.



CHAPTER 3
ACCUMULATION, PARTITION AND REMOBILIZATION OF
CARBOHYDRATE AND NITROGEN DURING THE GRAIN
FILLING OF DRY BEAN (Phaseolus vulgaris L.)
CULTIVARS

ABSTRACT

An efficient allocation of products of photo-assimilation is postulated as necessary to increase and stabilize yield in new dry bean (Phaseolus vulgaris L.) cultivars. The level, partition (harvest index) and late seed filling remobilization for water soluble sugars, starch, total non-structural carbohydrates and nitrogen were evaluated for different tissues among nine dry bean entries differing in plant morphology. Differences in sugars, starch, TNC and N were associated with cultivars and physiological stage. Significant increases in the level of TNC due to accumulation of starch in stems was found at the middle seed filling stage independently of cultivars. Nitrogen levels followed the same pattern. A highly significant stage x cultivar interaction was produced for the amount of starch in stems, roots and pod walls due to different remobilization to the seeds. The small bush architectural form remobilized higher amounts of TNC from the stem after the mid-seed filling stage than the other architectural forms (archetype, classic II, and tall erect bush). Archetypes remobilized starch and TNC. Classic II entries, Nep-2 and Black Turtle Soup maintained a high amount of accumulated starch and nitrogen in stems at physiological maturity. The interactions of stage x cultivars for the TNC and N content of the pod wall were significant. In

this organ the classic II form did not remobilize TNC and N as did the archetype forms. Although the harvest index (HI) did not correlate with yield, a modified HI (mHI) and the harvest nitrogen index (HNI) provided significant correlations ($r=0.83^{**}$ and 0.81^{**}) with yield, respectively. High mHI, HNI and harvest starch index (HSI) characterized the archetype lines producing the highest yields. On the other hand, remobilization of carbohydrates during late seed filling from all storage sites was greater from small bush than for classic II entries.

The results suggest that in order to maximize yield, partitioning and remobilization efficiency must be considered in a breeding program in addition to selection for increased sink capacity.

Additional index words: water soluble sugars, starch, total non-structural carbohydrate, yield, modified harvest index, remobilization factor, plant architecture, archetype.

INTRODUCTION

Increasing the availability of assimilates for grain development in dry beans (*P. vulgaris*) can best be accomplished by increasing whole plant assimilate accumulation and/or by increasing the proportion of stored assimilates that can be reallocated to the developing seeds. Breeding for yield and yield stability has been attempted by exploiting these physiological mechanisms through the use of the harvest index (HI) as a selection tool.

The harvest index is the ratio of grain (seed) weight to total above ground plant dry weight and is commonly used as an index of the amount of assimilate allocated to the economical sink of a plant. Donald (8) used

the HI as a selection criterion in cereals for increasing their yields. Harvest index can be viewed as a globalization of the partition mechanism, and the partitioning of photosynthates in terms of Duncan et al. (9) is a day-to-day process of the allocation of carbohydrates to grains that is assumed to be highly dependent on current photosynthesis during actual grain filling. Should current photo-assimilation be impeded by diseases, pests or climatic stresses, the reallocation of stored reserves could serve as a possible source for seed filling and, hence, stabilize yield.

The ability of a plant to allocate a high proportion of fixed carbon and nitrogen into the seed is an important component of the yield equation and has been shown to be under genetic control in cereals (8), soybeans (15), sugarbeets (22), and dry beans (26). Genetic differences in the accumulation and depletion of stem reserves have been reported among bean cultivars by Adams et al. (1). Although an increase of allocation of assimilates allocated to the seed has been considered as a selection criterion (high harvest index), the level of available or redistributable carbohydrates, accumulated in stem and leaves has been associated with the yield capacity of improved and high yielding new mungbean varieties (17). Physiological superiority expressed by a high partition of assimilates to the seed in peanuts (9), and in soybeans (12), respectively, has been suggested as the reason for the improved seed yields of newly released cultivars in these two legume crops. In corn, an improved 'Lancaster' population produced more dry matter, translocated dry matter to developing kernels at a faster rate and for a longer period of time than did testcrosses of the unimproved population (6). Apparent

efficiency of the leaf area in grain production of spring and winter wheats was measured by Watson (28) as the grain dry weight/leaf area duration ratio. This investigator concluded that the index of partition was higher for new and improved cultivars than for the standard ones. In the same order, cultivar differences in the grain/straw + glumes ratio among old and new wheat cultivars were associated with yield differences (2). The contribution of assimilates formed before anthesis and stored in barley stems may play an important role in grain filling and was calculated to be equal to 30 percent of the total seed weight (3). The stored carbohydrate could be remobilized into the seed or consumed by respiration, thus the loss of carbohydrate from the vegetative parts during grain filling gives only the maximum estimate of the contribution of the stored carbohydrate to the grain. This loss ranged from 0 to 70 percent in a number of crop species reviewed by Yoshida (29).

Although allocation of assimilate to seed has been modified by breeding in both cereals and grain legumes, this could have occurred equally as well as an indirect consequence of selecting for higher yield and other agronomic traits, including plant architecture (2,6,9,28). These achievements were obtained through long-term selection for yield within breeding populations aimed at maximizing yield by improving yield-related traits including yield components, plant morphology and disease and pest resistance. However, in most of the cases yield improvement was made without a clear understanding of which traits changed and to what physiological basis changes were related.

In dry beans, changes in plant morphology affecting the canopy architecture and leading to narrow-profile strains has been associated with improvements in seed yield due to an increase in seed number without a reduction in the weight of seed (Izquierdo, J.A., unpublished data,

1981). This modification of a yield component to produce an increase in yield as a result of increasing sink size could possibly be related to a better physiological efficiency in the partitioning of assimilates. The objective of this research was to study the pattern and the level of carbohydrate and nitrogen remobilization from storage sites during late seed filling. Specifically, an attempt was made to test the hypothesis that seed yield associated with architectural forms is associated with partitioning and remobilization of carbohydrates and nitrogen.

MATERIALS AND METHODS

Nine dry bean cultivars and breeding lines with determinate and indeterminate growth habit [Type I and II, according to the classification of the International Center for Tropical Agriculture (CIAT)], and contrasting plant architectures were planted at East Lansing, Michigan in 1980. The materials used were: 'Seafarer,' 'Sanilac,' 'Tuscola,' 'Nep-2,' C-14 and 61618, all white seeded, and the black seeded 'Black Turtle Soup' (BTS), 61380 and 61356. A randomized complete block design with four replications was used. Plots were eight rows, each 10 m in length and spaced 47 cm apart. Seed was precision drilled with a tractor mounted air planter and the within row spacing was 7-8 cm between plants. Standard fertility and herbicide management practices were used.

Yield was determined from samples taken at maturity from two, 2-m sections of row (1.88m^2). Seed moisture at harvest was determined and yields were adjusted to 16 percent moisture equivalent. Four physiological stages (PS) during reproductive development were established. These were: anthesis (A), middle pod elongation (MPE), middle seed filling (MSF),

and physiological maturity (PM). Sampling was conducted at each sampling period using procedures to dissect the plant described elsewhere (Izquierdo et al., 1981, unpublished data). At each (PS) a 1-m segment of row was removed from one of the four center rows and five random plants were subsampled and dissected into tap roots (R) by excising the plants at the ground level mark, stem (S) including the raceme peduncles, petioles (P) from the stem to the insertion point with a trifoliated leaf, and leaf blade (B) consisting of the trifoliated lamellae. At MSF and PM all pods (without peduncles) were harvested and divided into pod wall (PW) and seeds (G). The plant parts were immediately frozen at -10°C until drying in a forced air circulating oven at 100°C for one hour and 70°C for 36 hours. Dry weights for all plant components were obtained. Leaves, including petioles that had abscised, were collected every four days from an approximately 0.6 m^2 area using an abscission collection receptacle (ACR) (14). After collection dry weights of the fallen organs were determined and recorded.

Sugar and Starch Analysis

Soluble carbohydrates were determined by extracting water soluble sugars (WSS) according to the method of Black (4). Sugars were separated from the extract by HPLC by the procedure of Lester et al. (18). Starch was determined after solubilization in sodium hydroxide and hydrolysis to glucose. The glucose liberated from the starch digestion was determined quantitatively by the use of a Glucostat reagent kit and reference to HPLC glucose analysis. Total nonstructural carbohydrates (TNC) taken as starch + WSS as well as starch, WSS, and N was expressed as g.m^{-2} for each plant component at the four different physiological stages of each cultivar. N analysis was done for the abscised materials.

Nitrogen Analysis

Percentage of N was estimated by near-infrared reflectance (NIR) measurements on dry tissue samples using an infrared spectrophotometer (Neotec Corporation, Spectro computer model 41). Calibration of the instrument was done according to Rotolo (21) using reference samples with known N percentage determined by micro-Kjeldahl analysis. The minimum multiple correlation coefficient for N percent at four different wavelengths was found to be equal to 0.923**, n=26, for petiole tissue and the maximum, 0.983**, n=19, for seed. K's constants were calculated for each tissue by least square regression. The correlation coefficient among Neotec N percent-estimates and Kjeldahl N percent-values for each tissue are shown in Table 1.

Partitioning and Remobilization Parameters

Carbohydrate partitioning, efficiency and remobilization parameters for dry matter (DM), starch, WSS, TNC, and N were defined as follows: Harvest index (HI) = seed (DM or assimilate) yield/biological (DM or assimilate) yield (7,8,20); Modified harvest index (mHI) = seed (DM or assimilate) yield/total cumulative biological (DM or assimilate) yield (16). Total cumulative biological yield was calculated as biological yield for DM or any assimilate + DM or assimilate yield of abscised organs. The remobilization factor (RF) of stored reserves was modified from the proportion factor proposed by Gallagher (10). Then, $RF = RP/G \times 100$, where RF is defined as the absolute change in the redistributable pool during late seed filling (MSF - PM), and G is the incremental change in DM or assimilate content of the seeds. The redistributable pool was estimated by adding the DM or assimilate content of roots, stem, petiole,

leaves and pod wall to MSF. The RF of starch, WSS and TNC did not include leaves and petioles. The DM and N content of fallen leaves and petioles was included for the calculation of the RFN, HNI, and modified crop harvest index.

Plant Forms

Plant architecture group comparisons were established for the physiological traits. Architectural groups were as follows: a) small bush: which included the cultivars 'Seafarer,' 'Sanilac,' and 'Tuscola;'

b) Tall erect bush: the breeding line C-14; c) classic II: comprised of the cultivars 'Nep-2' and 'Black Turtle Soup;'

and d) the archetypes: breeding lines 61380, 61356 and 61618 with modified canopy architecture (13). All data were analyzed statistically using the ANOVA, least squares regression and correlation analysis.

RESULTS

Differences in starch, WSS and N among the various plant parts during reproductive development were related to the specific physiological role of each part. The source (L) was lower in TNC than the other parts but high in N and therefore had the lowest TNC/N ratio (Table 2).

The seeds (sink) contained about 40 percent starch and four percent WSS. These values agreed with proximate analysis determinations for dry seeds of P. vulgaris L. (25). The pod wall also served as a sink organ during early pod development and acted as a temporary storage site for TNC and N. Pods accumulated up to 24 percent TNC and 2.4 percent N. The stems and petioles accumulated TNC up to an average of 18 percent. Roots with 15 percent TNC content showed the highest TNC/N

mean ratio, which was presumably due to the low N content of the roots. In 1979, a small bush cultivar (Tuscola) and two classic II cultivars, Nep-2 and BTS, accumulated an average of 11.3, 14.1 and 22.1 percent of TNC in the roots, stems and petioles, respectively, during the reproductive development. The difference between years was due to the fact that less starch was allocated into roots and stems in 1979 (data not shown).

Significant differences were found for starch, WSS, TNC, N and TNC/N ratio between reproductive stages for most of the plant parts evaluated (Table 3). The entry (genotype) effects that were observed for TNC of the plant parts (except leaf) were statistically significant. Differences among entries for TNC of the stem were significant although WSS in the stem were not affected by the genotype.

Accumulation and remobilization of stem starch produced most of the variation and probably caused the significant differences noted for stem TNC. Leaf blades and petiole N content were not affected by genotype. Starch accumulation increased from anthesis and was maximum at the mid-seed filling stage (Table 4) in root, stem, petiole and pod wall. Starch was remobilized significantly by physiological maturity and significant changes were found for WSS in the stem but not in the root although the patterns of change were similar. The WSS were depleted from stems, petioles, leaf blades and pod walls by PM. Within the vegetative plant parts, N values peaked at MPE for roots and leaf blades and at MSF for stems and petioles. Significant changes of TNC and N in pod walls at PM were observed indicating remobilization had occurred. At the same time, significant increases of about 2.9, 5.1 and 2.5 fold occurred

for starch, WSS and N, respectively, in the seed. This finding indicated that allocation of assimilate during the late seed filling was strong.

Table 5 shows data for entries arranged by growth habits and architecture. When averaged over the entire period of reproductive development, the roots of architype plants accumulated the highest amounts of starch, WSS and N. Among the architype breeding lines, 61380 and 61618 accumulated significantly higher amounts of starch than 61356 and 61618 was able to maintain its starch storing ability until physiological maturity. In the present work, 61618 stored more starch than Nep-2, which has been reported to accumulate significant amounts of starch during the growing season. The classic II and architype plants allocated more starch to the stem than did the small and tall erect bush types. Architypes stored less starch in the stem than classic II, but the difference was not significant at MSF. When genotypes were compared individually, Nep-2 stored a significantly larger amount of starch in stem tissue than did the other entries, except for 61618. The water soluble sugar content of the stems was not significantly affected by architectural groups. However, WSS in roots of the architypes were significantly higher than in the small bush plants. Stems of classic II plants accumulated higher levels of carbohydrates (TNC) than stems of architype plants and both architectural groups stored significantly higher amounts of TNC in the stem than small and tall erect bush plants. Non-significant differences were found among genotypes for leaf starch, WSS, TNC, N or TNC/N ratio (data not shown). However, the leaves of classic II plants were higher in starch and N accumulation than architype leaves for the entire period of reproductive development.

The mean squares for the developmental stage x entry interaction of the analysis of variance are shown for all plant components and assimilates studied (Table 6). No significant interactions were observed for petiole and leaf blade for any of the assimilates. However, a significant interaction for stem starch accumulation was found (Figure 1). No changes in starch accumulation were observed in stems of classic II entries. Small bush and archetype stem plants, when compared with classic II, remobilized significant amounts of starch at PM. Tall erect bush plants did not accumulate significant amounts of starch in stems at MSF when the allocation of starch was maximum for the other architectural groups. Non-significant differences for stem starch per unit area were found among the archetype, classic II and small bush plants at MSF. Figure 2 shows the significant developmental stage x entry interaction for stem TNC ($\text{mg.g}^{-1}\text{d. wt.}$) observed in 1979 among cultivars representative of the small bush type (Tuscola) and Classic II (Nep-2 and BTS) architectural groups. The quantities of stem carbohydrate allocation were in good agreement for both years.

A highly significant stage x entry interaction was associated with pod wall TNC and N. In viewing this interaction graphically (Figure 3), remobilization of both TNC and N from pod walls during late seed filling occurred simultaneously. Pod walls of the classic II plants shows no mobilization of starch at PM. This finding was especially noticeable for Nep-2 and contrasted with the significant remobilization of the other groups.

Assimilate partitioning expressed as the harvest index (HI) was weakly but significantly correlated with yield ($r=0.47^*$, Figure 4). The effect of the HI could be better viewed when significant differences in

the amount of foliar abscission was considered. The percentage of N in the abscised materials and the total N losses due to abscission also differed significantly among entries (data not shown). When biological yield was adjusted for losses due to abscission, the mHI showed a much higher correlation with yield ($r=0.83^{**}$) (Figure 4). The harvest nitrogen index was correlated well with yield ($r=0.81^{**}$) and both indices, HI and HNI correlated well with each other ($r=0.78^{*}$).

The remobilization factor (RF) for starch, WSS, and N are shown in Table 7. The cultivars, Seafarer, Sanilac, and Tuscola had the highest RF's among all entries for starch, WSS and N. Nep-2 and BTS produced the lowest RF's. Changes in N allocation and remobilization for plant components of Tuscola (the highest NRF among entries) and Nep-2 with the lowest NRF are shown in the Figure 5. The SRF was negatively correlated with yield ($r=-0.62^{*}$) (Figure 6). However, when data of 61380 (architype) were not considered, the correlation coefficient was $r=-0.75^{*}$. The breeding line 61380 produced the highest yield (3577 kg/ha) and was characterized by a SRF of 32.2. The line 61618 showed a SRF between the range of its two parents, Nep-2 and BTS, suggesting genetic control, while architypes 61380 and 61356 with higher SRF produced higher and significantly higher yields than their two parents, respectively.

Changes in several physiological traits were observed to be associated with an increase in seed yield for classic II and architype groups over the bush types. These groups had longer filling periods and a slower rate with a significantly higher yield (Table 8). Apparently the higher potential accumulation of redistributable assimilates at MSF in the small

bush group does not lead to a significant increase in yield over erect bush type. On the other hand, C-14 with a low redistributable TNC and N, produced a non-significant although higher yield than the small bush entries.

Harvest index did not show any appreciable difference. The mHI was lower than HI due to an increased Biological Yield (accounted for by foliar abscission). Differences in the mHI were associated in the archetype group with higher yield. In the same order, HSI, H WSS I and HNI were significantly higher than in the classic II genotypes. The remobilization factor for N, starch, and WSS showed values over 100 per-cent in the bush forms and this may indicate complete reallocation, losses due to respiration, and losses due to abscission in the case of SRF and WSS RF's in which reallocation from stem, root and pod wall but not petiole and leaves were included. Lower RF's values were obtained for the classic II and archetype groups, but archetype remobilized significantly higher stored N and WSS than classic II entries.

DISCUSSION

The accumulation of carbohydrate N in different storage tissues indicated that the allocation of assimilates to roots and stems was not terminated by the initiation of seed filling. Since the highest values for stem and root starch occurred at MSF, the work reported herein supported the idea of a diversion from storing in the allocation mechanism. Stem carbohydrate reserves have been shown to be involved in late seed filling in P. vulgaris (24). Adams et al. (1) found phenotypic variation for stored starch in stems of 23 cultivars using an IKI-starch indicator technique. The accumulation values reported in our work are in agreement

with Martinez (19) and Waters (27). Data for stem starch allocation in our work expressed as mg.g^{-1} d.wt. or per unit of area (g.m^{-2}) showed a strong physiological stage x entry interaction involving starch accumulation and remobilization (Figures 1 and 2) and agreed with the significant stage x genotype interaction reported by Adams et al. (1).

Since the physiological aspects of photosynthesis and C-assimilate partitioning are integrated in time and space, resources of plants having a particular plant morphology could be affected differently. For example, morphology determines the number of fruiting branches available for photosynthate produced. On the other hand, length of seed filling influences seed size. When one only measures economic yield, one considers only a single, economically important output from the total physiological system. From the plant breeder's point of view in breeding for improved C-assimilate partitioning, the parameters most easily measured are Biological Yield and HI. Biological Yield rarely has been shown to be correlated with yield due primarily to inefficient partitioning (29). Thus, measurements of HI can help to identify and define the translocation capacity, and, thereby, help identify varieties with a high partitioning potential. The ultimate partitioning of dry matter between reproductive and vegetative plant parts is indicated by the HI. A mHI has been associated with increased seed yield among plant densities for a determinate cultivar of dry beans (16) and in soybean, harvest indices and harvest nitrogen indices were positively correlated with yield (15). These results provide evidence that certain strains are more efficient than others in mobilizing both dry matter and N to the seed.

Similarly, there is evidence for the existence of the same relationship among strains of dry beans pertaining to contrasting architectural groups (Figure 4). Our range for the HNI (0.61-0.86) agreed with values for this parameter found by Jeppson (15).

A larger number of seeds m^{-2} and greater seed weight produced by the archetype 61380 were associated with greater yield of this line compared to most strains of white and black beans (Izquierdo et al., 1981, unpublished data). Modification in plant architecture does not necessarily have to lead to increased efficiency in translocation although yield advantages of the improved varieties over old standard cultivars has been associated with changes in physiological efficiency (6,9,12,17). In our case, the morphological model characterized by the archetypes has produced not only a more desirable plant type from the agronomic standpoint (lodging resistance, and ease of mechanical harvest) but has been associated with high yields due to increased physiological efficiency involving filling duration, partitioning and remobilization of assimilates. The remobilization factor for late seed filling separated genotypes according to their growth habit and the length of their filling periods (Table 7). A high RF was associated with a short filling period while genotypes with delayed leaf fall (Nep-2 and 61618) had long filling periods and did not significantly remobilize accumulated assimilates from the root, stems and pod walls. In these cases and specifically for Nep-2 (classic II), the storing process continued until PM causing a negative RF value. This indicated a competitive allocation instead of remobilization.

