

CONTROL OF ABSCISSION OF FLOWERS
AND FRUITS OF PHASEOLUS VULGARIS L.

Dissertation for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
SURANANT SUBHADRABANDHU
1976



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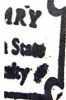
Ph.D. degree in Department of Crop
and Soil Sciences

M. W. Adams

Major professor

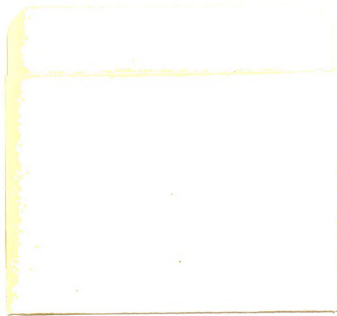
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ABSTRACT

CONTROL OF ABSCISSION OF FLOWERS AND FRUITS OF PHASEOLUS VULGARIS L.

By

Suranant Subhadrabandhu

Abscission of flowers and fruits was studied in two dry bean (Phaseolus vulgaris L.) cultivars, "Black Turtle Soup," an indeterminate, semi-vine type, and "Seafarer," a determinate bush type. Under normal greenhouse and field conditions, these two cultivars exhibited differences in percent pod abscission and flowering pattern. "Black Turtle Soup" had a longer flowering period, produced fewer flowers and exhibited less flower and pods abscission than "Seafarer." In spite of the above differences, seed yields from the two cultivars were not significantly different.

Environmental conditions favorable for photosynthesis, such as long days and carbon dioxide enrichment applied during the reproductive phase in the greenhouse increased vegetative growth and leaf area, and decreased pod abscission. "Black Turtle Soup" was more responsive than "Seafarer."

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Long days and carbon dioxide enrichment promoted vegetative growth and seed yield, increased free sugar and starch in the vegetative parts, and reduced pod abscission.

"Black Turtle Soup" contained more sugar and starch in vegetative tissues than did "Seafarer," particularly in stem and leaf. The levels of free sugar and starch in seeds were similar in the two cultivars.

Bean populations having a low or high abscission potential were established by either increasing or decreasing competition between flowers. Abscission probabilities based on a predetermined relationship between pod size and abscission were assigned to subgroups within each population. Levels of endogenous abscisic acid, phaseic acid and dihydrophaseic acid were determined in methanol extracts of both pod and pedicel, using gas liquid chromatography. None of the treatments affected abscisic acid, phaseic acid or dihydrophaseic acid level in pedicels. Abscisic acid and dihydrophaseic acid levels in pods were higher in "Seafarer" than in "Black Turtle Soup." Populations with high abscission potential from both cultivars also contain higher abscisic acid levels in the pod. The data obtained here cannot explain the role of abscisic acid and its related compounds in flower and pod abscission of dry bean.

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By

Suranant Subhadrabandhu

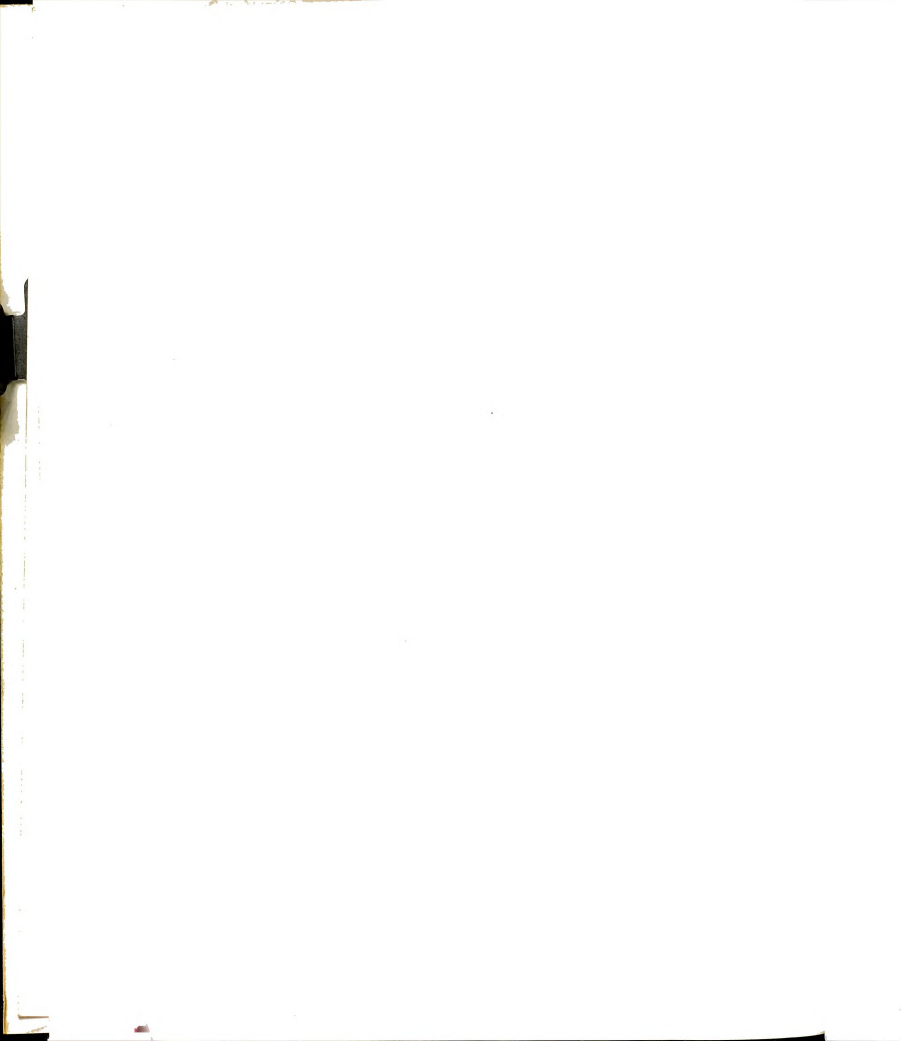
A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

1976



DEDICATION

To my parents,
wife and sons.

I wish
gratitude to
and Dr. F. G.
valuable advice
course of this
criticism of

I am
experience of
Dr. D. Penne

A great
Hanover who
thank Dr. D.
served on the
study. Thank
field assistant
and encouragement
kindly assistance

I wish
encouragement
study. Since
her sacrifice

ACKNOWLEDGMENTS

I wish foremost to express my sincere thanks and gratitude to my advisers, Dr. M. W. Adams, Dr. D. Penner, and Dr. F. G. Dennis Jr., for their encouragement, valuable advice, guidance and interest throughout the course of this investigation and for their constructive criticism of this manuscript during its preparation.

I am most honored and grateful to have had the experience of working in both Dr. F. G. Dennis' and Dr. D. Penner's laboratories.

A grateful acknowledgment is extended to Dr. J. W. Hanover who served on the guidance committee. I wish to thank Dr. D. A. Reicosky and Dr. E. A. Mielke who also served on the guidance committee in some parts of this study. Thanks are also extended to Mr. J. L. Taylor for field assistance and to Dr. J. V. Wiersma for suggestions and encouragement. Special thanks to my Thai friends who kindly assisted in field planting in 1974.

I would like to thank my father for his kind encouragement and endless support during my graduate study. Sincere thanks to my loving wife, Pannee, for her sacrifices, understanding, and encouragement

especially in
this study and
of this manus
thanks for th
Apinya, for a

Lastl
support grant
out my stay :

especially in time of frustration during the course of this study and also to her valuable help in preparation of this manuscript. To my sons, Dhanant and Dhanat, many thanks for their unsuspecting sacrifices and to my sister, Apinya, for assisting in preparation of this manuscript.

Lastly, I wish to acknowledge the financial support granted me by the Rockefeller Foundation throughout my stay in America.

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INTRODUCTION

Abscission of flowers and immature fruits is characteristic of many economic plants, which produce excessive numbers of flowers, including dry beans (Phaseolus vulgaris L.), and may be an important factor limiting yield. To prevent abscission of flowers and pods the factors controlling their abscission must be understood. Abscission may be regulated by hormones or by the level of nutrients available, chiefly carbohydrates and/or proteins.

The objectives of this study were to test two hypotheses concerning abscission, namely (a) abscission is controlled by carbohydrate level vs. (b) abscission is controlled by abscisic acid level.

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CHAPTER 1

LITERATURE REVIEW

Introduction

Abscission is the process by which an organ, or part of an organ, separates from the main body of the plant. In fruits and leaves an abscission zone can be identified at the base of the organ or its supporting stalk which is characterized by smaller, less lignified cells. An abscission layer usually develops through this zone, which eventually brings about separation of the organs. In nature abscission occurs at defined stages in the life of a deciduous organ or following traumatic or accidental interruptions of its development, and it may be influenced by environmental changes. Also, some chemical message, sent to the abscission zone, is usually assumed to be responsible for the regulation of abscission layer formation. Physiologists have long searched for evidence of involvement of plant hormones in this phenomenon. These messengers are presumed to be synthesized outside of the abscission zone itself (82). The induction of these hormonal changes is believed to

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be controlled either by environmental factors or by internal ones, such as competition between different plant parts (82).

The physiology of fruit abscission parallels that of leaf abscission, suggesting similar regulatory mechanisms (55). Two arguments support such a hypothesis, first based on the presumed homology of the two organs (55), the second on analogies in their behavior. Hormones are produced in both the fruit and in the leaf blade, and injury to a fruit may result in rapid abscission, analogous to that observed on deblading.

Analyses of hormone levels and responses to growth regulators suggest that a simple, direct mechanism for the control of fruit abscission is unlikely (85). This should not be surprising in view of the complexity of the fruit. Unlike leaves, fruits enclose megasporangia which have a complex development of their own. Also, they are heterotrophic and therefore more prone to correlative control.

Despite the proposed analogy between leaf and fruit abscission (55) several differences are noteworthy. For example, immaturity and active growth are associated with persistence in leaves, but with abscission in fruit. In some instances (e.g., avocado, tomato), abscission occurs only in young fruit; the mature fruit does not develop a complete abscission layer.

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Since many reviews have dealt with leaf abscission (5, 6, 18, 55, 56, 90), this review will be limited to abscission of reproductive structures.

Genetics Control of Reproductive
Structure Abscission

Evidence for genes control of abscission can be grouped into two parts flowering time and rate of abscission (23, 107). The blossoms of early flowering lines are often damaged by adverse environmental conditions such as early spring frost, and abscise prematurely. The same thing happens in the very late flowering varieties. This is evident in some fruit trees, and certain introduced varieties of field crops.

Evidence for the existence of genes controlling time of flowering was obtained for Phaseolus vulgaris L. (23). In a cross between early and late flowering cultivars, complete dominance for early flowering was observed in F_1 , and a good fit to 3:1 and 1:1 ratios of early to late flowering plants was observed in F_2 and in $P_2 \times F_1$ generations respectively. Similar results were reported in snap beans, and the dominant gene controlled the early flowering character (28). However, this is not always the case. In the cross of White Seeded Tendergreen (early flowering) x Bush Blue Lake OSC 949-1864 (late flowering), the late flowering character was dominant (24). In the cross of G.N. 1140 (early flowering) x

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Nebraska #1 selection (late flowering), the time of flowering is controlled by two major genes, with earliness being dominant to lateness. This indicates involvement of more than one locus for the gene expressing time of flowering. In Goiano and Mexico 450, bean cultivars of tropical origin which are daylength insensitive, Ortega (79) found continuous variation of flowering time in F_2 , backcross 1 and backcross 2, suggesting that flowering time was quantitatively inherited. He concluded that most of the genes involved in the control of flowering time exhibited additive effects and lack of dominance. Thus genes controlling time of flowering appear to differ among varieties. Daylength plays a major role in controlling earliness and in adaptation of cultivars to new habitats (36). Therefore, environment, and especially daylength, may interact with genes in the control of time of flowering.

Genes may control the rate of abscission of reproductive structures, as well as time of flowering. Early work of Heinicke (50) showed marked differences in the percentage of immature fruit abscission in three apple varieties. Since the trees were growing in the same orchard, the rate of fruit drop must have been determined genetically. Cowpea varieties differ in percentage of aborted ovules (75). Soybean (107) and garden bean (13) varieties exhibit different rates of

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blossom and pod drop. In the latter species negative correlations between total number of blossoms per plant vs. yield per plant, and percentage blossom and pod drop vs. yield per plant were reported (13).

Types of Abscission

Under natural conditions, the abscission of reproductive structures ensues when one or more of the following events occurs.

- (1) Lack of pollination due to unfavorable environmental conditions or absence of insects, which is followed by abscission of the flower;
- (2) Failure of the pollen tube to reach the ovule usually results in the flower abscission. This may be due to genetically controlled incompatibility between the pollen tube and the style.
- (3) In some species, fertilization occurs and the ovule is formed; however, during fruit development the ovule ceases growth and abscission of the young fruit follows. In soybeans, pod abscission was found to occur during the early stages of embryo development, 3 to 7 days after anthesis (59). Competition for carbohydrates, mineral nutrients, and growth regulators may be responsible for this type of abscission.

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- (4) Fruit maturation. Abscission of fruit at maturity is common in some fruits, however, this type of abscission does not commonly occur in field crops.

Factors Controlling Reproductive
Structures Abscission

Environmental Factors

The abscission of reproductive structures is very responsive to environmental factors, including light, temperature, CO₂, relative humidity, and moisture stress.

Light intensity. Both photosynthetic effects and photoperiodic effects of light influence abscission. The carbohydrates resulting from photosynthesis are utilized directly for deposition of cell walls. When environmental factors favor photosynthesis but restrict overall growth, cell walls are thicker and abscission is less likely to occur (9). The opposite is true when photosynthesis is limited. Cell walls are thinner and abscission rates are higher. Cotton boll drop is increased from 46 to 86% by shading (30). Pea yields are reduced 50% under 50% shade (71). Shading of soybean plants increases the abscission of pods (69). In deciduous fruit trees abscission of young fruit is greater on twigs deficient in carbohydrate or with few leaves (19).

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Photoperiod. Ojehohon et al. (77) reported that long days induce abscission of flower buds on the main axis of three South American cultivars of Phaseolus vulgaris L., and in subsequent experiments with one of these cultivars they showed that the buds began to fail to develop in long days at about the stage when meiosis occurred. This happened regardless of whether light intensity were high or low (78). Long photoperiods also increase the percentage of flower and pod abscission in soybeans (60, 106). Information on the physiology of the response is only fragmentary (52).

Various reports indicate that long days favor high levels of auxins, gibberellins and abscisic acid (9, 127, 128). Hormonal changes in leaves associated with decreasing day length could be one factor in the initiation of leaf abscission in the fall (9). With regard to vernal leaf abscission, increasing daylength leads to an upsurge of hormone synthesis, especially in buds (9). Consequently, buds and developing shoots became strong sinks, and the auxin moving downward from the buds altered the auxin gradient across the abscission zones of the old leaves. This would serve to promote vernal leaf abscission.

Temperature. Under natural growing conditions, high temperature increases flower and pod abscission in soybean (106), temperatures above 40°C being especially

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effective (69). Cessation of pod growth at 40°C possibly is due to lowered rates of photosynthesis, since net photosynthesis of soybeans is very low at this temperature (40). In lima bean, the daily rate of blossom abscission was positively correlated with the maximum temperature and possibly the attendant low humidity (22). In young cotton fruits, abscission increased during the period of warm nights (30°C) (43). Abscission of flower buds, flowers and young fruits is frequently correlated with periods of hot weather (118). Various metabolic processes are adversely affected by excessive heat (104). Such adverse metabolic effects probably mediate the high temperature induction of flower and young fruit abscission.

Carbon dioxide. Marked increases in plant production have been obtained by carbon dioxide enrichment of greenhouse atmosphere (119). Soybean yields have been increased when plants were grown in a carbon dioxide enriched atmosphere (20). Increasing carbon dioxide concentration during the reproductive stages may increase storage capacity and yield. The number of ear-bearing tillers in barley was increased by such treatment (41), whereas in rice both grain number and grain size were increased (126). Carbon dioxide enrichment only during grain filling can also increase yield (41, 126). Carbon dioxide enrichment at flowering increased the number of

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Pods in soybeans under field conditions, but seed size was reduced, whereas enrichment during pod filling increased both seed size and yield (45). Increasing the concentration of carbon dioxide in the atmosphere from 350 to 1,000 ppm decreased abscission of young cotton fruits by nearly 50% (43). Carbon dioxide enrichment also increased the yield of sugar beet and kale (39), as well as many greenhouse crops (119). These results indicate that plants grown under carbon dioxide enrichment are better able to retain fruits.

Although there are few reports on its effects on abscission in intact plants, carbon dioxide retards abscission in explants; it reduces the rate of abscission appreciably (4), and counteracts the promotive action of ethylene (3).

Relative humidity. Low relative humidity, together with high temperature, promotes abscission in lima bean flowers and fruits (22, 63). High humidity alone increases pod set and retention, but is detrimental when combined with low temperature (38). In peanuts, high relative humidity favors the development and retention of fruits (64).

Soil moisture stress. Moisture stress during the flowering and pod filling period increases abscission of flowers and fruits in garden beans (13), and cotton (37).

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Soil moisture stress alters hormone levels in plants. Among the changes reported are: decreases in diffusible auxin (49) and cytokinin activity (54); increases in ethylene release (68) and abscisic acid levels (122, 127, 128). All these changes would favor abscission.

Factors such as nutrient deficiency (69), excess rainfall (14) and severe defoliation (67) also favor abscission of reproductive structures.

Internal Factors

In lima beans, position on the raceme influences flower abscission (22). Fruit setting occurred acropetally until a "capacity set" was attained; the remaining flowers then abscised. Therefore, pods occurred largely on the basal portion of the raceme, the terminal part being characteristically barren. Ojehomon (76) examined the factors controlling pod retention in Vigna unguiculata, in which only the pods of the basal racemes, the first to flower, were normally retained. Autoradiographs showed that the upper flowers did receive some labelled assimilate from the subtending leaf. Ovaries which failed to develop tended to be smaller at the time of flower opening, to grow more slowly, and eventually to lose weight. However, they would abscise even if comparable in size to those on the basal racemes, unless the latter were removed. Thus, the basal racemes appeared to promote abscission

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in the more distal ones, not simply by sequestering all the assimilates from the subtending leaf, but probably through the action of diffusible hormones.

Although both Luckwill (66) and Wright (120) reported an inverse relationship between levels of auxin-like hormones and fruit abscission, the nature of the hormones analyzed remains uncertain. Their nature was better defined in subsequent studies (73, 85, 87), but Powell and Pratt (85) concluded that extracted auxins probably do not directly control abscission.

Van Steveninck showed that in lupine the first pods formed promoted abscission of the remaining flowers on the cluster (108, 109, 110, 111, 112). Both auxin and anti-auxin could substitute for the effect of the pod, naphthaleneacetic acid (NAA) and 2, 3, 5 triiodobenzoic acid (TIBA) being the most effective. He concluded that the controlling factor may be an "antiauxin" (110). A search for abscission accelerating factors in lupine revealed the presence of an auxin-like material which delayed abscission of pods, but promoted abscission of flowers (112).

Studies of auxin applications to fruit are inconclusive. Synthetic auxins may increase abscission (flower and young fruit) (12), or increase persistence (mature fruit and seedless fruit) (33). Hartmann proposed that if auxin increase persistence, antiauxin

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should promote abscission (46). Application of anti-auxins to mature olives promoted abscission, apparently confirming this suggestion. However, both auxin and "antiauxin" promote abscission in lupine flowers (110). Auxins alone may be insufficient to account for fruit abscission (55). Evidence associating abscission stimulators in fruit has accumulated (111, 112), culminating with the identification of abscisic acid (ABA) in cotton fruit (10, 74).

Carbohydrate Availability

Carbohydrates are the primary source of reserve energy stored in the vegetative organs of plants. They accumulate during periods of high photosynthetic activity when synthesis exceeds utilization. Conversely, these reserve carbohydrates are degraded when utilization exceeds synthesis, and are essential for survival (99). The level of carbohydrate reserves may be influenced by numerous cultural and environmental factors (16, 58, 88, 94, 97).

Under conditions of low leaf area, low light intensity or supra-optimal temperature, the energy balance is likely to be negative, since the demand exceeds supply (16). Under such conditions, the reserve carbohydrates are likely to be utilized. Decreases in reserve carbohydrates are usually observed just after

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defoliation (88). Surplus carbohydrates can be restored when sufficient leaf area has developed to exceed the energy requirement of the crop.

Reserve carbohydrates mentioned in this sense are synonymous with the term "total available carbohydrates" mentioned in many papers (116), and include all carbohydrates which can be used as a source of energy or as building material, either directly or indirectly. Generally, in higher green plants, the bulk of available carbohydrates consists of sugars, fructosans, dextrin and starch (116), whereas hemicellulose and cellulose serve only as structural materials.

Although the term "total available carbohydrates" (TAC) had been widely used, Smith (96) introduced the term "total nonstructural carbohydrate (TNC)" as a replacement for "total available carbohydrate" to avoid confusion with animal physiology, ruminants being able to obtain energy from at least part of the structural carbohydrates.

Carbohydrate Determination

Extraction

Various extraction and analysis techniques have been reported for plant carbohydrates. Almost all the available literature deals with grasses and forage crops (16, 88, 99, 113); however, these methods have been

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adapted for horticultural (11, 121) and forest crops (84, 114).

In certain cases the form of carbohydrate stored by a given species dictates the techniques (99). In others, the choice may depend on the convenience and judgment of the investigator. This has made it difficult to evaluate critically data from different laboratories.

To develop an extraction technique, one must know the form of carbohydrate stored in the plant. Many legumes accumulate sucrose and starch (97), as do tropical and subtropical grasses (95). TNC has been extracted from these species with takadiastase enzyme preparations (116) or with acid (88). On the other hand, grasses native to temperate latitudes accumulate sucrose and fructosan (101, 102). Therefore, TNC from these species has been extracted with dilute acid solution (88), or with water (113), since fructosan is readily soluble in water. Fructosan-storing grasses may also accumulate very small amounts of water-insoluble carbohydrates (95).

The extraction of reducing sugars is less complicated than that of TNC. Reducing sugars consist mainly of glucose and fructose, which can be extracted by using 80% ethanol. Extraction in boiling 80% ethanol for 4 hours was found to be sufficient to remove all the sugar in barley leaves (124). Later, Yemm and Willis (125) extracted soluble sugars at 37°C with absolute alcohol,

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followed by two further extractions with 70% ethanol. Extraction of white clover tissue with hot 80% ethanol for two hours removed all the glucose and fructose from the plant (62). Recent studies also report satisfactory results using 80% ethanol for soluble sugars (11, 121).

Analysis

Four commonly used carbohydrate analysis techniques are: (a) anthrone, (b) phenol-sulfuric, (c) Nelson's arsenomolybdate and (d) Shaeffer-Somogyi Micro copper (53).

Role of Carbohydrates in Abscission

In woody plants, rapid vegetative growth imposes a high demand for carbohydrates and mineral nutrients, and abscission of immature fruits may result from the inability of the fruits to compete successfully with vegetative tissues and with each other for carbohydrate (1, 103). If competition is increased by partial or complete leaf removal, the rate of abscission increases, as evident in cotton (32, 70), and soybean fruits (67). The environment can affect abscission partly by the effect on photosynthetic rate, as discussed previously.

The role of carbohydrate in the abscission process is not clear. Carbohydrate is used as a source of energy in many metabolic processes which may affect abscission. However, there is growing evidence for the

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role of plant hormones in abscission (6, 18), and the role of carbohydrates may be related to that of hormones (6).

Role of Abscissic Acid (ABA)
in Abscission

The recent discovery of ABA (7) aroused the interest of many physiologists conducting abscission studies. Bornman (15) found that Streptocarpus leaves contained five times as much ABA in autumn as in mid-summer. Application of cotton extracts to intact young fruits or to defruited pedicels of cotton strongly promoted abscission (7). Application of ABA to leaves or entire plants in the field usually accelerated leaf abscission (98). However, repeated applications were sometimes required to obtain a response (98).

Davis and Addicott (26) reported a strong correlation between ABA content and abscission in cotton fruits. However, their data are for cumulative abscission, rather than rate of abscission. Critical analysis reveals that ABA content was better correlated with fruit growth rate than with abscission. Further, in immature peach fruit the concentration of an ABA-like inhibitor is greater in persisting than in abscising fruit (129). Finally, application of synthetic ABA to fruit has little or no effect on abscission (47, 48, 130).

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The physiology of the ABA effect is not well understood, and convincing evidence for its role in fruit abscission is still lacking. High levels of ABA were observed in young nonabscising leaves, whereas the levels were lower in old and abscising leaves (81, 105). ABA is most effective on explants (2, 7, 8, 25, 83, 97); intact plants respond only to very high concentrations or to repeated applications (21, 31, 35, 47).

Although abscission of flowers and immature fruits is becoming a problem in many economic crops, its cause is still unknown. This creates difficulty in an effort to solve the problem of abscission. Due to its complex process, abscission can be influenced by many factors, therefore care should be taken in any study on abscission.

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CHAPTER 2

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L.

I. VARIETAL DIFFERENCE IN FLOWERING PATTERN AND ABSCISSION

Abstract

Developmental patterns and abscission of reproductive structures (flowers and pods) were studied in both greenhouse and field experiments with three cultivars of dry beans (Phaseolus vulgaris L.). The pattern of flower production, pod retention, number of flowers produced and percentage of reproductive structures abscised varied with cultivar. The pattern of flower production varied from a concentrated skewed pattern for cultivar Seafarer to a longer more normally distributed pattern for cultivar Black Turtle Soup. In general, the first-formed flowers had the highest probability of setting pods and producing mature seed.

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Introduction

The seed yield is determined primarily by the number of flowers per plant, the percentage fruit set, the number of seeds per fruit, and seed size. If abscission could be prevented or decreased, yield of dry beans might be increased, provided other physiological limits were not encountered.

Dry bean, in common with many other crop plants grown for seed, produce many more flowers than mature fruit. One of the reasons that maximum yield is not obtained in this crop is abscission of flowers and immature pods. Swen (9) reported that from 78 to 87% of the reproductive potential in 5 varieties of soybeans was lost by abscission. In field beans the estimated loss varies from a low of 75 to a high of 97% (3, 4, 7, 8), and a figure of 80% was reported in lupins (2).

In order to increase yields, information is needed on flowering patterns, patterns of abscission, and the basic cause or causes of abscission. In this paper the patterns of flowering, abscission, and fruit growth and development under field and greenhouse conditions are described in three dry bean cultivars with contrasting growth habits. The information obtained hopefully will serve as a base for further studies on the genetic and physiological causes of abscission.

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Materials and Methods

Greenhouse Experiment

Three dry bean cultivars, Seafarer (bush), Black Turtle Soup (semi-vine) and Michelite (vine) were selected for their contrasting growth and flowering habits. Four seeds of each cultivar were planted in 20 35-cm pots in the greenhouse in early April with temperature maintained at $26 \pm 5^{\circ}\text{C}$ at East Lansing. Ten days after emergence the seedlings were thinned to one uniform plant per pot. At flowering time, 15 of each cultivar were selected for uniformity and flowers that opened each day were counted and tagged with color-coded wire, using a different color each day. These flowers were observed until maturity. At maturity the number of filled pods, plant dry weight and the yield components were recorded. Analysis of variance and correlation analysis were carried out where appropriate.