Recently, the hypothesis of stress tolerance due to remobilization of reserves was tested (11) and is still under study.¹ Maintenance of the filling rate in a starch-storing cultivar was observed under stress but yield was significantly reduced. The ability to withstand a stress by assimilate remobilization is not necessarily linked to the storing capacity. Partition and remobilization capacity are both needed.

Remobilization factors in this study were well correlated with each other, with r 's of 0.83, 0.85 and 0.81 for starch-WSS, starch-N and WSS-N, respectively, but negatively correlated (overall correlation) with yield. The archetype 61380 outyielded the other archetype lines although there were no differences in the filling parameters. The yield advantage in this case could be attributable to the higher partitioning and later remobilization observed for this entry compared to the others studied. Removal of assimilates is related to sink capacity differences. Streeter (23) reported that increasing fruit load in soybean plants by increasing light intensity at early pod development depleted stem and petiole TNC. On the other hand, another experiment (5) showed that pod removal increased TNC in soybean tissues. The archetype 61380 had a stronger metabolic sink than 61618 due to large seed size although there were no differences in seed number per square meter. The increased sink load could have been the "trigger" for the increased partitioning and later remobilization in 61380 compared to 61618. On the other hand, 61618 produced a high yield and was stable under different environments (Ghaderi, 1981, unpublished data). The line

¹Adams, M.W.; D.A. Reicosky; S. Garcia and J.A. Izquierdo. 1981. Starch storage and stress resistance in dry beans. Agronomy Abstracts (in press) in 1981 Annual Meetings, ASA-CSSA-SSSA, 29 November - 4 December, Atlanta, Georgia.

61618 had higher partitioning than BTS and Nep-2 but lower than 61380 in our non-stress conditions. If late remobilization is triggered by stress conditions it could be one of the mechanisms involved in yield stability.

Since our experiments were conducted in the absence of apparent stresses, no conclusions concerning remobilization and stability can be made. On the other hand, these results do allow the suggestion that in order to maximize yield, partitioning and remobilization efficiency must be considered in a breeding program in addition to selection for increased sink capacity. This suggestion is consistent with the fact that bush type entries were characterized by a short but rapid filling period, high partitioning and high remobilization. However, these entries, as compared to the other types, are susceptible in different degrees to photosynthetic leaf area reduction due to physical and biological stresses. Once the photosynthetic mechanism became impaired in bush type plants, seed filling was dependent on remobilization. Furthermore, the sink demand was too great for remobilized assimilate to sustain filling, hence, sink load was reduced due to abscission. The modification in the plant architecture for bush beans has not led to significant yield increases. Despite this fact, C-14 with its Nep-2 genetic background has no apparent physiological superiority over the small bush cultivars in terms of remobilization; however, it showed a longer filling period and a higher yield.

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Table 1. Correlation coefficient and regression equation for Kjeldahl-N percent (y) Neotec-N percent readouts (x)

Tissue	r	n	y
Leaf blade	0.988	31	$y=0.1044 + 0.9753x$
Petiole	0.897	26	$y=-0.00136 + 1.0035x$
Stem	0.964	31	$y=-0.0409 + 1.014x$
Root	0.885	29	$y=0.00863 + 1.99601x$
Pod wall	0.978	26	$y=0.00022 + 1.00073x$
Seed	0.981	25	$y=0.001 + 1.0001x$

Table 2. Mean value ($\text{mg} \cdot \text{g}^{-1}$ d.wt.) and standard deviation for starch, water soluble sugar (WSS), nitrogen (N) and total nonstructural carbohydrate to nitrogen (TNC/N) ratio of nine dry bean genotypes during the reproductive period

Plant Component	TNC		N	TNC/N
	Starch	WSS		
	$\text{mg} \cdot \text{g}^{-1}$ dry weight			
Seed	392.1 ± 64.7	37.4 ± 22.7	38.8 ± 3.1	11.1 ± 2.1
Pod Wall	212.6 ± 93.3	35.3 ± 22.3	24.1 ± 8.0	10.4 ± 3.2
Leaf Blade	115.5 ± 39.2	8.6 ± 8.1	36.4 ± 8.2	3.5 ± 1.3
Petiole	148.2 ± 36.5	34.8 ± 24.7	17.2 ± 4.0	10.9 ± 2.9
Stem	151.3 ± 31.8	30.4 ± 23.6	18.8 ± 5.5	10.4 ± 3.6
Root	139.4 ± 60.1	11.2 ± 8.5	10.8 ± 2.8	14.7 ± 7.0

Table 3. Mean squares from ANOVA of starch, water soluble sugars (WSS), total nonstructural carbohydrates (TNC), nitrogen (N) and TNC/N ratio during four stages of the reproductive development of nine dry bean genotypes

Source	df	Starch	WSS	TNC	N	TNC/N
<u>Root</u>						
Stage	3	49.1**	0.03	50.0**	0.01*	537.3**
Error a	3	1.8	0.09	1.9	0.02	18.8
Entry	8	14.4**	0.15*	17.3**	0.05**	48.0**
Error b	32	0.9	0.05	1.1	0.001	11.6
<u>Stem</u>						
Stage	3	1931.6**	110.5*	2443.7**	16.2**	161.7**
Error a	3	27.9	22.0	9.8	0.3	2.2
Entry	8	159.1**	4.2	191.6*	0.9*	22.2**
Error b	32	33.6	7.9	63.5	0.3	2.9
<u>Petiole</u>						
Stage	3	69.2**	14.6**	133.2**	1.1**	17.2
Error a	3	1.5	0.3	2.8	0.05	6.4
Entry	8	10.2**	0.5	14.0**	0.1	12.2
Error b	32	3.0	0.3	4.0	0.06	8.1
<u>Leaf</u>						
Stage	3	1423.7**	13.1**	1683.4**	162.5**	8.3**
Error a	3	94.3	2.5	111.8	2.1	3.7
Entry	8	110.3	1.7	183.2	3.5	0.4
Error b	32	104.5	1.4	108.2	2.6	1.4
<u>Pod Wall</u>						
Stage	1	7251.6**	531.4**	11368.8**	78.9*	41.8**
Error a	1	1.3	1.0	1.8	0.1	1.1
Entry	8	816.6**	26.7**	977.4**	8.4**	13.1
Error b	16	50.5	2.4	75.9	0.9	8.3
<u>Seed</u>						
Stage	1	81434.1**	1470.3*	108011.9**	567.5**	25.1**
Error a	1	10.2	6.0	4.4	1.4	0.01
Entry	8	3014.7**	29.7**	3654.2**	26.8**	7.8*
Error b	16	107.6	4.6	105.5	3.9	2.0

*, ** Mean squares significantly different at the 0.05 and 0.01 probability level.

Table 4. Mean values for starch, water soluble sugars (WSS), nitrogen (N) and total nonstructural carbohydrate (TNC) /N ratio for nine dry bean genotypes at four reproductive stages

		Reproductive Stage			
		Anthesis	Mid-Pod Elongation	Mid-Seed Filling	Physiological Maturity
		g.m ⁻²			
<u>Root</u>					
Starch		2.21 c [†]	3.27 b	5.97 a	2.87 b
WSS		0.27	0.32	0.29	0.22
N		0.23 b	0.28 a	0.27 ab	0.24 ab
TNC/N		10.63 c	12.49 bc	22.77 a	13.01 b
<u>Stem</u>					
Starch		8.33 c	21.47 b	38.58 a	20.89 b
WSS		2.70 b	5.97 a	5.77 a	0.86 c
N		1.50 b	3.21 a	3.30 a	1.73 b
TNC/N		7.35 d	8.65 c	11.91 b	13.91 a
<u>Petiole</u>					
Starch		5.14 b	7.03 a	6.67 a	2.72 c
WSS		1.95 a	2.08 a	1.18 b	0.12 c
N		0.68 a	0.76 a	0.81 a	0.26 b
TNC/N		10.56	12.23	9.22	11.01
<u>Leaf</u>					
Starch		16.86 b	22.24 a	18.89 ab	3.33 c
WSS		1.95 a	2.08 a	1.18 b	0.12 c
N		6.36 b	7.83 a	5.46 b	0.87 c
TNC/N		2.92 b	3.41 b	3.38 b	4.52 a
<u>Pod Wall</u>					
Starch		- ^{††}	-	52.30 a	23.92 b
WSS		-	-	10.53 a	2.84 b
N		-	-	5.60 a	2.64 b
TNC/N		-	-	11.49 a	9.39 b
<u>Seed</u>					
Starch		-	-	49.30 b	144.42 a
WSS		-	-	3.10 b	15.88 a
N		-	-	5.16 b	13.10 a
TNC/N		-	-	10.97 b	11.97 a

[†] Means followed by the same letter in rows do not differ significantly by DMRT at the five percent probability level.

^{††} Data not observed.

Table 5. Dry bean architectural group mean value of starch, WSS, N and TNC/N ratio on plant components over reproductive stages

Architectural Group	TNC		N	TNC/N
	Starch	WSS		
	g.m^{-2}			
	<u>Root</u>			
Small bush	2.25	0.14	0.18	13.17
Tall erect bush	3.13	0.30	0.26	12.87
Classic II	3.71	0.29	0.29	14.02
Architype	5.14	0.40	0.31	17.36
LSD .05	0.88	0.25	0.06	3.62
	<u>Stem</u>			
Small bush	18.26	3.78	2.69	8.29
Tall erect bush	16.39	4.11	2.23	10.08
Classic II	25.39	4.37	2.48	12.10
Architype	22.36	4.40	2.22	12.05
LSD .05	6.03	-	0.68	1.68
	<u>Petiole</u>			
Small bush	4.94	1.13	0.63	9.68
Tall erect bush	3.69	1.26	0.47	10.71
Classic II	6.32	1.71	0.68	12.25
Architype	5.64	1.30	0.63	11.37
LSD .05	1.93	0.79	-	-

Table 6. Mean square of developmental stage x entry interactions for starch, water soluble sugars (WSS), total nonstructural carbohydrate (TNC), nitrogen (N) and TNC/N ratio of nine dry bean entries at four stages during the reproductive development. DF=24

Plant Component	Starch	WSS	TNC	N	TNC/N
Root	4.3**	0.06	4.5**	0.005	45.1**
Stem	89.3**	7.2	103.8	0.4	7.2**
Petiole	3.7	0.5	5.0	0.07	8.0
Leaf	109.6	1.4	116.8	1.7	1.5
Pod Wall	1178.0**	17.3**	1428.7**	4.9**	10.5
Seed	1347.9**	18.1	1720.4**	10.7	3.32

*, ** Mean square significantly different at the 0.05 and 0.01 probability level.

Table 7. Assimilate remobilization factor during late seed filling for nine dry bean genotypes

Entry	TNC		N
	Starch	WSS	
	%		
Nep-2	-30.4	32.1	44.3
61380	32.2	34.0	46.6
61356	27.6	70.8	91.7
61618	2.6	82.8	67.0
BTS	26.4	2.8	60.6
Seafarer	107.2	178.2	146.2
Sanilac	135.5	192.7	144.2
Tuscola	82.4	121.2	171.7
C-14	24.6	130.2	84.5

Table 8. Yield, seed filling parameters, and carbohydrate and nitrogen utilization efficiency indices of standard and morphologically improved dry bean genotypes

	Growth Habit			
	Type I		Type II	
	Small bush	Tall erect bush	Classic	Archetype
Yield (kg/ha)	2185	2366	2717	3201**
Linear Filling Period [†] (day)	5.6	7.0*	11.5	11.3
Linear Filling Rate [†] (mg.seed ⁻¹ .day ⁻¹)	14.58*	10.97	9.32	10.81*
Plant TNC Redistributable (g.m ⁻²) ^{††}	125.10**	85.20	116.35	114.47
Plant N Redistributable (g.m ⁻²) ^{††}	16.71*	10.95	13.67	12.89
Harvest Index	0.49	0.49	0.48	0.50
Modified Harvest Index	0.35	0.36	0.37	0.41*
Harvest N Index	0.71	0.69	0.73	0.81**
Harvest Starch Index	0.79*	0.71	0.69	0.80**
Harvest WSS Index	0.85	0.83	0.77	0.84**
N Remobilization Factor (%)	154.7**	84.5	52.4	68.4*
Starch Remobilization Factor (%)	108.3**	24.6	28.4	20.8
WSS Remobilization Factor (%)	164.1*	130.2	17.4	62.5**

[†]Data taken from Izquierdo et al. (unpublished, 1981).

^{††}At Mid-Seed Filling.

*, ** Significant difference within growth habit types at the 0.05 and 0.01 percent probability level.

Figure 1. Stem starch allocation changes during the reproductive development of standard and architecturally improved dry bean cultivars

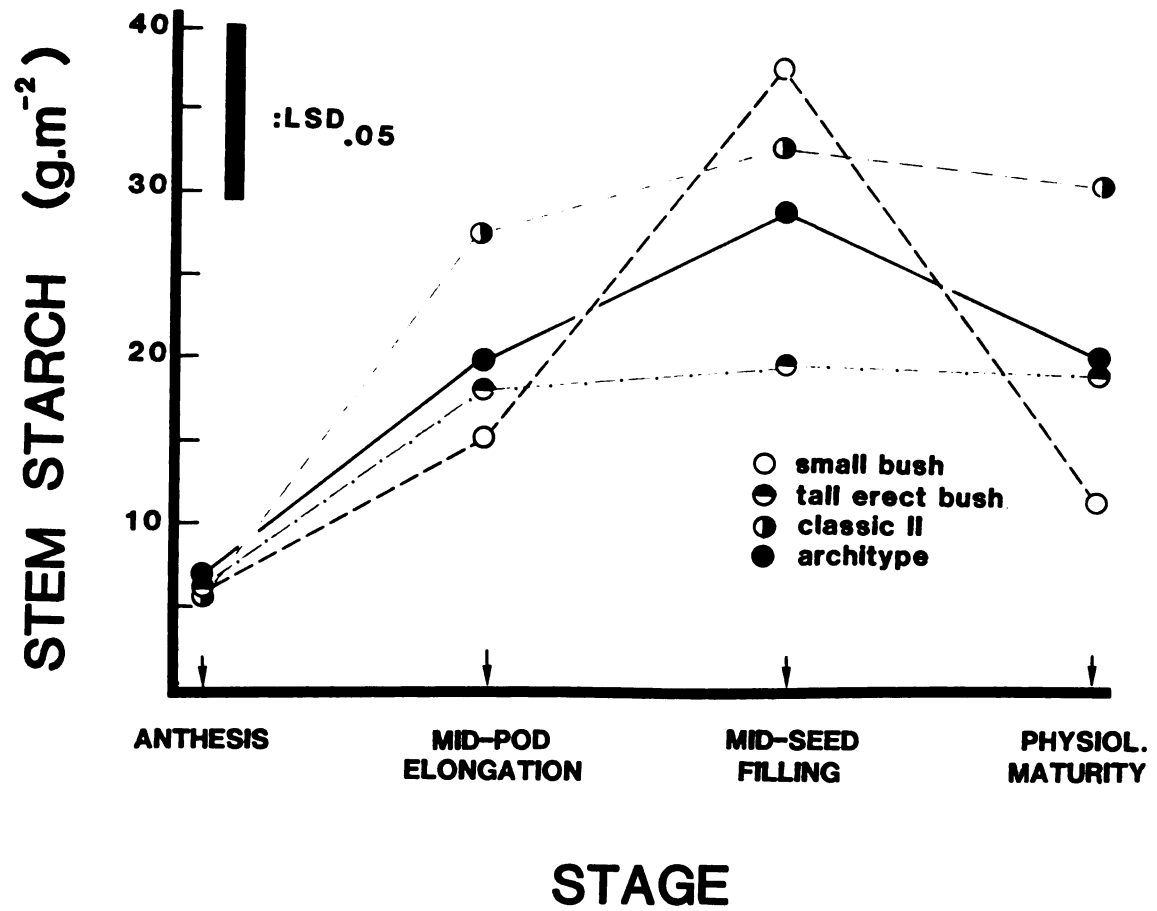


Figure 2. Stem nonstructural carbohydrate (TNC=starch+sugars) content at different stages of the reproductive development for small bush and classic II architectural forms dry bean cultivars observed in 1979

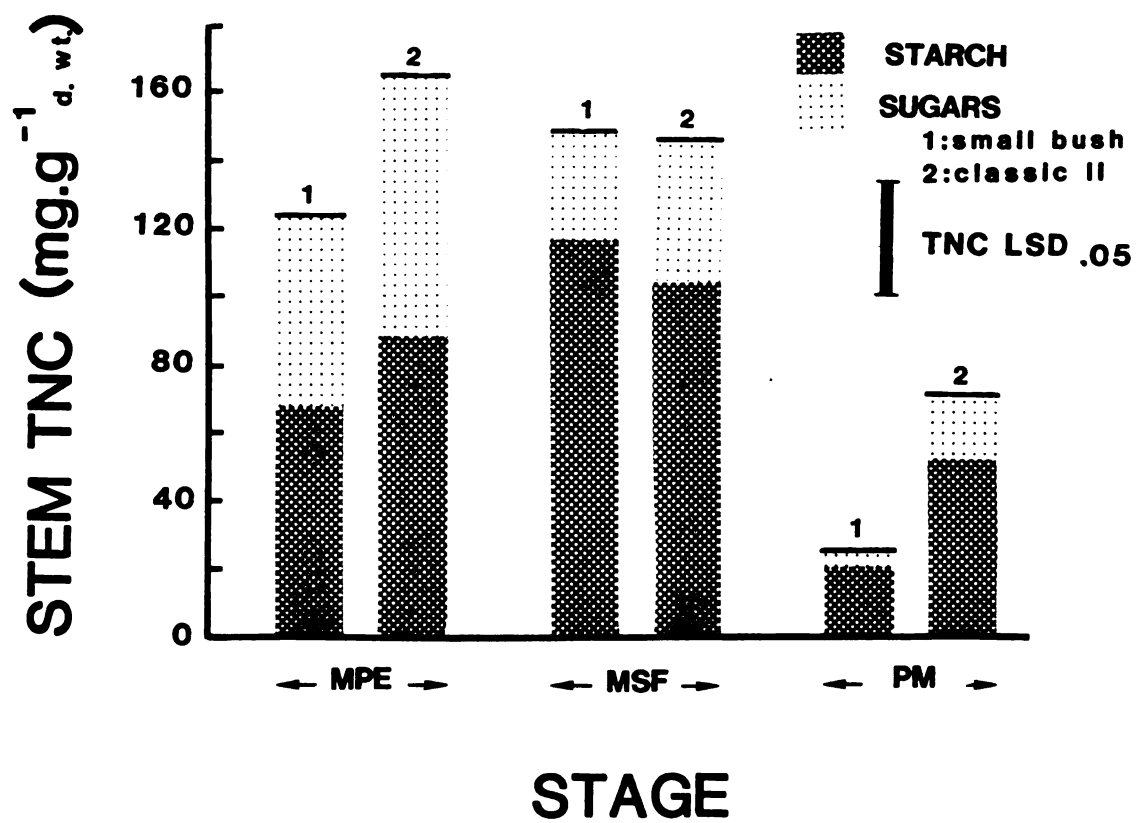


Figure 3. Pod wall nonstructural carbohydrate (TNC) and nitrogen (N) allocation changes during late seed filling among architectural forms of dry bean cultivars

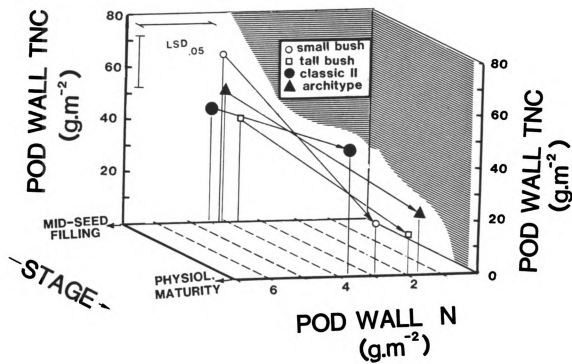


Figure 4. Modified harvest index and harvest nitrogen index relationship to yield for dry bean cultivars with differing plant architecture (●: architype; ●: classic II; O: small bush; and ●: tall erect bush)

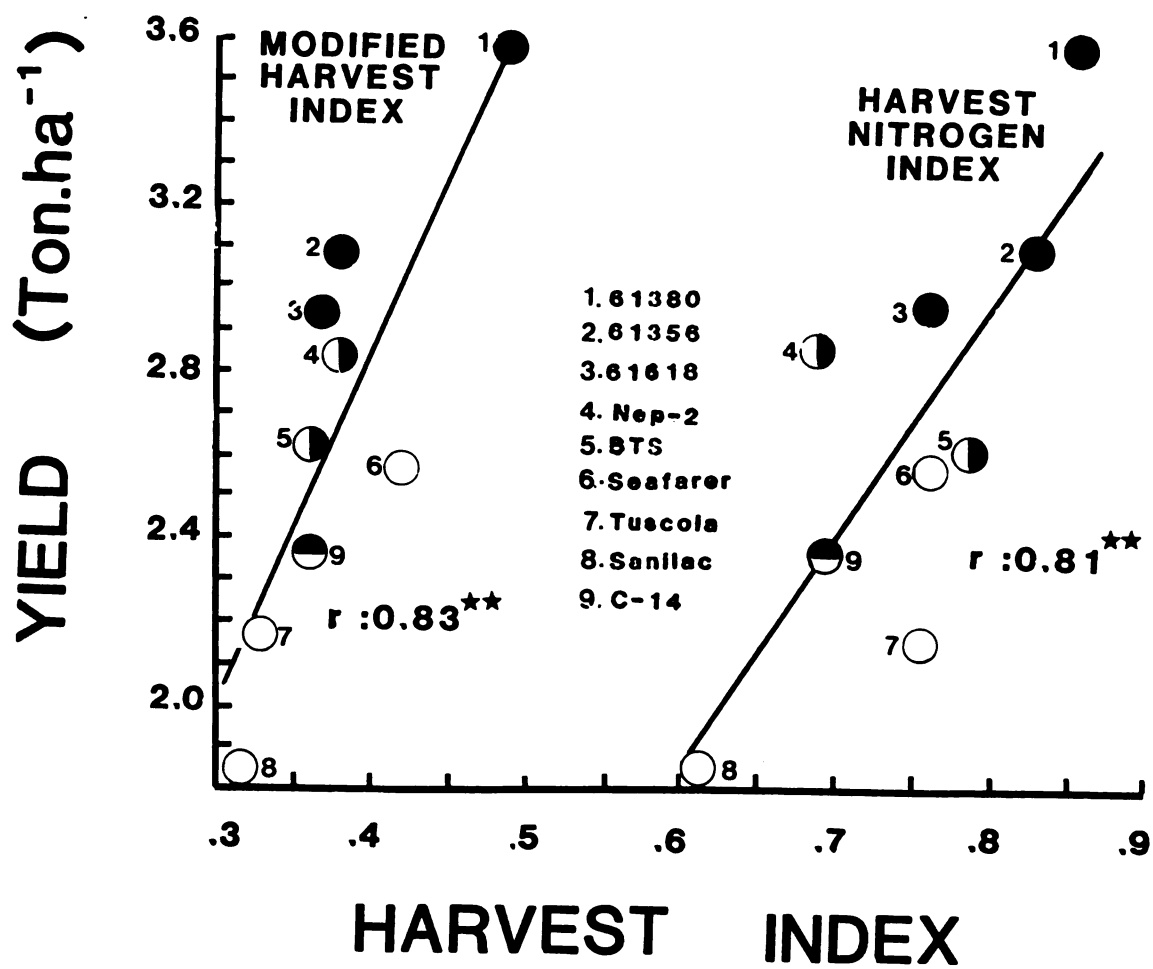


Figure 5. Nitrogen allocation and remobilization among plant components of cultivars 'Tuscola' and 'Nep-2' during reproductive development. Area in between dotted and solid lines and indicated with the arrows is N losses by foliar abscission (leaf blades + petioles)

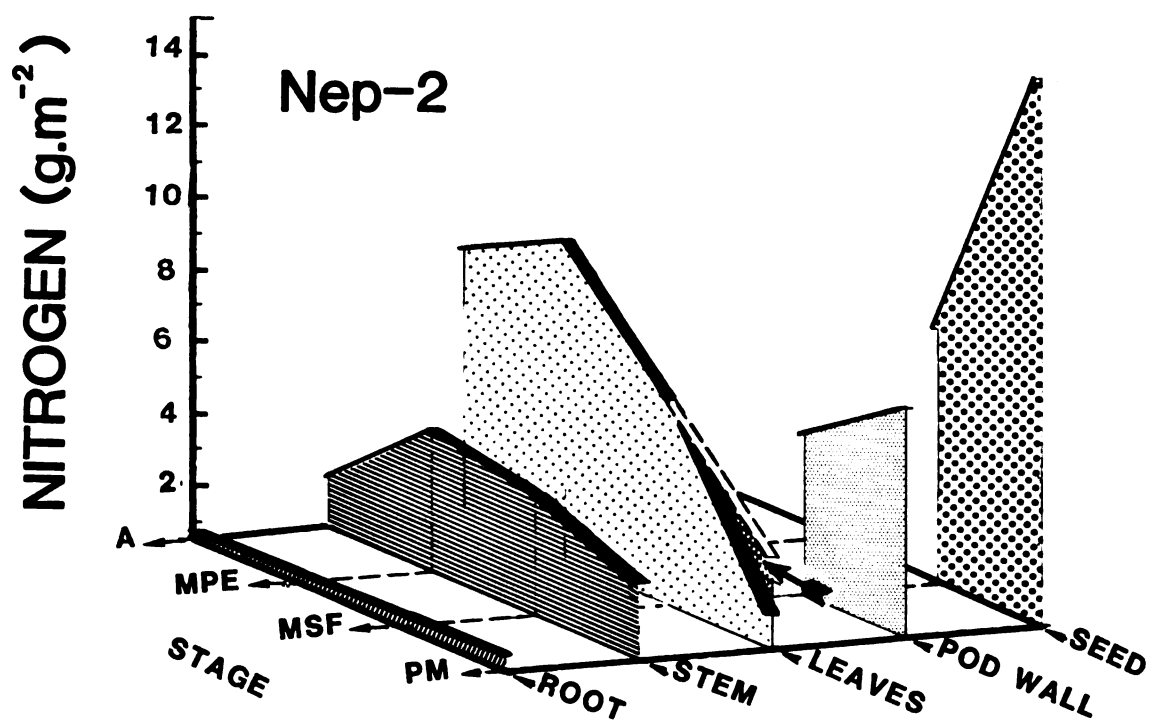
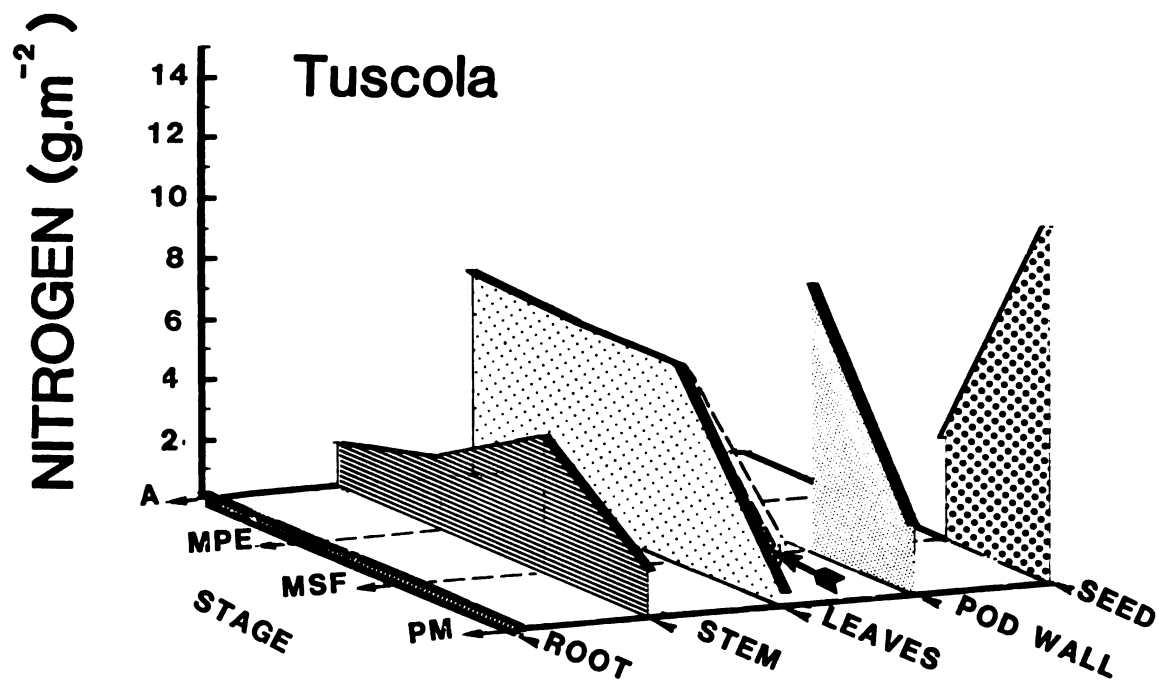
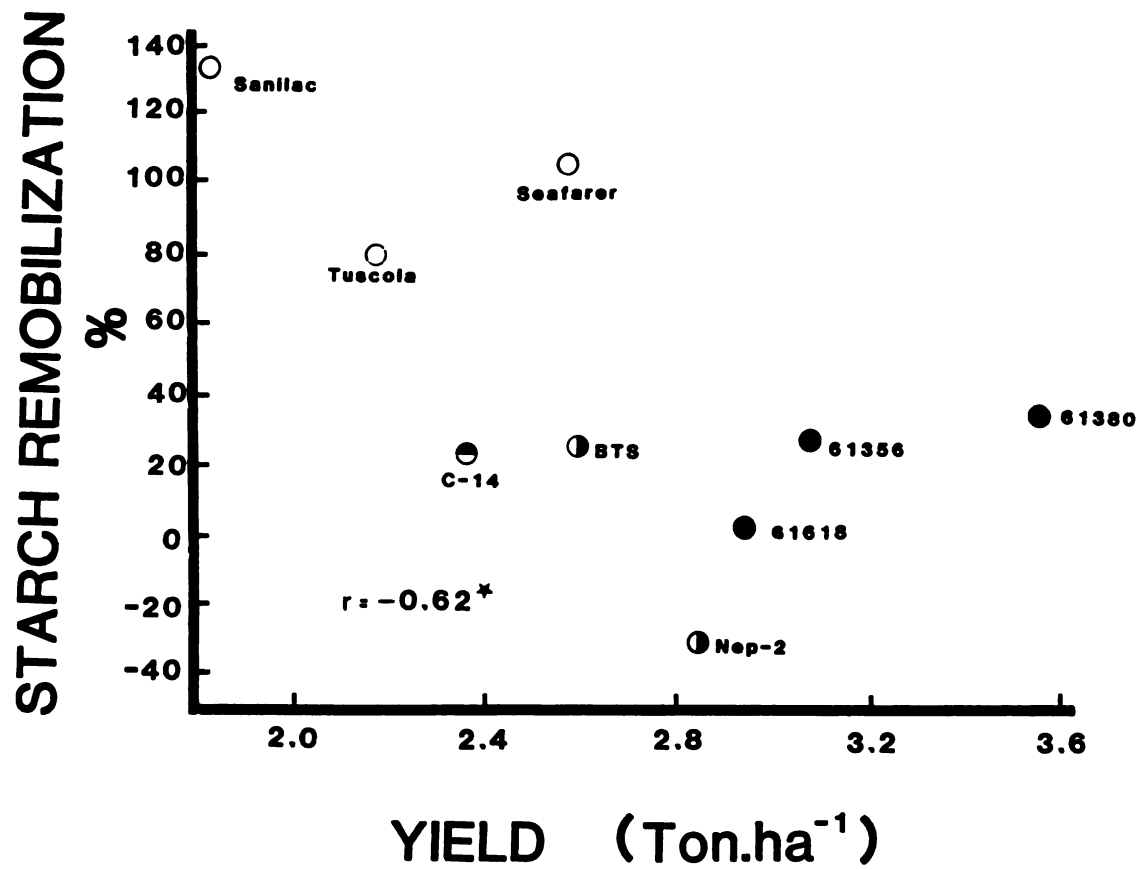


Figure 6. Yield and starch remobilization factor relationship between dry bean genotypes with differing plant architecture (●: architype; ①: classic II; O: small bush; and ②: tall erect bush)



CHAPTER 4

A COLLECTION RECEPTACLE FOR FIELD ABSCISSION STUDIES IN COMMON BEAN¹

ABSTRACT

A nontagging, nondestructive, continuous, and inexpensive method was developed to evaluate abscission of reproductive organs in dry beans (Phaseolus vulgaris L.) under field conditions. Abscission collection receptacles (ACR) were built, using Saran[®] screen (1.5 x 2.0 mm mesh) and 2.5 x 5.0 cm redwood stock. Receptacles were placed in the field over a 1.25 m segment of row, and the floor was carefully fitted around competitively growing plants at the two to three true leaf stage. The method was tested on dry bean cultivars, 'Tuscola,' 'Nep-2,' and 'Black Turtle Soup,' selected because of their contrasting growth and flowering habits. Reproductive organs were collected every four days and taken to the laboratory where the data were quantified. Samples required three minutes per ACR. Abscission could be broken down into flower and pod drop components. Pod abscission accounted for most of the shedding of reproductive organs. The abscission of pods under 10 mm length accounted for 64 to 82 percent of all reproductive structures abscised. The ACR was useful to study the seasonal patterns of flowering, abscission, and pod retention of genotypes. Differences in

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these parameters were detected among the three cultivars studied in this experiment. Low coefficients of variation associated with data collection indicated a good degree of precision in the experiments. Compared to unenclosed plants, the ACR had no significant effect on growth, vigor, yield, and yield components of enclosed plants.

Additional index words: Phaseolus vulgaris L., Dry beans, Reproductive organs, Flower and pod shedding, Field methodology.

INTRODUCTION

The abscission of reproductive organs during the flowering and fruiting period in the grain legumes is often greater than 50 percent. Binkley (1) studied six garden bean (Phaseolus vulgaris L.) cultivars and showed shedding of flowers among genotypes ranging from 44.3 to 76.2 percent. In soybeans, Glycine max (L.) Merr., one study (10) reported that levels of flower and pod abscission ranged between 43 and 81 percent in four cultivars, while Swen (7) found that between 70 to 87 percent of the reproductive potential of five cultivars was lost. Similar observations have been made for cowpeas [Vigna unguiculata (L.) Walp., 3], broad beans [Vicia faba L., 2, 5], yellow lupine [Lupinus luteus L., 11], and peanuts [Arachis hypogaea L., 4].

Dry beans are an important food crop in the USA, but the decreasing yields over the past two decades (9) have been of major concern. Several lines of evidence suggest that if the shedding of reproductive parts in beans could be prevented or decreased, the yields might be increased (6, 8, 12). The possibility for improving yield in beans by controlling abscission should stimulate interest in this area of research.

This paper describes the construction and usefulness of a collection method we developed to study abscission in dry beans. The technique has great utility for field abscission studies. Randomization need not be restricted as which might occur when cultivars contrasting in flower color are always planted in adjacent rows to guarantee the separation of abscised reproductive structures (10). In addition, the investigator is not hampered by limitations on the number of replications or treatments desired.

The method is designed to be used in field plots planted at commercial population densities; the receptacle is inexpensive to build, and allows one to collect data rapidly and with a good degree of precision. Moreover, the gathering of reproductive parts is continuous and sampling can be done at whatever daily interval (in our case every four days) the investigator chooses, even during periods of inclement weather.

MATERIALS AND METHODS

Construction of a Receptacle

Our method involves the construction and field placement of an abscission collection receptacle (ACR). An ACR is 1.25 x 0.50 x 0.50 m in dimension, made from plastic Saran screen (1.5 x 2.0 mm mesh), and cut as illustrated (Figure 1a). The plastic screen is attached to 2.5 x 5.0 cm redwood (other wood stock or tubular materials of appropriate dimensions are suitable). Two pieces of redwood stock cut 1.25 m long serve as top supports (Figure 1a). The Saran screen is nailed on each side as shown (Figure 1a) under a piece of flat molding (1.25 cm wide) to the supports. The ends of the ACR are reinforced by fastening the mesh under a piece of molding to 2.5 x 5.0 cm corner braces 0.75 m long (Figure 1b). The

end of each corner brace is cut into a V-shape to facilitate anchoring the box in the soil (Figure 1b).

The bottom of the ACR has a longitudinal cut one cm wide and 1.20 m long (the cut should be made to give approximately 2.5 cm of uncut floor at each end) to facilitate fitting the mesh floor around the stems of the plants contained within. Special care must be taken while anchoring an ACR in the field plot row in order to secure the floor around each plant but to avoid damage to neighboring plants. This can easily be accomplished if two persons work together to position the receptacle.

Field Evaluation

Three dry bean cultivars, 'Tuscola' (semi-vine), 'Nep-2' (bush), and 'Black Turtle Soup' (BTS; semi-vine) were selected to test the ACR technique because of their contrasting growth and flowering habits. Seed was precision drilled with a modified air planter into 80 m rows spaced 0.5 m apart. Spacing within the row was six to seven cm between plants (approximately 14 to 16 plants/m). Each cultivar was bordered on either side by itself.

Four 1.25 m segments of row were marked off at random for Tuscola, Nep-2, and BTS, respectively. An ACR was carefully placed over a segment and the floor of the receptacle was carefully fitted around the plants. Each ACR was further anchored into the soil by using pieces of steel wire two mm thick and 25 cm long. These anchors were bent into a U-shape and fastened to the bottom of the ACR and into the middle of row between adjacent borders.

Abscission was evaluated every four days throughout the flowering period by collecting all abscised reproductive structures from each ACR.

The first collection date began four days after the first open flower in the row was noticed. Abscised flowers and pods were collected between 0900 and 1000 hours each collection date by carefully sweeping the ACR floor with a fine bristled brush. After collection, the abscised materials were carefully placed into glassine envelopes, sealed, and taken to the laboratory where they were counted and/or measured using a 10X bifocal magnifying lens.

When mature, all plants were harvested from each ACR, weighed, and pods removed. Seed yield per 1.25 m row (g), pod number per plant, seed number per pod, and 100 seed weight (g) were measured. Data were also taken on biological yield (g) and harvest index (ratio). Biological yield and harvest index are defined here as total above ground plant dry weight, and the ration of seed yield to biological yield, respectively.

RESULTS AND DISCUSSION

Significant differences were detected among cultivars for reproductive organ production and abscission (Table 1). The percentages of flower abscission found agreed with those reported in other dry bean studies (1, 6). In addition, using the ACR enabled us to distinguish between abscission of flowers and pods throughout the flowering and fruiting period. Pod drop accounted for 64 to 82 percent of the total reproductive structures abscised, with the shedding of small pods less than 10 mm in length accounting for most of this.

Many studies on abscission in beans and other grain legumes relied on methodology that involved daily counting and tagging of flowers. Binkley (1) counted and color-coded 16,000 bean flowers during his study.

Counting and tagging practices are tedious and time consuming, and the fatigue encountered can lead to a lack of precise data.

Sampling (including the collection and counting operations) of each receptacle at each four day sampling period required about three minutes. Hence, the total time needed to obtain data for all four replications of the three cultivars investigated in each sampling period was about 45 minutes. The coefficient of variation (Table 1) for each trait suggested that we obtained a good degree of error control in the measurements.

Abscission studies in beans have had other shortcomings. Data from greenhouse or growth chamber experiments often have limited usefulness because of an insufficient number of plants tested per genotype or restrictions on the number of treatments imposed. In addition, data from field abscission studies often are taken on plants growing under spacings that are unrealistic and do not reflect an acceptable population density. Field-grown plants should be free from biases caused by lack of suitable interplant competition.

Van Schaik and Probst (10) designed a collection technique for studying the shedding of reproductive parts in soybeans under field conditions. Their method overcame many of the objections listed above. Nevertheless, the utility of the procedure was limited because cultivars with purple colored flowers had to be planted adjacent to rows containing white flowered cultivars.

In addition to evaluating total abscission of a number of cultivars, the ACR can be used to study seasonal patterns of flowering, abscission, and pod retention. Figure 2 shows the results of evaluating flower and pod abscission of Tuscola, Nep-2, and BTS throughout the postbloom

period. Measurements were made on plants of each cultivar growing in the field at densities similar to a commercially grown crop.

There were no statistically significant differences for biomass produced, seed yield, yield components, and harvest index of plants which grew enclosed by an ACR and those growing in random 1.25 m segments elsewhere in the plot (Table 2). This finding substantiated our hypothesis that the ACR would have no significant effect on plant growth which possibly could be caused by shading or mulching. In addition, plants confined to the ACR showed no visible differences for height or vigor when compared to plants growing free from enclosure (Figure 3).

CONCLUSIONS

The ACR method we described has a high degree of utility in field abscission studies in beans. Nevertheless, two disadvantages are associated with the method. First, an investigator may be interested in following the development of specific flower buds from anthesis through physiological maturity. This would require tagging or color coding flowers of interest on plants within the receptacle. The second disadvantage is that there may be some restriction of air movement through plants growing within an ACR. Restricted air movement through the lower canopy of bean plants could possibly create an environment favorable to development of leaf blights and white mold caused by Sclerotinia sclerotiorum. Disease development associated with the ACR would be more of a problem in humid climates than in the upper Great Lakes area.

The information that can be obtained by the investigator on flower and pod drop using the ACR method and the precision and flexibility gained over other techniques reported in the literature for studying abscission in dry beans far outweighs the disadvantages.