Field Experiment

Ten dry bean cultivars were grown in field plots at East Lansing in the summer of 1974. Each plot was a double row, 15 m long with rows 1.5 m apart. Plants were spaced 50 cm apart in the row. A randomized complete block design was used with 4 replications and 60 plants per replication per cultivar. Flowers from 10 plants

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At maturity, the plants were harvested and analyzed as described above.

Results

Greenhouse Experiment

Seafarer and Michelite produced significantly more flowers than Black Turtle Soup; however, their higher rates of abscission resulted in a nonsignificant difference between cultivars in number of pods retained (Table 1). No cultivar differences occurred in stem weight, pod weight, or total plant weight, but the differences were seen in root weight (Table 1). With the nonsignificant difference in vegetative weight, no significant difference in seed yield among cultivars was obtained (Table 1). Cultivar differences in yield components were found in seeds per pod and weight per seed but not in number of pods or yield (Table 1). In general, the phenomenon of yield component compensation is demonstrated by these data. Michelite had a high number of pods, low seeds per pod and low seed weight but had the same yield as Black Turtle Soup (Table 1). On the other hand, Black Turtle Soup, with a low pod number, high seeds per pod and high average seed weight, also had a yield similar to the others. This suggests

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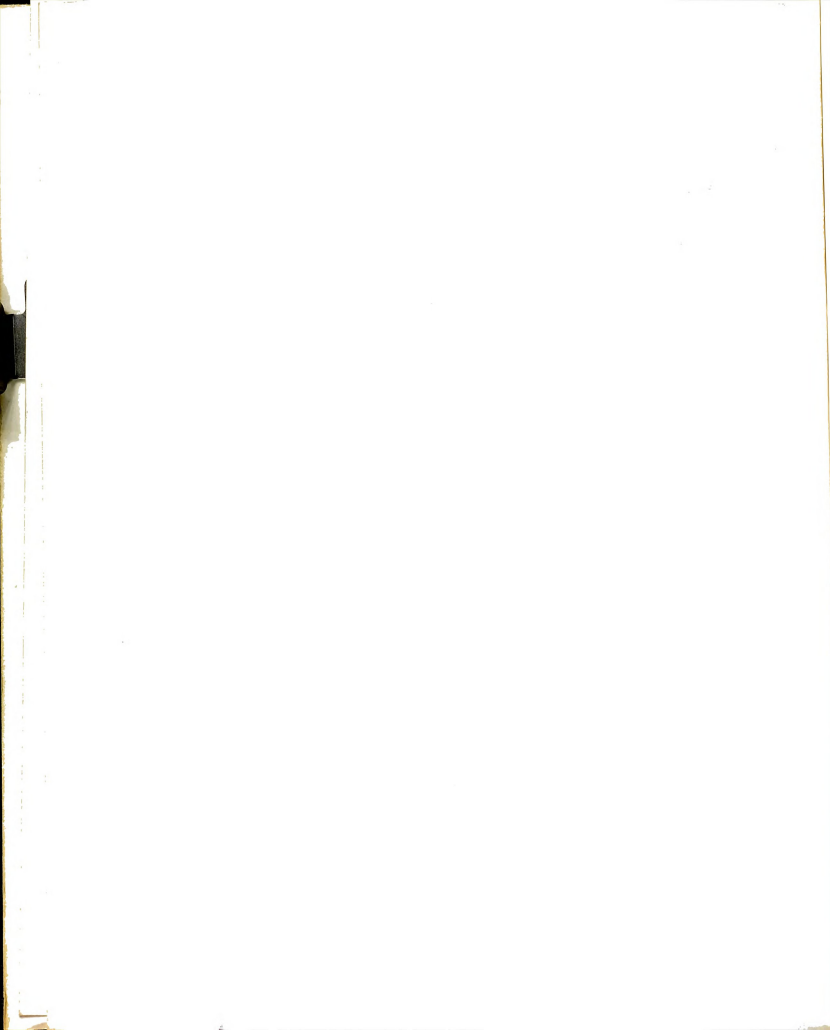
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Table 1

Effects of Cultivar on Yield Components in the Greenhouse^a

Character	Cultivar		
	Seafarer	Michelite	Black Turtle Soup
No. Flowers/plant	40.9 a	44.9 a	19.0 b
No. Pods/plant	15.2 m	19.5 m	13.7 m
% Abscission	62.8 y	56.6 y	27.9 x
<u>Dry wt./plant (g)</u>			
Stems	5.4 a	4.7 a	3.5 a
Roots	5.1 mn	6.6 n	3.0 m
Pods	16.8 x	16.7 x	20.4 x
Total	27.3 p	31.0 p	27.0 p
#seeds/pod	4.1 a	4.2 a	5.5 b
wt./seed (g)	0.21 y	.16 x	.22 y
seed wt./plant (g)	12.7 m	14.1 m	15.7 m

^aMeans within a given character followed by similar letters are not significantly different at the 1% level by Tukey's Test.

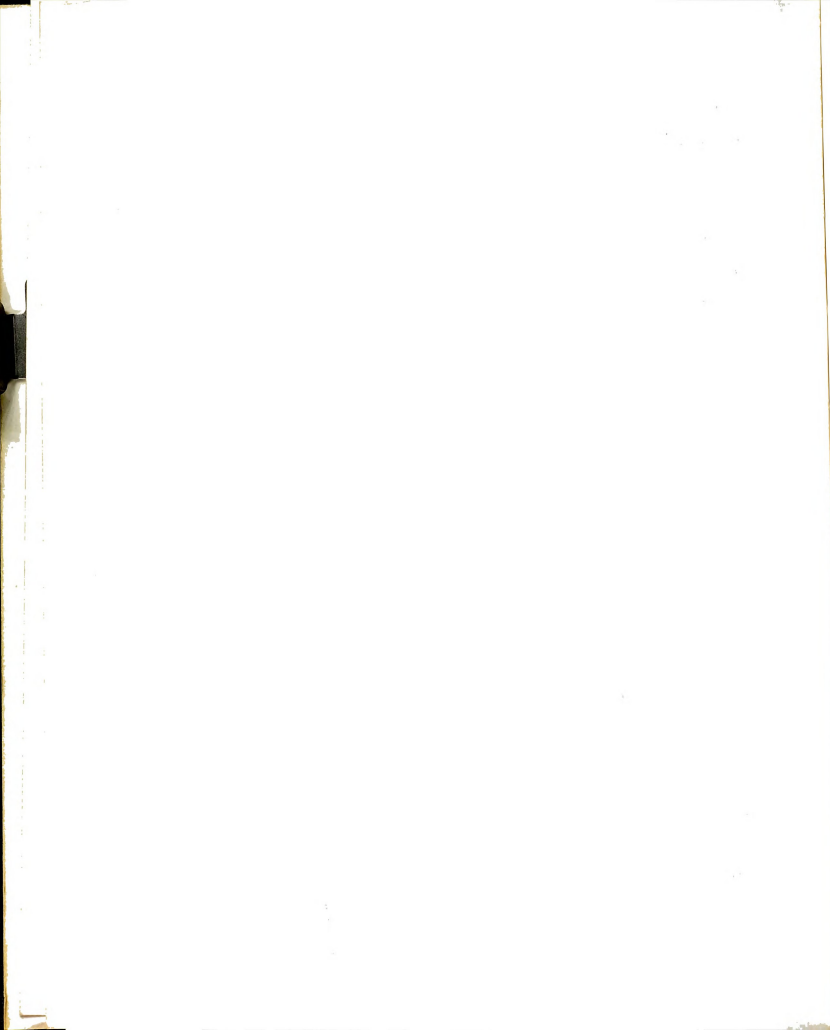


that there is a yield limit set by the plant but that there are several ways to get to that end point via variations in level of yield components.

Seafarer had a short and highly concentrated flowering period (6 days) reaching its peak of flower production in 3 days from beginning of the first flower. Michelite and Black Turtle Soup, on the other hand, had a longer and less concentrated flowering period (15-18 days) with their peak of flower production at 8 days from the opening of the first flower (Fig. 1). To determine which flowers were most likely to set pods and produce seed, the data were expressed as pods produced on a given day that are retained to maturity, as a percentage of the total number of pods harvested (Fig. 2). The peak of pod retention for Seafarer was at 2 and 3 days while its peak of flower production was at 3 days (Figs. 1 and 2). The peak of pod retention for Michelite and Black Turtle Soup was at 4 days while their peaks of flower production were at 8 days.

Field Experiment

The 10 cultivars studied can be classified into 3 groups, according to the number of flowers produced; those which produced the highest number of flowers were Michelite, 0639, and 0686, those with the next highest were Pinto 114, Seafarer, Black Turtle Soup and Jamapa, and those which produced the lowest number of flowers



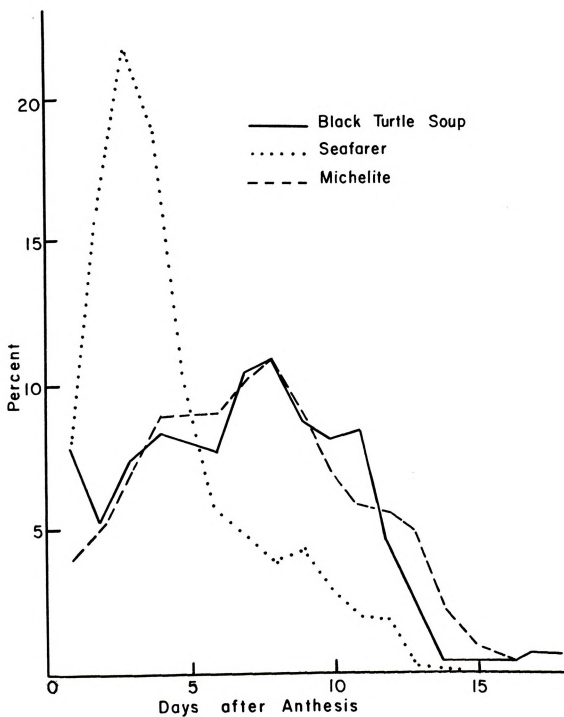
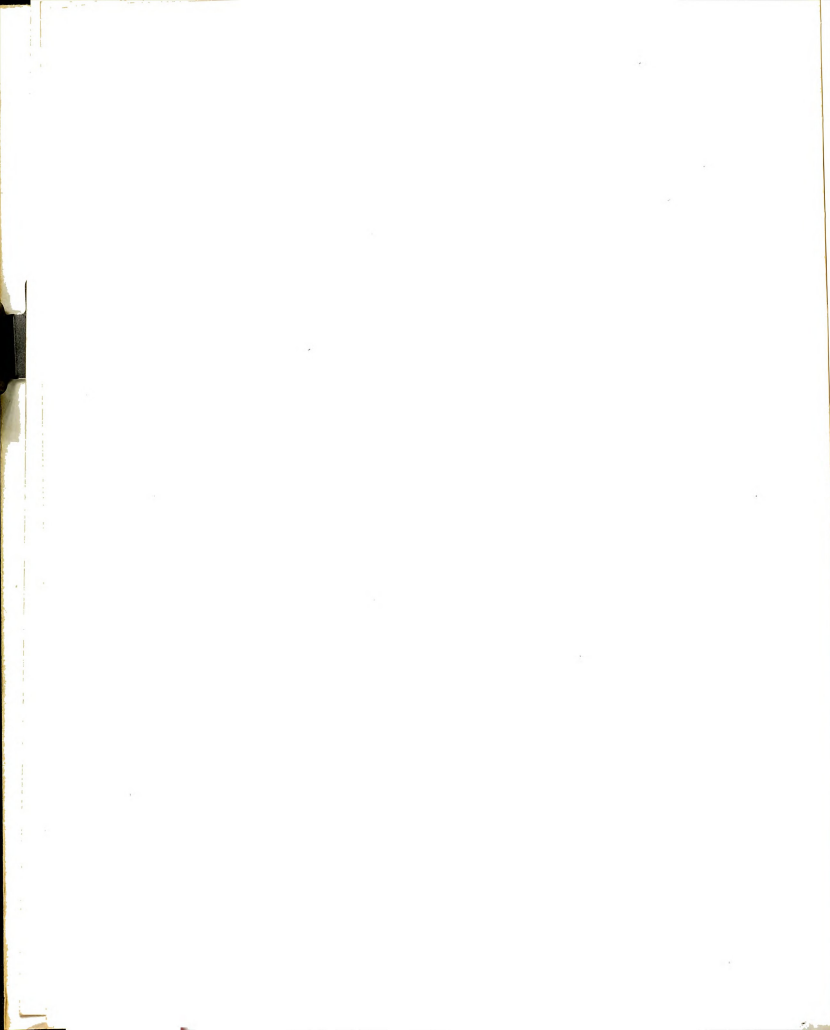


Fig. 1. Flower production in a specific day as a percentage of total flowers produced under greenhouse conditions.



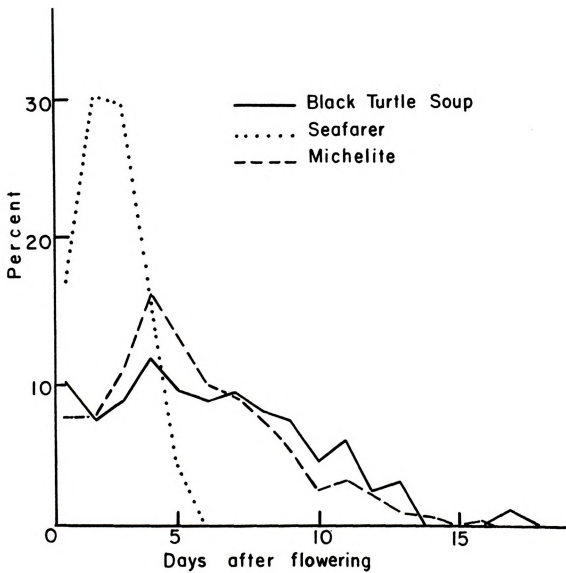
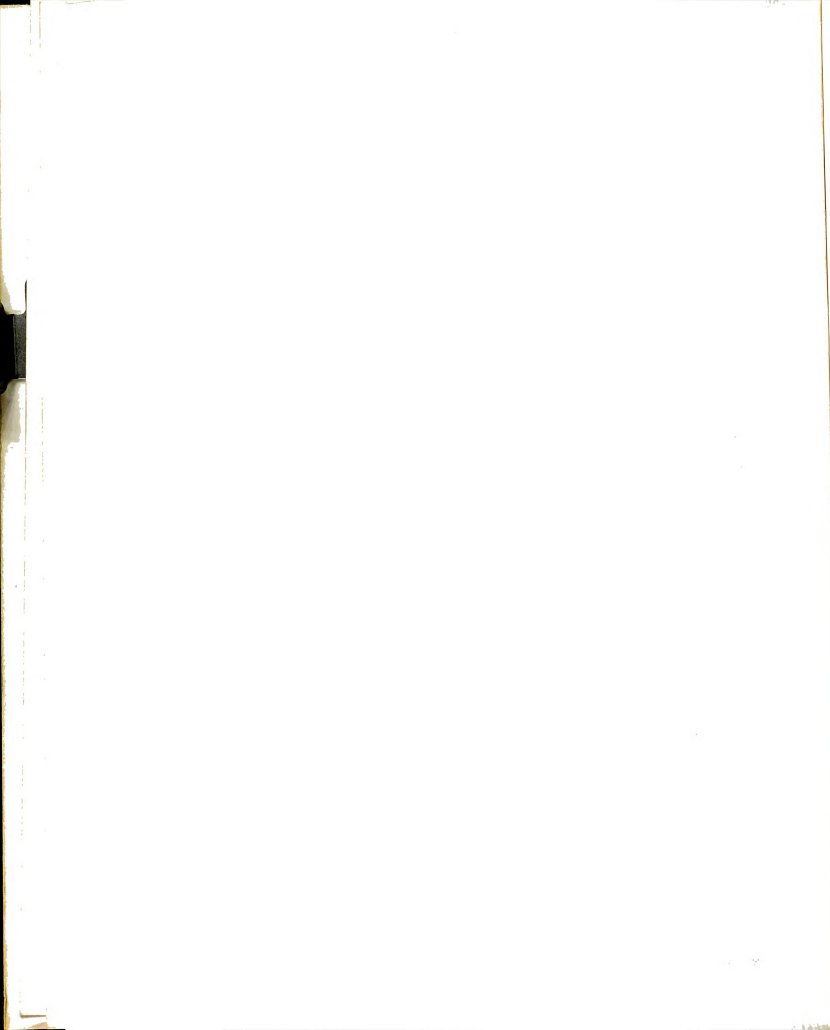


Fig. 2. Pods retained from flowers borne on a specific day, as a percentage of total pods at harvest grown under greenhouse conditions.



were Cran-028, Montcalm and Swedish Brown (Table 2). A similar trend was seen among these cultivars in the number of pods retained to maturity, that is, cultivars which produced more flowers had a tendency to retain higher number of pods (Table 2). However, the abscission rate did not follow the trend of flowers and pod production; plants with fewer flowers and fewer pods had the abscission rate as high as those with higher number of flowers and pods (Table 2). Cultivar differences were seen in total plant weight which resulted in the difference in seed weight per plant (Table 2).

The flowering pattern of the three cultivars selected for detailed study indicated Seafarer to have a slight earlier peak of flower production in 7 days from beginning of the first flower than Michelite and Black Turtle Soup (11-12 days) (Fig. 4). The peak of pod retention in Seafarer occurred at 5 days after the first flower which was ahead of that in Michelite and Black Turtle Soup (Fig. 5). In all three cultivars, the flowers that were borne earlier had a higher chance of setting and developing to maturity (Fig. 6).

Discussion

Abscission data from the field and greenhouse grown plants indicates that there is more abscission in the field (Table 1 and 2). This higher abscission rate under the field conditions in all cultivars may be

Table 2

Mean Values per Space-planted plants of flowers produced, Pods Retained at Harvest and Percentage of Flower and Pod Abscission

Table 2

Mean Values per Space-planted Plants of Flowers Produced, Pods Retained at Harvest and Percentage of Flower and Pod Abscission

Cultivars	Number of Flowers	Number of Pods	% Abscission	Seed wt. (g) Per Plant	Total Plant Wt. (g)
Michelite	281 a	82 ab	71 ab	51 b	94 bed
0679	259 ab	84 a	68 b	44 bc	79 cdef
0686	222 b	73 abc	66 b	55 b	110 ab
Pinto 114	178 c	58 cd	66 b	87 a	131 a
Seafarer	168 c	53 d	68 b	33 c	54 f
Black Turtle Soup	147 cd	68 bcd	52 c	57 b	102 bc
Jamapa	147 cd	64 cd	56 c	51 b	88 bcde
Cran-028	107 de	35 e	68 b	48 bc	72 def
Montcalm	100 e	23 e	76 a	50 b	87 bcde
Swedish Brown	97 e	33 e	66 b	41 bc	63 ef

Note: Letters not in common indicate significant differences by the Duncan's Multiple Range Test (5% level).

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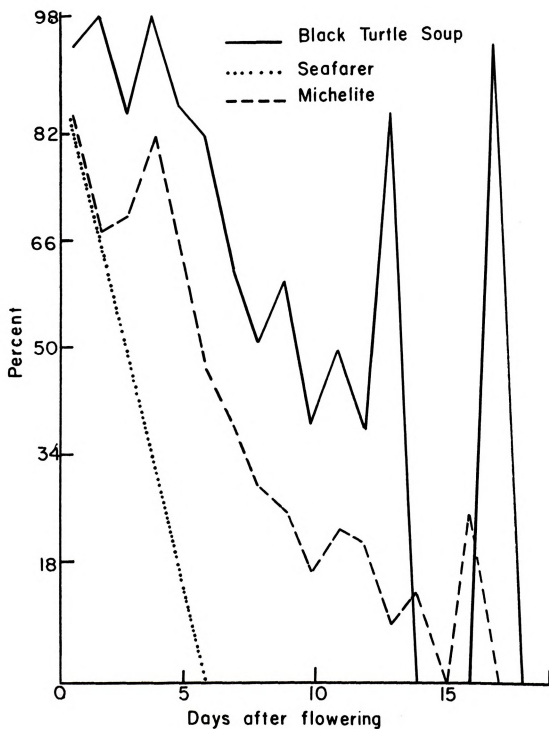
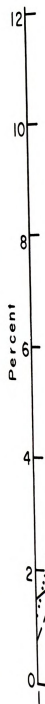


Fig. 3. Pods retained per day as a percentage of flowers produced on that day (data from greenhouse grown plants).



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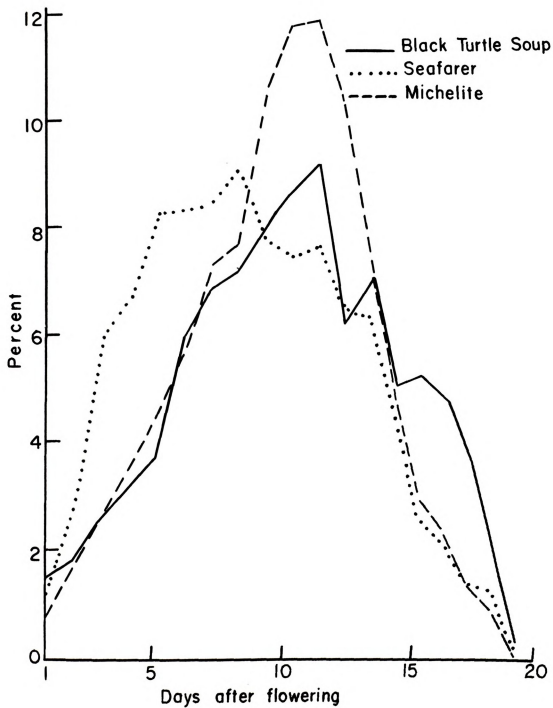


Fig. 4. Flower production in a specific day as a percentage of total flowers produced under field conditions.

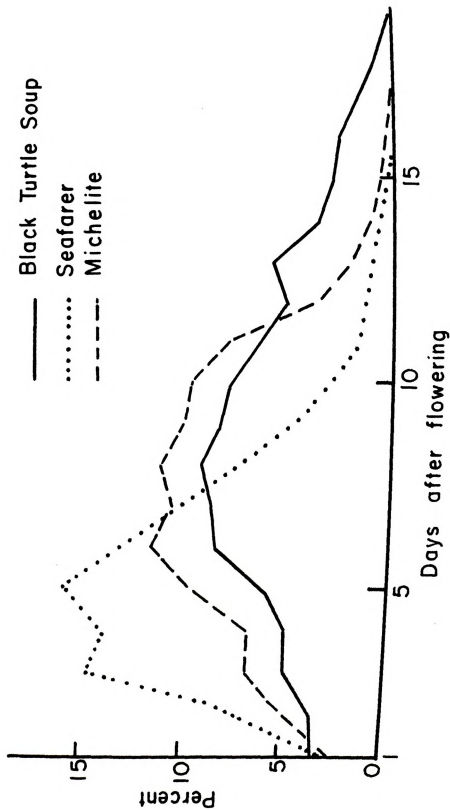


Fig. 5. Pod retained from flowers borne on a specific day, as a percentage of total pods at harvest grown under field conditions.

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attributed to greater variations in the environmental conditions such as moisture stress, heat, wind, pest and diseases to which the plants were occasionally subjected. Also it was noticed that under the field conditions a much greater number of flowers were produced as compared to that of greenhouse grown plants (Table 1 and 2). A high rate of abscission in the field probably can be associated with the greater number of flowers produced on field-grown plants. A high negative correlation between the yield per plant and the percentage of flower and pod abscission was reported in garden beans (1). Apart from the higher abscission rate under the field, cultivar differences in abscission existed under both growing conditions. Black Turtle Soup, which produced the least number of flowers, had the lowest while Michelite and Seafarer had the highest percentage of abscission (Table 1 and 2).

The pattern of flowering was longer in all cultivars under the field-grown plants as compared to that of the greenhouse-grown plants (Fig. 1 and 4). This may be due to the longer daylength in summer when the plants were grown in the field, and better growth rates at that time (Table 1 and 2), the same as was shown in soybean (10). The patterns of pod retention for the three cultivars were similar under both greenhouse and field. Seafarer had an earlier peak for pod retention than those of Michelite and Black Turtle Soup. This pattern of pod

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retention peaks indicates that the flowers that are produced first are most likely to be retained to produce ripe pods containing good seeds (Fig. 3 and 6). This phenomenon was also shown in lupin (11) and cowpea (5, 6). This may be explained either by assuming that early flowers have the first share of nutrients for their development, thus having a greater chance of survival, or by the release of an inhibitory substance to inhibit flowers set at a later time.

Although Seafarer and Michelite differ widely in growth habit and flowering patterns, they share approximately 92% of their germplasm in common (Adams, per com.). These two cultivars have similar percentage of abscission in either greenhouse or field-grown conditions (Table 1 and 2). This indicates that there may be separate genetic and physiological factors controlling abscission which are not affected by growth habit. These factors must also be considered in breeding to better fit the plant to its environment especially when gross changes in plant architecture are proposed.

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Black Turtle Soup
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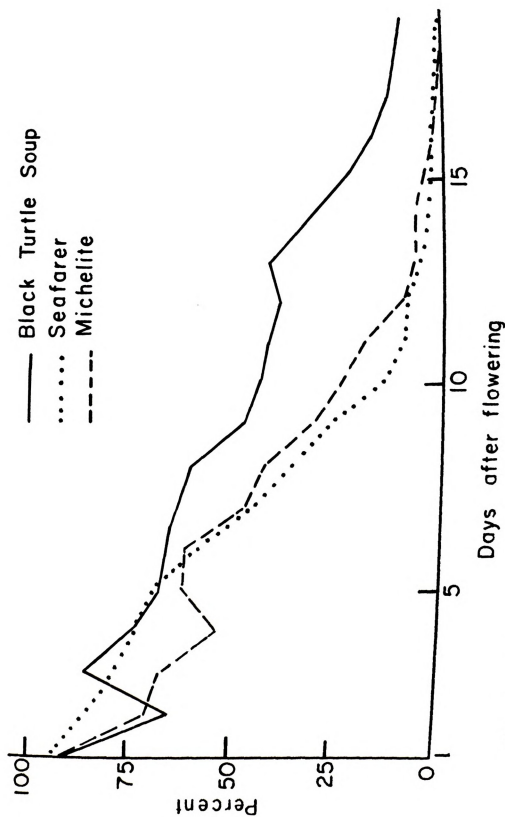


Fig. 6. Pods retained per day as a percentage of flowers produced on that day (data from field-grown plants).

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CHAPTER 3

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L.

II. GROWTH AND POD ABSCISSION AS AFFECTED BY DIFFERENT DAYLENGTHS

Abstract

Greenhouse-grown plants of two cultivars of dry bean (Phaseolus vulgaris L.) were subjected to 8, 13, and 18-hour photoperiods after the flower buds became visible. The numbers of flowers that opened on each plant were counted daily. Plants were harvested at peak flowering (10 days after initiating photoperiodic treatment), at pod filling (20 days), or at maturation (40 days). Weights of roots, stems, leaves, fruits and seeds were recorded, and leaf areas determined. Pod abscission was greater under short photoperiods and differed for the two cultivars. Plants were larger and yielded more seed under longer daylengths.