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Table 1. Reproductive organ production and abscission of three dry bean cultivars grown competitively in the field and determined using an ACR

Cultivar	Total reproductive organs per ACR		Reproductive organs abscised per ACR				Mature pods harvested per ACR		Plants per ACR
	no.	no.	Flower		Pod		Total	% [‡]	
			no.	% [†]	no.	%	no.	% [‡]	no.
Tuscola	623	97	32	202	67	299	47.9	324	13
BTS	837	199	36	358	64	557	66.5	280	14
Nep-2	883	108	18	484	82	592	67.0	287	16
L.S.D. (0.05)	-	-	-	-	-	-	-	30	-
(0.01)	94	59	-	88	-	93	-	-	-
C.V. (%)	15.8	10.2	10.9	8.4	12.3	6.4	12.3		

[†] % = fraction of total abscised reproductive organs.

[‡] % = fraction of total reproductive organs per ACR.

Table 2. Comparative yields, harvest indexes, and yield components for dry beans growing within the ACR and free of enclosure[†]

Plants growing in 1.25 m of field plot row	Yield components				
	Biological yield	Seed yield	Harvest index	Pods/	
				plant	100 seed weight
	— g/1.25 m row —	ratio	— no. —	g	
Enclosed	503.2	273.2	0.52	21.3	6.1
Free	457.0	243.1	0.51	18.5	6.2
F-ratio [‡]	NS	NS	NS	NS	NS
C.V. (%)	16.7	10.5	13.2	14.7	12.2
					6.7

[†]Data averaged over replications (four) and cultivars (three).

[‡]Differences are statistically nonsignificant (NS) at five percent probability level.

Figure 1. Abscission collection receptacle (ACR) for abscission studies. A. Top view of receptacle showing construction before assembling sides and ends. B. Assembled and anchored ACR with mesh floor fitted around enclosed plants

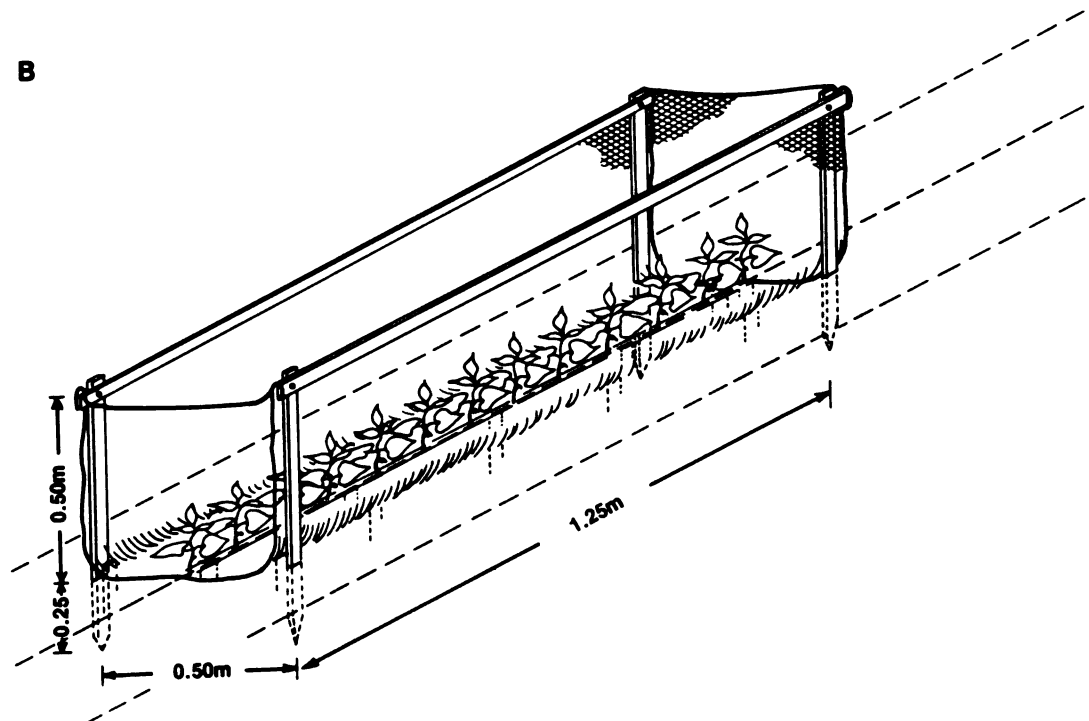
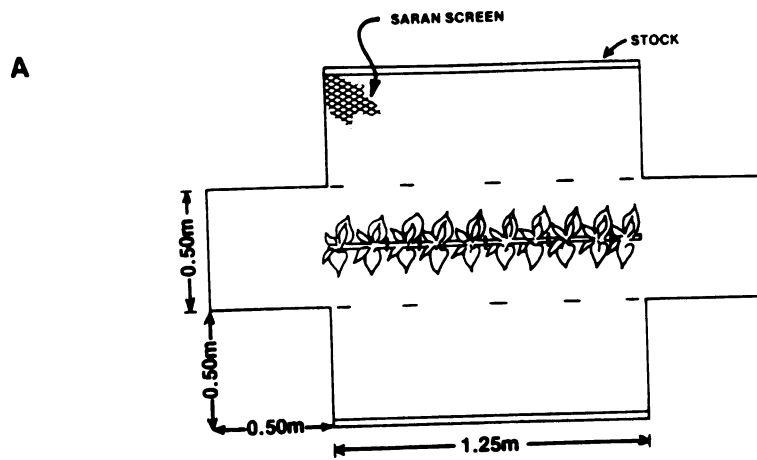


Figure 2. Abscission profiles of flowers (A) and pods (B) of three dry bean cultivars throughout the post bloom period determined using abscission collection receptacles. Each point is the mean of four replications. The vertical bar delineating the L.S.D. indicates the value for a significant difference between three cultivar means within a single sampling date

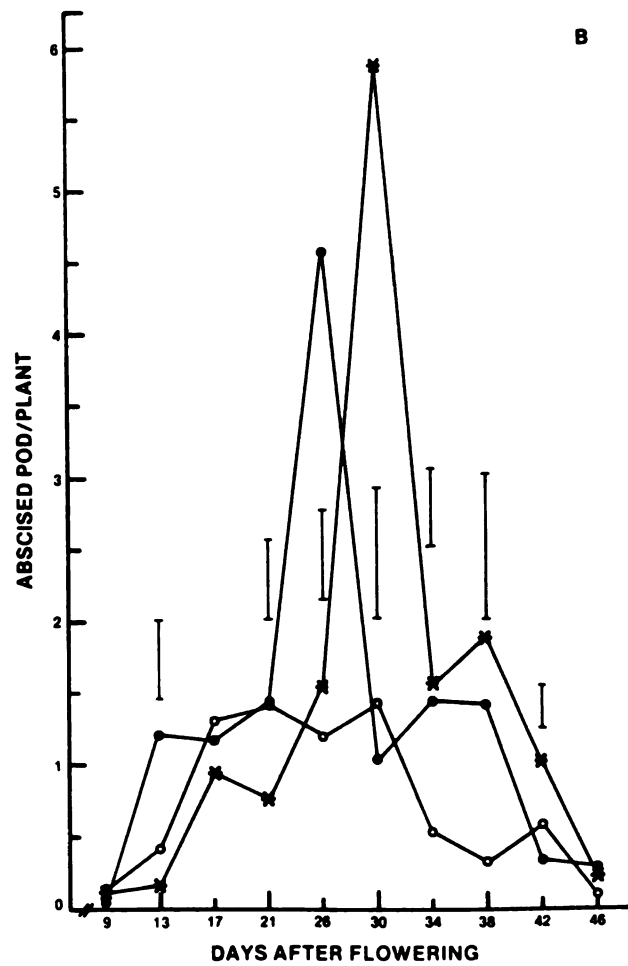
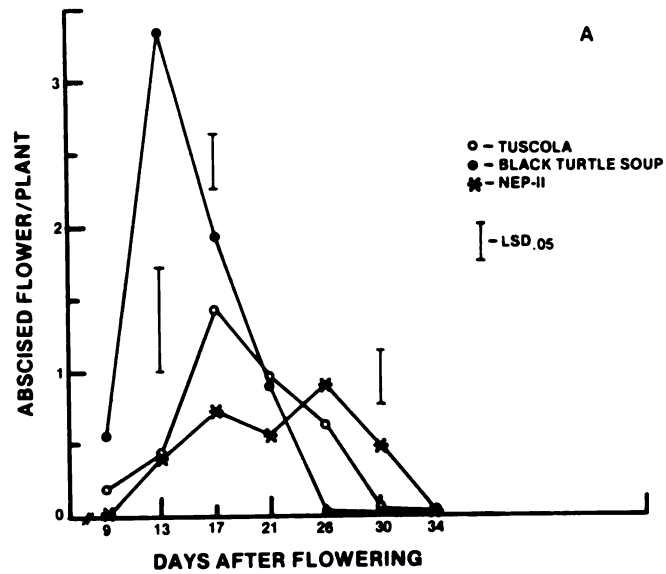


Figure 3. Field grown plants confined to an ACR and growing free from enclosure



CHAPTER 5

FLOWER, POD AND LEAF ABSCISSION OF DRY BEANS (PHASEOLUS VULGARIS L.) AS RELATED TO ETHYLENE PRODUCTION, NITROGEN CONTENT, AND CARBOHYDRATE LEVEL

ABSTRACT

Reproductive abscission is limiting the yield of dry beans. High yield has been reported in new architectural forms. Strong involvement of assimilate availability and growth regulators have been suggested as regulatory mechanisms of the abscission in dry bean and in other legume crops. The vegetative and reproductive abscission of nine dry bean entries with differing plant morphology were evaluated to establish relationships between carbohydrates (water soluble sugars, starch, and total nonstructural carbohydrate), nitrogen, and ethylene evolution from reproductive organs. Pod abscission accounted for 61 percent of the total abscission. Bush (determinate) entries produced higher rates of flower and pod abscission than the classic II and archetype (indeterminate) forms. The highest rate of ethylene production from flowers was observed in the cultivar Sanilac and the breeding line 61618. This was associated with the highest rate of total reproductive abscission. When compared with the classic II architectural form, the small bush entries had an increased rate of abscission and a lower level of total nonstructural carbohydrate in stems during the pod elongation stage. A total non-structural carbohydrate to nitrogen ratio of about eight seemed to stimulate abscission during the pod elongation stage. On the other hand,

a total nonstructural carbohydrate to nitrogen ratio of 12 was associated with decreased abscission. Foliar abscission accounted for 70 percent of the leaf dry matter losses and 80 percent of the foliar nitrogen was reallocated. A high potential for nitrogen remobilization was associated with delayed leaf senescence in the classic II and archetype forms.

Additional index words: abscission collection receptacle, water soluble sugars, nonstructural carbohydrates, yield potential, yield losses.

INTRODUCTION

More than 50 percent of the reproductive structures produced on plants of common bean (Phaseolus vulgaris L.) abscise. Hence, reproductive abscission is thought to be a major factor in reducing the yield potential of dry edible beans. Izquierdo and Hosfield (13) reported shedding of reproductive structures of 48 percent, 66 percent, and 67 percent for the cultivars 'Tuscola,' 'Nep-2,' and 'Black Turtle Soup,' respectively. These results were determined from field grown plants using an abscission collection receptacle (ACR) (13) and agreed with previous bean abscission work (8, 21). Control mechanisms of reproductive abscission in beans and in other legume crops have been postulated to involve developmental competition within the raceme for C-assimilates. Plant hormones, specifically endogenous ethylene, may also regulate abscission. Pod retention in a dry bean crop determines the portion of the yield potential achievable in any set of environmental conditions. It is probable that yield could be increased by reducing reproductive abscission. Yield advantages have been reported for some architectural forms by Adams (2). However, little information is available which describes the abscission levels in any dry bean cultivar. The role of

carbohydrates in their regulation of abscission is unclear (22) and ethylene has been postulated as the promotion factor in reproductive abscission (11, 15).

This study was conducted to determine fruit production, abscission level and rate of dry bean strains with different architectural forms. Ethylene monitoring from flowers and pods was conducted to establish differences in the rate of production of this growth regulator and its possible relationship to levels of abscission. Total nonstructural carbohydrates (TNC) and nitrogen (N) status were determined to relate abscission levels to the general assimilate level for each architectural form.

LITERATURE REVIEW

Fruit setting and pod retention is acropetal in legumes (19). Abscission of flowers or small pods occurs on practically every raceme of the plant. There is evidence that suggests that the basal and older pods regulate the abscission of new flowers and small pods in several species of grain legume. This has been substantiated in cowpea (Vigna unguiculata L., 19), lupin (Lupinus luteus L., 26), lima bean (Phaseolus lunatus L., 10), faba bean (Vicia faba L., 16), soybean (Glycine max L. Merr., 30) and in common bean (P. vulgaris, 21, 22, 24). It has been postulated that the regulation of abscission is due to the inability of younger fruits as they develop to compete successfully with each other or with vegetative tissue for assimilates (23, 30) and this situation is aggravated when the level of available carbohydrates is low (22, 25). Low water soluble sugars (WSS) and starch content of pod walls of aborting bean pods was reported by Tanaka and Fujita (25) as an

indication of a shortage of carbohydrates during pod wall growth which led to pod abscission.

There is also evidence that suggests that abscission in legumes is under hormonal control (5, 6, 22, 24). Ojehomon (19) examined factors controlling abscission in cowpeas and concluded that the basal racemes in the plant or the basal flowers of the inflorescence promoted abscission in the more distal ones, not simply by sequestering the assimilate from the subtending leaf, but probably through the action of diffusible hormones. Based on the hypothesis that more mature pods are more potent sinks within the raceme, Adedipe et al. (6) studied the effect of benzyladenine on ^{14}C -assimilate import in pods of cowpeas. He found that the mature pods were more competitive and suggested that pod abscission could be due to a deficiency in endogenous cytokinins in the younger pods which in turn resulted in an inability for C-assimilate mobilization. Other work showed reduced abscission of young bean pods when older fruits were removed (24). Tamas et al. (24) suggested that the effect the mature pod had on the abscission of flowers and young bean pods was due to differential levels of abscisic acid. Further work was conducted by Subhadrabandhu (22), who found that bean populations with high abscission potential also contained higher abscisic acid levels in the pod than populations with low potential abscission. This finding (22) supported Tamas et al.'s work (24).

The abscission of flowers and developing bean pods occurs at the junction of the pedicel and peduncle and is delineated by a narrow constricted zone of cells (28). In this zone, separation of cells is restricted to four or five rows of parenchyma cells. No differences in structure of

the abscission zone of flowers and pod were found when compared to the foliar abscission zone (28). Solubilization of pectic substances, increased calcium oxalate crystals and partial disintegration probably of the middle lamella area characterized cell separation during abscission (29). One of the striking features of reproductive abscission in dry beans is the speed with which the observed structural changes in the cell wall occur. Reproductive abscission occurs within 48 hours in contrast with the foliar abscission which generally requires eight days (28).

Increased cellulase activity during and prior to cell separation requires ethylene for activation and secretion to the abscission layer (1). Wright and Osborne (31) showed a specific and positional growth response to ethylene in the cells of the abscission layer of Phaseolus vulgaris L. This unique, non-auxin like, ethylene inductive growth was described as cell enlargement and occurred only in one row of cells of the abscission layer. These authors referred to this layer of cells as the target cells for ethylene abscission promotion (20). Causative effect of ethylene on abscission symptomatic growth has been attributed to this growth regulator (20).

Endogenous ethylene has been reported by many workers to be closely associated with abscission in many plant species (1). It has been reported to cause flower and pod shedding in broad bean (11) and reproductive abscission in P. vulgaris (15). It was speculated that the ethylene produced by the first flowers and pods could induce the inhibition of carbohydrate mobilization during early development of the younger developing pods (15). Variation between genotypes for ethylene production from flowers and pods was associated with abscission patterns (14, 15).

Watkins and Cantliffe (27) concluded that competition for metabolites by early developing cucumber fruits over later fruits or the production of growth hormones by developing seed which inhibit further other fruit development were the causes of the regulation in fruit set. Furthermore, It has been reported that when auxin transport was inhibited from the inside of the fruit ovary causing an increase in the auxin concentration within the ovary tissue, fruit set was enhanced (7, 27). A critical auxin level inside the ovary or a critical balance between inside levels and that directly next to the ovary was postulated as the regulatory mechanism for fruit set (27). A relation between auxin and ethylene metabolism was proposed after the finding that auxin (IAA) induced endogenous ethylene production by stimulation of synthesis of ACC-synthetase, an intermediary enzyme in the methionine to ethylene pathway (32). The Molish theory of "exhaustion death" was discussed by Nooden and Lindoo (18). Molish proposed that the diversion of nutrients to the reproductive parts of the plant at the expense of the vegetative parts was the cause of senescence. Nutrient diversion or senescence hormonal signaling (18) are not believed to be purely passive mechanisms. They involve interaction of growth regulators. Obtaining a legume plant that can supply the needs of the developing fruits without dying in the process could insure a greater chance for survival or inclusively greater yield and yield stability.

MATERIALS AND METHODS

Genetic Materials and Plant Architecture

Nine strains of dry beans were used as entries in this study. The entries represented four distinct architectural forms and two growth

habits which are described in detail elsewhere.¹ The architectural forms were selected on the basis of differences in the length of time to maturity, reproductive growth pattern, and yield.

Planting and Sampling Procedures

The nine entries were grown in the field in 1980 at East Lansing, Michigan. Seed was precision drilled into eight row plots with a tractor mounted air planter. Rows were 10 m in length and spaced 47 cm apart. Within row spacing was seven to eight cm giving between 14 and 16 plants per meter of row. Plots were arranged in a randomized complete block with four replications. Standard practices for herbicide and fertilizer application were used. In late September, mature plants were removed by hand from two, 2-m sections of row (1.88 m^2) of individual plots and threshed by hand. Just prior to threshing, data on yield components were recorded. Yield components consisted of number of pods per plant, number of seeds per pod and weight of 100 seeds. After threshing, seeds were analyzed for moisture content and weighed for yield (g) per plot. Yields were adjusted to 16 percent moisture content. Determinations of dry matter, water soluble sugars (WSS), starch, and nitrogen (N) were made on stem and leaves at four different physiological stages (PS), anthesis (A), mid-pod elongation (MPE), mid-seed filling (MSF), and physiological maturity (PM). These stages are described elsewhere.¹ Plants from 1-m of row were harvested from one of the center rows of each plot at each of the above mentioned PS. The stem and leaves were frozen at -19°C and dried in a forced air circulating oven at 100°C for one hour and 70°C for 36 hours.

¹Chapter 2 (Izquierdo, J.A., 1981, unpublished).

Sugars and Starch Analysis

The extraction of WSS was completed using essentially the method of Black (9) for defatted soybean meal. Sugars were separated and quantified using high performance liquid chromatography (HPLC) according to the procedure of Lester et al. (17). Starch was determined after first solubilizing it in sodium hydroxide and then hydrolizing to glucose using enzymes (17). The glucose liberated by the starch digestion was determined quantitatively by the use of a Glucostat reagent kit and HPLC analysis.

Nitrogen Analysis

Percentage of nitrogen was estimated by near-infrared reflectance (NIR) measurement on dry tissue samples using an infrared reflectance spectro (Neotec Corporation, Model 41). The method of sample preparation and analysis are described elsewhere.²

Vegetative and Reproductive Abscission Data Collection

Abscission collection receptacles (ACR) described by Izquierdo and Hosfield (13) were placed in one of the center rows of each replication. Abscised materials, which included flowers, pods, petioles and leaf blades were collected every four days after 50 percent flowering (DA 50 percent F) had occurred for each entry. Collection of foliar material was done by hand and flowers and pods were removed from the floor of each ACR using a battery operated hand-held vacuum cleaner manufactured for cleaning automobiles. The use of the vacuum cleaner

²Chapter 3 (Izquierdo, J.A. 1981, unpublished).

reduced the sampling time compared to using a brush and was well-suited to collecting abscised reproductive parts. All the collected materials from each entry were kept separately in glassine envelopes until they could be counted. Leaf blades and petioles were placed into paper bags for drying as described above for dry matter determinations. Reproductive abscission was measured as described elsewhere (13) and the level and rates of flower and pod abscission were calculated on a per square meter and day basis. Total number of pods produced per ACR were counted at maturity. The pods were hand threshed and the seed yield determined. Data on yield components and seed yield from a 1.25-m row segment of non-enclosed plants were observed to establish comparison with the data from enclosed plants as were done previously (13). The rate of foliar abscission was calculated on the same basis with the dry weights of leaf blades and petioles. Nitrogen analysis as described above was conducted on the foliar abscised material.

Ethylene Production Rate

Endogenous ethylene production from reproductive non-abscising organs was measured. Fresh flowers, one day old flowers and small pods (less than 35 mm in length) were detached from field grown plants and placed into 20 cc Vacutainers[®]. The Vacutainers were fitted with a rubber septum to permit the withdrawing of gas samples with a syringe. A one cc sample of gas was taken from each Vacutainer after a period not exceeding one hour (14, 15). The gas samples were injected in a gas-liquid chromatograph (GLC) equipped with a flame ionization detector (FID) and column appropriate for ethylene detection. Fresh weight of the flowers and pods--ten per tube--were obtained after the gas sampling.

Each field grown entry was sampled for ethylene production from reproductive organs at A, MPE, and early seed filling. Ethylene samples were always taken between 0800 and 0900 on the respective sampling date. Care was taken to choose flowers and pods from healthy plants and from the nodal positions corresponding to the middle canopy region of each plant. No appreciable ethylene evolution occurred through the rubber septum. This was substantiated using a control which consisted of a vial and a rubber serum stopper. Induced-wound ethylene evolution from excised segments of fruit peduncles was estimated to be equal to 0.15 nl.g^{-1} after one hour of accumulation. This value was subtracted from the data of the ethylene produced by flowers and pods.

RESULTS

Significant differences among entries were detected for the total number of flowers produced and reproductive structures abscised (Table 1). Reproductive abscission was broken down into two components: 1) Shedding due to flowers; and 2) Shedding due to pods. Entries characterizing the small bush architectural form produced significantly higher numbers of flowers than the architypes and BTS (Classic II).

Flower abscission accounted for an average of 39 percent of the total abscission but only for 20 percent of the total number of reproductive structures produced per ACR. The cultivars 'Sanilac,' and 'Tuscola' and the breeding line 61618 abscised significantly higher numbers of flowers per ACR than did the cultivars 'Seafarer,' 'Nep-2' and the breeding lines 61380 and C-14. Differences in flower abscission were not associated with any architectural form. Pod abscission accounted for an average of 61 percent of the total abscission. Pod abscission

(abscised pod/ACR) was significantly higher for Seafarer and Sanilac than the other entries (Table 1). On the other hand, the Tuscola, also a small bush architectural form, abscised significantly less pods than the Seafarer and Sanilac. This finding supports our earlier work (13) showing low pod abscission for the cultivar Tuscola.

The archetype 61380 abscised significantly fewer pods per ACR than the classic II cultivars Nep-2 and all the entries comprising both bush forms (Table 1). Significant differences in total reproductive abscission per ACR were observed. The archetype and classic II architectural forms abscised significant fewer organs than did the cultivars with small bush forms and non-significantly less than the tall erect bush breeding line C-14. In spite of the above differences in abscission the number of mature pods harvested per ACR did not follow the same pattern (Table 1). The cultivar Sanilac produced significantly higher number of pods per ACR than the breeding lines C-14, 61356 and 61618.

A significantly higher rate of flower abscission ($\text{flower} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was observed at 17 DA 50 percent F for the small bush architectural forms than for the other three forms (Figure 1a). On the other hand, the peak for flower abscission of classic II plants occurred at 22 DA 50 percent F. The tall erect bush strain (C-14) showed the same abscission pattern for flowers as did the small bush. The large number of flowers abscising early in reproductive development (17 DA 50 percent F) agreed with Izquierdo and Hosfield (13).

Two maximum peaks in the pod abscission rate were observed for the small bush forms at 17 and 32 DA 50 percent F, respectively (Figure 1b). In the former, the small bush abscission rate was significantly higher than

for the other three architectural forms. When the second peak occurred, only significant differences between the classic II and tall erect bush forms were found. Architypes showed a non-significant but higher pod abscission at 37 DA 50 percent F than the other forms. At PM all forms showed low rates of abscission (Figure 1b).

Significant differences among entries in their endogenous ethylene production rate were found at the MPE stage of reproductive development (Table 2). The differences, however, were not associated with any particular architectural form. Sanilac and 61618 produced the highest amount of ethylene per fresh weight and unit of time in flowers and pods at MPE, however, the rate of production was only significantly higher than the rate for Nep-2 and Seafarer. A very low rate of ethylene production from small pods occurred at the beginning of the seed filling period.

Figure 2 shows significant differences in the rate of foliar abscission at 37 DA 50 percent F. The bush (small and tall erect) entries had a higher but non-significant rate of leaf shedding at 32 DA 50 percent F for the four architectural forms and they maintained significant differences in the rate by 37 DA 50 percent F than classic II (Figure 2). The architypes showed an approximately similar rate as classic II entries at 37 DA 50 percent F. By PM all architectural forms abscised leaves at about the same rate, $4.5 \text{ g (dry weight) } \cdot \text{ m}^{-2} \cdot \text{ day}^{-1}$, although the rate for the small bush entries was non-significantly higher than the others.

Significant changes in leaf dry matter were observed during ontogeny (Table 3). The architype 61356 lost a significantly higher amount of its dry matter from MPE to PM than did BTS, Tuscola and C-14. On the other

hand, losses in foliar nitrogen (change) did not follow the same pattern as for losses in dry matter. Higher losses of foliar N were observed for 61380 (architype) compared to the classic II and the bush architectural entries (Table 3). The leaf dry matter abscission was affected little by either strain or architectural form. Only Sanilac abscised significantly higher dry matter than Seafarer (Table 3). On the other hand, differences in loss of N due to abscission were significant. The architypes lost more due to abscission than the other forms, however, the losses of 61380 and 61618 were significantly higher than of those of Seafarer. The percentage of N lost by foliar abscission followed the same pattern as the percentage of dry matter lost by abscission (Table 3).

On the average, foliar abscission of all entries accounted for 70 percent of the losses in dry matter of vegetative tissue among entries but only 21 percent of the losses in N. This finding tempts us to speculate that N is remobilized from leaves prior to the separation and shedding of leaves. Architype breeding line 61380 had a significantly higher potential for reallocation of foliar N into developing seeds than the breeding lines 61356, C-14 and Sanilac and Tuscola. Figure 3a shows that in the small bush entries the maximum reproductive abscission (flowers plus pods) occurred in a sequential fashion with time and was accompanied by an increased accumulation of N and TNC in the stems. On the other hand, a reduced abscission level was observed for the classic II entries (Figure 3b) and architypes (Figure 3c) while either accumulation of assimilates had ceased by MPE or increased in a lower proportion for small bush plants during the same period of development. The rate of ethylene production was maximum by MPE in all architectural forms and first occurred prior to the peak of reproductive abscission.

Significant differences in seed yield were observed at maturity (Table 4). The breeding line 61380 produced significantly higher yields than 61618, C-14, BTS, Nep-2, Seafarer, Sanilac, and Tuscola. Sanilac produced the lowest yield but this was not significantly lower than that of Tuscola. Yield abscission losses were calculated estimating an even probability of normal development to produce a productive pod filled with the same number and size of seed for all abscised organs. It was assumed also, the non-existence of component compensation among the yield component pod/m^2 , seed/pod, and seed size. The yield potential was calculated by adding the yield abscission losses together with the actual yield (Table 4). Yield abscission losses accounted for an average over all entries of 54 percent of the yield potential and a non-significant negative correlation of $r=-0.45$ between actual yield and calculated abscission losses.

DISCUSSION

The results showed that the total reproductive abscission averaged over the nine bean entries was 48 percent and ranged from 42 for 61380 (architype) to 54 percent for Sanilac (small bush) bean (Table 1). Abscission levels in P. vulgaris of 44 to 76 percent have been reported previously by Binkley (8). Differences among cultivars for percent abscission have been reported by Izquierdo and Hosfield (13) and Subhradrabandhu (22) reported that BTS had lower reproductive abscission than Seafarer. The data from the present study agree with these reports.

Differences among entries for total abscission were principally due to the abscission of small pods (less than 35 mm in length) and an average

of 61 percent of the total abscission involved pods. In this regard, the archetypes of 61380 and 61618 had the lowest percentage of pod abscission, while contrary-wise 61618 had the highest reproductive abscission which was due to a high floral abscission. Most pod abscission measured in our study occurred while pods were very small. Since pods abscised at such an early stage of development one might suggest that the lack of fertilization was mainly responsible for abscission. However, it has been reported that only one ovule needs to be fertilized to prevent pod drop in P. vulgaris (12). Furthermore, stress enhanced pod abscission was stated not to be caused by failure in fertilization by Harterlein (12). This has been supported with data for soybean abscission (30).

Abscission may result from water stress or from competition among developing pods for nitrogen, other nutrients and carbohydrates. Another cause of abscission is probably related to hormonal regulation of abscission of younger developing structures in a raceme, mainly by the older fruit. Regulatory control also could be exerted through hormone availability, hormone balance or hormone inhibition of assimilate mobilization to developing seeds. Differences between cultivars for ethylene production by reproductive structures has been reported by Izquierdo and Hosfield (14) and related to levels of reproductive abscission (14). El-Beltagy (11) suggested ethylene as the cause of abscission in broad beans and specific response to ethylene by target cells located at the peduncle of pods has been described in beans by Osborne (20) and Webster (29). Ethylene production rate in our study was maximum at the MPE stage (Table 2). The breeding line 61618 and the Sanilac produced the highest rates of ethylene released from flowers and pods and these entries had the maximum percents of total abscission.

In spite of the close relationship found between ethylene production and reproductive abscission for 61618 and Sanilac, Nep-2, with about the same level of abscission had the lowest rate of ethylene production at MPE (Tables 1 and 2).

Recently, Wiebold et al. (30) speculated that increased abscission in canopy regions receiving low irradiance might be a consequence of nonavailability of photosynthates in soybean racemes. Localized competition among older and younger developing pods, at each "phytomic unit" proposed by Adams (4), could cause a localized abscission.

Carbohydrate availability and level were studied as regulatory agents in abscission. Subhradrabandhu (22) reported that carbon dioxide enrichment and long days applied during the reproductive phase decreased pod abscission due to a high accumulation of carbohydrates in the stems of BTS. Higher IKI-starch score values have been associated with higher pod retention and yield of Nep-2 and BTS than the Tuscola by Izquierdo et al. (15). The data in this study support these reports (Figure 3). When compared with the classic II architectural form the small bush beans had an increased rate of total abscission associated with lower TNC level by the MPE stage (Figure 3a, b). It is suggested that an apparent competitive accumulation of TNC and N in the stem occurred during this period for the small bush form cultivars. This accumulation is coincidental with increased abscission and supports the idea that a reduced level of available carbohydrate is triggering the abscission of small pods. On the other hand, lower levels of abscission for the classic II and archetype entries than for the small bush entries were associated with higher TNC and N levels at MPE. It is tempting to speculate that the ratio of TNC/N in stem tissue is associated with abscission. A TNC/N

ratio of about eight at MPE seemed to increase abscission at MSF. The availability and interaction between TNC and N appear to be related to the regulatory mechanism in reproductive abscission although a strong effect of ethylene cannot be ruled out.

Although foliar abscission accounted for 70 percent of the leaf dry matter changes during reproductive growth, an average of 80 percent of the N was reallocated from leaves. It has been postulated (18) that reallocated N is utilized in seed filling. However, the N reallocation differences among entries did not explain entirely the differences in senescence and foliar abscission rate. It is necessary to include the level of N for potential remobilization. Archetypes and classic II entries had higher remobilizable leaf N than the bush forms and lower foliar abscission rate late in the reproductive period. This higher potential for N remobilization was associated with delayed leaf canopy senescence and a longer growing period than for the bush forms. The bush entries seemed to follow the nutrient diversion principle (18) and late remobilization of assimilate from leaves and other vegetative parts to developing seeds is coincidental with rapid senescence and death.

All architectural forms maintained a basal rate of foliar abscission during pod development and early seed filling. Since photosynthetically active sources lost by abscission during this early period was not important, perhaps photosynthesis was sufficient for both vegetative and reproductive needs. Accumulation of TNC and N in a particular storage organ could have caused competition sufficiently large among developing structures to cause their abscission. Breeding strategies for early TNC and N accumulation and late flowering during an extended growth season

are postulated as key factors in increasing yield in this crop. Genotypic differences for these characters indicated the existence of genetic variability but not necessarily associated with any architectural form. In some cases, the new architectural form, the archetype, offers a possibility for a potential expression of a minimum abscission leading to high yields.

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Table 1. Production and abscission of reproductive structures of nine dry bean strains comprising four architectural forms, growing in the field and determined using an abscission collection receptacle (ACR)

Architectural form and entry	Total reproductive organs per ACR	Reproductive organs abscised per ACR				Mature pods harvested per ACR		Plants per ACR
		Flower	Pod	Total		per ACR	per ACR	
	No.	No.	% ^z	No.	%	No.	No.	No.
Archetype								
61380	308 c ^y	61 b	20 bcd	67 d	22 d	128 d	42 b	180 ab
61356	333 c	73 ab	22 abc	89 bcd	27 cd	161 cd	49 a	170 b
61618	332 c	92 a	28 a	74 cd	22 d	166 cd	52 a	165 b
Classic II								
BTS	331 c	72 ab	22 abc	76 cd	23 d	147 cd	45 ab	184 ab
Nep-2	355 bc	58 b	16 cd	107 bc	29 bc	165 cd	46 ab	189 ab
Small bush								
Seafarer	402 b	54 b	13 d	161 a	40 a	215 ab	53 a	187 ab
Sanilac	466 a	94 a	20 bc	159 a	34 ab	253 a	54 a	212 a
Tuscola	393 b	91 a	23 ab	103 bc	26 cd	194 bc	49 ab	199 ab
Tall erect bush								
C-14	330 c	52 b	16 cd	120 b	36 ab	172 bcd	49 ab	160 b

^zPercent fraction of total reproductive organs per ACR.

^yMean separation in columns by Duncan's multiple range test, five percent level.

Table 2. Rate of ethylene production from reproductive structures at different stages during the reproductive development of nine dry bean strains comprising four architectural forms

Architectural form and entry	Reproductive stages		
	Anthesis (flowers)	Mid-pod elongation (flowers+small pods)	Early seed filling (small pods)
	———— ethylene nl.g ⁻¹ (fresh wt.).h ⁻¹ ————		
Architype			
61380	14.35	14.00 abc ^z	0.48
61356	10.53	11.54 abc	0.49
61618	11.27	21.12 a	0.54
Classic II			
BTS	9.75	17.91 abc	0.46
Nep-2	13.29	8.97 bc	0.86
Small bush			
Seafarer	14.25	19.46 ab	0.20
Sanilac	11.88	22.22 a	0.49
Tuscola	12.28	17.69 abc	0.24
Tall erect bush			
C-14	12.27	18.61 ab	0.29

^zMean separation in columns by Duncan's range test, five percent level.

Table 3. Changes in dry matter and nitrogen of leaves during reproductive development and losses of dry matter and nitrogen due to leaf abscission of nine dry bean entries comprising four architectural forms

Architectural form and entry	Changes in leaves during reproductive development ^x		Losses due to abscission ^y		Percent of change due to abscission		Remobilizable leaf N
	Dry matter	N	Dry matter	N	Dry matter	N	
	g.m ⁻²		g.m ⁻²		%		g.m ⁻²
Architype 61380	197.2 ab ^z	9.2 a	131.7 ab	1.7 a	68.3 b	18.4 b	7.4 a
61356	235.4 a	6.8 cd	126.7 ab	1.5 ab	55.4 ab	22.0 ab	5.3 b
61618	195.8 ab	8.4 ab	123.8 ab	1.8 a	67.6 ab	21.4 ab	6.6 ab
Classic II							
BTS	166.4 b	8.0 b	119.2 ab	1.5 ab	72.7 ab	21.4 ab	6.5 ab
Nep-2	201.8 ab	8.1 b	134.8 ab	1.6 ab	67.5 ab	20.0 ab	6.4 ab
Small bush							
Seafarer	192.1 ab	7.4 c	113.5 b	1.2 b	59.7 ab	16.9 bc	6.1 ab
Sanilac	183.7 ab	6.8 cd	138.9 a	1.4 ab	75.9 ab	20.6 ab	5.3 b
Tuscola	164.7 b	6.1 d	133.0 ab	1.5 ab	81.1 a	24.6 a	4.5 c
Tall erect bush							
C-14	175.8 b	7.4 c	129.9 ab	1.6 ab	73.5 ab	21.6 ab	5.8 b

^xPlant leaf dry weight loss from mid-pod elongation to physiological maturity. Leaf includes petiole.

^yDetermined using an abscission collection receptacle.

^zMean separation in columns by Duncan's multiple range test, five percent level.

Table 4. Estimated losses in yield due to abscission, actual yields and yield potential of nine dry bean entries comprising four architectural forms

Architectural form and entry	Estimated yield loss due to abscission ^x	Actual yield	Yield potential ^y
		kg. ha ⁻¹	
Architype			
61380	2661	3577 a ^z	6239
61356	3185	3076 ab	6262
61618	3188	2949 b	6137
Classic II			
BTS	2904	2589 bcd	5494
Nep-2	2798	2845 b	5644
Small bush			
Seafarer	3496	2569 bcd	5066
Sanilac	3443	1823 e	5266
Tuscola	2822	2162 de	4984
Erect small bush			
C-14	3027	2366 cd	5394

^x(reproductive abscission/m²) · (seed/pod) · (seed weight).

^yYield potential = Estimated yield loss due to abscission + actual yield.

^zMean separation in columns by Duncan's range test, five percent level.

Figure 1. Abscission rate for flowers (a) and pods (b) associated with four architectural forms of dry beans throughout the post bloom period determined using abscission collection receptacles

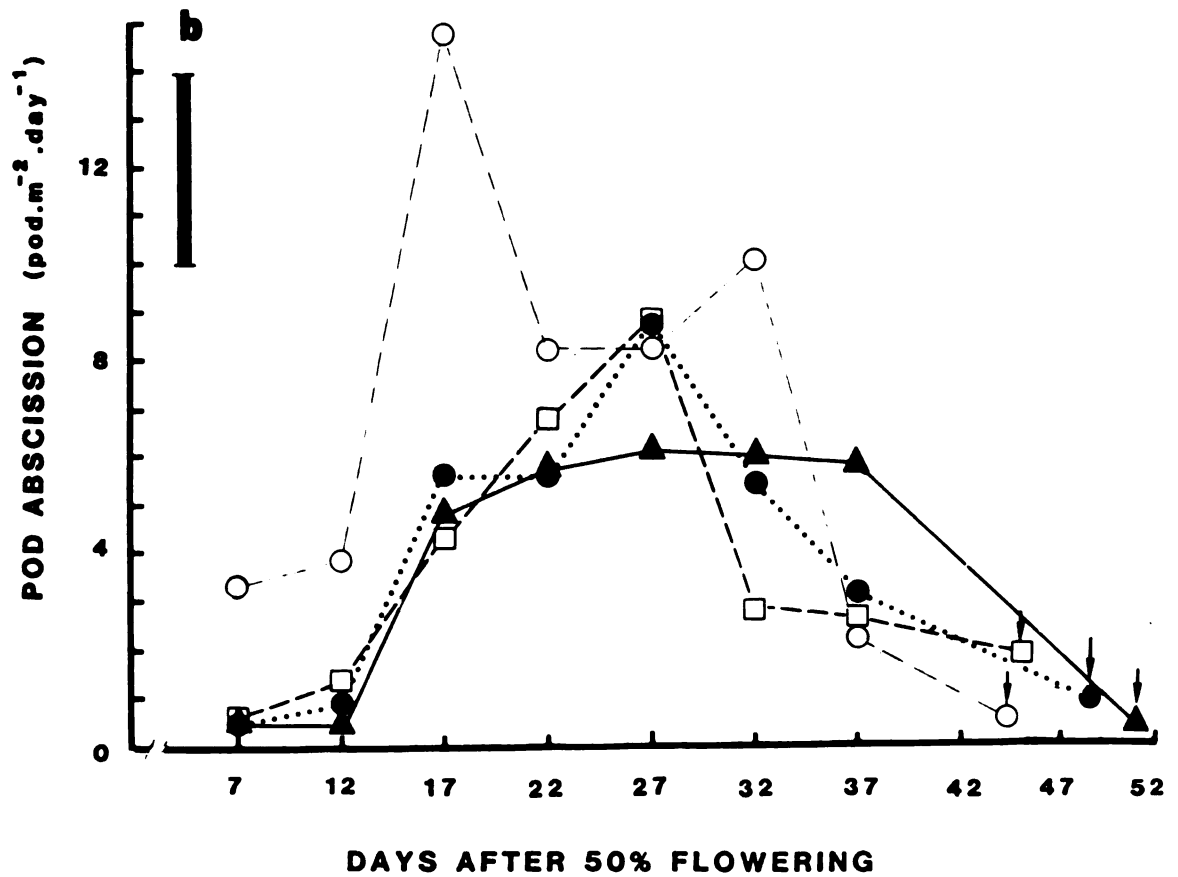
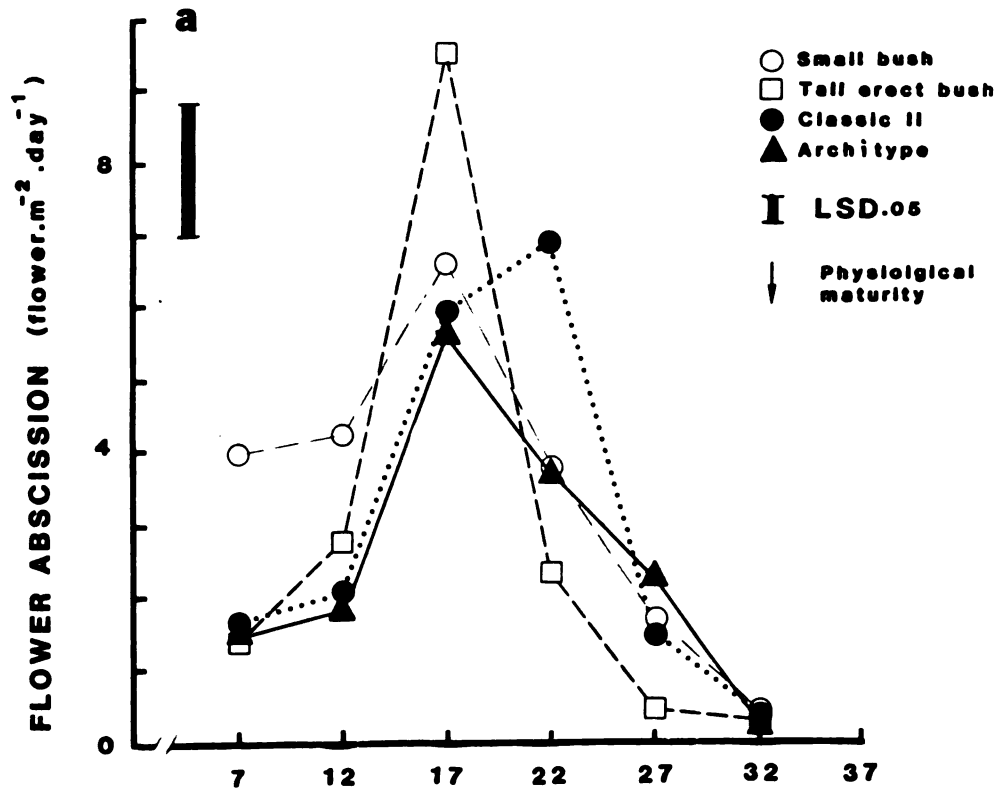