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Introduction

A number of environmental factors have been cited as the cause of abscission of reproductive structures. Among these factors are extremes of temperature, humidity, soil moisture, light duration and intensity, inadequate plant nutrition, disease, insect infestation, and mechanical forces such as wind and rain.

Abscission may be promoted by a deficiency of photosynthate. For example, shading increases abscission in cotton (5, 6, 7), soybean (3, 11) and vining peas (13). Factors which reduce the amount of light reaching the plant canopy, such as cloudy weather (9, 12) and close spacing (2) increase abscission in young cotton fruit (6, 12), and soybean (10). Partial or complete defoliation also increases abscission. Most of these results can be attributed to a deficiency of photosynthate.

Abscission can occur at several stages in ontogeny. However, Meadley and Milbourn (13) showed that pod abscission in pea was markedly increased when plants were shaded from flowering onwards. In order to meet the increased demand for photosynthate during fruit development either photosynthetic rates or leaf area must be increased. In soybean the rates of leaf photosynthesis are much higher during the pod filling stages (4, 8).

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The purpose of this study was to measure the effects on growth and pod abscission of differential daylengths.

Materials and Methods

Two dry bean cultivars, "Seafarer" and "Black Turtle Soup" were chosen for study because they differed in flowering habit and rate of pod abscission (Chapter 2). Three seeds were planted in each of 150 35-cm pots in the greenhouse in early April, 1975 at East Lansing. Ten days after emergence the seedlings were reduced to one plant per pot. At flower initiation 10 uniform plants of each cultivar were harvested, and separated into root, stem (including petioles), and leaf. Leaf area per plant was measured and, after freeze drying of all plant parts, dry weights were determined.

At the time of flower initiation 90 uniform plants of each cultivar were selected, and randomly divided into three groups of 30 plants, which were placed under 8, 13, or 18-hour photoperiods in the same greenhouse. For the 8-hour day, black polyethylene curtains were opened at 8 a.m. and closed at 4 p.m. each day throughout the experiment. The 13- and 18-hour treatments consisted of natural light plus supplemental lighting with a mixture of high intensity from fluorescent and incandescent lights. The intensity of the light at the plant level was 70,000-75,000 lux, ample for maximum

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photosynthesis. A black screen separated the treatments to avoid any interference. The greenhouse temperature was maintained at 25-29°C in the daytime and 18-21°C at night.

All plants were numbered, and the flowers that opened each day were recorded to give the number of flowers produced. Plants were harvested at peak flowering (10 days after the beginning photoperiodic treatment), at pod filling (20 days), and at maturity (40 days). The experiment was analyzed factorially with three factors, harvesting time, cultivar, and daylength. In each harvest, 10 plants per cultivar were used for all treatments, and the parameters measured in each harvest were:

- (1) Number of pods and number of seeds per plant (second and third harvest only);
- (2) Number of trifoliate leaves per plant (first and second harvest only, since leaves had senesced on mature plants);
- (3) Leaf area per plant (first and second harvest only);
- (4) Root, stem (including petiole), leaf, seed and pod dry weight.

The above experiment was repeated in 1976, using the same greenhouse, cultivars and lights as before. However, 25 cm pots were used instead of 35 cm pots.

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Results and Discussion

Pod Abscission

Both cultivars produced more flowers and retained more pods as daylength increased (Table 1). In 1975, percent pod abscission was markedly reduced in Black Turtle Soup under 13-hour day, while Seafarer did not show this reduction until daylength was extended to 18 hours (cultivar x daylength significant at 1%). However, no interaction was evident in 1976.

Pod abscission was not recorded at peak flowering since the pods were still attached to the plants. However, at pod filling many pods had abscised. More than one-half of the pods lost having fallen in the first 20 days after anthesis in both cultivars. In Seafarer a greater portion of the pods abscised at the early stages of pod development (Table A-1, A-2, Appendix A). Under the 8-hour day many pods abscised at the pod filling stage in both cultivars (Table A-1, A-2, Appendix A). In general, considering both years increasing daylength from 8 to 13 to 18 hours reduced pod abscission in both cultivars (Table 1). At the mature stage pod abscission decreased progressively as daylength increased (Fig. 1A). Abscission data recorded at the pod filling stages included both late flowers and young pods. The abscission of these structures may involve hormonal levels as well as nutrients. Similarly, shading of peas after flowering increased pod abscission (12).

Table 1
Number of Flowers, Number of Pods, and Percentage of Pod

Table 1
Effects of Daylengths and Harvesting Time on Number of Flowers, Number of Pods, and Percentage of Pod
Abscission of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1975 and 1976
(data represents means for treatments)^a

	Number of Flowers		Number of Pods		% Abscission	
	1975	1976	1975	1976	1975	1976
I. Harvesting Time						
Peak flowering	17.2 a	11.5 a	16.4 c	10.4 c	-	-
Pod filling	17.4 a	13.6 b	9.9 b	7.3 b	36.2 a	42.1 a
Maturity	18.7 a	12.8 ab	7.6 a	5.5 a	53.7 b	54.1 b
II. Cultivar						
Black Turtle Soup	10.8 m	8.3 m	8.6 m	6.3 m	30.5 m	38.2 m
Seafarer	24.7 n	17.0 n	14.0 n	9.2 n	59.4 n	62.0 n
III. Daylengths						
8 Hours	10.1 x	10.4 x	5.9 x	5.9 x	53.7 z	57.9 z
13 Hours	18.3 y	12.4 y	10.2 y	7.7 y	47.4 y	46.8 y
18 Hours	24.8 z	13.2 z	17.8 z	9.7 z	33.7 x	39.7 x
Interactions						
I x II	n.s.	n.s.	**	**	n.s.	n.s.
I x III	n.s.	n.s.	*	*	**	n.s.
II x III	**	n.s.	**	n.s.	**	n.s.
I x II x III	n.s.	n.s.	**	n.s.	n.s.	n.s.

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

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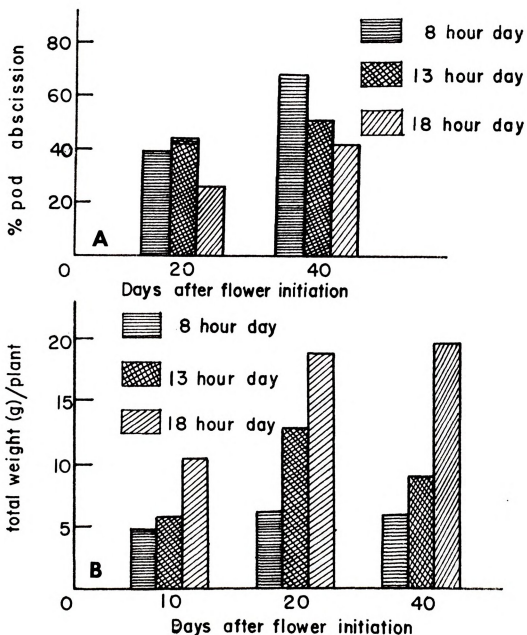


Fig. 1. Interaction between developmental stages and daylengths on percentage of pod abscission (A), and total plant weight (B). (Data taken from 1975, averaged over two cultivars.)

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Competition for nutrients between flowers, young pods and growing apices was probably severe under the 8-hour day. The correlation between percentage of pod abscission and number of flowers produced was significant in Black Turtle Soup under 8- and 13-hour days but not under the 18-hour photoperiod (Table 2). The positive correlation agrees with data for garden bean in which abscission of flowers and pods is greater in varieties with high flower number (1). However, under the 18-hour photoperiod the number of flowers borne per plant was negatively correlated with abscission (Table 2). The negative correlation was insignificant in both cultivars under the 18-hour day. Because Seafarer is determinate, vegetative growth competed less with fruit set than was the case in the indeterminate Black Turtle Soup. Thus the correlation between abscission and flower number was significant only at the 13-hour photoperiod (Table 2).

The preponderance of negative relationships between percentage of pod abscission and the characteristics representing vegetative growth at the 18-hour photoperiod, though individually not always statistically significant (Table 2) nevertheless implies that the plants of both cultivars are producing photosynthate sufficient for both an increase in growth and a removal of competition between developing pods.

Table 2
Correlation Coefficients Between Percentage of Pod Abscission or Leaf Area and Other
Parameters in Two Dry Bean Cultivars Subjected to Different Day Length Treatments

Table 2

Correlation Coefficients Between Percentage of Pod Abscission or Leaf Area and Other Parameters in Two Dry Bean Cultivars Subjected to Different Daylength Treatments After Flowering (data taken at the pod filling stage from 1975 grown plants)

Parameters	Black Turtle Soup			Seafarer		
	8 Hours	13 Hours	18 Hours	8 Hours	13 Hours	18 Hours
% Pod Abscission vs:						
Flowering period	.22	.28	.28	-.20	.28	.25
Number of flowers	.71a	.74b	-.24	.34	.61a	-.04
Number of pods	.09	.29	-.47	-.57	-.26	-.73b
Number of seeds	.77b	.58	-.31	.23	.31	-.78b
Seed weight	.64a	.59	.18	.47	.49	-.20
Root weight	.53	.27	-.55	.13	.13	-.33
Stem weight	.44	.61a	-.24	-.03	.21	-.42
Leaf weight	.61a	.40	-.43	-.13	.30	-.38
Leaf number	.69a	.46	-.19	-.26	.06	-.04
Leaf area	.51	.57	-.51	-.18	.17	-.40
Leaf Area vs:						
Flowering period	.73b	.13	.13	.60a	.33	.43
Number of flowers	.74b	.69a	.74b	.75b	.48	.85b
Number of pods	.67a	.51	.79b	.78b	.51	.87b
Number of seeds	.67a	.88b	.61a	.64a	.89b	.49
Seed weight	.69a	.65a	.06	.55	.72a	.50

^aSignificant at 5% level.

^bSignificant at 1% level.

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Leaf Development

Leaf number, area, and weight increased significantly with daylength (Table 3). Leaf area and leaf weight per plant were significantly greater in Black Turtle Soup than in Seafarer in 1975; only the latter difference was significant in 1976. However, the number of leaves per plant was not affected by cultivar, documenting the larger leaf size in the Black Turtle Soup (Table 3). Leaf number and area per plant did not change significantly with time in 1975 (Table 3) indicating that no leaf growth occurred after the pods were set.

Leaf area was positively correlated with yield components in all daylengths (Table 2). This is consistent with many reports that greater photosynthetic capacity results in higher yield. Leaf area was significantly correlated with length of flowering time in both cultivars under 8-hour day, but not under longer photoperiods (Table 2). Yield (seed weight) was significantly correlated with leaf area under 8 and 13-hour days in Black Turtle Soup (Table 2). However, no significant correlation existed between leaf area and yield for Seafarer plants under 8 and 18-hour days.

Plant Development

Weight of all vegetative parts increased with daylength in both cultivars and in both years (Table 4, A-5, and A-6). This was associated with a greater number

Table 3

Effects of Daylengths, Harvesting Times and Cultivars on Leaf Weight Per Plant, Leaf Area Per Plant and Number of Trifoliate Leaves Per Plant Grown Under Greenhouse Conditions in the Year 1975 and 1976 (data represents means for treatment)^a

	Leaf wt/Plant (g)		Leaf Area/Plant (cm ²)		Number of Trifoliate Leaf/Plant	
	1975	1976	1975	1976	1975	1976
I. Harvesting Time						
Peak flowering	3.7 a	2.3 a	1394 a	901 a	17 a	12 a
Pod filling	4.6 b	2.5 a	1472 a	1131 b	16 a	13 b
II. Cultivar						
Black Turtle Soup	4.7 n	2.5 m	1624 n	1149 n	16 a	12 m
Seafarer	3.6 m	2.3 m	1242 m	974 m	17 a	13n
III. Daylengths						
8 Hours	2.9 x	1.6 x	1172 x	839 x	14 x	10 x
13 Hours	3.8 y	2.1 y	1460 y	1026 y	16 y	12 y
18 Hours	5.7 z	3.5 z	1667 z	1320 z	19 z	15 z
Interactions						
I x II	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
I x III	n.s.	*	n.s.	n.s.	n.s.	n.s.
II x III	**	n.s.	**	n.s.	*	n.s.
I x II x III	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

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and percentage of pods retained (Table 1). Greater vegetative growth (Table 3 and 4) was also associated with lower abscission (Table 1) when 1975 values for Black Turtle Soup are compared with those for Seafarer.

The weight of the vegetative portions of the plants in this experiment did not increase after flowering; root and stem weights tended to decrease (Table 4), while leaf weight remain unchanged (Table 3). Total plant weight increased from peak flowering to the pod filling stages (Table 4), as a result of increasing pod weight. It could be assumed from these results that, after flowering, pod development comprises such a strong sink for assimilate (or nutrients) that pods are effective and successful competition with vegetative organs. A more likely explanation is simply that the vegetative organs have reached their final size, as determined by genetic potential in this environment, and that these organs are, in fact, no longer competing for the available photosynthate (or nutrients) with the pods.

Seed Yield

The number of normal-sized seeds produced per plant was greater for both cultivars under longer day-length (Table 5), resulting in greater seed weight per plant. Weight per seed was not affected in 1976 (Table 5); effects varied with cultivar in 1975. Black Turtle Soup seeds were larger under 13 and 18 hour than

Table 4
Effects of Daylengths, Harvesting Times and Cultivars on the Weight per Plant of Root, Stem and Total Plant Grown Under Greenhouse Conditions in the Year 1975 and 1976 (data represents means for treatment)^a

	Root wt/Plant (g)		Stem wt/Plant (g)		Total Plant wt (g)	
	1975	1976	1975	1976	1975	1976
I. Harvesting Time						
Peak flowering	1.9 c	1.0 a	2.0 b	1.2 a	7.2 a	4.8 a
Peak filling	1.1 b	1.0 a	2.0 b	1.5 b	12.5 c	9.3 b
Maturity	0.9 a	0.9 a	1.6 a	1.2 a	11.3 b	7.5 b
II. Cultivar						
Black Turtle Soup	1.4 n	0.9 m	1.9 n	1.2 m	11.0 n	6.4 m
Seafarer	1.1 m	1.1 n	1.7 m	1.4 n	9.6 m	7.4 n
III. Daylengths						
8 Hours	0.8 x	0.5 x	1.3 x	0.9 x	5.7 x	3.9 x
13 Hours	1.0 y	0.8 y	1.6 y	1.1 y	9.2 x	6.4 y
18 Hours	2.0 z	1.5 z	2.7 z	1.9 z	16.1 z	10.3 z
Interactions						
I x II	n.s.	n.s.	*	n.s.	n.s.	n.s.
I x III	n.s.	*	*	*	**	**
II x III	n.s.	*	**	n.s.	n.s.	n.s.
I x II x III	n.s.	n.s.	n.s.	n.s.	*	n.s.

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

Table 5

Effects of Daylength on Number of Seeds per Plant, Total Seed Weight per Plant and Weight per Seed in Two Dry Bean Cultivars Grown in 1975 and 1976 Seasons^a

	No. Seed/Plant		Total Seed Wt. (g)		Wt/Seed (g)	
	1975	1976	1975	1976	1975	1976
I. Cultivar						
Black Turtle Soup	38.8 a	25.9 a	5.4 a	5.1 a	0.22 a	0.14 a
Seafarer	35.0 a	23.7 a	4.8 a	5.7 a	0.23 a	0.18 b
II. Daylength (hrs.)						
8	15.3 x	11.5 x	2.4 x	2.3 x	0.23 x	0.16 x
13	28.9 y	26.6 y	4.9 y	5.7 y	0.24 x	0.17 x
18	66.4 z	36.4 z	8.0 z	8.2 z	0.22 x	0.16 x
<u>Interaction</u>						
I x II	n.s.	n.s.	n.s.	n.s.	**	n.s.

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under 8-hour daylengths, whereas the reverse was true for Seafarer.

Within the same variety, plants having greater growth before flowering usually associate with lower abscission level. Also favorable environmental conditions after flowering are required for seed development and fruit retention.

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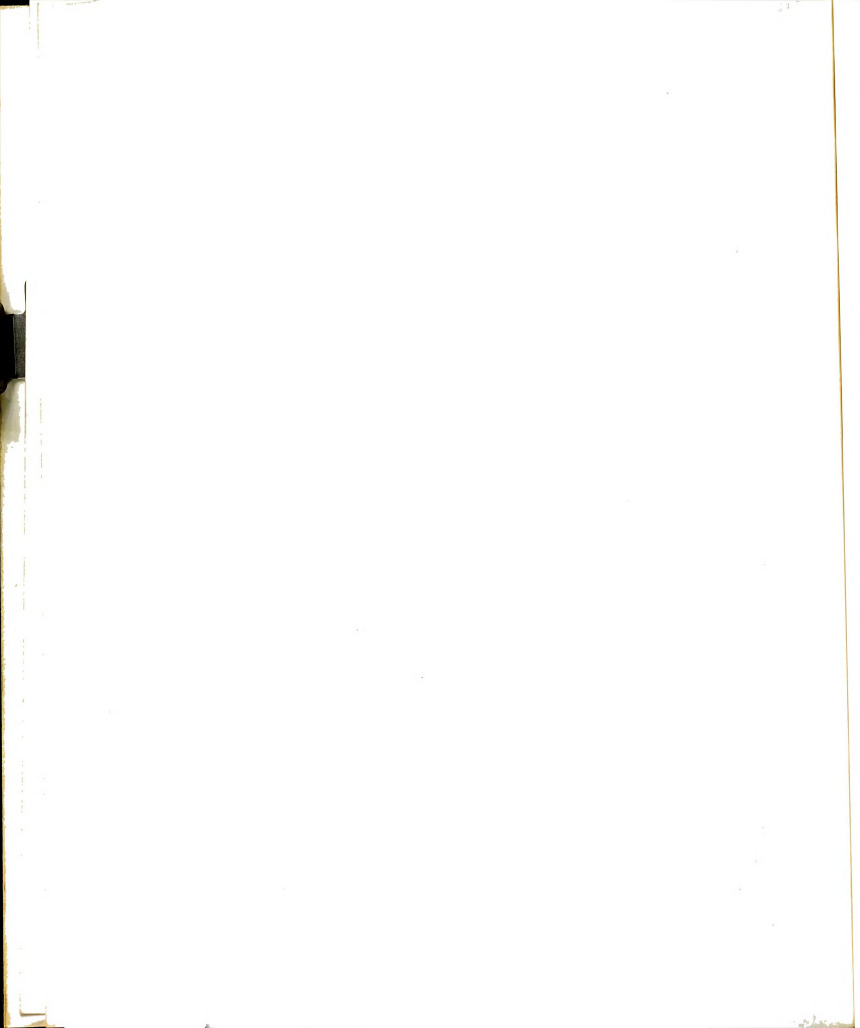
CHAPTER 4

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L.

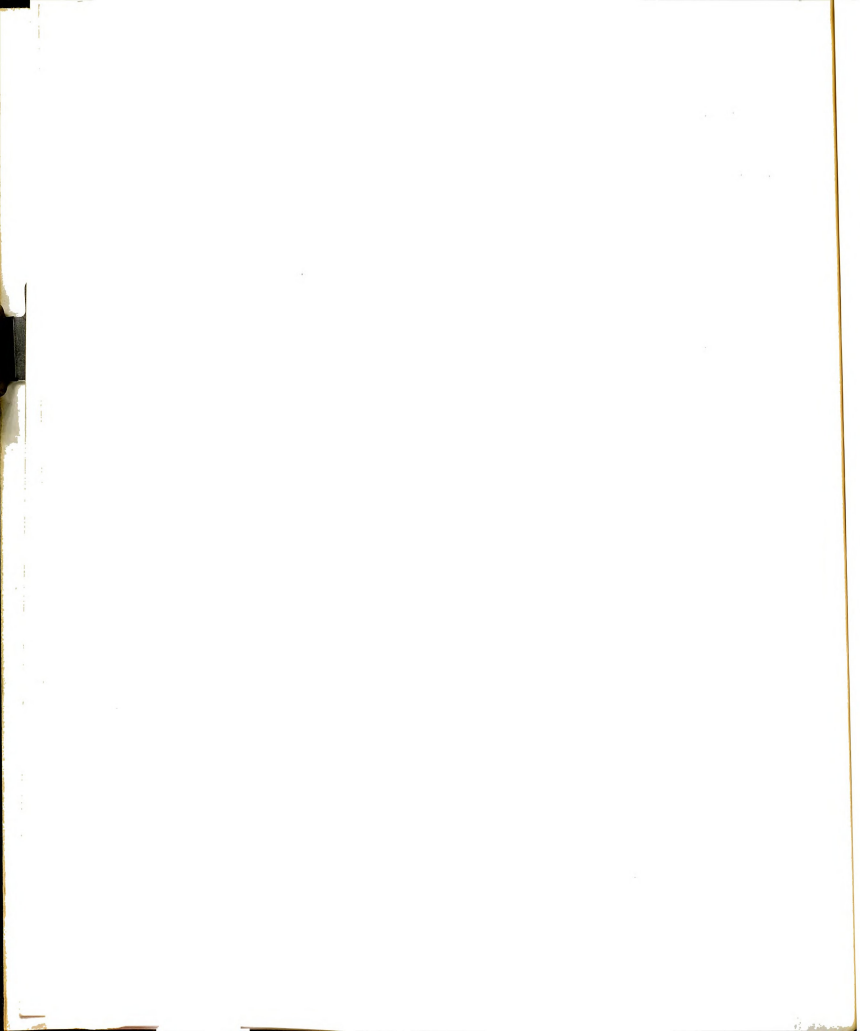
III. RELATIONSHIP OF POD ABSCISSION TO DIFFERENTIAL LEVELS OF CARBOHYDRATES PRODUCED BY VARIATION IN DAYLENGTH

Abstract

"Black Turtle Soup" and "Seafarer" dry bean (Phaseolus vulgaris L.) cultivars were subjected to 8, 13 and 18-hour photoperiods in the greenhouse during their reproductive phase. Free sugar, starch, and total non-structural carbohydrate concentration of root, stem, leaf, seed, and pod wall were determined at different stages during pod development. Free sugar concentration increased with photoperiod in all tissues. Higher starch concentration was found in all tissues except in the root where there was no difference in starch concentration between the short (8-hour) and the long (18-hour) days. Black Turtle Soup, an indeterminate cultivar, contained more free sugar in all tissues than Seafarer, a determinate cultivar. Black Turtle Soup contained more starch in stem and leaf, but not in root and seed. Free sugars in root and leaf rose from peak flowering to pod filling, then



decreased. However, free sugars in stem, seed, and pod wall declined as the pod matured. In general, starch concentration of vegetative organs (root, stem, and leaf) decreased as the plants matured, while that of the seeds increased. The general pattern of higher available carbohydrate under long photoperiods was associated with greater vigor, higher yield, and reduced pod abscission. Pod abscission data indicated an inverse relationship to available carbohydrate concentration in vegetative organs.



Introduction

Seed yield is determined by the number of flowers produced, the percentage of fruit set, the number of seeds per fruit, and seed size. Flower and young fruit abscission is extensive in many economic crops (4, 6, 14, 15), and is often related to environmental conditions, especially those that influence photosynthesis (3).

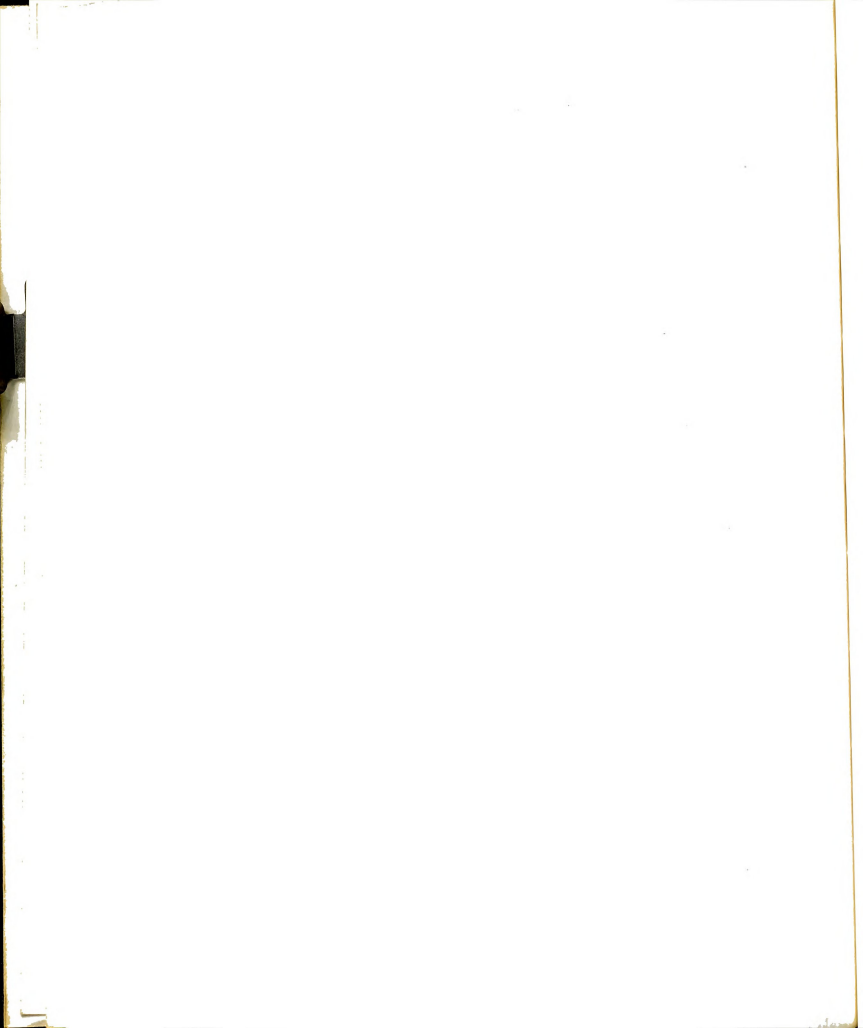
Abscission of young fruits may be controlled by levels of nitrogenous or carbohydrate reserves (5, 16). Spraying cotton plants with 20% sucrose and 1% nitrogen as urea actually increased abscission (1). However, the endogenous carbohydrate level was not influenced. Girdling increased carbohydrate level, and a 2% urea spray increased the nitrogen level (1). However, combining the two treatments considerably increased boll abscission. These results raise a question on the role of carbohydrate in fruit abscission (1).

In previous work, pod abscission was reduced and seed yield increased in dry beans by exposure to long photoperiods during the reproductive phase (see Chapter 3). The present study was designed to determine the effect of photoperiod on levels of available carbohydrates.

Materials and Methods

Sample Preparation

Two dry bean cultivars, "Seafarer" and "Black Turtle Soup," were chosen because of differences in plant



type, flowering habits, and pod abscission rates. Seeds were planted in 35-cm pots in the greenhouse at East Lansing in early April 1975. Growing conditions have been described previously (see Chapter 3).

Plants were harvested at (a) flower initiation, just before beginning photoperiod treatments, (b) peak flowering, 10 days after flower initiation, (c) pod filling, 20 days after flower initiation, and (d) maturity, 40 days after flower initiation. At each harvest 10 uniform plants of each cultivar were separated into root, stem (including petioles), leaf, pod, and seed. The samples were freeze-dried, weighed, ground in a Wiley mill having a 40-mesh sieve, and stored in scintillating vials at room temperature prior to extraction.