Figure 2. Abscission rate for leaves of dry beans associated with four architectural forms throughout the post bloom period determined using abscission collection receptacles

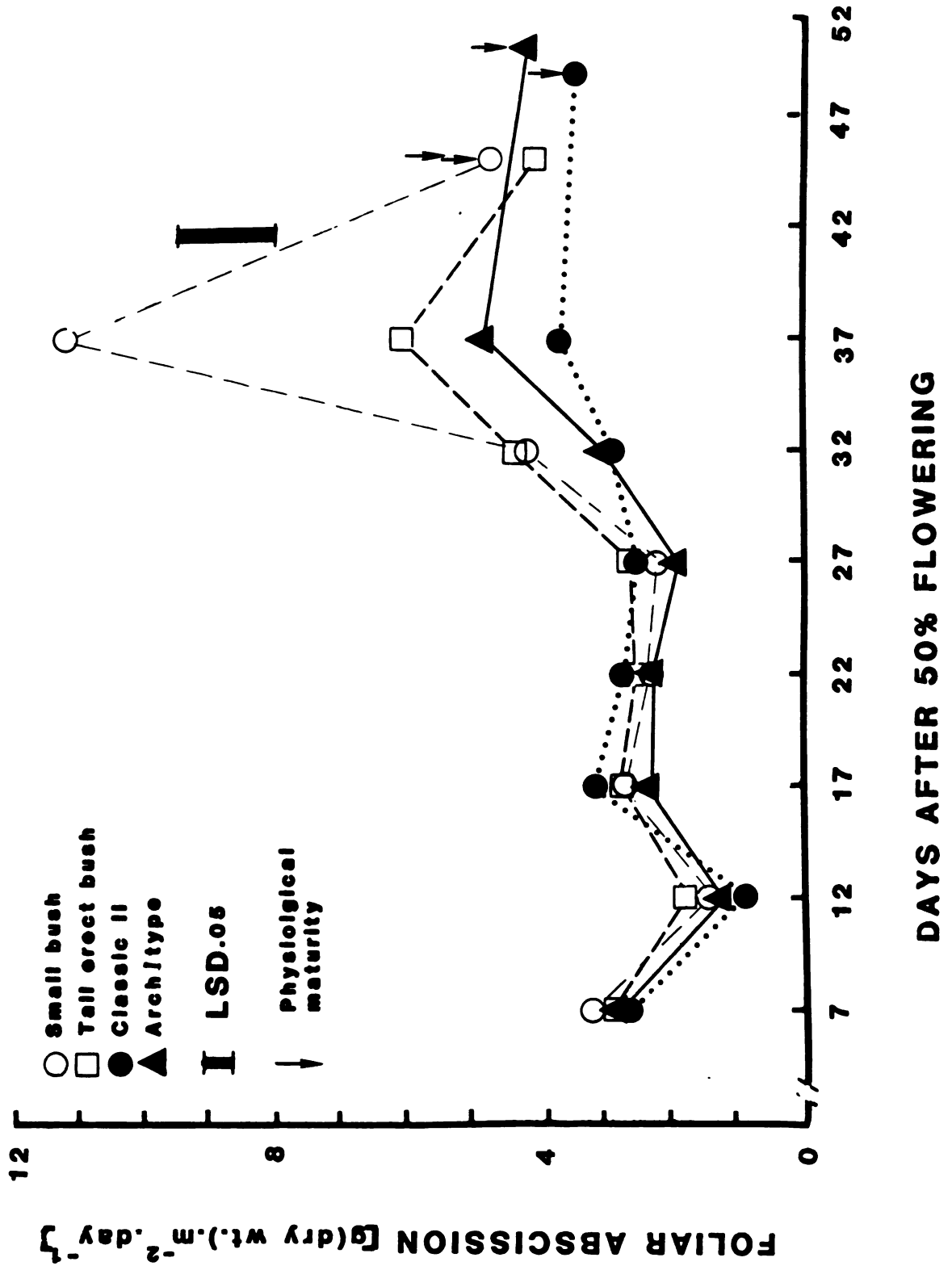
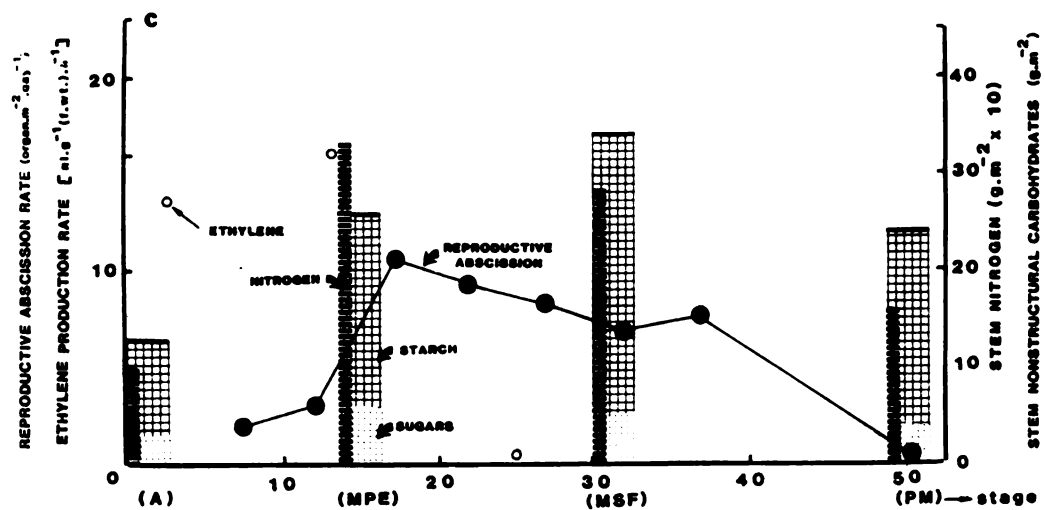
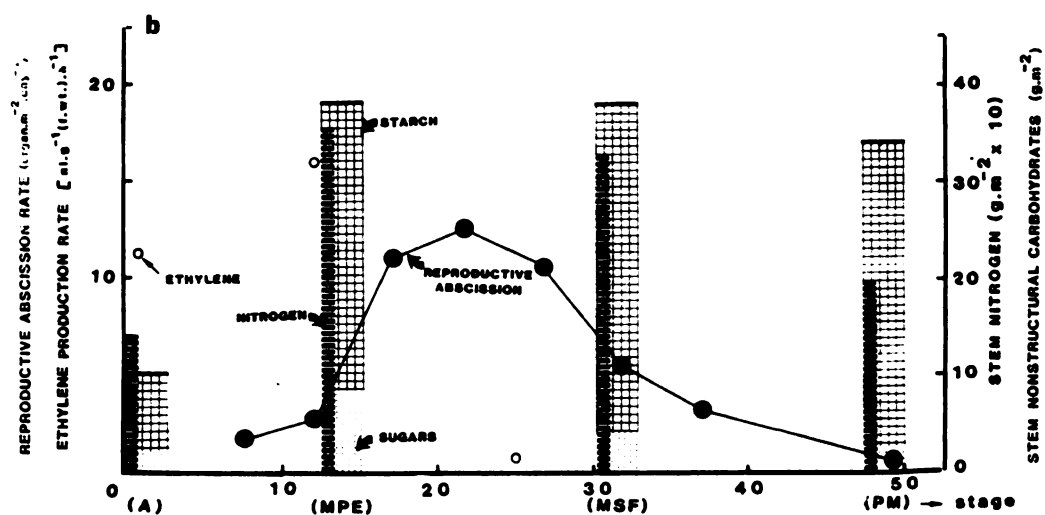
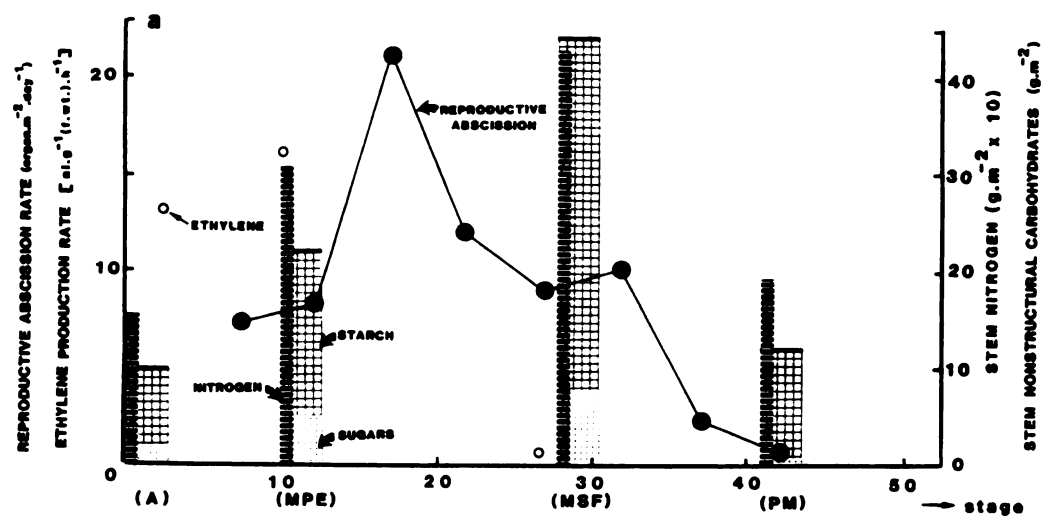


Figure 3. Abscission rate, ethylene production and stem assimilate level during ontogeny of small bush (a), classic II (b), and architype (c) architectural dry bean forms



DAYS AFTER 50% FLOWERING

SUMMARY AND CONCLUSIONS

In the cereals and grain legumes the unimpeded transport of photosynthate and nitrogen to the "sink" is important for normal grain development. High yields have been associated with cultivars that have large sinks and which partition C-assimilate efficiently. Moreover, yield stability of grain crops may be associated with remobilization of reserve nonstructural carbohydrates and nitrogen from storage organs during periods of stress.

In dry edible beans (Phaseolus vulgaris L.) improving the efficiency of the grain filling process has been an objective of breeders for the past decade. Selection for recombinants with high harvest indices has been part of the dry bean breeding strategy of several programs. Recently, breeders have become interested in characterizing genotypes for their rate and duration of seed filling and remobilization of stored starch during reproductive development. Physiological efficiency in regard to partitioning and remobilization is viewed as an important means for improving yields of dry bean cultivars.

During the past few years, a significant modification in the architecture of semi-determinate dry bean plants has been achieved. The new architectural form ("archetype") is characterized as tall, erect, and amenable to growing in narrow rows. In addition, "archetype" strains are higher yielding than the widely grown and accepted cultivars they are replacing. It is tempting to speculate that the advantage associated with the "archetype" is due to a larger sink (increase in the number of pod bearing nodes), more efficient grain filling, and less reproductive abscission.

To study C-assimilate partitioning, remobilization of nonstructural carbohydrates and nitrogen, and abscission in dry beans this thesis research was undertaken.

Specific objectives were to: 1) ascertain relationships between bean cultivars with differing plant architecture and rate and duration of seed filling and abscission, and 2) elucidate whether the yield advantage of the "architype" can be explained by a more efficient C-assimilate partitioning than other architectural forms.

The thesis research was implemented by evaluating partitioning, remobilization and abscission on several tissues of dry beans and at several stages during their reproductive development. Water soluble sugars, starch, and nitrogen content were determined on roots, stems, petioles, leaves, pod walls, and seeds in each of two years. In 1979, three strains were sampled at four day intervals throughout the reproductive growth period. In 1980, nine strains were evaluated at four reproductive stages (anthesis, mid-pod elongation, mid-seed filling, and physiological maturity).

The strains used were characterized by four architectural forms and belonged to type I and II growth habits as defined by the Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia. Architectural form A were small bush plants (CIAT type I) and were made up of the cultivars 'Seafarer,' 'Sanilac,' and 'Tuscola.' These cultivars belong to the navy commercial class and account for most of the navy bean grown in the United States. Architectural form B was characterized by tall and erect bush plants (CIAT type I). The breeding line C-14 was the only architectural form B entry. The cultivars 'Black Turtle Soup' and

'Nep-2' were characteristics architectural form C plants. These were semi-determinate entries (CIAT type II) that lodged at maturity. The breeding lines 61380, 61356, and 61618, comprised the "architypes" and were characteristic architectural form D plants (semi-determinate; CIAT type II).

During the course of the research several seed filling parameters were determined from sample data fitted to a regression equation appropriate to the cubic model. The relationship between reproductive and vegetative abscission was studied by measuring the level and the pattern of each. In addition, the amount of ethylene evolved from flowers and small pods was measured and correlated with abscission. Experiments to quantify abscission under field conditions were made feasible by the development of appropriate methodology. One method was the construction and placement of abscission collection receptacles (ACR).

The following conclusions are made on the basis of this research:

- 1) Yield differences among the entries were more associated with the length of the seed filling period than with the rate of seed growth. The architypes and the cultivars Black Turtle Soup and Nep-2 showed more than a two-fold increase in the duration of the filling period when compared with the standard bush cultivars.

- 2) Dry matter remobilization from stems and pod walls, the most important sources of remobilization, was negatively and significantly correlated with duration of the seed filling. A large remobilization factor for dry matter characterized the standard bush form. These cultivars filled seeds at the highest rates and for the shortest period to produce the lowest yield. The high yield of the architype 61380 and 61356 may be due to the longer filling period than the other architectural forms associated to a high dry matter remobilization from storage sites to the seeds.

3) Differences in sugars and starch (total nonstructural carbohydrates) and nitrogen were associated with entries and physiological stages over the entire reproductive growth period. However, a significant increase in the level of total nonstructural carbohydrates due to accumulation of starch in the stems was found at middle seed filling and was independent of entry. Nitrogen followed the same pattern as did TNC.

4) The highly significant interaction of entry x physiological stage for carbohydrates in stems, roots, and pod walls was due to differential remobilization to the seeds. The small bush entries (form A) remobilized larger amounts of TNC from the stems to the seeds after mid-seed filling than the other architectural forms. The archetypes remobilized carbohydrate but the classic II entries (Nep-2 and Black Turtle Soup) did not.

5) The modified harvest index and the harvest nitrogen index were the parameters that correlated the best with yield.

6) Reproductive abscission limits the yield of dry beans. Fifty percent of the theoretical yield is lost by abscission and 61 percent of the total abscission was accounted for the dropping of small pods. The bush forms produced higher rates of flower and pod abscission than the classic II and some of the archetypes.

7) Ethylene is viewed as being one of the regulating factors in reproductive abscission in dry beans. The highest rate of ethylene production from flowers was observed for Sanilac and 61618. This was associated with highest rate of total reproductive abscission.

8) Assimilate availability was implicated as being strongly involved in the regulation of abscission. Competitive storage of TNC and N in stems seemed to stimulate reproductive abscission in the small bush entries during the early reproductive development. A TNC/Nitrogen ratio of about

eight stimulate abscission during the pod elongation stage. On the other hand, a TNC/Nitrogen ratio of 12 was associated with decreased abscission.

9) Foliar abscission accounted for 70 percent of the dry matter losses of the leaves, and 80 percent of the foliar nitrogen was reallocated before abscission. Delayed senescence was associated with larger pool of remobilizable nitrogen.

10) The abscission collection receptacle was an appropriate method for studying abscission in the field. The advantages are due to the method's feasibility, practicality, continuity and reduced cost.

11) Starch status determined by the IKI-starch score method allows for only gross separation of starch storing and non-starch storing genotypes. It also requires the investigator to establish a reference to starch content determined in the laboratory.

12) The yield superiority of the architype is based on an extended seed filling period and high partitioning of carbohydrates and nitrogen. A larger sink than the other entries, a lower abscission rate, and larger seed size were associated with the yield superiority. On the other hand, remobilization could be a mechanism to keep yield high under adverse conditions (stability), and also to allow for maximum yield under non-stress conditions.

13) The results of this work suggest that in order to maximize and stabilize yield in dry beans, selection for efficient partitioning and remobilization must be incorporated as a major objective of the breeding programs in addition to the selection for only an increased sink capacity.

APPENDICES

APPENDIX A

Table 1. Method of analysis of nonstructural carbohydrates in dry bean tissues

A) EXTRACTION OF SOLUBLE SUGARS

1. Place 500 mg dry tissue samples ground to pass a 45 mesh sieve in 50 cc centrifuge plastic tubes.
2. Add 25 ml 80 percent ethyl alcohol and cap tubes.
3. Homogenize 40 minutes at 85°C in a shaking water bath. Stir periodically with glass stirrer to avoid decantation.
4. Centrifuge for nine minutes at 10,000 rpm.
5. Extract supernatant into 50 cc centrifuge plastic tubes. Dry remaining pellet fraction 12 hours at 65°C and transfer to 25 ml plastic bottle. Cap bottles and store at -3 to 0°C.
6. Add to the extract two ml ten percent lead acetate. Centrifuge three minutes at 10,000 rpm and extract supernatant again into 50 cc centrifuge plastic tubes.
7. Add to the extract two ml ten percent oxalic acid. Centrifuge three minutes at 10,000 rpm and extract supernatant into 40 ml volumetric glass tubes.
8. Immerse the glass tubes in a boiling water bath and evaporate to about 19 ml. Adjust final volumen to 20 ml with distilled water.
9. Add 0.1 ml saturated benzoic acid solution for preservation.
10. Transfer to 25 ml plastic or glass bottles, cap tightly and store at -3 to 0°C.

B) SOLUBLE SUGAR ANALYSIS

1. Prefilter two ml of extract (A.9) with a C18 SepPak^R.
2. Inject 15 µl of the filtrate into the port of a high pressure liquid chromatograph acconditioned with a µ-Bondapak column for carbohydrate separation. The solvent phase is 70:30 CH₃CN:H₂O (v/v) pH 4.8, flowing at 2.0 ml·min⁻¹.

Appendix A Table 1 (continued)

-
3. Use high purity standard for sugar qualitative and quantitative determination. Prepare one mg/ml in 80 percent alcohol standards of individual and joined sugars. Use co-chromatograms and standard retention times for qualitative identification. Peak area sample/peak area standard ratio times concentration and dilution factors will give you the amount (mg/g d.wt.) for each sugar (Appendix A, Figure 1).

C) STARCH ANALYSIS

1. Starch solubilization and alkaline digestion.
 - a. Redry pellet fraction (A.5) three hours at 65°C.
 - b. Place 200 mg of the redried pellet into 15 ml centrifuge plastic tubes.
 - c. Add five ml 0.5N sodium hydroxide and cap tubes.
 - d. Homogenize one hour at 35°C in a shaking water bath with frequent vortexing.
 - e. Neutralize by adding five ml 0.5N acetic acid. Centrifuge one minute at 10,000 rpm.
2. Enzymatic breakdown to glucose
 - a. Transfer one ml supernatant (C.1.4) into ten ml glass tubes.
 - b. Add one ml ten mg/ml amyloglucosidase (Sigma^R) 2200 U/g, 0.2 ml 0.1 mg/ml Alpha amylase (Sigma^R) 1270 U/g and 0.2 ml 5 µl/ml Beta-amylase (Sigma^R) 1140 U/g and incubate one hour at 55°C. The enzyme solutions are prepared fresh in 0.1M sodium acetate pH 4.8 buffer solution.
3. Glucose Analysis
 - a. By HPLC analysis inject 15 µl of the hydrolizate (C.2.2) into a HPLC as described before (B). Analyze for glucose.
 - b. Buy a Glucostat Reagent-Assay Kit^R (Sigma No. 510).
 1. Take 0.5 ml of the hydrolizate (C.2.2) into 15 ml centrifuge plastic tubes.
 2. Add 5.5 ml distilled water.
 3. Add two ml 0.3N barium hydroxide and two ml 0.3N zinc sulfate.