Determination of Free Sugars

The method used was a modification from Laidlaw and Reid (7). Free sugars were extracted by refluxing 100 mg samples in 80% ethanol in a water bath at 60°C for two hours, with occasional shaking. Samples were filtered through Whatman #1 paper and the filtrate was evaporated under vacuum at 50°C to near dryness. Volume was adjusted to 25 ml with distilled water. The solution was clarified with 10% lead acetate and then delead with potassium oxalate (8). Volume was adjusted, to 50 ml in the case of root and pod wall and 100 ml for

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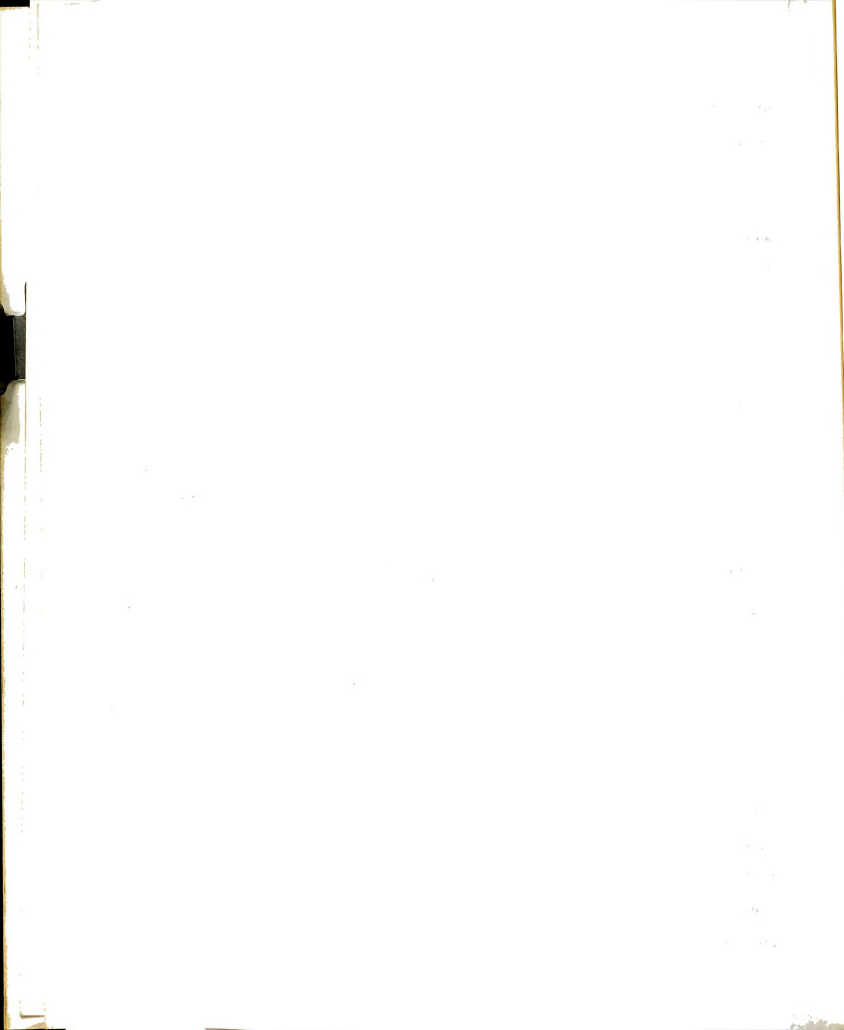
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stem, leaf and seed tissues, with distilled water prior to analysis.

For analysis of free sugars, 5 ml of 70% anthrone reagent (19) was added to each 1.0 ml of extract. Before and after the addition of anthrone reagent the tube was immersed in cold water and shaken to obtain thorough mixing. The solution was heated in boiling water for 10 minutes, cooled to room temperature and absorbance was determined at 620 nm. Sugar content was expressed as glucose equivalents per gram dry weight.

Determination of Total Non-
structural Carbohydrates
(TNC)

The extraction employed was modified from Smith (11). One hundred mg of tissue was placed in a 45 by 400 mm test tube, 15 ml distilled water was added, and the solution was boiled for 5 minutes to gelatinize the starch. After cooling to room temperature, 10 ml of buffer, pH 4.45, and 10 ml 0.5% takadiastase (Clarase 900) enzyme solution were added. The tubes were shaken in a water bath at 45°C for 44 hours (17). The solution was filtered through Whatman #1 paper into a 125 ml Erlenmeyer flask, and 2 ml of 10% neutral lead acetate was added to precipitate the proteins. After centrifugation at 12,000 xg for 5 minutes, the supernatant fluid was decanted into a second 125 ml flask containing 100 mg powdered potassium oxalate. These mixtures were kept



overnight in the refrigerator. The solution was stored overnight at 4°C, then centrifuged at 12,000 xg for 10 minutes, filtered through Whatman #52 paper, and made up to 200 ml with distilled water. TNC was determined colorimetrically at 620 nm using the anthrone-reagent technique as described earlier (19), and expressed as mg glucose per gram dry weight.

Since TNC in legumes consists mainly of free sugars and starches (11, 12), starch concentration was estimated as the difference between TNC and soluble sugars.

The data were analyzed factorially using 10 plants per treatment (one plant per replication).

Results and Discussion

Free Sugar

In general, free sugar levels increased with photoperiod in root, stem, leaf, seed and pod wall (Table 1). However, in the leaf highest levels occurred in plants subjected to 13-hour days (Table 1). Under the 18-hour daylength the movement of assimilate out of the leaf might have been more rapid, resulting in less free sugar in the leaf.

Free sugars were higher in all tissues of Black Turtle Soup than in Seafarer (Table 1), indicating either a difference in rate of assimilation of carbon dioxide or a difference in rate of translocation of sugar, or

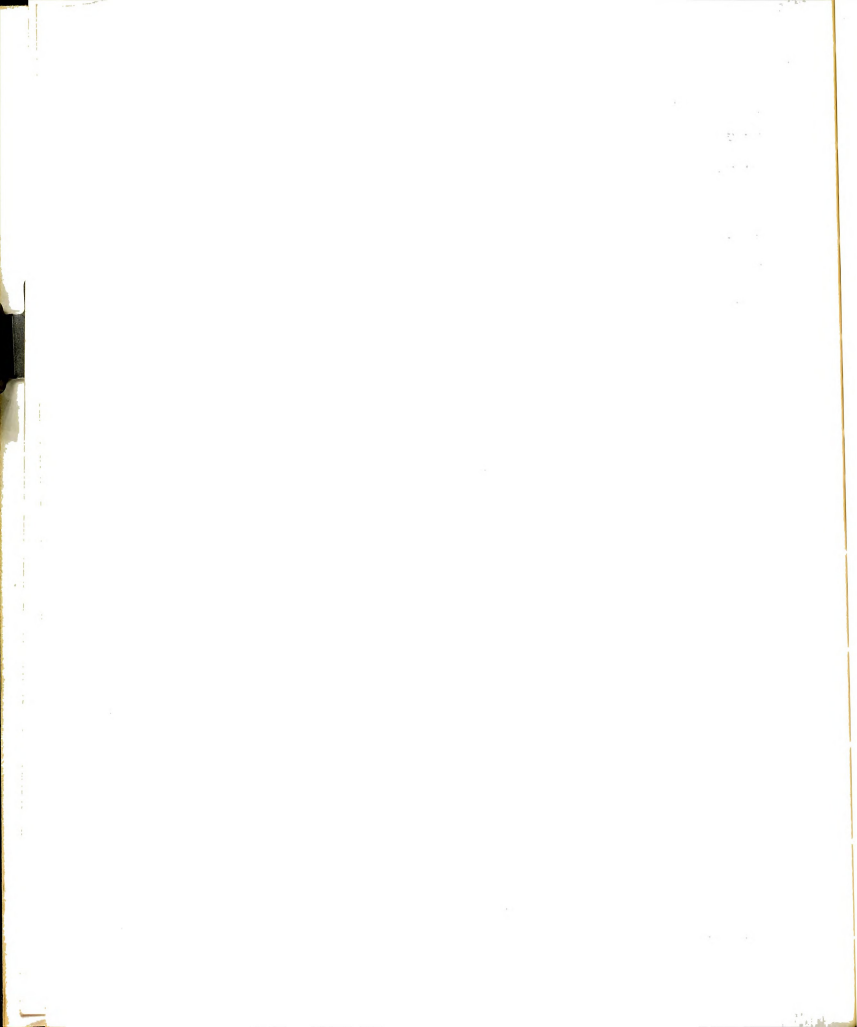
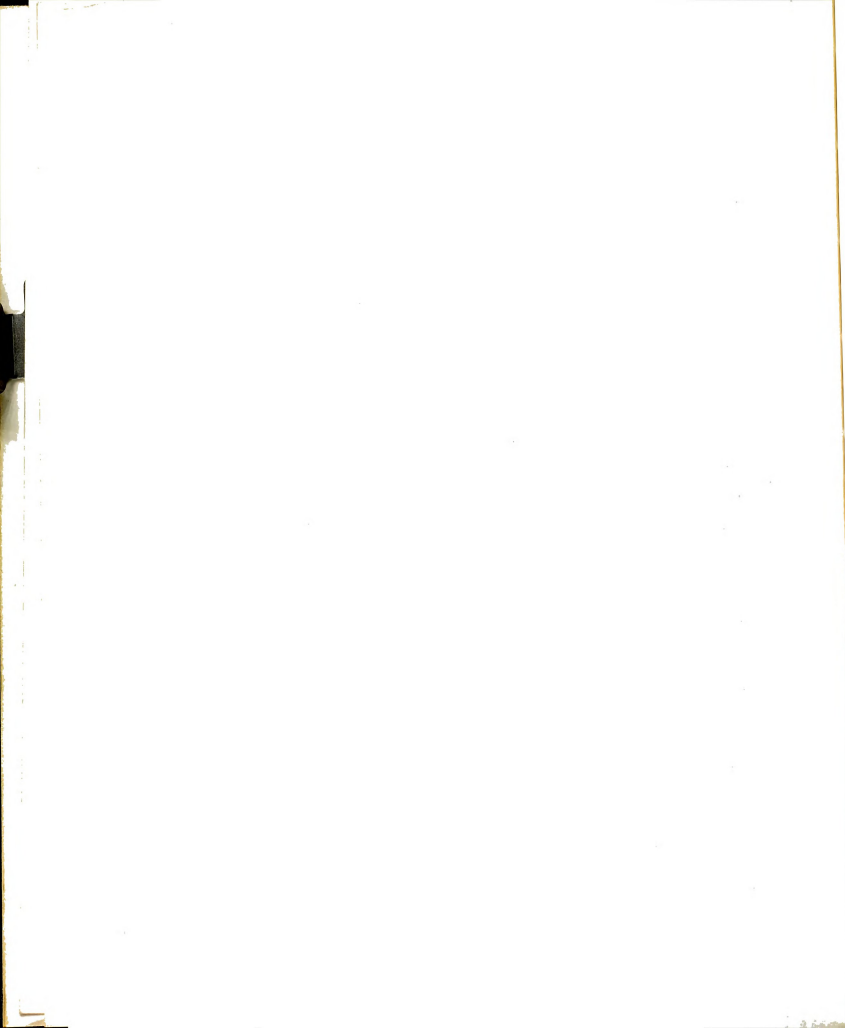


Table 1
Developmental Stages, Cultivars and Daylength Effects on Free Sugar Level
in Various Plant Parts^a (mg. glucose per g. dry weight)

		Mg Glucose per g Dry Weight				
		Root	Stem	Leaf	Seed	Pod
I. Time						
	Peak flowering	12.4 a	74.6 c	55.5 a	-	176 c ^b
	Pod filling	17.1 c	62.7 b	66.1 b	66.6 a	141 b
	Maturity	13.7 b	34.9 a	-	71.5 a	26.1 a
II. Cultivar						
	Black Turtle Soup	16.2 m	67.9 m	68.8 m	70.2 m	122.4 m
	Seafarer	12.7 n	47.0 n	52.8 n	67.8 m	106.8 n
III. Daylength						
	8 hours	12.1 x	45.4 x	52.8 x	56.7 x	110.7 x
	13 hours	14.9 y	61.2 y	67.2 z	66.9 y	106.7 x
	18 hours	16.3 z	65.7 z	62.4 y	83.3 z	126.4 y
Interactions						
	I x II	**	**	*	**	**
	I x III	**	**	**	*	**
	II x III	**	*	*	n.s.	**
	I x II x III	n.s.	*	**	n.s.	*

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.



both. Differences in rates of translocation of ^{14}C assimilates among bean cultivars have been reported (18).

Differences in response of the two cultivars to increasing daylength was evident in free sugar accumulation (Table 2). Free sugar concentration of root, stem, and leaf was proportional to photoperiod in Black Turtle Soup, but not in Seafarer (Table 3). In the latter, the effects of photoperiod were nonsignificant in root, stem, and leaf sugars which were not increased by extending the photoperiod from 13 to 18 hours. This could be due to the differences in growth habit, for Black Turtle Soup plants continue growth after the reproductive stage is attained. Seafarer, on the other hand, is determinate and makes only slight additional growth after the reproductive phase has been reached. This may have reduced free sugar content under longer photoperiods (Table 3). Cultivar did not affect free sugar levels in seed and pod wall except under the 18-hour photoperiod (Table 3). This may be due to the greater ability of Black Turtle Soup to accumulate free sugars in these organs under longer daylength.

In roots of Black Turtle Soup free sugar rose from flower initiation to pod filling, then decreased at maturity (Table 2). However, in Seafarer, free sugar levels did not change between pod filling and maturity. The accumulation of free sugar in roots at the later

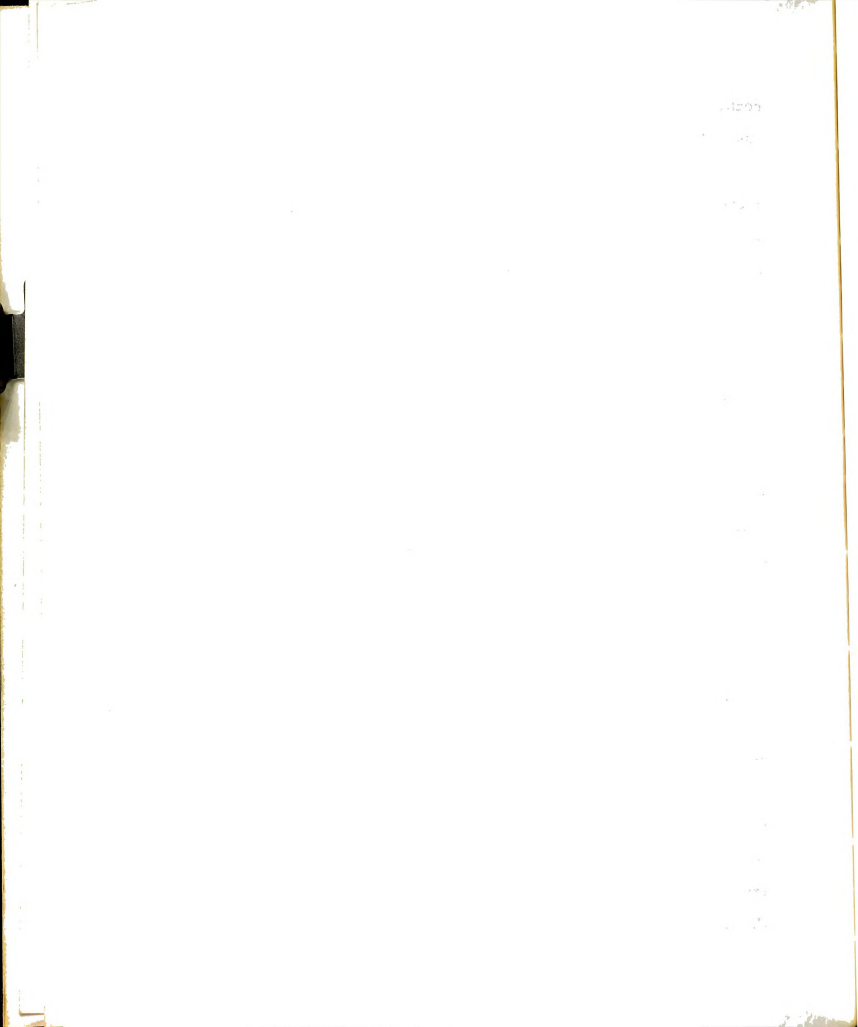


Table 2
Effects of Cultivar and Time of Sampling on Free Sugar Concentrations
(mg glucose/g dry weight) in Bean Tissues^a

Time After Flower Initia- tion (days)	Cultivar	Tissue				
		Root	Stem	Leaf	Seed	Pod Wall
0	Black Turtle Soup	11.5 a	117.1 g	103.5 e	-	-
	Seafarer	13.2 b	55.1 cd	44.1 a	-	-
	Mean	12.3 p	86.1 s	73.8 r	-	-
10	Black Turtle Soup	14.9 b	88.4 f	61.7 c	-	187 d
	Seafarer	9.9 a	60.9 d	49.3 a	-	166 c
	Mean	12.4 p	74.6 r	55.5 p	-	176 r
20	Black Turtle Soup	20.2 c	76.8 e	75.9 d	73.3 b	158 c
	Seafarer	14.0 b	48.6 c	56.3 b	59.9 a	124 b
	Mean	17.1 q	62.7 q	66.1 q	66.6 p	141 q
40	Black Turtle Soup	13.3 b	38.6 b	-	67.1 ab	22.7 a
	Seafarer	14.1 b	31.3 a	-	75.8 b	29.5 a
	Mean	13.7 r	34.9 p	-	71.5 p	26.1 p

^a Means within columns and sets (abc, pqr) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

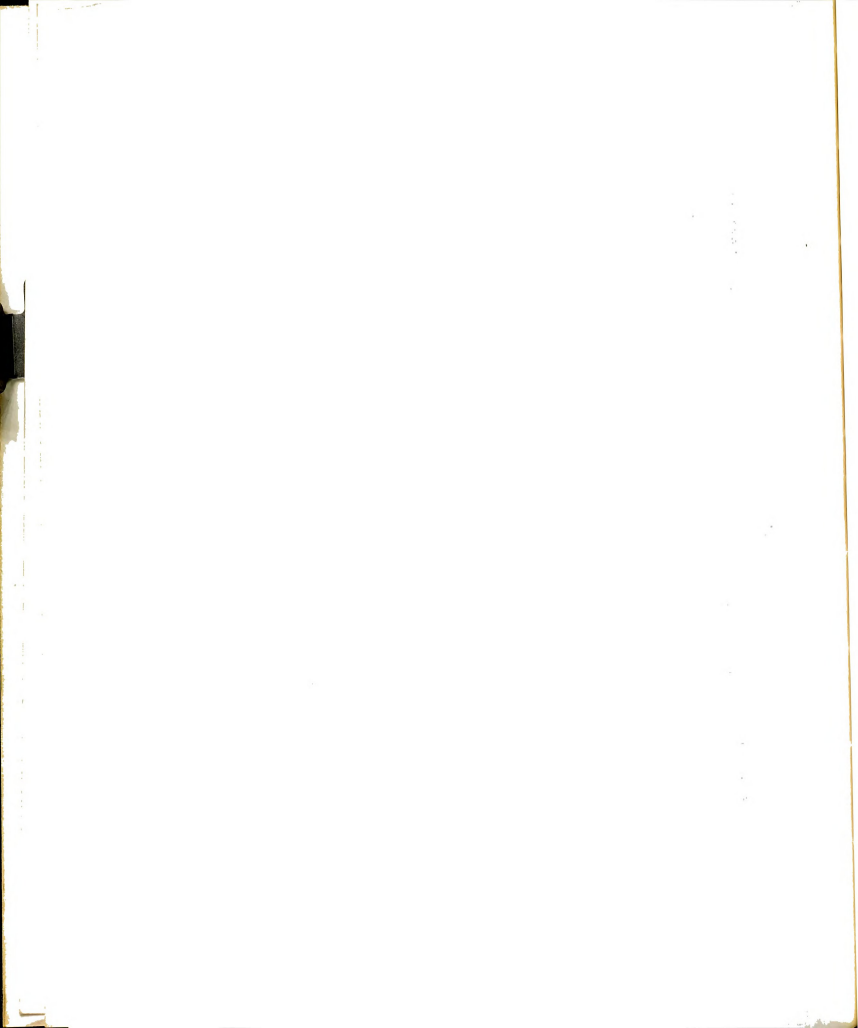
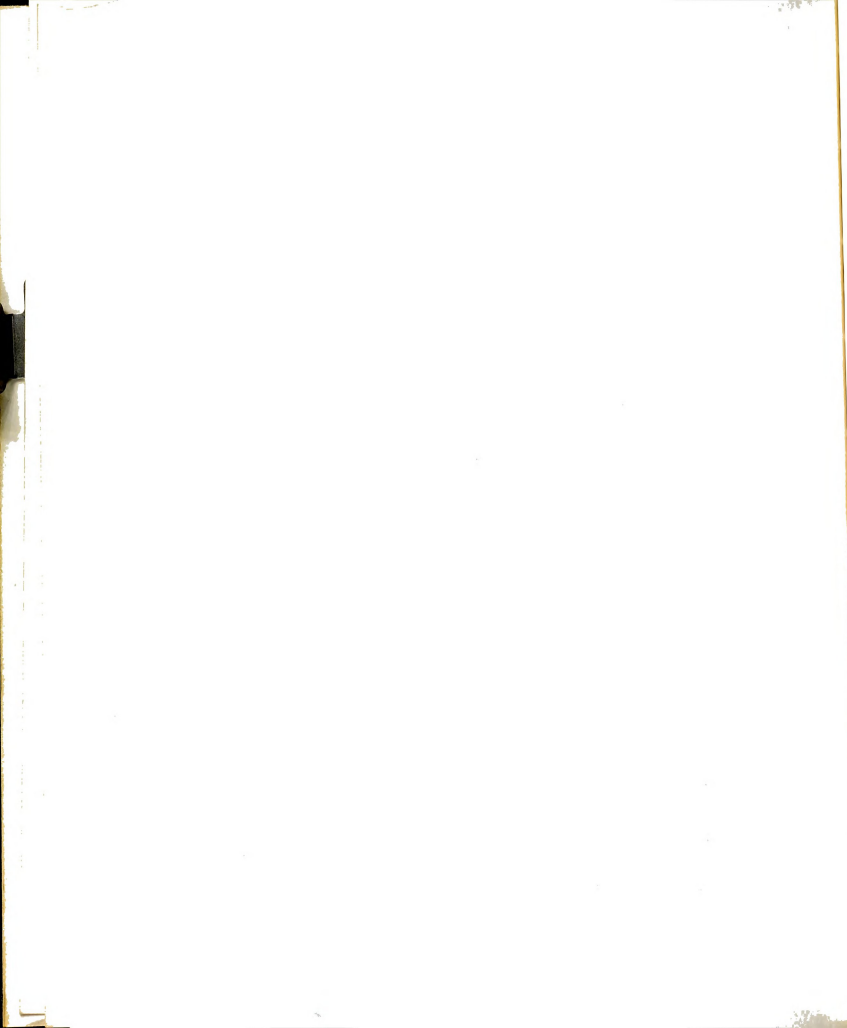


Table 3
Effects of Photoperiod and Cultivar on Free Sugar Concentration (mg/g dry wt)
in Bean Tissues^a

Photoperiod (hours)	Cultivar	Tissue				
		Root	Stem	Leaf	Seed	Pod Wall
8	Black Turtle Soup	12.3 a	53.6 b	58.3 b	94.5 ab	115 a
	Seafarer	12.0 a	32.7 a	47.4 a	87.7 a	106 a
	Mean	12.1 x	45.4 x	52.8 x	91.9 x	110.5 x
13	Black Turtle Soup	16.4 b	71.5 c	76.9 d	103.8 bc	110 a
	Seafarer	13.4 a	50.8 b	57.4 b	101.6 b	103 a
	Mean	14.9 y	61.2 y	67.2 z	102.7 y	106.5 x
18	Black Turtle Soup	19.8 c	78.7 d	71.2 c	128.8 d	142 b
	Seafarer	12.7 a	52.8 b	53.5 b	112.7 c	111 a
	Mean	16.3 z	65.4 z	62.4 y	120.8 z	126.5 y

^aMeans within columns and sets (abc, xyz) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



stages of pod development in Seafarer may imply that there is a genetically programmed characteristic of this variety, or that root sink strength exceeds stem or pod strength. The level of free sugar in stem decreased as the pods matured in both cultivars (Table 2). Free sugar in leaves increased from peak flowering to pod filling (Table 2). The marked reduction in leaf free sugar from flower initiation to peak flowering stages in Black Turtle Soup may be due to the movement of sugar from the leaves to the flowers. The decreased abscission of flowers and young pods at peak flowering of Black Turtle Soup as compared to Seafarer (Chapter 3) may be related to the drop in leaf sugar level at this stage. Levels of free sugar in seeds were not affected by cultivar, but fell rapidly between peak flowering and pod filling (Table 2 and 3). In both cultivars the sugar level in pod walls rapidly decreased as the seed matured (Table 2). This may reflect redistribution from the pod walls to the growing seeds, although a decreased rate of photosynthesis in aging pod walls may also be held accountable.

Interactions between photoperiod and developmental stages were noted for sugar concentration of root, stem, leaf, seed and pod wall (Table 4). In the root, at peak flowering and at pod filling, free sugar level increased as photoperiod was extended to 13-hour, but no further increase occurred at 18-hour (Table 4). Levels were

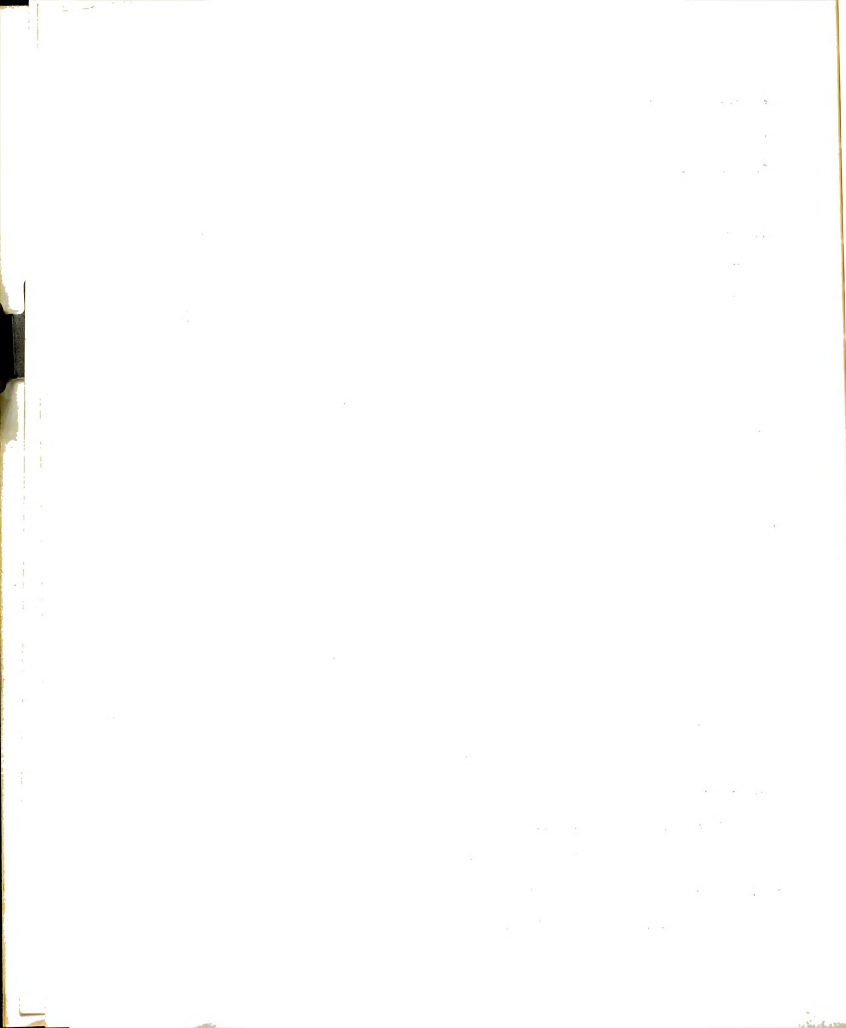
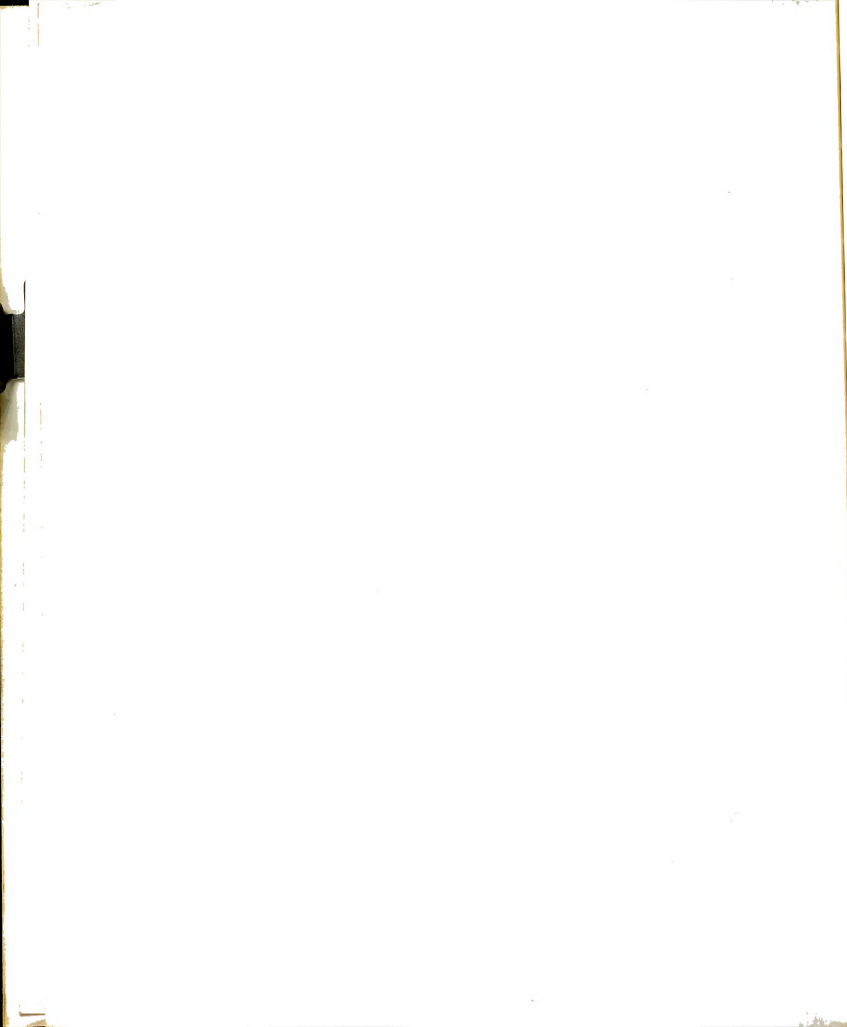


Table 4
Effects of Photoperiod and Time of Sampling on Free Sugar Concentration
(mg/g dry weight) of Bean Tissues^a

Photoperiod (hour)	Time After Flower Initia- tion (days)	Tissue			
		Root	Stem	Leaf	Pod Wall
8	0	12.3 ab	86.1 g	73.8 c	-
	10	10.4 a	67.6 d	44.1 a	159 cd ^b
	20	14.9 d	47.3 c	61.5 b	145 c
	40	11.1 ab	21.3 a	-	64.3 b
	Mean	12.2 x	55.6 x	59.8 x	56.7 x
13	0	12.3 ab	86.1 g	73.8 c	-
	10	13.6 cd	81.4 f	60.8 b	174 d
	20	18.5 e	66.8 d	73.5 c	122 b
	40	12.5 abc	35.3 b	-	61.0 b
	Mean	14.2 y	67.4 y	69.3 z	72.9 bc
18	0	12.3 ab	86.1 g	73.8 c	-
	10	13.2 bcd	74.9 e	61.5 b	195 e
	20	18.0 e	74.1 e	63.2 b	156 c
	40	17.5 e	48.2 c	-	89.5 d
	Mean	15.2 z	70.8 z	66.2 y	77.1 c
					83.3 z
					126.1 y

^aMeans within columns and sets (abc, xyz) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.



proportional to photoperiod at maturity. In stems, the levels of free sugars at the peak flowering stage were similar under all photoperiod (Table 4), with the 18-hour treatment slightly lower than the 13-hour. At pod filling and at maturity, level was proportional to photoperiod. Under all photoperiods stem free sugar decreased as the pods reached maturity (Table 4) possibly due to redistribution from the stem to the growing pods. Free sugar in leaves was significantly lower under 8-hour than under longer photoperiods at the peak flowering stage (Table 4), possibly because of a light period insufficient for maximal photosynthesis. However, the level increased at the pod filling stages under both the 8 and 13-hour daylengths, but not under the 18-hour photoperiod (Table 4). This may be due to the stimulating effect of longer daylength on sugar movement out of the leaf. Free sugar concentration in seeds was proportional to photoperiod at all sampling dates, with maximum differences at pod filling, when the 18-hour treatment remained high relative to the 8- and 13-hour treatments (Table 4). The concentration decreased in all daylength treatments from peak flowering to pod filling. At maturity, however, the concentration increased slightly under 8- and 13-hour daylengths, while decreasing slightly under the 18-hour treatment. The increase in free sugar levels in seeds under the 8- and 13-hour daylengths was

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accompanied by a decrease in stems and roots (Table 4). Free sugar levels in pod wall decreased independently of photoperiod as maturation advanced (Table 4), possibly due to re-allocation to the growing seeds. In pea, the pod exports all of its assimilate to the enclosed seed (2).

Starch

In vegetative tissues starch levels did not consistently increase with photoperiod (Table 5), levels in roots being lower under the 18-hour day in both cultivars (Table 6). No cultivar difference in starch level was evident under any of the daylength regimes. However, differences were seen in stems of Black Turtle Soup under the 13- and 18-hour daylengths (Table 6) since it stored more starch in stems than Seafarer. Also, Black Turtle Soup, which showed a greater growth response to longer daylength (13, and see Chapter 3), had a higher level of starch in the stems under the longer daylengths. This response did not occur in Seafarer. The starch level was found significantly higher only in leaves of Black Turtle Soup under the 18-hour day (Table 6). The level of starch in seed and pod wall was not affected by increasing daylengths (Table 6). No cultivar differences for starch were found in these organs under the longer daylengths (13 and 18 hours).

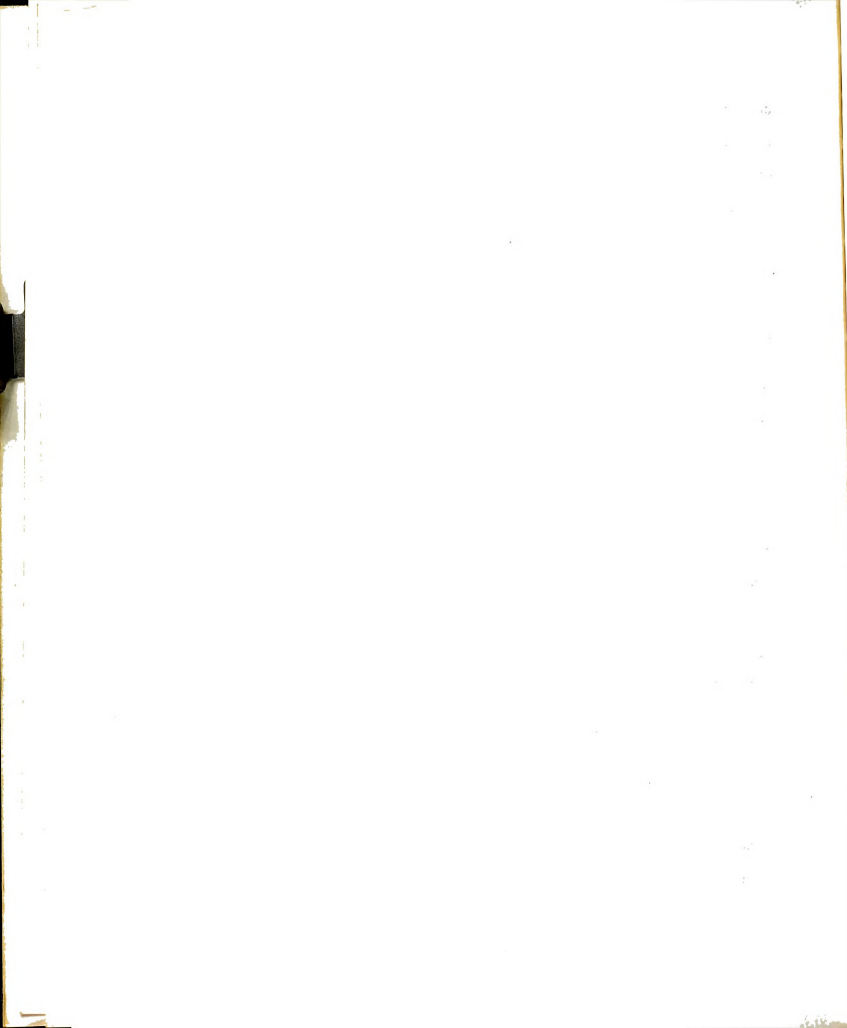


Table 5
Developmental Stages, Cultivars and Daylength Effects on Starch Level in
Various Plant Parts^a

		Mg Glucose per g Dry Weight				
		Root	Stem	Leaf	Seed	Pod
I.	Time					
	Peak flowering	20.4 b	115.2 b	89.9 b	-	56.5 b ^b
	Pod filling	16.4 a	117.4 b	28.7 a	389.0 c	357.8 c
	Maturity	21.8 b	25.3 a	-	343.3 b	38.4 a
II.	Cultivar					
	Black Turtle Soup	19.9 m	108.3 n	77.2 n	363 m	142.4 m
III.	Seafarer	19.1 m	63.6 m	41.3 m	369 m	159.4 n
	Daylength					
	8 hours	18.8 x	54.9 x	46.3 x	332 x	126 x
	13 hours	23.9 y	79.0 y	46.9 x	167 y	402 z
Interactions	18 hours	15.9 x	123.9 z	84.6 y	364 y	159 y
	I x II	*	**	**	n.s.	**
	I x III	**	**	**	**	**
I x II x III	II x III	n.s.	**	**	*	*
	I x II	**	**	**	n.s.	n.s.
	I x III	**	**	**	n.s.	n.s.

^aMeans followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeeds not separate from pod.

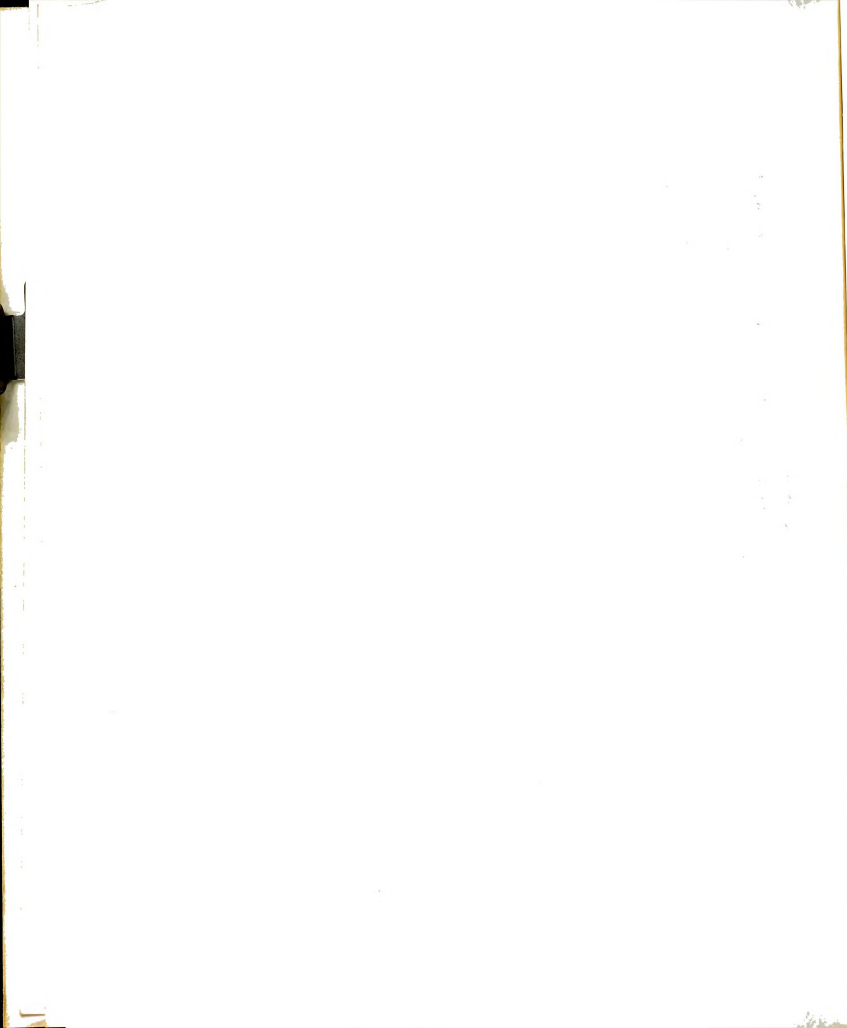
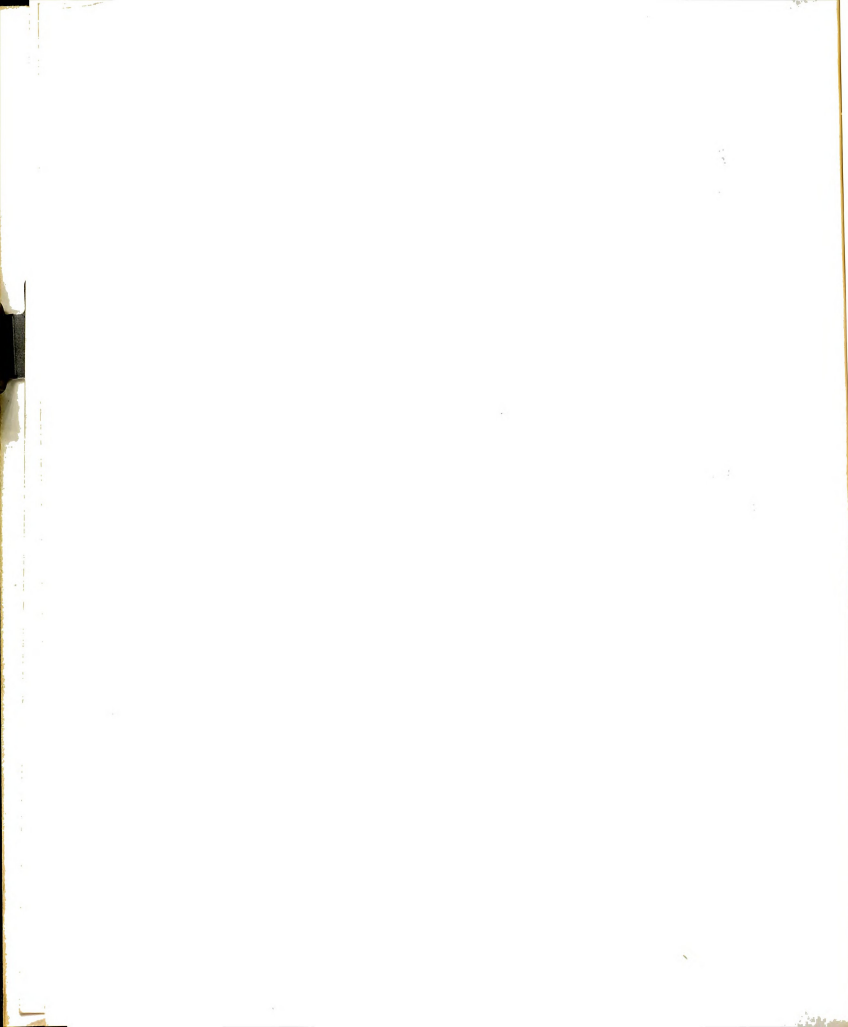


Table 6
Effects of Photoperiod and Cultivar on Starch Concentration (mg/g dry weight)
in Bean Tissues^a

Photoperiod (hours)	Cultivar	Tissue				
		Root	Stem	Leaf	Seed	Pod Wall
8	Black Turtle Soup	17.8 ab	62.6 a	49.3 a	227 a	107 a
	Seafarer	19.7 bc	47.2 a	43.3 a	250 b	145 b
	Mean	18.8 x	54.9 x	46.3 x	239 x	126 x
13	Black Turtle Soup	24.4 d	102.8 b	58.5 a	286 cd	167 c
	Seafarer	23.5 cd	55.3 a	35.3 a	287 d	168 c
	Mean	23.9 y	79.0 y	46.9 x	287 z	167 y
18	Black Turtle Soup	17.6 ab	159.5 c	123.9 b	268 bc	153 bc
	Seafarer	14.2 a	88.3 b	45.4 a	258 b	165 c
	Mean	15.9 z	123.9 z	84.6 y	263 y	159 y

^aMeans within columns and sets (abc, xyz) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



The pattern of starch accumulation in roots during pod development of the two cultivars showed that at the onset of flowering Black Turtle Soup stored more starch in roots than Seafarer (Table 7). This difference remained until the peak flowering stage. However, when seeds started to develop, the starch level in the roots of Black Turtle Soup dropped to the same level as Seafarer and subsequently there were no cultivar differences (Table 7). Black Turtle Soup stems contained higher starch levels in the flower initiation and pod filling stages than Seafarer; cultivar differences in starch level in the stems disappeared at maturity (Table 7). The high starch level in the stem of Black Turtle Soup may have been due to the indeterminate character and prolonged flowering behavior of this cultivar. This ability to continue vegetative growth after flower initiation can also result in higher starch level in leaves of Black Turtle Soup (Table 7). No differences were evident between cultivars for the starch level in seeds during pod development (Table 7). The starch level in immature pods of both cultivars was lower at the peak flowering stage. At the pod filling stage when seeds could be separated from the pod wall, starch levels in green pod wall of both cultivars rose considerably (Table 7). At maturity the seeds still contained a high

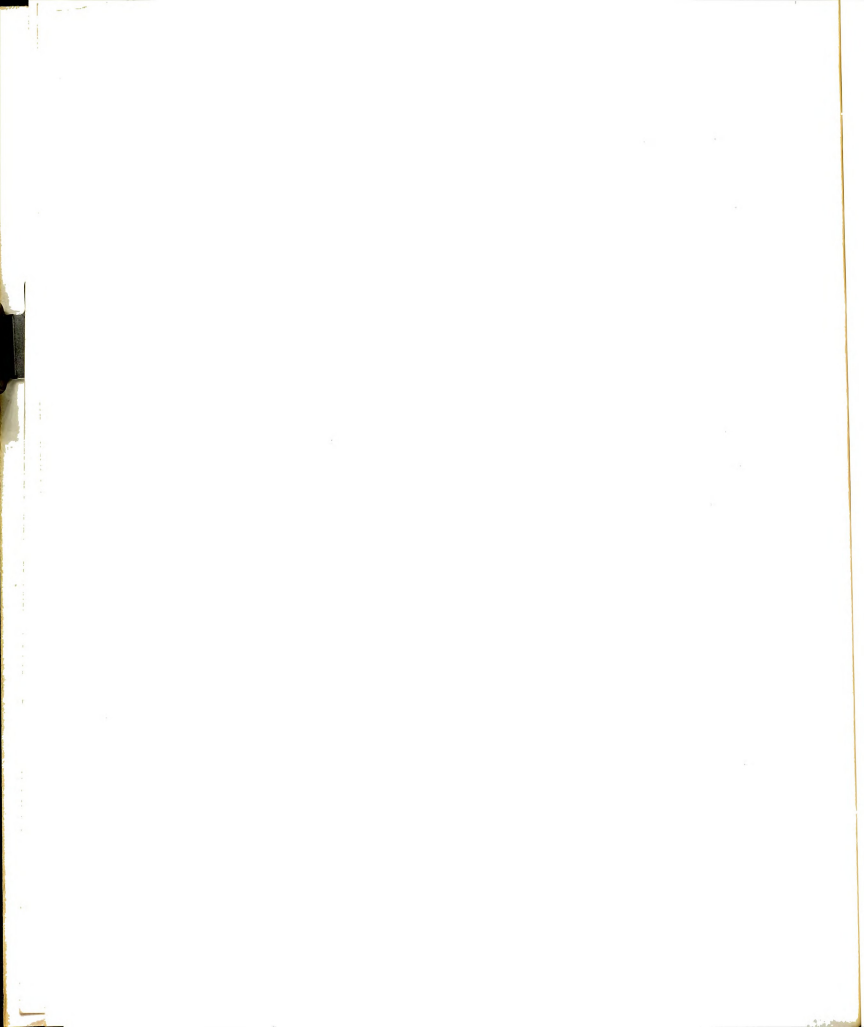
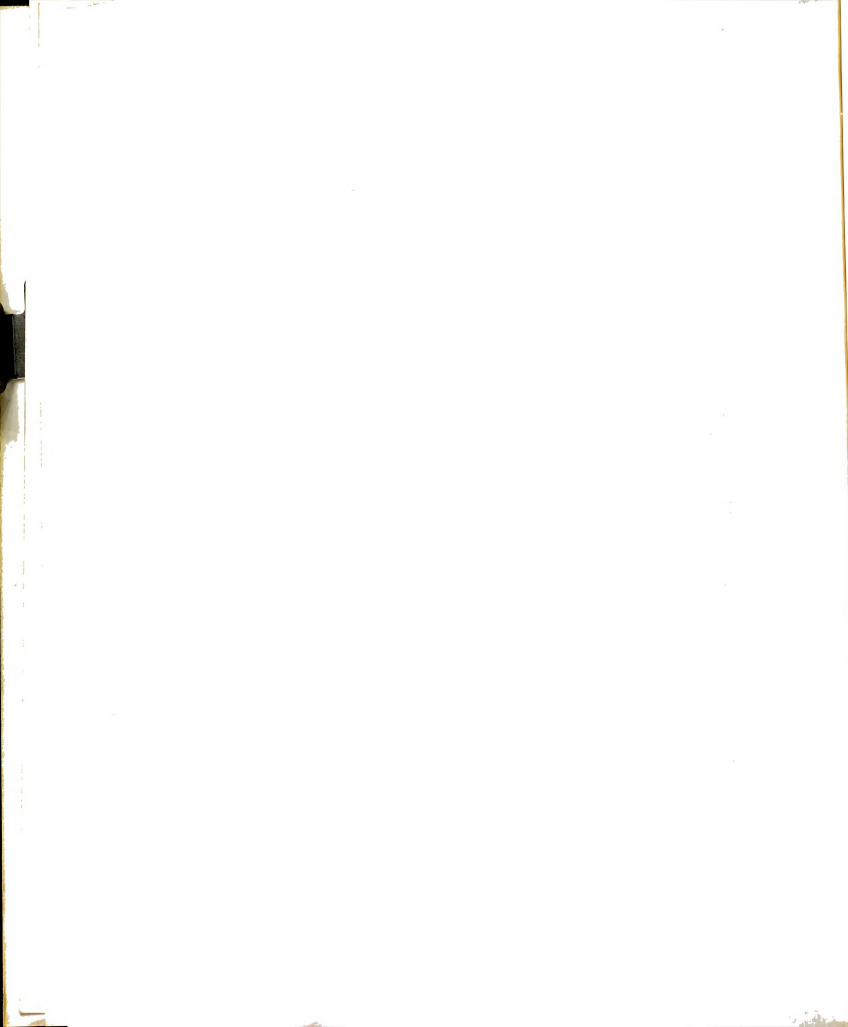


Table 7
Effects of Cultivar and Time of Sampling on Starch Concentration (mg glucose/g dry weight) in Bean Tissues^a

Time After Flower Initia- tion (days)	Cultivar	Tissue			
		Root	Stem	Leaf	Pod Wall
0	Black Turtle Soup	21.2 cde	62.4 b	37.1 a	-
	Seafarer	7.1 a	51.1 b	33.3 a	-
	Mean	14.1 p	56.7 q	35.2 p	-
10	Black Turtle Soup	23.0 e	142.9 d	121.4 c	54.9 b ^b
	Seafarer	17.9 bcd	87.5 c	58.3 b	58.2 b
	Mean	20.4 q	115.2 r	89.9 q	56.6 q
20	Black Turtle Soup	15.2 b	156.7 d	33.0 a	379.8 b
	Seafarer	17.5 bc	78.0 c	24.3 a	398.3 c
	Mean	16.4 p	117.4 r	28.7 p	389.0 q
40	Black Turtle Soup	21.6 cde	25.4 a	-	347.0 a
	Seafarer	22.0 de	25.2 a	-	339.5 a
	Mean	21.8 q	25.3 p	-	343.3 p

^aMeans within columns and sets (abc, pqr) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.



starch content (Table 7), but starch in the matured, yellow pod wall dropped to a very low level (Table 7).