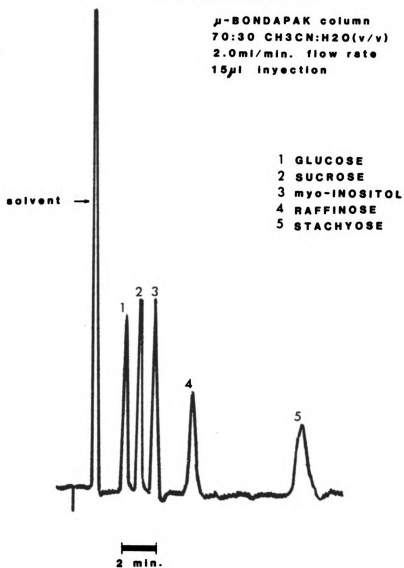
Appendix A Table 1 (continued)

-
4. Centrifuge three minutes at 10,000 rpm.
 5. Take 0.5 ml supernatant into ten cc glass test tubes and add five ml of the enzyme-color reagent solution (Sigma Technical Bull. No. 510).
 6. Incubate 12 minutes at 37°C and read absorbance at 450 nm.

Figure 1. HPLC Chromatogram of the free sugars in dry bean (Phaseolus vulgaris L.) tissues

HPLC condition:

μ -BONDAPAK column
70:30 CH₃CN:H₂O(v/v)
2.0ml/min. flow rate
15 μ l injection



APPENDIX B

Relationships of pod and seed development with stem IKI-starch score during the reproductive period of the cultivars Tuscola (Figure 1), Black Turtle Soup (Figure 2), and Nep-2 (Figure 3) grown in 1979

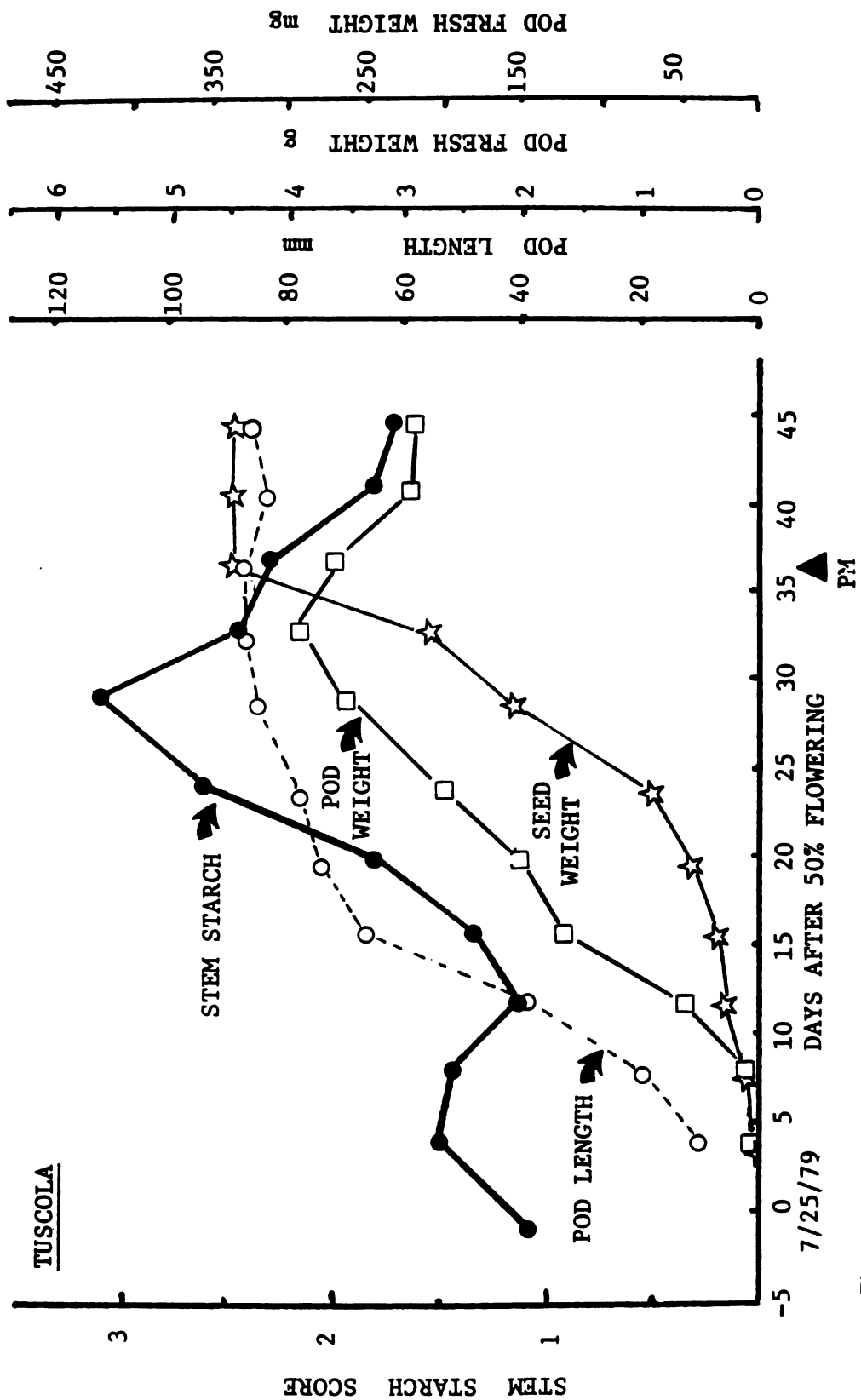


Figure 1.

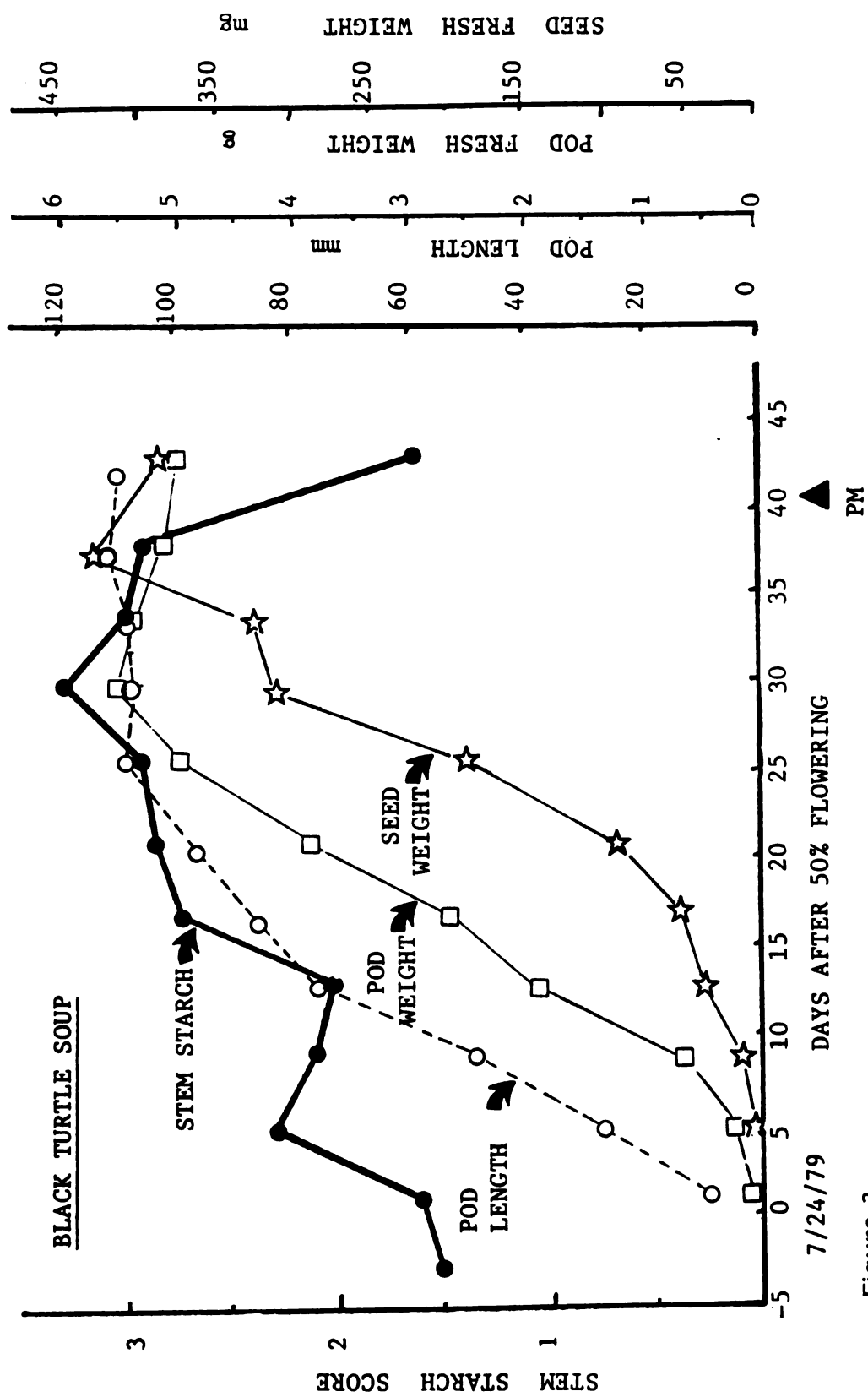


Figure 2.

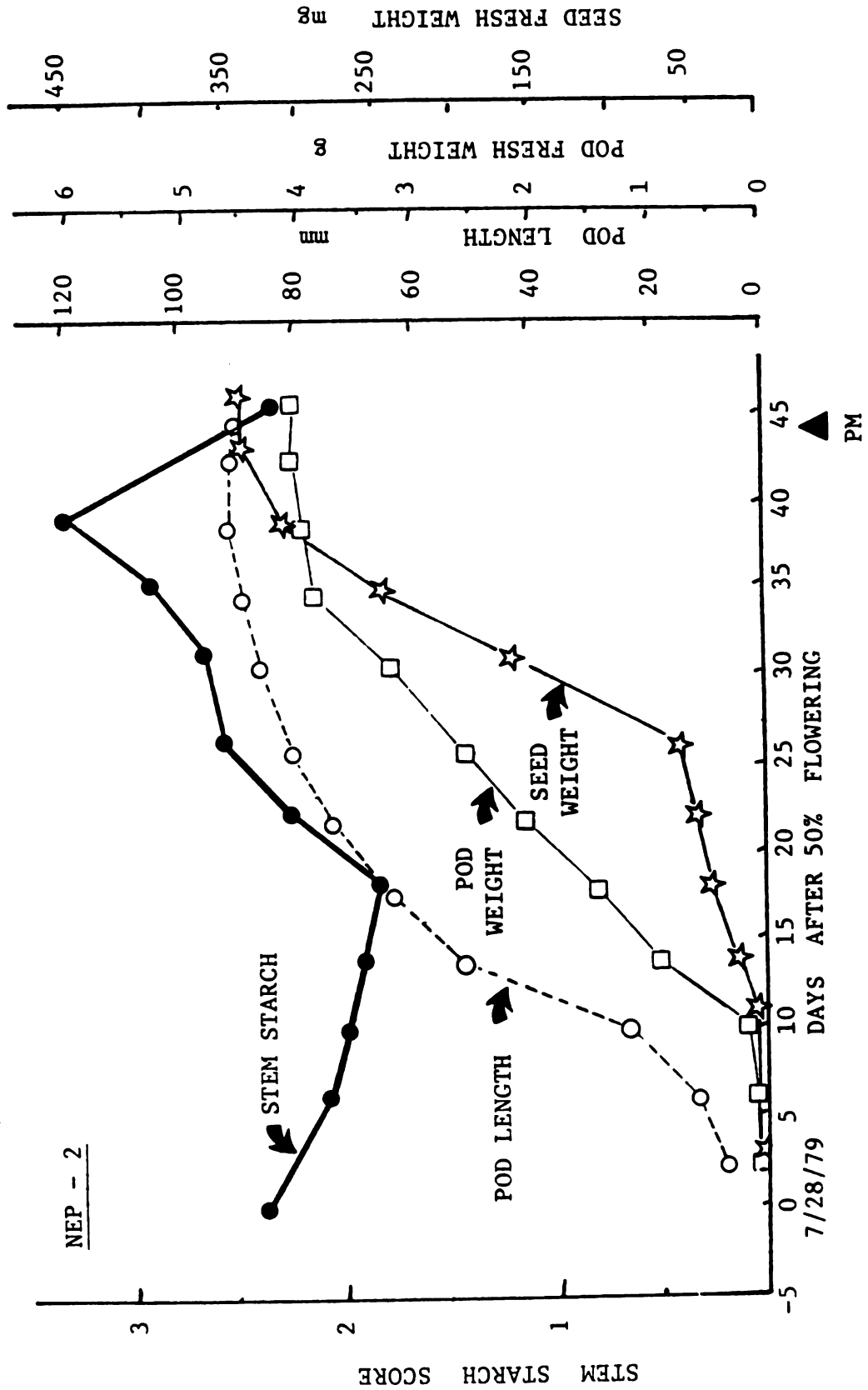


Figure 3.

APPENDIX C

Relationships of pod development and abscission with stem IKI-starch score and ethylene production rate during the reproductive period of the cultivars Tuscola (Figure 1), Black Turtle Soup (Figure 2), and Nep-2 (Figure 3) grown in 1979

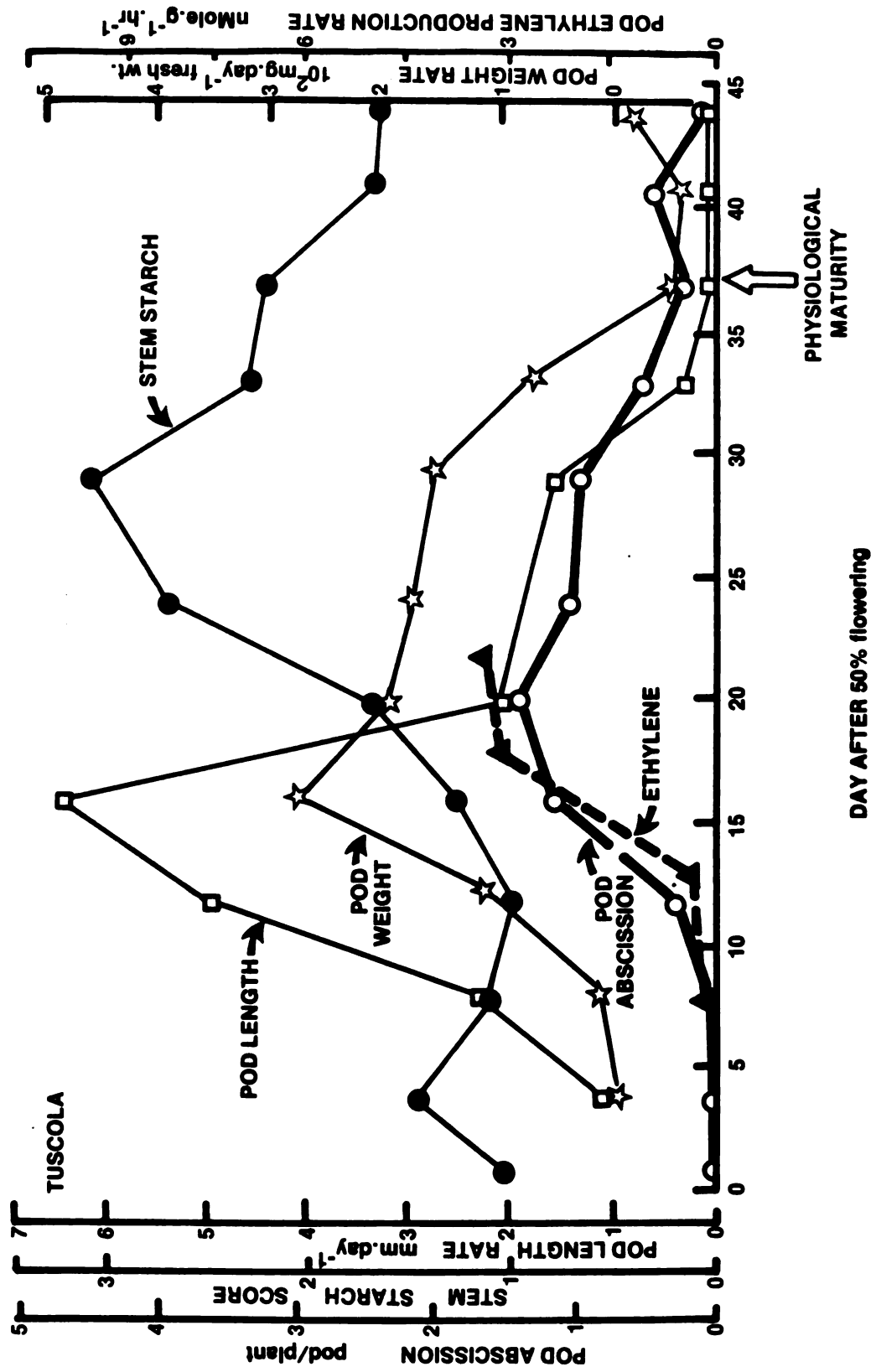


Figure 1.

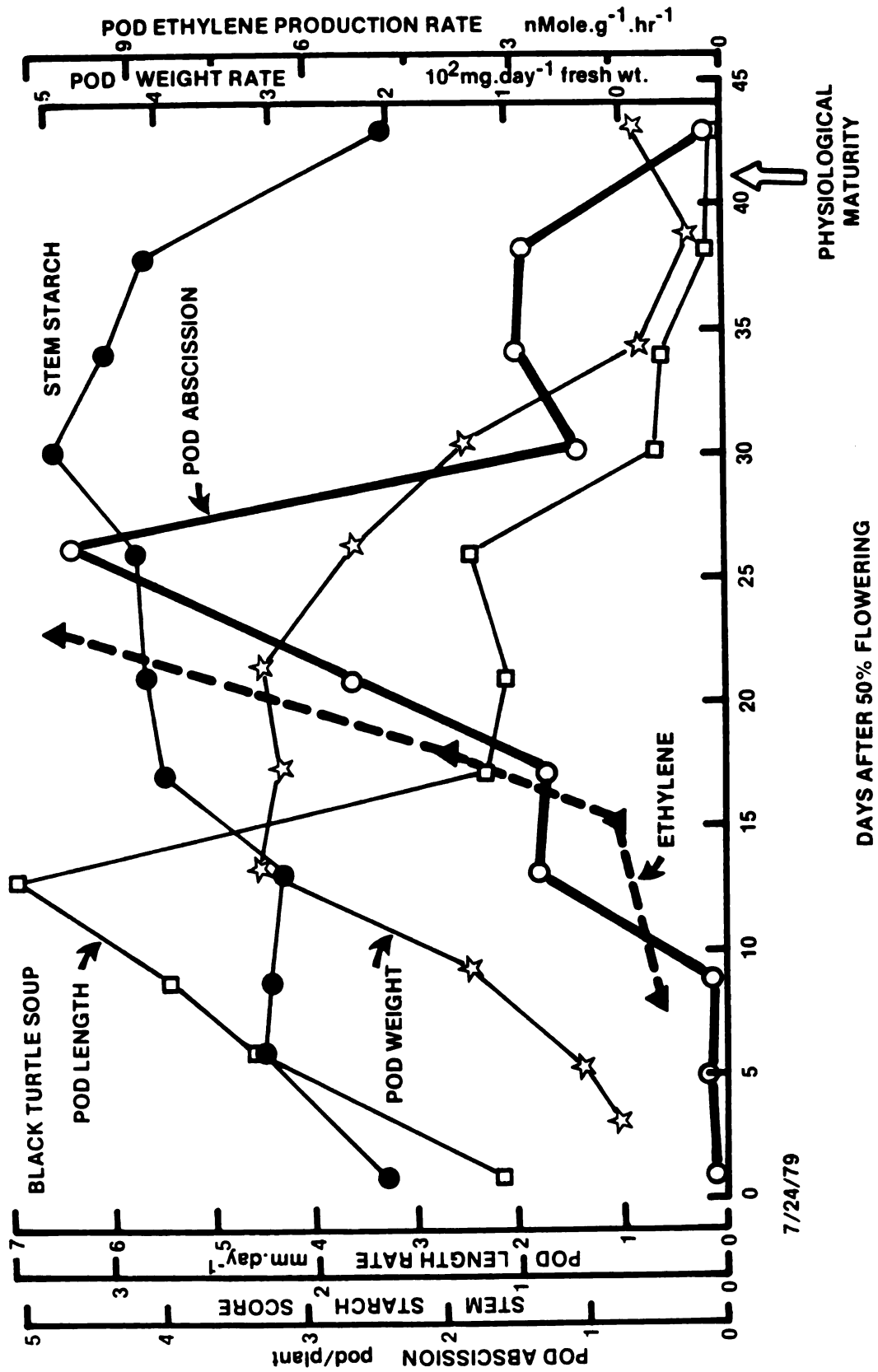


Figure 2.