Under the 8- and 13-hour daylength, the starch level in roots followed a similar pattern for both cultivar (Table 8). It was high at peak flowering, dropped markedly at the pod filling stage where carbohydrate reserve was in great demand for embryo development, and increased again at maturity where the final size of various organs had been achieved (Table 8). Under the 18-hour daylength the plants retained more flowers and pods (see Chapter 3, Table 1), thus more carbohydrates may have been available to support these reproductive organs and less was left for the root. This trend was especially evident at peak flowering (Table 8) where the starch level in root decreased. From peak flowering to pod filling where more than one-half of pod abscission had occurred, the plants had adjusted the number of pods to be retained. This may have caused a rise in starch level in roots at the pod filling stage under the 18-hour daylength. The interaction between daylength and stage of pod development on starch level in stems was shown in Table 8. The longer the daylength, the more starch was found in the stems at peak flowering and pod filling (10 and 20 days after flower initiation). At maturity, no significant differences were found for starch levels in stems between the 13- and 18-hour daylengths, but a significantly

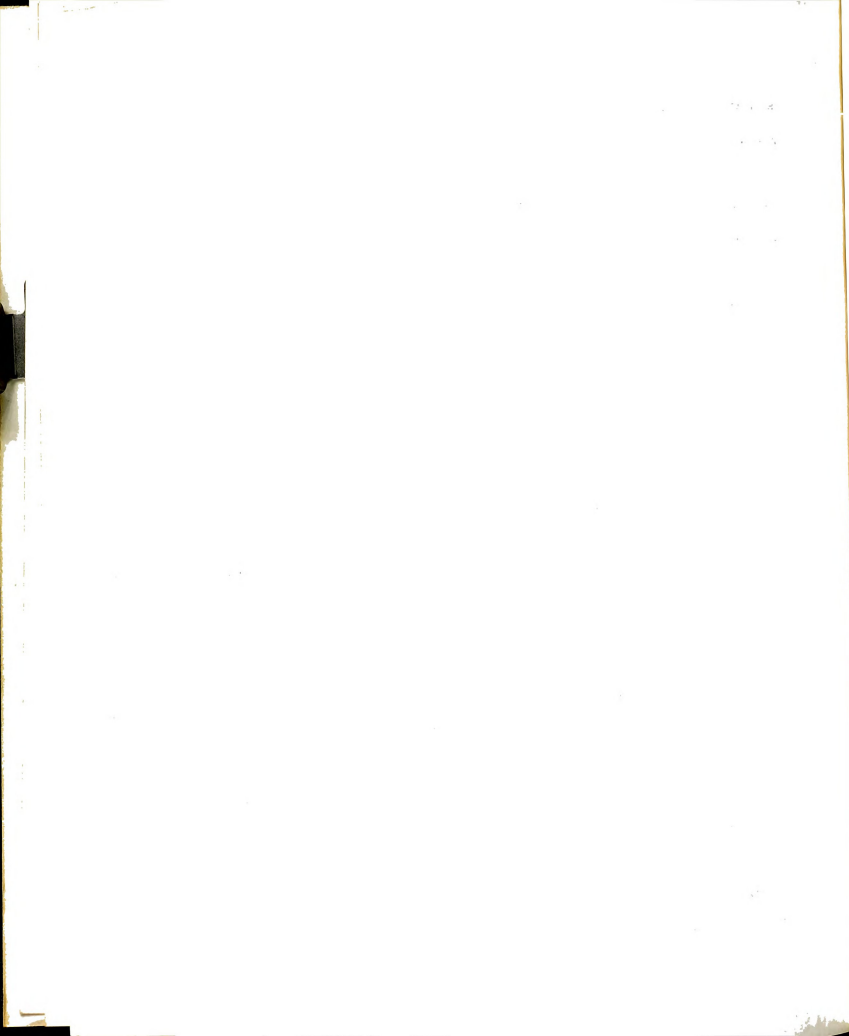
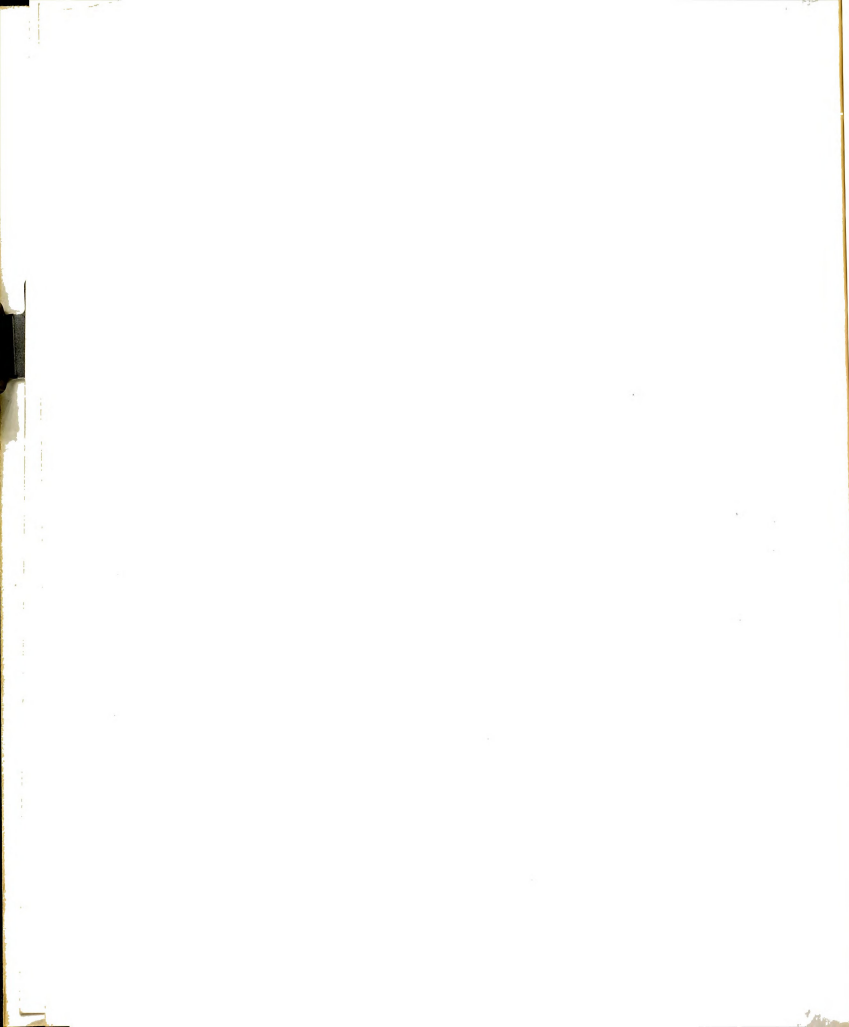


Table 8
Effects of Photoperiod and Time of Sampling on Starch Concentration
(mg glucose/g dry weight) of Bean Tissues^a

Photoperiod (hour)	Time After Flower Initia- tion (days)	Tissue				
		Root	Stem	Leaf	Seed	Pod Wall
8	0	14.2 ab	56.7 b	35.2 b	-	-
	10	25.5 cd	83.1 bc	75.5 c	-	52.4 b
	20	12.5 a	69.3 b	17.0 a	367 b	309.2 c
	40	18.3 b	12.4 a	-	297 a	16.4 a
	Mean	17.6 x	55.4 x	42.6 x	332 x	126 x
13	0	14.2 ab	56.7 b	35.2 b	-	-
	10	28.1 d	95.5 cd	47.3 b	-	56.3 b
	20	17.5 b	108.1 d	46.6 b	442 c	418.1 e
	40	26.2 d	33.5 a	-	361 b	28.2 a
	Mean	21.5 y	73.4 y	43.0 x	401 z	167 y
18	0	14.2 ab	56.7 b	35.2 b	-	-
	10	7.8 a	167.1 e	146.8 d	-	61.0 b
	20	15.0 b	174.7 e	22.4 ab	357 b	346.0 d
	40	20.9 bc	29.9 a	-	371 b	70.5 b
	Mean	15.5 x	107.1 z	68.1 y	364 y	159 y

^aMeans within columns and sets (abc, xyz) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

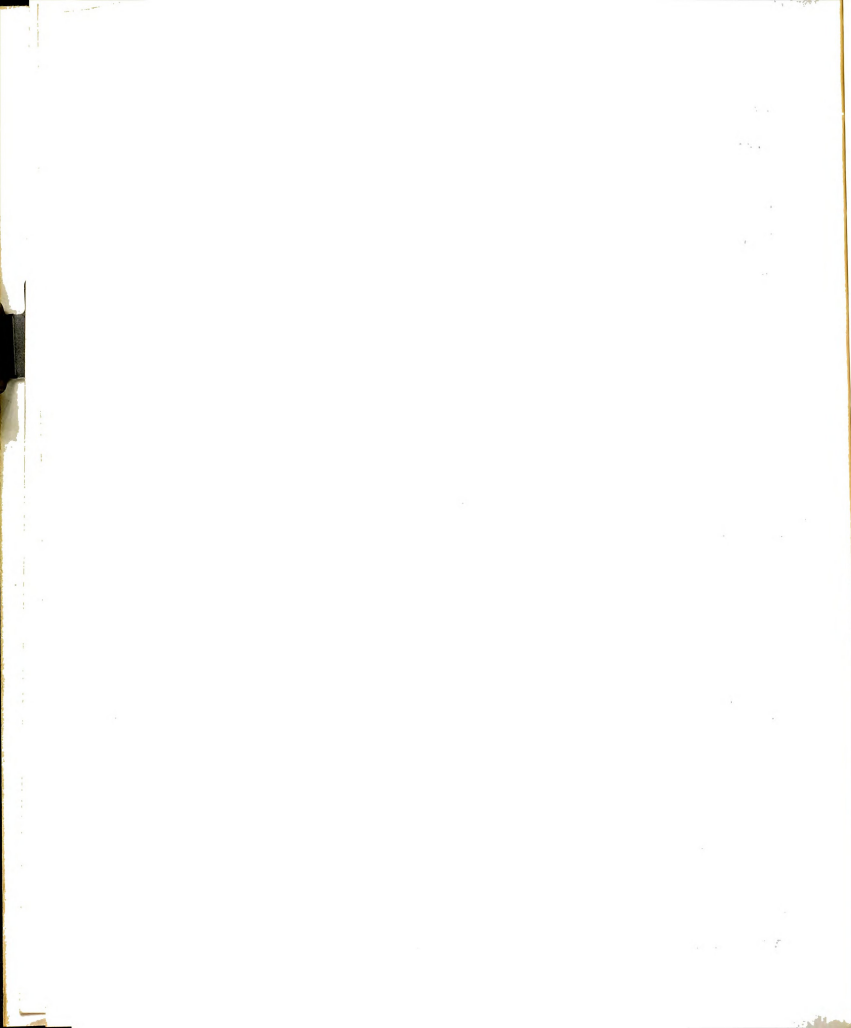
^bSeed not separate from pod.



lower starch level was found under the 8-hour regime (Table 8). The starch level in leaves reached the maximum at peak flowering and then declined rapidly. This was seen in both 8- and 18-hour daylength treatment (Table 8), while in the 13-hour day the starch level did not drop at the pod filling stage. No explanation for this is apparent. The starch level in seed and pod wall reached a maximum at pod filling and declined at maturity (Table 8). The rate of decline was more rapid in the pod wall than in the seed (Table 8) possibly due to the export of starch from pod wall to seed as was shown in field pea (2). This pattern was seen in all three daylength regimes, except no decrease was seen in starch level in the seed at maturity in the 18-hour day (Table 8). Perhaps the great decrease in starch in stems from pod filling to maturity may be related to the changes in the level of starch in seeds under this 18-hour day (Table 8).

Relationship of Pod Abscission
to Levels of Available
Carbohydrates

Increasing the daylength during the reproductive phase increased plant weight, seed yield, and pod retention in these two dry bean cultivars. In this study increasing the daylength after flower initiation also caused an increase in free sugar and starch levels in roots, stems and leaves. A relationship may exist between available carbohydrate in the vegetative organs and percentage of



pod abscission as was suggested in the nutritional hypothesis first put forward by Mason (9). In this study no precise relationship could be established between percentage of pod abscission and available carbohydrate levels in the vegetative organs of these two cultivars (Table 9). However there was a general trend of negative correlation between percentage of pod abscission and available carbohydrates in most organs. This indicated that the higher the carbohydrate levels, the lower the abscission rate. The data presented here, though consistent with Mason's explanation, do not prove the level of available carbohydrates to be the cause of pod abscission in beans. Since abscission is a complex process, other factors than carbohydrate levels, such as nitrogenous levels or even endogenous hormonal levels, may play a part in determining pod abscission. Future studies toward establishing the balance of these factors in relation to pod abscission are needed.

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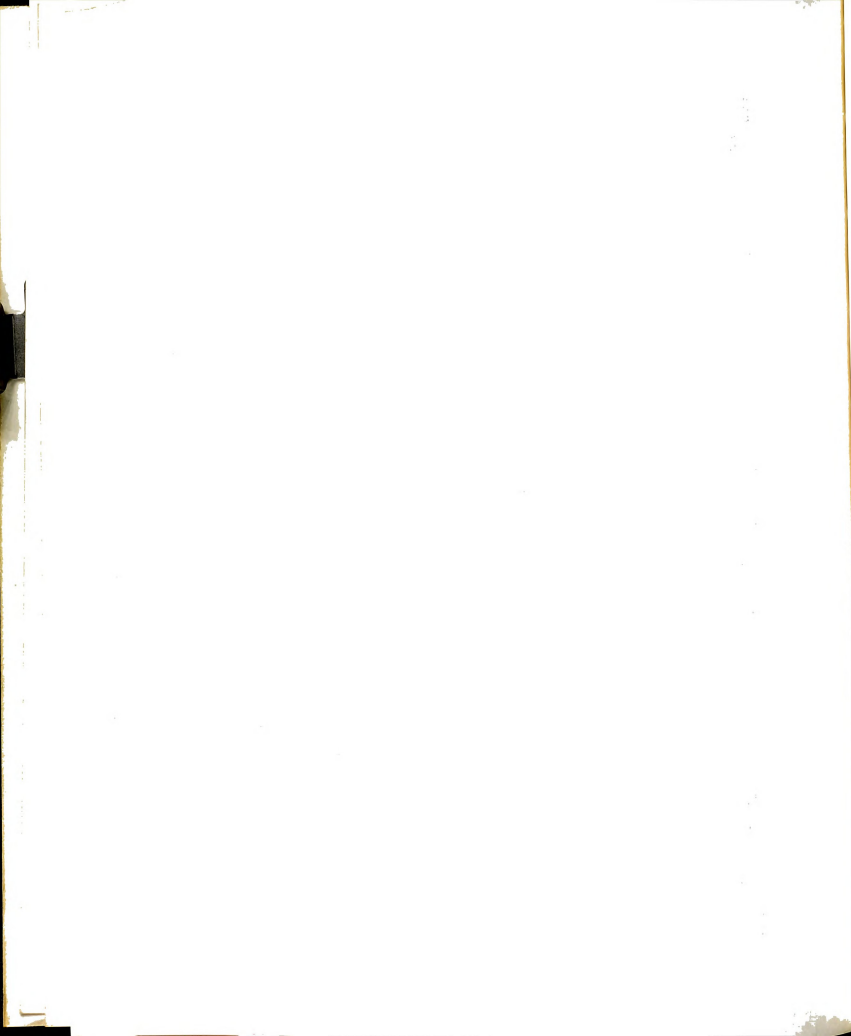
Table 9

Correlation Coefficients Between Percentage of Pod Abscission and Available Carbohydrate in the Vegetative Tissues of the Two Drybean (*Phaseolus vulgaris* L.) Cultivars Grown Under 3 Daylengths

Characters	Black Turtle Soup				Seafarer			
	8 Hours	13 Hours	18 Hours	8 Hours	13 Hours	8 Hours	18 Hours	
I. At pod filling stage								
Free sugar in root	.05	-.41	.11	-.48	.31		.41	
Free sugar in stem	.11	.16	.07	-.70 ^a	-.33		-.33	
Free sugar in leaf	-.26	-.39	.15	-.09	.12		.33	
Starch in root	.43	.22	.15	-.39	-.10		-.25	
Starch in stem	-.46	-.75 ^b	.41	-.88 ^b	-.33		-.13	
Starch in leaf	-.01	-.57	.45	.14	.67 ^b		.07	
II. At maturity								
Free sugar in root	.10	-.21	-.12	-.27	-.23		.32	
Free sugar in stem	.63 ^b	-.61 ^a	-.06	-.38	-.66 ^a		.33	
Starch in root	.58	.01	-.53	-.30	-.09		.35	
Starch in stem	-.01	-.57	-.38	-.35	-.01		-.29	

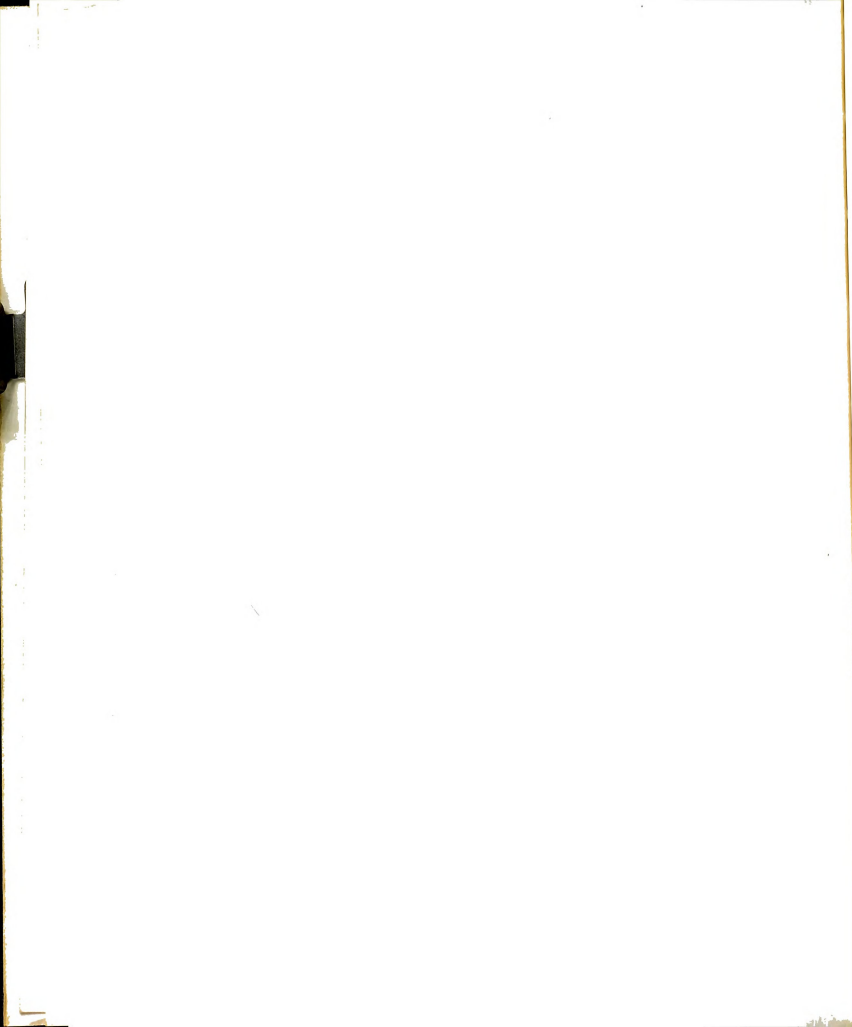
^aSignificant at 5% level.

^bSignificant at 1% level.

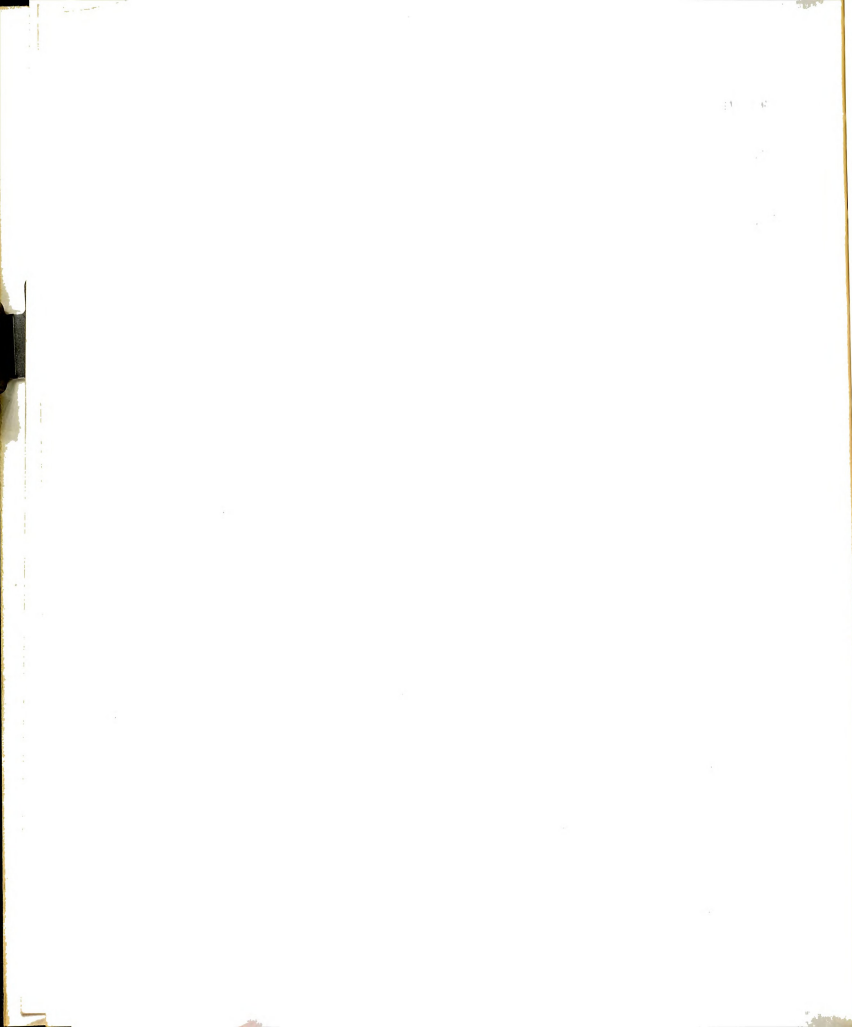


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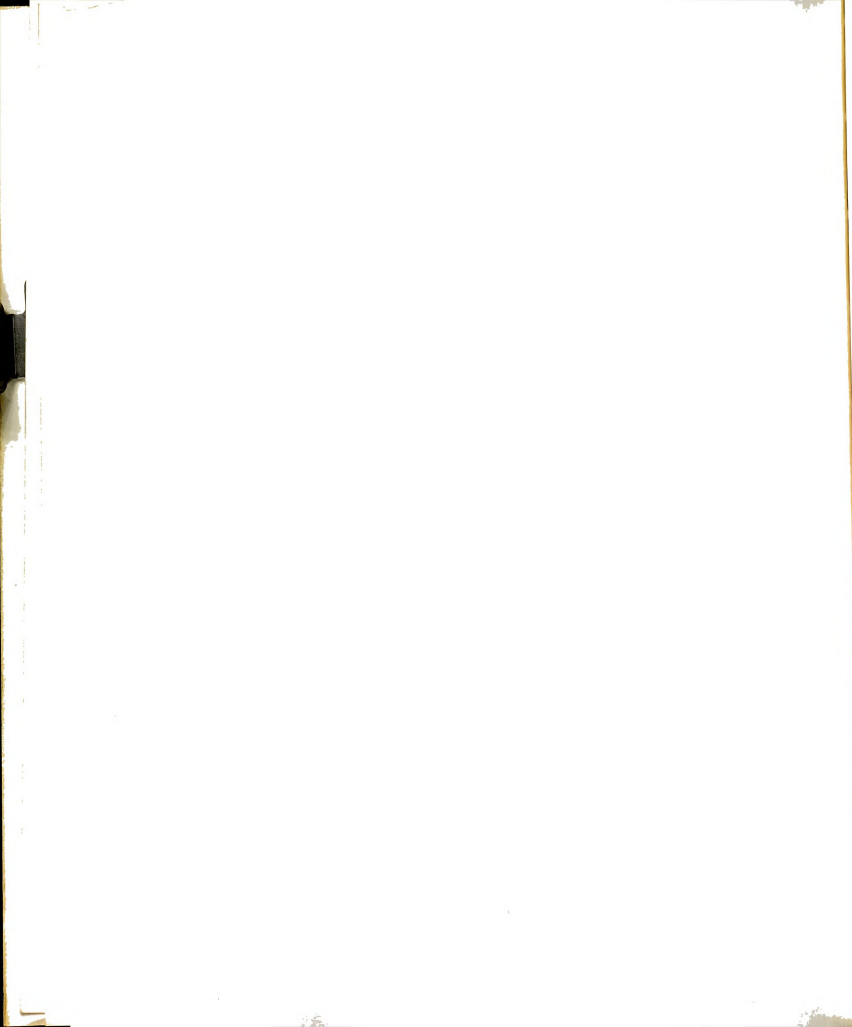
CHAPTER 5

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L.

IV. GROWTH AND POD ABSCISSION AS AFFECTED BY CARBON DIOXIDE LEVELS

Abstract

Abscission of young pods was studied in the greenhouse in two Phaseolus vulgaris L. cultivars over two seasons. Plants were grown under 300 (ambient air) and 800 ppm carbon dioxide after their flower buds became visible. High carbon dioxide level reduced pod abscission, increased plant size and seed yield. The relationship between pod abscission and growth is discussed.



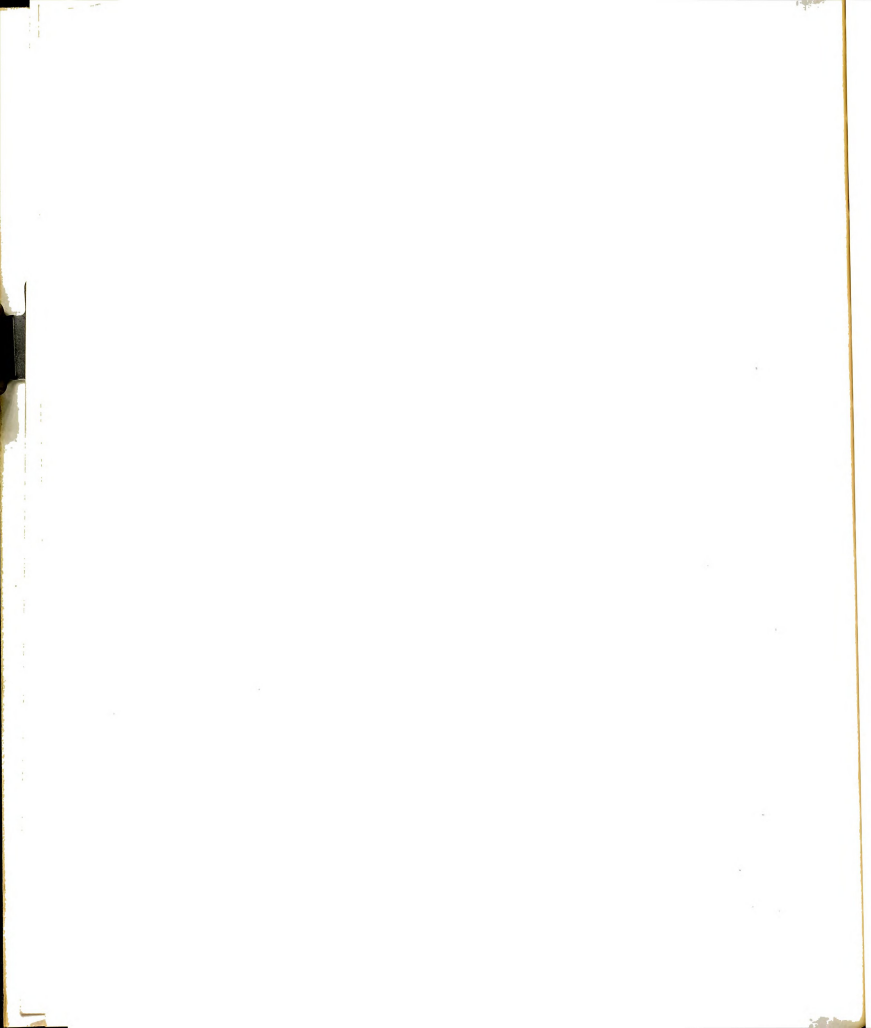
Introduction

Since the report of Wittwer (5) on increasing crop yield by carbon dioxide enrichment, numerous reports have confirmed his observations. Yields of field-grown soybean have been increased nearly 30% by carbon dioxide enrichment (1,200 ppm) (4), as a result of both an increase in number of pods filled and a decrease in pod abortion. In cotton an increase in carbon dioxide concentration in the atmosphere decreased abscission of floral buds and bolls (3). In barley (2), rice (6), and soybean (4) increasing the carbon dioxide concentration during the reproductive phase increased yield.

Growing dry bean plants under long photoperiods after flowering increased yield (see Chapter 3). This was associated with less pod abscission and larger plants. The study reported here was designed to determine the effects of increasing carbon dioxide levels during the pod development period on growth and pod abscission of dry beans.

Materials and Methods

Two dry bean cultivars, "Seafarer" and "Black Turtle Soup," were grown in the greenhouse at East Lansing in the spring of 1975 and 1976 (for procedures, see Chapter 3). When the plants reached the flower initiation stage, 30 of each cultivar were placed in each of two clear polyethylene chambers (7.2 by 3 by 3 meters).



In each chamber air drawn in from one end was released at the other end. Carbon dioxide was fed into the mixing chamber of carbon dioxide and air. The gas mixture was introduced into one chamber with a fan at the rate of 148 cubic meters per hour. The concentration at the plant level was maintained in the range of 750 to 850 ppm, as maintained with an infra-red gas analyzer. This was continued for 40 days.

Ambient air was blown into the second chamber at the same rate. The carbon dioxide concentration was in the range of 300 to 350 ppm. Three harvests were made, pod abscission and growth were measured as before (Chapter 3).

Results and Discussion

Pod Abscission

Plant subjected to a high carbon dioxide level produced more flowers and retained more pods than the control (Table 1). Response was similar in both cultivars (Table 2). Data for both 1975 and 1976 showed the same trends (Table 1). Pod abscission was reduced more by carbon dioxide level in Black Turtle Soup than in Sea-farer (Table 2). This was associated with larger plant (Table 3), more leaves, greater leaf area and leaf weight per plant in Black Turtle Soup (Table 4).

Pod abscission was not recorded at peak flowering (10 days after flower initiation). At pod filling stage

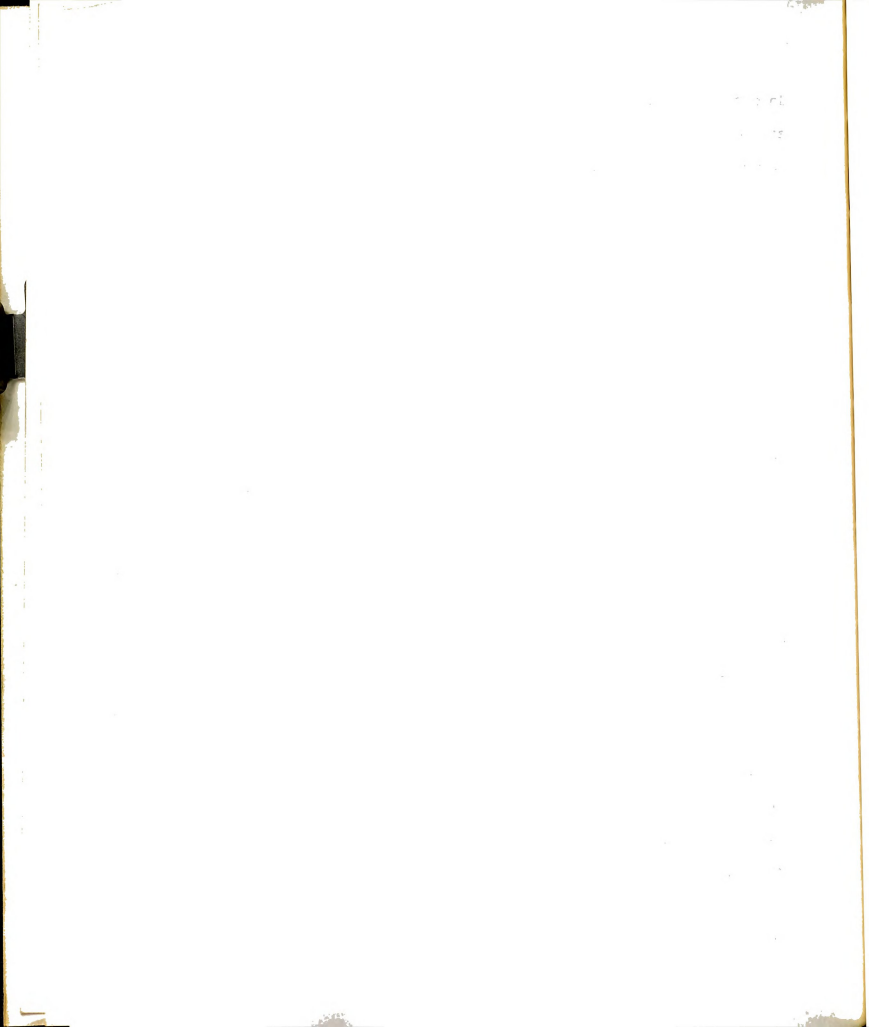


Table 1

Stages of Pod Development and Carbon Dioxide Levels Effect on Number of Flowers,
Number of Pods and Percentage of Abscission in Two Dry Bean Cultivars
Grown Under the Two Seasons^a

	No. Flowers		No. Pods		% Abscission	
	1975	1976	1975	1976	1975	1976
I. Developmental Stages						
Peak flowering	16.8 a	12.3 a	14.3 c	10.9 b	-	-
Pod filling	15.8 a	12.9 a	11.5 b	8.2 a	25.1 a	28.4 a
Maturity	15.7 a	15.5 b	8.8 a	7.3 a	41.1 b	47.3 b
II. Cultivar						
Black Turtle Soup	10.5 m	8.3 m	8.8 m	6.5 m	21.9 m	20.5 m
Seafarer	21.6 n	18.8 n	14.3 n	11.0 n	44.3 n	55.2 n
III. CO ₂ Level						
300 ppm	14.6 x	10.4 x	9.3 x	6.0 x	44.2 y	46.5 y
800 ppm	17.6 y	16.7 y	13.8 y	11.5 y	22.0 x	22.2 x
Interactions						
I x II	*	n.s.	**	**	n.s.	n.s.
I x III	n.s.	n.s.	**	n.s.	n.s.	n.s.
II x III	n.s.	n.s.	n.s.	n.s.	n.s.	*
I x II x III	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

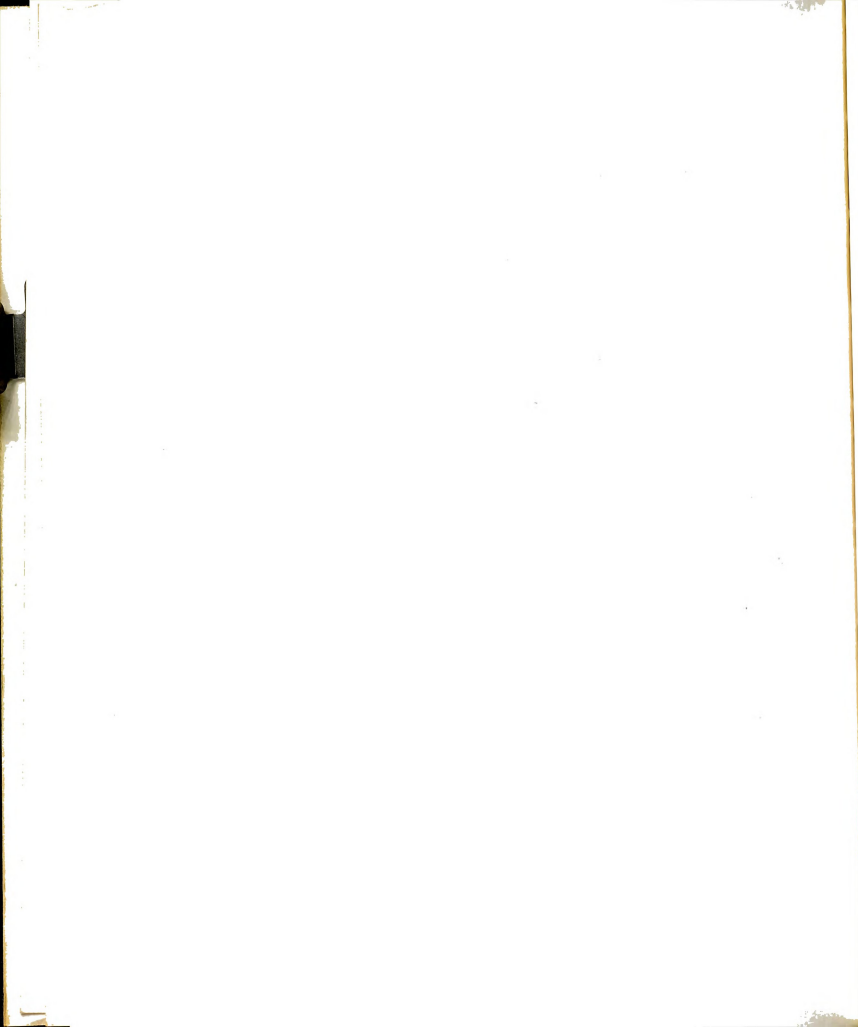


Table 2

Effects of Carbon Dioxide Levels on Number of Flowers, Number of Pods Retained, and Percentage of Pod Abscission in Two Dry Bean Cultivars Grown under the Two Seasons (data are means at all harvesting stages)^a

Carbon Dioxide Levels (ppm)	Cultivar	No. Flowers/Plant		No. Pods/Plant		% Pod Abscission	
		1975	1976	1975	1976	1975	1976
300	Black Turtle Soup	9.2 a	5.4 p	5.5 a	4.1 p	34.48 b	26.09 q
	Seafarer	20.0 c	15.3 r	8.1 b	7.9 q	53.88 c	66.88 s
800	Black Turtle Soup	11.9 b	11.3 q	11.4 c	9.0 q	9.30 a	14.88 p
	Seafarer	23.3 d	22.0 s	13.7 d	14.1 r	34.75 b	43.57 r

^aMeans within a given parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

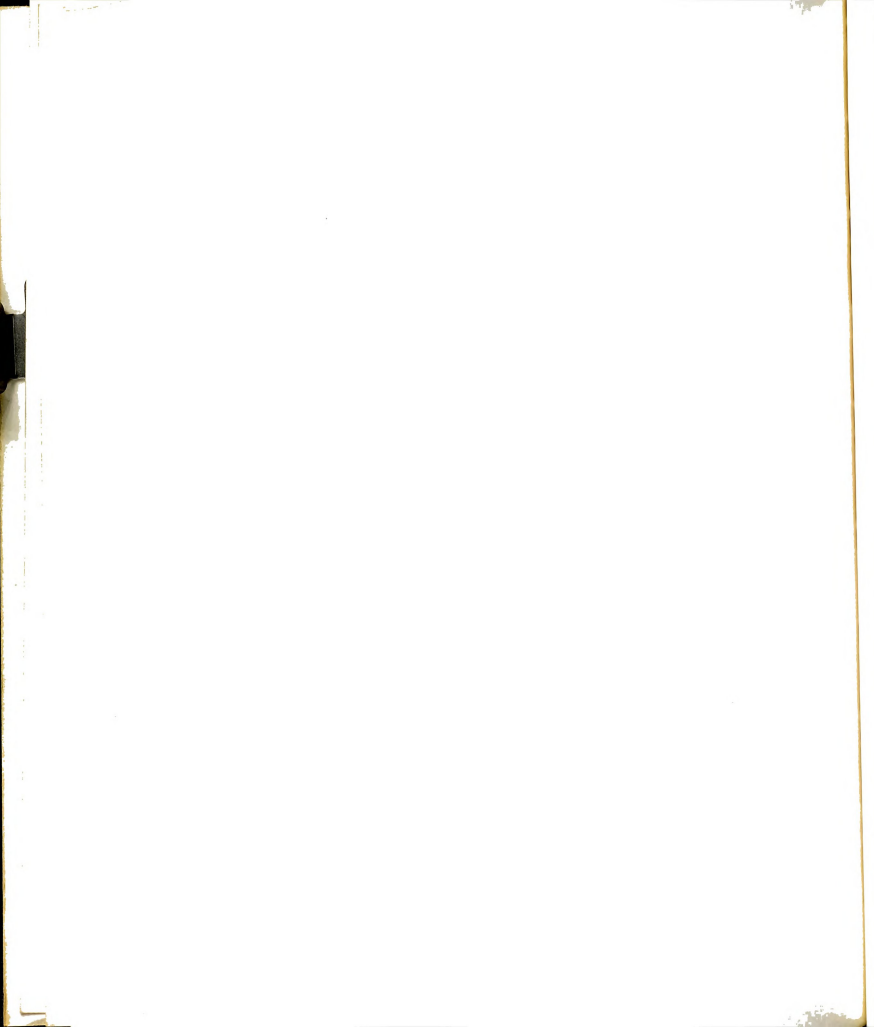


Table 3

Effects of Carbon Dioxide Levels on Dry Weight Per Plant of Root, Stem and Total Plant Weight in Two Dry Bean Cultivars Grown Under the Two Seasons (data are means at all harvesting stages)^a

Carbon Dioxide Levels (ppm)	Cultivar	Root Wt./Plant (g)		Stem Wt./Plant (g)		Total Plant Wt. (g)	
		1975	1976	1975	1976	1975	1976
300	Black Turtle Soup	1.0 a	1.2 q	1.3 a	1.0 p	7.0 a	5.9 q
	Seafarer	1.0 a	0.7 p	1.4 a	0.8 p	6.8 a	3.9 p
800	Black Turtle Soup	1.6 c	2.1 s	2.3 c	2.2 r	13.4 c	10.1 s
	Seafarer	1.4 b	1.4 r	1.9 b	1.9 q	11.6 b	7.6 r

^aMeans within a given parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

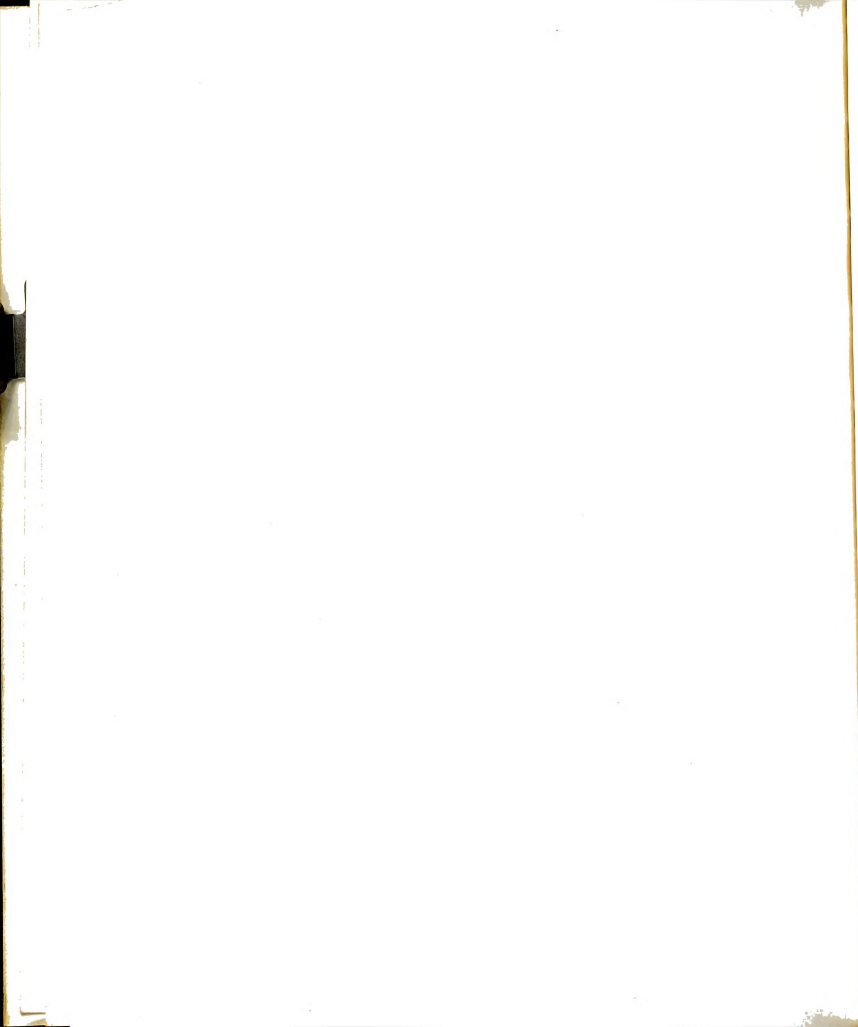
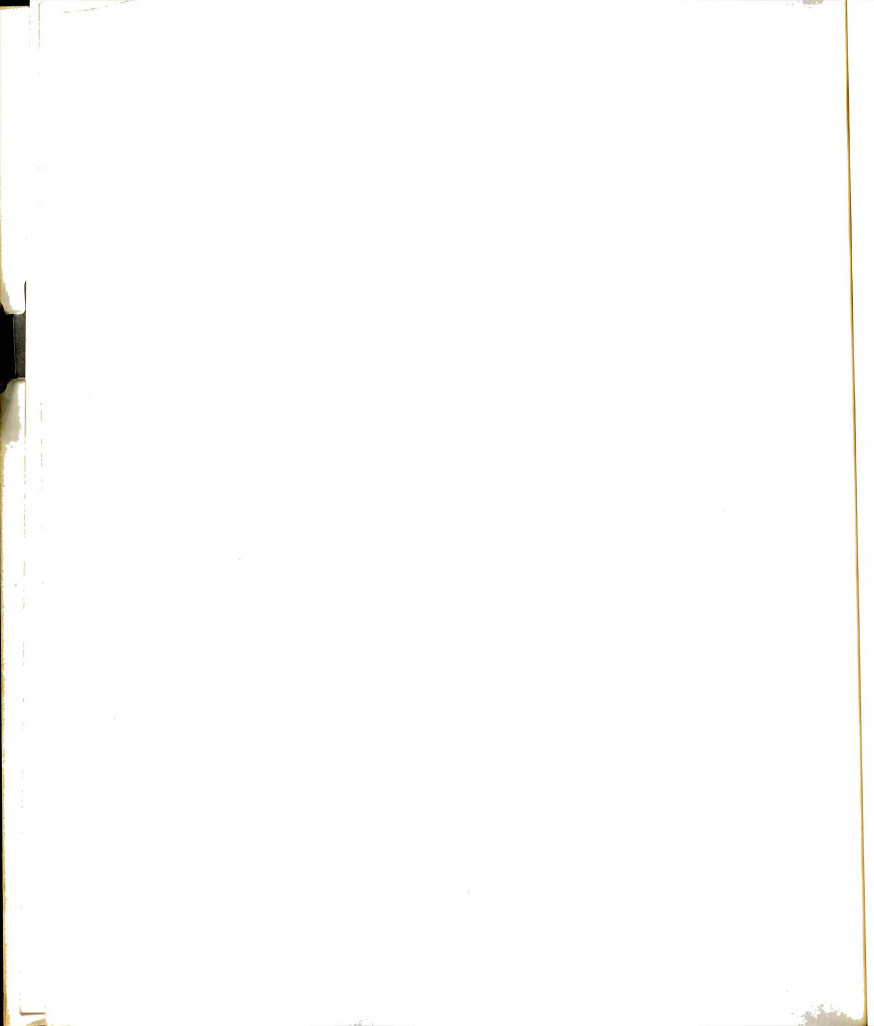


Table 4

Effects of Carbon Dioxide Levels on Leaf Area Per Plant, Number of Leaf Per Plant and Leaf Weight Per Plant in Two Dry Bean Cultivars Grown Under the Two Seasons (data are means at all harvesting stages)^a

Carbon Dioxide Levels (ppm)	Cultivar	Leaf Area/Plant (cm ²)		Number Trifoliolate Leaf/Plant		Leaf Weight/Plant (g)	
		1975	1976	1975	1976	1975	1976
300	Black Turtle Soup	668 a	420 p	11 a	11 p	2.4 b	2.5 q
	Seafarer	659 a	342 p	13 a	10 p	2.0 a	1.6 p
800	Black Turtle Soup	930 b	1043 r	19 b	14 r	5.0 d	6.3 s
	Seafarer	739 a	723 q	13 a	12 q	3.4 c	3.2 r

^aMeans within a given parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



and at maturation, high carbon dioxide reduced pod abscission in both cultivars (Table 1, Appendix C tables C-1 and C-2). About half of the pod abscised at pod filling stage in Black Turtle Soup under the control treatment, but only one-third were lost at this same stage when this cultivar was grown under high carbon dioxide (Table C-1). However, for Seafarer, a cultivar with a high abscission level, about two-thirds of pod loss occurred at the pod filling stage when they were grown under ambient carbon dioxide. This ratio was decreased to one-half when high carbon dioxide level was supplied to the plants (Table C-1). Similar results were obtained in 1976 (Table C-2). Two interpretations are offered for these results. First, high competition for carbohydrates occurred during the early stages of pod development, and this competition will determine the amount of pods to be retained. This was supported by the high portion of pods abscised at pod filling in relation to that at maturity when plants were grown under a low carbon dioxide level. The second explanation was shown in the drop of this ratio of pod abscision at pod filling and at maturity with carbon dioxide enrichment. This indicated that more carbohydrate was made available under a high carbon dioxide regime for feeding young pods at this stage. Percentage of pod abscission obtained by carbon dioxide enrichment was similar to that obtained by increasing daylength, as reported earlier (Chapter 3).

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Leaf Development

With high carbon dioxide levels more leaves per plant were obtained. This resulted in greater leaf area and higher leaf weight produced by the plant (Table 5). With a low carbon dioxide level there was no significant difference in number of leaves and leaf area per plant of the two cultivars, but when the plants were subjected to the higher carbon dioxide level cultivar differences in number of leaves and leaf area were obtained. Black Turtle Soup exhibited greater response to increasing carbon dioxide than Seafarer (Table 4). This response occurred in both the 1975 and 1976 experiments (Table 4). This high response to increasing carbon dioxide level in Black Turtle Soup can be related to its growth habit. Black Turtle Soup is a semi-vine bean and the plant can still make some vegetative growth after flowering. Therefore, when more carbohydrate was synthesized under with a high carbon dioxide level, vegetative growth may also be promoted and this resulted in more leaves being produced. For Seafarer, a determinate type, vegetative growth does not continue much after the plant reaches the reproductive phase, therefore, more carbohydrate produced by carbon dioxide enrichment did not result in more leaves being produced (Table 4). However, the high carbon dioxide treatment did result in lower percentage of pod abscission. A negative correlation between percentage

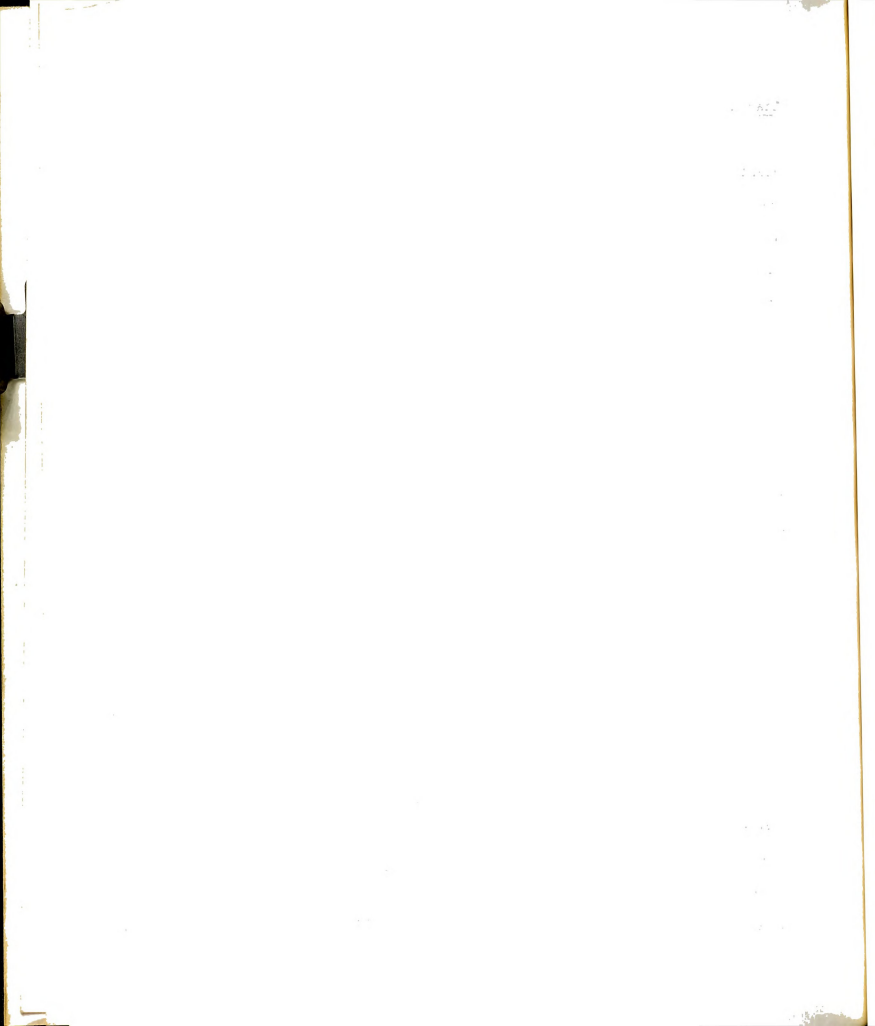
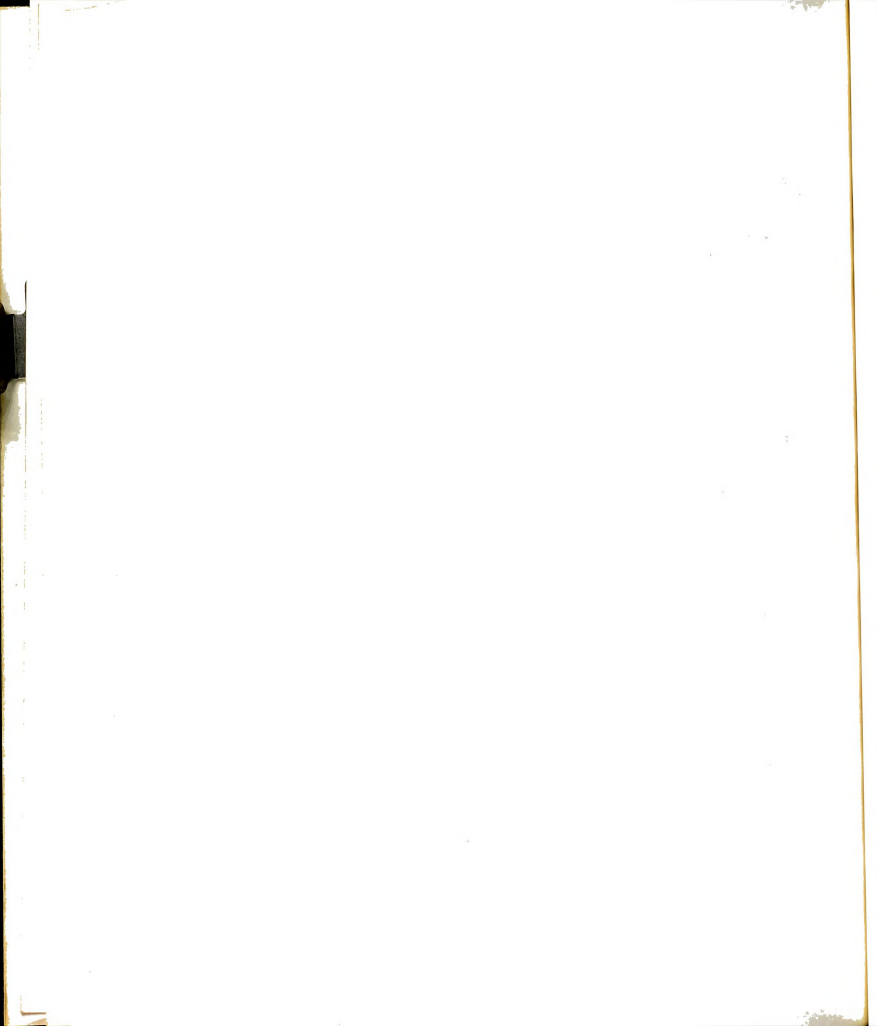


Table 5

Stages of Pod Development and Carbon Dioxide Levels Effect
on Number of Leaf and Leaf Area per Plant in Two Dry
Bean Cultivars Grown Under the Two Seasons^a

	No Leaf		Leaf Area/ Plant (cm ²)	
	1975	1976	1975	1976
I. Developmental Stages				
Peak flowering	15.8 b	10.7 a	742 a	549 a
Pod filling	12.6 a	12.9 b	756 a	716 b
Maturity	-	-	-	-
II. Cultivar				
Black Turtle Soup	15.2 m	12.3 n	799 m	732 n
Seafarer	13.3 m	11.3 m	699 m	533 m
III. CO ₂ Level				
300 ppm	12.2 x	10.2 x	663 x	381 x
800 ppm	16.2 y	13.4 y	835 y	883 y
<u>Interactions</u>				
I x II	*	**	n.s.	n.s.
I x III	n.s.	**	**	**
II x III	**	*	**	**
I x II x III	*	n.s.	n.s.	n.s.