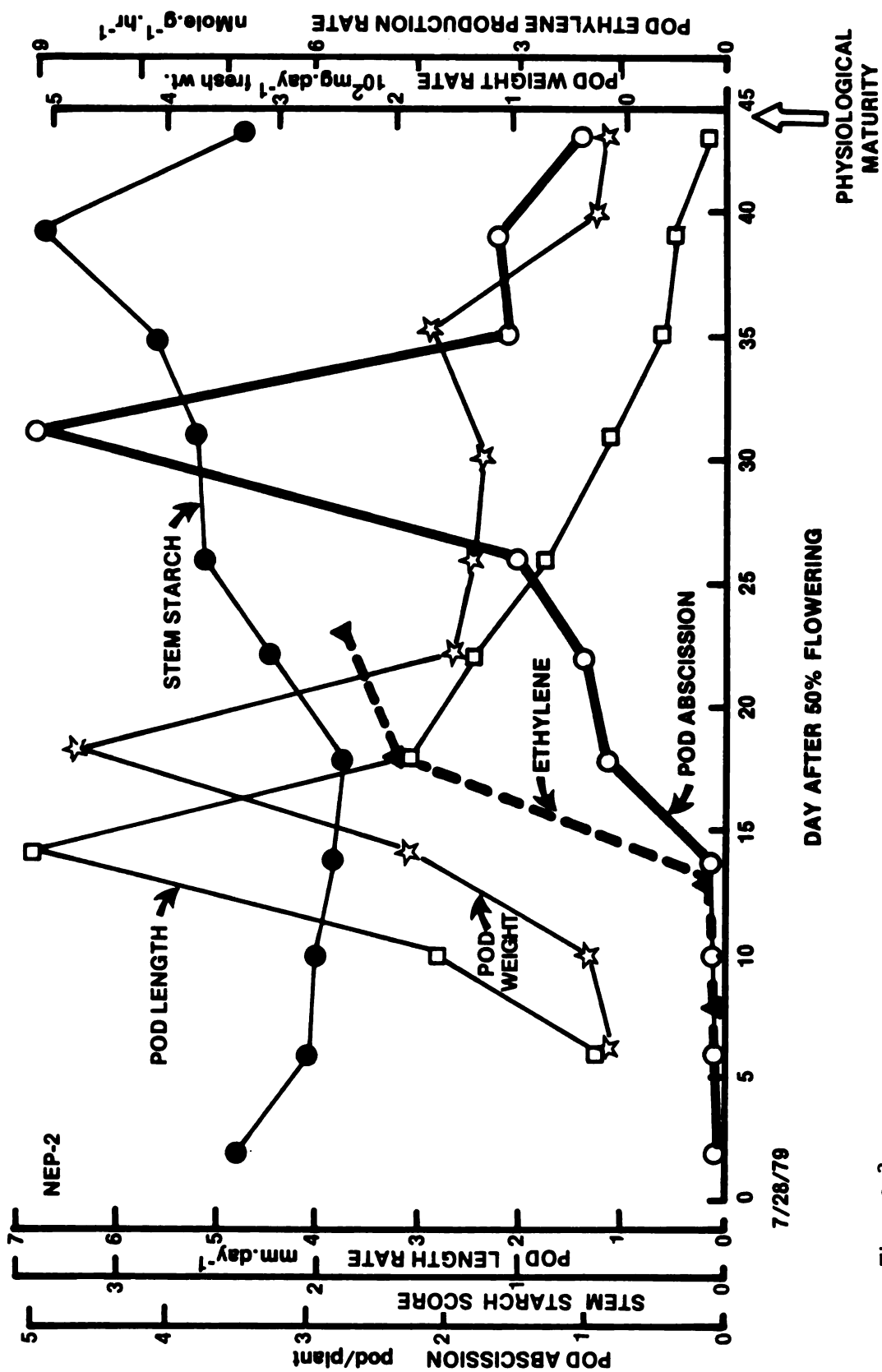


Figure 3.

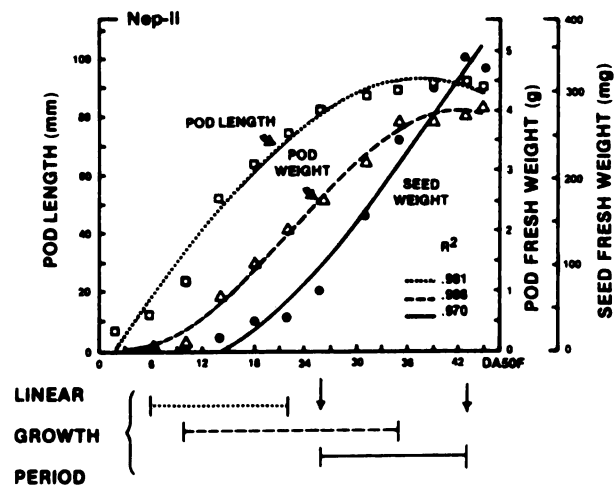
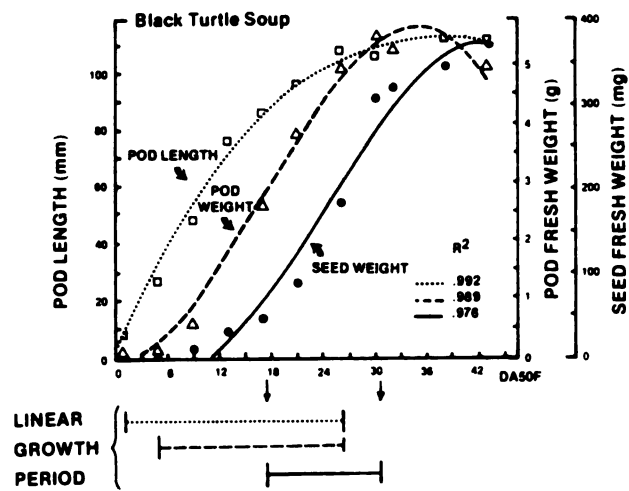
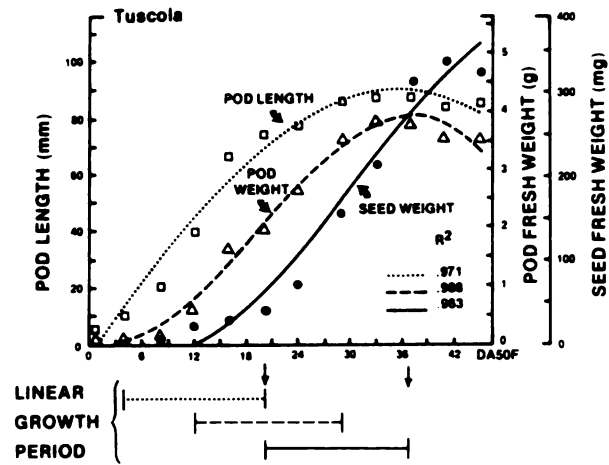
APPENDIX D

Table 1. Regression and determination coefficients for the cubic polynomial regression equation of the mean pod length, mean pod fresh weight and the mean seed fresh weight on days after 50 percent flowering of three dry bean cultivars grown in the field in 1979, N = 12[†]

Parameter	Cultivar	β_0	β_1	β_2	β_3	100R ²
Pod Length (mm)						
	Tuscola	-2.86	4.31	-0.021	-0.0007	96.3
	BTS	0.47	7.15	-0.143	0.0008	99.2
	Nep-2	-7.82	4.17	-0.009	-0.0008	98.1
Pod Fresh Weight (g)						
	Tuscola	0.009	-0.033	0.011	-0.0001	98.8
	BTS	0.03	-0.0007	0.013	-0.0002	98.9
	Nep-2	-0.007	-0.042	0.008	-0.0001	99.6
Seed Fresh Weight (mg)						
	Tuscola	23.96	-10.08	0.75	-0.008	96.3
	BTS	15.70	-12.12	1.16	-0.016	97.6
	Nep-2	33.45	-10.42	0.64	-0.005	97.0

[†] Each observation is the mean value of four field replicated samples of 15 pod each.

Figure 1. Data points of pod length, pod fresh weight and seed fresh weight fitted by cubic polynomial models, determination coefficients and linear growth period for the dry bean cultivars Tuscola, Black Turtle Soup and Nep-2 grown in 1979



APPENDIX D

Tables 2, 3, and 4. Linear growth rate and period for pod elongation (Table 2), pod fresh weight increase (Table 3), and seed fresh weight increase (Table 4) of the cultivars Tuscola, Black Turtle Soup and Nep-2 grown in 1979

Table 2. **LINEAR GROWTH PERIOD**

POD ELONGATION 				
	RATE (b) mm/day	R^2 	PERIOD days	S - E DA50%F ¹
Tuscola	4.39	.972	16	4-20
B.T.S.	4.11	.980	24	3-27
Nep-II	4.16	.967	16	6-22

¹ days after 50% flowering

Table 3. **LINEAR GROWTH PERIOD**

	<u>RATE (b)</u> g/day	<u>R²</u>	<u>PERIOD</u> days	<u>S - E</u> DA 50%F ¹
Tuscola	.163	.981	17	12-39
B.T.S.	.228	.991	25	5-30
Nep-II	.144	.996	25	10-35

1 days after 50% flowering

Table 4. **LINEAR GROWTH PERIOD**

SEED WEIGHT INCREASE

	<u>RATE (b)</u> mg/day	<u>R²</u>	<u>PERIOD</u> days	<u>S - E</u> DA50%F
Tuscola	16.76	.952	17	20-37
B.T.S.	19.58	.971	15	17-32
Nep-II	17.42	.975	17	26-42

1 days after 50% flowering

APPENDIX E

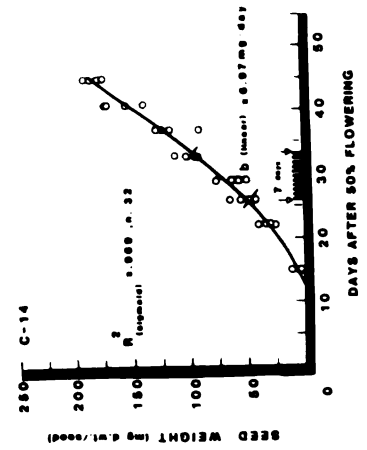
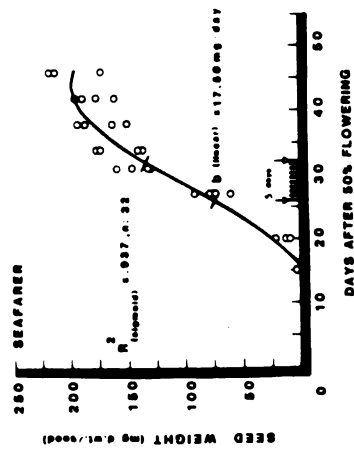
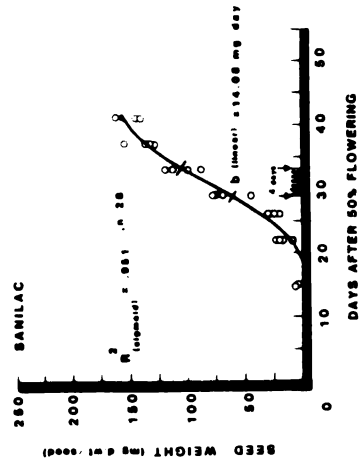
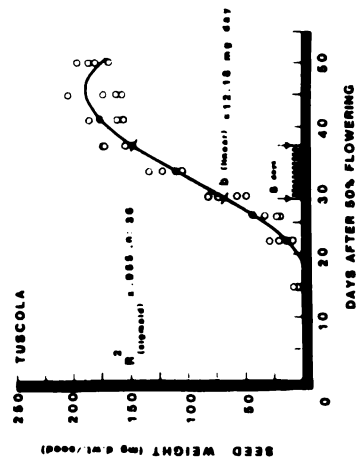
Table 1. Regression and determination coefficients for the cubic polynomial regression equation of the pod length, pod dry weight and the seed dry weight on days after 50 percent flowering of nine dry bean entries grown in the field in 1980

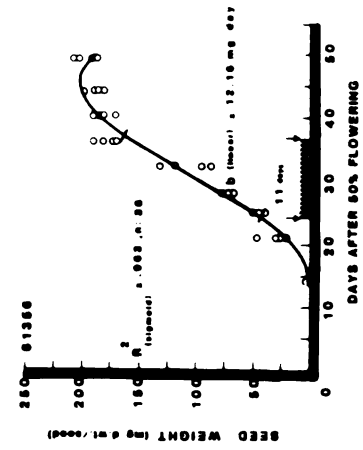
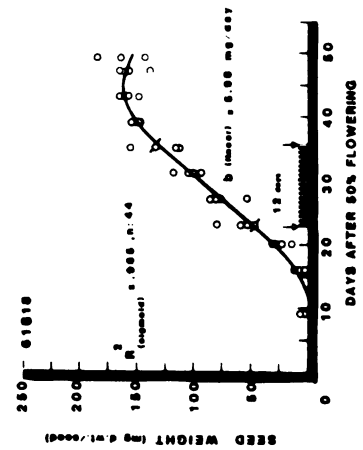
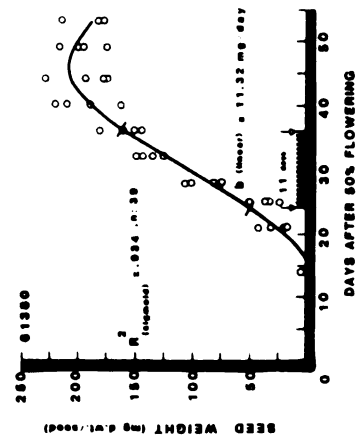
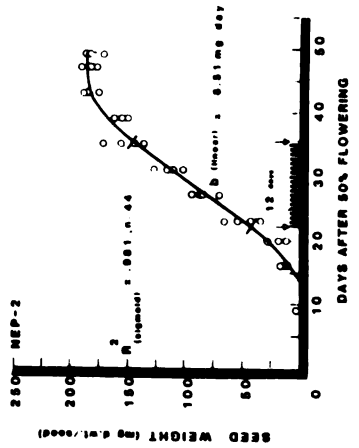
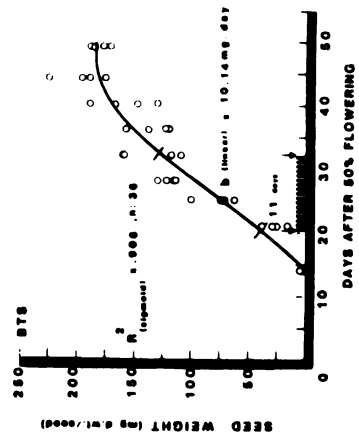
Parameter	Entry	β_0	β_1	β_2	β_3	$100R^2$	n [†]
Pod Length (mm)							
	61380	-56.6256	13.4328	-0.3785	0.0033	92.8	43
	61356	-78.4289	16.1597	-0.5000	0.0047	92.4	40
	61618	-4.5022	9.9307	-0.3108	0.0030	90.7	48
	Nep-2	9.0163	7.2699	-0.2266	0.0022	90.9	48
	BTS	-38.8030	11.7906	-0.3281	0.0029	91.7	40
	Seafarer	-20.9085	8.2072	-0.2147	0.0017	92.6	36
	Sanilac	-55.7686	14.6021	-0.4846	0.0052	89.2	32
	Tuscola	-44.3415	10.3313	-0.2733	0.0023	91.7	40
	C-14	-7.7986	10.3277	-0.3414	0.0036	78.3	36
Pod Dry Weight (g)							
	61380	0.2835	-0.0598	0.0041	-0.00005	93.8	44
	61356	-0.0134	-0.0122	0.0020	-0.00002	94.6	40
	61618	0.0373	-0.0105	0.0019	-0.00003	95.6	48
	Nep-2	0.1355	-0.0327	0.0029	0.00004	96.7	48
	BTS	0.2471	-0.525	0.0029	-0.00005	95.4	40
	Seafarer	0.4646	-0.0842	0.0047	-0.00006	91.4	36
	Sanilac	0.3036	-0.0492	0.0028	-0.00003	95.3	32
	Tuscola	0.1586	-0.0317	0.0021	-0.00002	96.4	40
	C-14	-0.5061	0.0785	-0.0024	0.00003	96.4	36
Seed Dry Weight (mg)							
	61380	123.3101	-21.2165	1.0333	-0.0115	93.9	39
	61356	216.8186	-31.3166	1.3589	-0.0148	96.3	36
	61618	51.0540	-11.0148	0.6564	-0.0079	96.5	44
	Nep-2	70.4618	-14.0718	0.7835	-0.0092	98.1	44
	BTS	-43.8972	-1.1168	0.3598	-0.0049	90.8	36
	Seafarer	104.1177	-20.4141	1.0839	-0.0129	93.7	32
	Sanilac	392.7247	-51.5442	2.0414	-0.0129	93.7	32
	Tuscola	276.5534	-37.5328	1.5147	-0.0160	94.2	36
	C-14	-8.4975	-1.1126	0.1393	-0.0004	92.9	32

[†]Data points observed after seven DA 50 percent F.

APPENDIX E

Figure 1. Seed dry weight data points fitted by a cubic polynomial regression model, determination coefficient, linear growth rate and linear growth period of nine dry bean entries grown in 1980





APPENDIX F

Table 1. Coefficients of regression, determination and partial correlation of the multiple linear regression analysis of seed weight (mg/seed) (y) on days after 50 percent flowering (DA 50 percent F) (x_1)[†] and pod dry weight (g/pod) (x_2) according with the model $y = b_0 + b_1x_1 + b_2x_2$ for nine dry bean entries grown in 1980

	β_0	β_1	β_2	$100R^2$	r_{y,x_1}	r_{y,x_2}	r_{x_1,x_2}	n
Seafarer	-67.4588	3.7593	98.7995	94.0	0.950	0.949	0.920	32
Sanilac	-72.1684	2.8294	107.1265	94.1	0.951	0.960	0.943	28
Tuscola	-51.2807	2.1647	126.9824	92.1	0.942	0.955	0.959	36
61380	-41.3459	1.5600	113.5301	92.3	0.920	0.956	0.926	39
61356	-87.3991	5.3883	31.0918	91.3	0.954	0.930	0.959	36
61618	-35.4839	1.6912	100.5867	95.1	0.958	0.970	0.950	44
Nep-2	-43.4979	2.4475	96.9238	96.1	0.968	0.973	0.960	44
BTS	-14.4614	0.0012	140.0683	95.8	0.931	0.979	0.951	36
C-14	-66.8362	2.6103	103.0040	97.6	0.972	0.980	0.956	32

[†]Data observed after seven DA 50 percent F.

APPENDIX F

Table 2. Correlation coefficient between dry matter (g/plant part) and starch (mg/plant part) for root, stem, petiole, leaf blade, pod wall and seed during the reproductive development of nine dry bean entries grown in 1980, N = 72

Plant part	r
Root	0.66
Stem	0.89
Petiole	0.86
Leaf Blade	0.81
Pod Wall[†]	0.79
Seed[†]	0.95

[†]N = 36

APPENDIX F

Table 3. Correlation coefficients among the nitrogen content (mg/g d.wt.) of different plant parts of nine dry bean entries during the reproductive development and grown in 1980, N = 72

	Stem	Petiole	Leaf Blade
Root	0.73	0.60	0.61
Stem		0.82	0.83
Petiole			0.73

APPENDIX G

Table 1. Multiple linear regressions (K's) and determination coefficients for the regression of percent of nitrogen (Kjeldahl) on the reflectance at four wavelengths determined for different dry tissues of bean plants by a near infrared analyzer (Neotec Model 41) set with pulse points of $P_1=272$, $P_2=579$, $P_3=622$, and $P_4=899$

Tissue	K's					$100R^2$	n
	β_0	β_1	β_2	β_3	β_4		
Seed	4.3541	133.0548	75.6465	280.5939	36.3203	97.3	21
Pod Wall	1.0357	-111.3777	224.8033	324.1995	-137.4021	95.7	21
Leaf Blade	0.1525	61.2496	115.5667	278.6883	-146.4693	94.8	35
Petiole	1.4470	-1.2085	247.4109	38.0827	127.5805	87.3	26
Stem	1.6900	133.1479	223.6057	37.9619	93.2862	91.2	33
Root	0.8680	111.5652	301.5051	15.3221	69.0013	87.8	32

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