^a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



of pod abscission and leaf area per plant was also noticed in both cultivars under both levels of carbon dioxide (Table 6). However, at 300 ppm carbon dioxide, at which leaf area may be more important in supplying carbohydrate for pod retention, a highly significant correlation occurred. This significant correlation was seen in the indeterminate cultivar, Black Turtle Soup. In Seafarer, the determinate type bean, no significant correlation between leaf area and percentage of pod abscission was found. At the high carbon dioxide level (800 ppm), more ideal for photosynthesis, leaf area per se may not be as critical for supporting the young pods, therefore, no significant correlation between leaf area and pod abscission was found (Table 6).

The number of leaves per plant was significantly lower at the pod filling stage as compared to peak flowering (Table 5). This was due to the loss of some old leaves at pod filling. However, leaf area and leaf weight per plant were not significantly different at these two stages. This indicated that very little or no leaf growth occurred after peak flowering in 1975. This was in contrast to the 1976 data where there were indications of leaf growth after this stage (Table 5).

Plant Development

Greater growth and larger plants were observed with the carbon dioxide enrichment treatment. Increase

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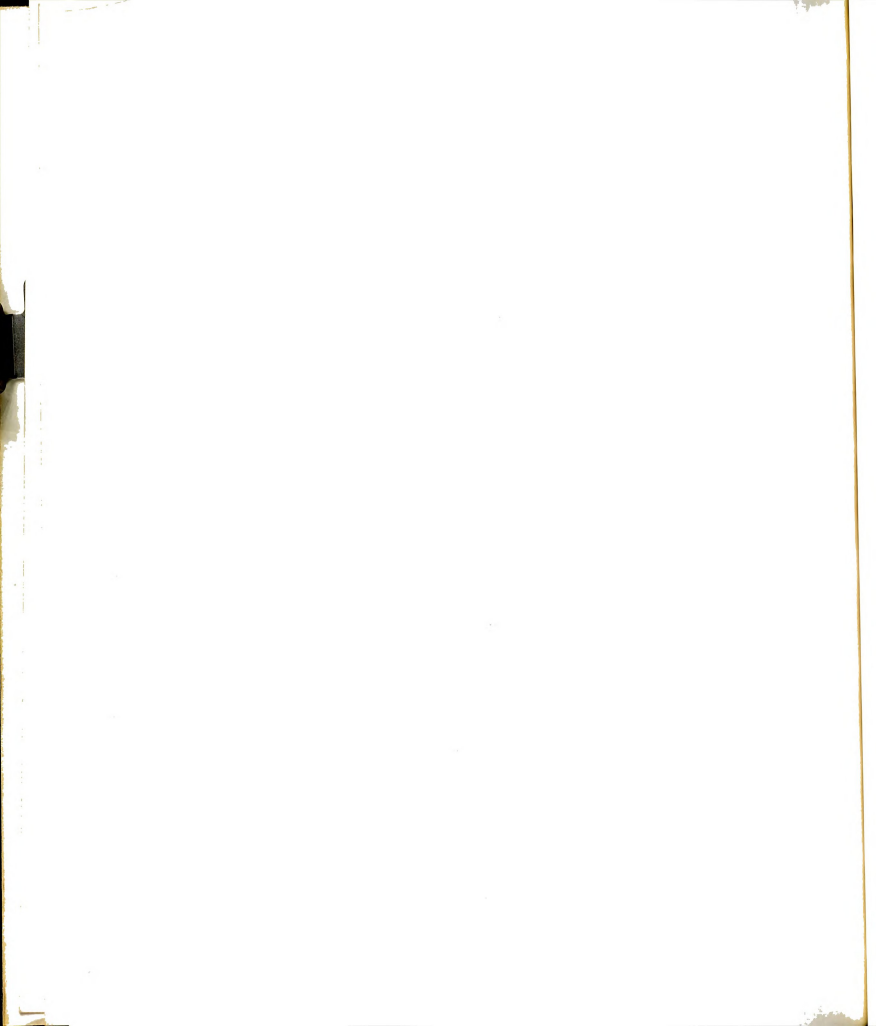
Table 6

Correlation Coefficients Between Percentage of Pod Abscission and Other Growth Characters in Two Dry Bean Cultivars Subjected to Different Carbon Dioxide Levels After Flowering (data taken at pod filling stage)

Characters	Black Turtle Soup		Seafarer	
	300 ppm CO ₂	800 ppm CO ₂	300 ppm CO ₂	800 ppm CO ₂
Root weight	.62 ^a	-.33	-.24	.42
Stem weight	-.03	-.68 ^a	-.23	-.11
Leaf weight	-.80 ^b	-.36	-.32	.08
Leaf number	-.39	-.02	.09	.03
Leaf area	-.76 ^b	-.47	-.22	-.14

^aSignificant at 5% level.

^bSignificant at 1% level.



in root, stem, leaf and total plant weight occurred in both cultivars (Table 3) in both years of study. The increase in vegetative growth with the high carbon dioxide level in both cultivars was associated with a higher number of pods retained (Table 2).

Black Turtle Soup produced more dry weight in the vegetative organs than the Seafarer (Table 3). The greater growth response with high carbon dioxide enrichment was also evident by reduced pod abscission in Black Turtle Soup. Whether the higher vegetative weight determined pod abscission was not known, but the data show a relation between these characters (Table 6).

Total plant weight was greater with the carbon dioxide enriched treatment after flowering, while under the ambient carbon dioxide level this weight was decreased (Table 2). This may be due to the loss of senescing leaves at maturation. The slightly higher total plant weight at maturity under high carbon dioxide enrichment was due to the increased weight of reproductive organs (seeds and pods). This was also seen in decreased weight of root and stem (Table C-4) from peak flowering to maturation. This loss in vegetative weight compensated for an increase in reproductive weight. This dynamic situation in weight allocation affected the yield of a plant. Competitive ability of various organs at any developmental stage of plants grown under a particular environment would undoubtedly influence pod abscission.

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Seed Yield

Plants growing under the high carbon dioxide level (800 ppm) produced more mature seeds. This was seen in both cultivars (Table 7). The more seed produced, the greater the seed weight per plant. The high number of seed produced under the high carbon dioxide level resulted in slightly smaller seeds produced in 1975 (Table 7). This may have been due to the competition between the more numerous seeds in the pods. However, this seed size difference was not observed in 1976 (Table 7).

Cultivar differences in seed yield existed in response to increasing carbon dioxide concentration. Under the high carbon dioxide level, Black Turtle Soup produced more seed and had higher yield than Seafarer in both years (Table 7). This greater response by Black Turtle Soup was also seen in vegetative growth and pod abscission.

The correlation between percentage of pod abscission and other reproductive structures at pod filling was given in Table 8. At the ambient carbon dioxide level, the number of flowers produced in both cultivars was positively correlated to percentage of pod abscission. This suggested that under this carbon dioxide level at the pod filling stage, competition for carbohydrate occurred between the flowers and young pods. The more reproductive organs, the more competitive force and the

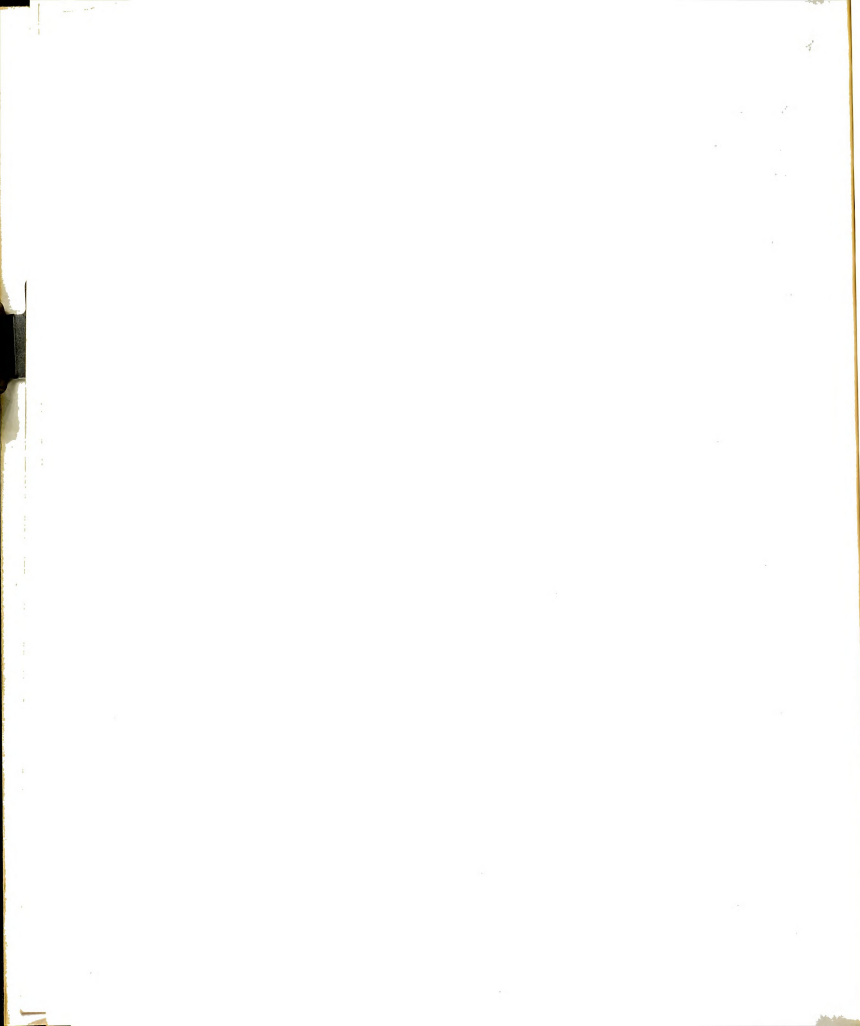


Table 7

Effects of Carbon Dioxide Levels on Number of Seeds Per Plant, Seed Weight Per Plant and Weight of One Seed in Two Dry Bean Cultivars Grown Under Two Seasons (data are means at all harvesting stages)^a

Carbon Dioxide Levels (ppm)	Cultivar	No. Seeds/Plant		Seed Wt./Plant (g)		Weight/Seed (g)	
		1975	1976	1975	1976	1975	1976
300	Black Turtle Soup	23 a	22 p	4.1 b	4.0 p	0.17 b	0.16 p
	Seafarer	16 a	21 p	2.5 a	3.1 p	0.15 ab	0.15 p
800	Black Turtle Soup	53 c	54 r	8.1 c	7.1 q	0.13 a	0.13 p
	Seafarer	39 b	37 q	6.9 c	5.7 q	0.13 a	0.18 q

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

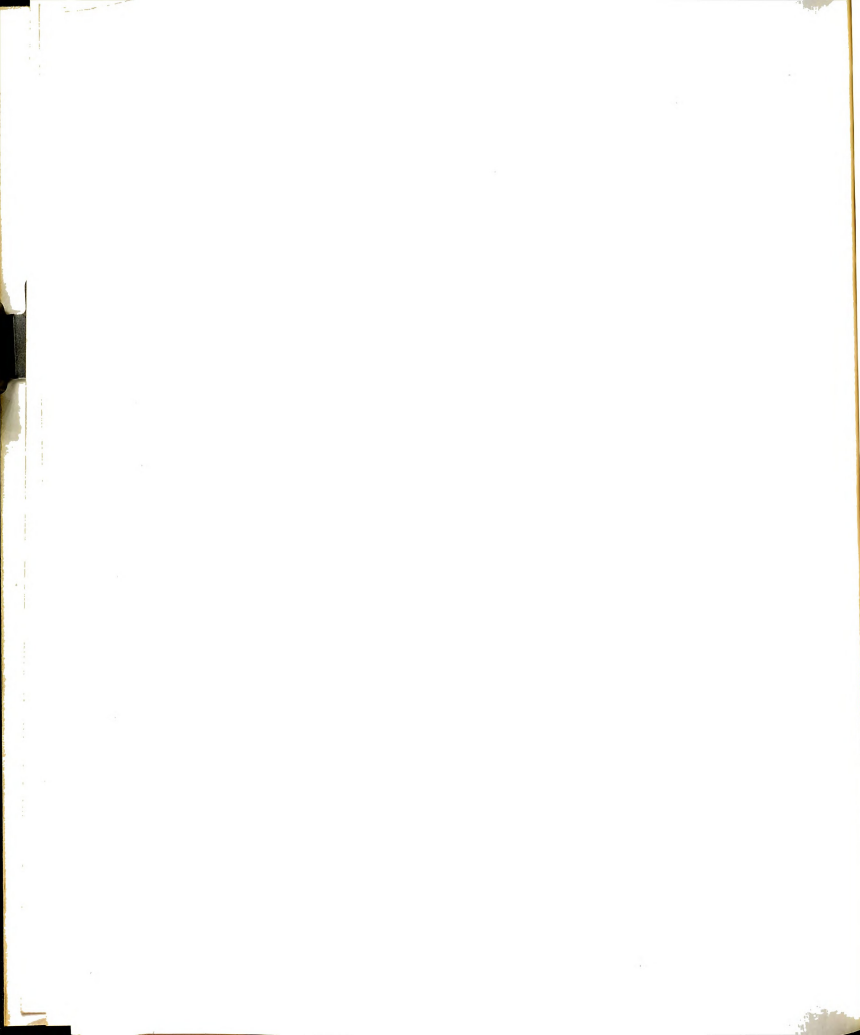


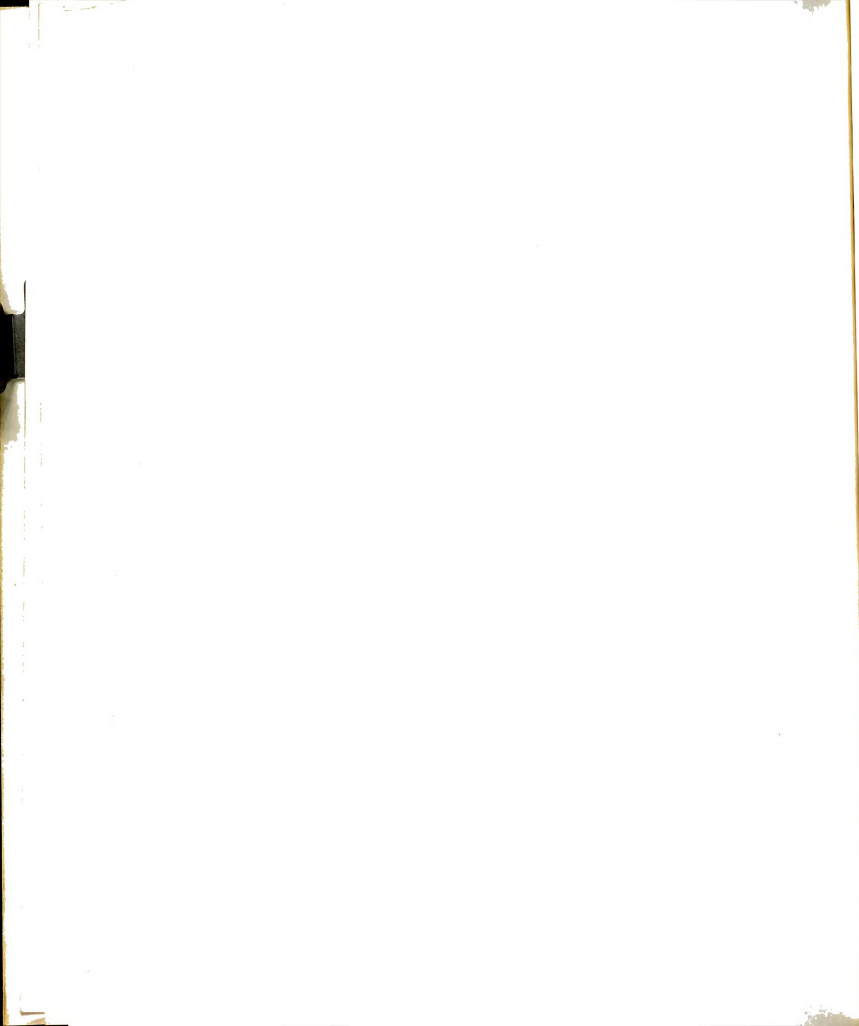
Table 8

Correlation Coefficients Between Percentage of Pod Abscission and Other Reproductive Characters in Two Dry Bean Cultivars Subjected to Different Carbon Dioxide Levels After Flowering

Characters	Black Turtle Soup		Seafarer	
	300 ppm CO ₂	800 ppm CO ₂	300 ppm CO ₂	800 ppm CO ₂
I. At Pod Filling Stage				
Flowering period	.30	-.12	-.18	.36 ^a
Number of flowers	.78 ^b	-.26	.63 ^a	-.46
Number of pods	-.58	-.57	-.37	-.01
Number of seeds	.48	-.21	-.00	.78 ^b
Seed weight	.85 ^b	.52	.42	
II. At Maturity				
Flowering period	.59 ^a	-.55	.33	-.25
Number of flowers	.88 ^b	.11	.44 ^b	.60 ^a
Number of pods	.46	-.41	-.86 ^b	-.73 ^b
Number of seeds	.70 ^a	-.57	-.47	-.49
Seed weight	.77 ^b	-.36	-.37	-.41

^aSignificant at 5% level.

^bSignificant at 1% level.



more they would abscise. However, when the plants were grown under the high carbon dioxide level, a negative correlation was seen in Black Turtle Soup while the positive correlation was still observed in Seafarer (Table 8). The negative correlation in Black Turtle Soup may have resulted from a greater vegetative growth response by this cultivar to the higher carbon dioxide level. Therefore, flowers and young pods had a greater share of the assimilate produced, thus fewer pods would have to sacrifice themselves by abscising. However, for Seafarer which is a determinate plant, vegetative growth did not occur after flowering, the plants exhibited less growth response to the increased carbon dioxide level. Also this cultivar produced many flowers in a short flowering time as compared to Black Turtle Soup (see Chapter 2). Thus the demand for food from these flowers and young pods was made in a short time period; even if plants had grown larger under the high carbon dioxide, the increase in growth may not have been sufficient to meet the demand from those flowers and pods. Therefore, a high percentage of pod abscission still occurred as more flowers were produced.

Negative correlation between percentage of pod abscission and yield (seed weight) at maturity indicated that as percentage of abscission went up lower yield resulted. This was seen in Black Turtle Soup grown at

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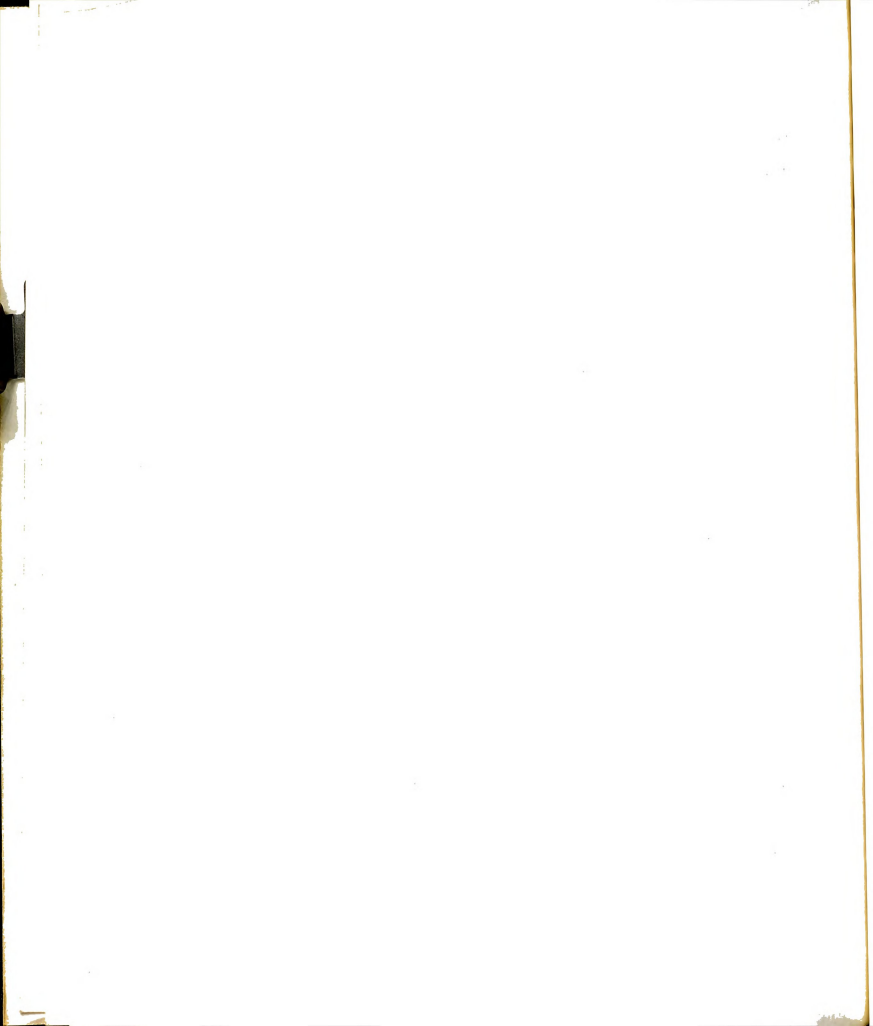
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300 ppm carbon dioxide and in both cultivars at the 800 ppm carbon dioxide level (Table 8). Although pod abscission can affect seed yield, in dry beans there are many components affecting yield (1). Thus, non-significant negative correlations under these conditions may be explained. It is possible that percentage of pod abscission might be significantly correlated to any one of the yield components instead of total yield in this case. The significantly positive correlation of 0.77 between percentage of pod abscission and seed yield in Black Turtle Soup grown under ambient air (300 ppm carbon dioxide) may be explained as follows. The limited photosynthesis may have been insufficient for retaining many pods. Thus the competition among pods for growth could result in a condition that the more pods abscised the greater the chance for the remaining pods to grow.

The previous study of cultivar response to increasing daylength showed positive response to daylength in both cultivars, but Black Turtle Soup seemed to exhibit a greater response than Seafarer (Chapter 3). A similar result was also found when these two cultivars were grown under high carbon dioxide concentration. These two experiments pointed out two things. First, Black Turtle Soup had greater response when grown under conditions favoring photosynthesis after flowering. The second was that since both extending daylength and



carbon dioxide enrichment gave similar results in pod abscission, seed yield, and growth rate, there must be similar physiological responses of plants that result from these two environmental factors. These physiological responses may be responsible for determining the abscission capacity of the plants. If that physiological factor is not carbohydrate availability, then it must be some factors influenced by or closely associated with the levels of carbohydrate.

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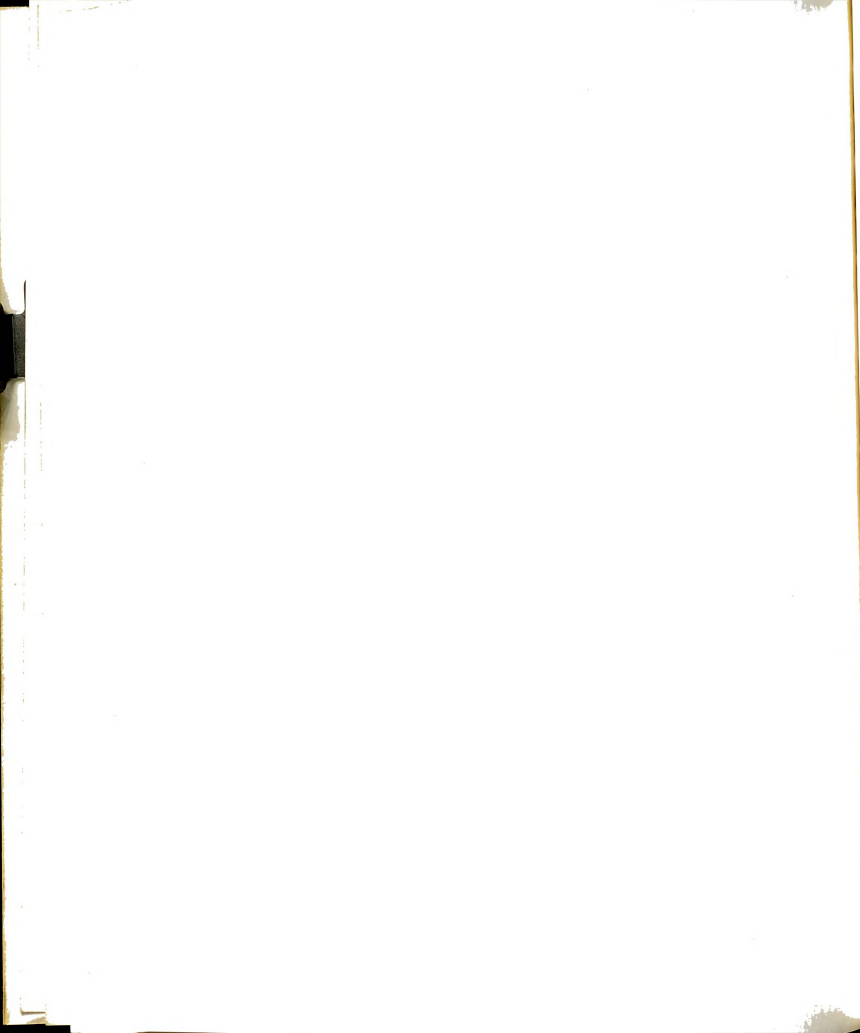
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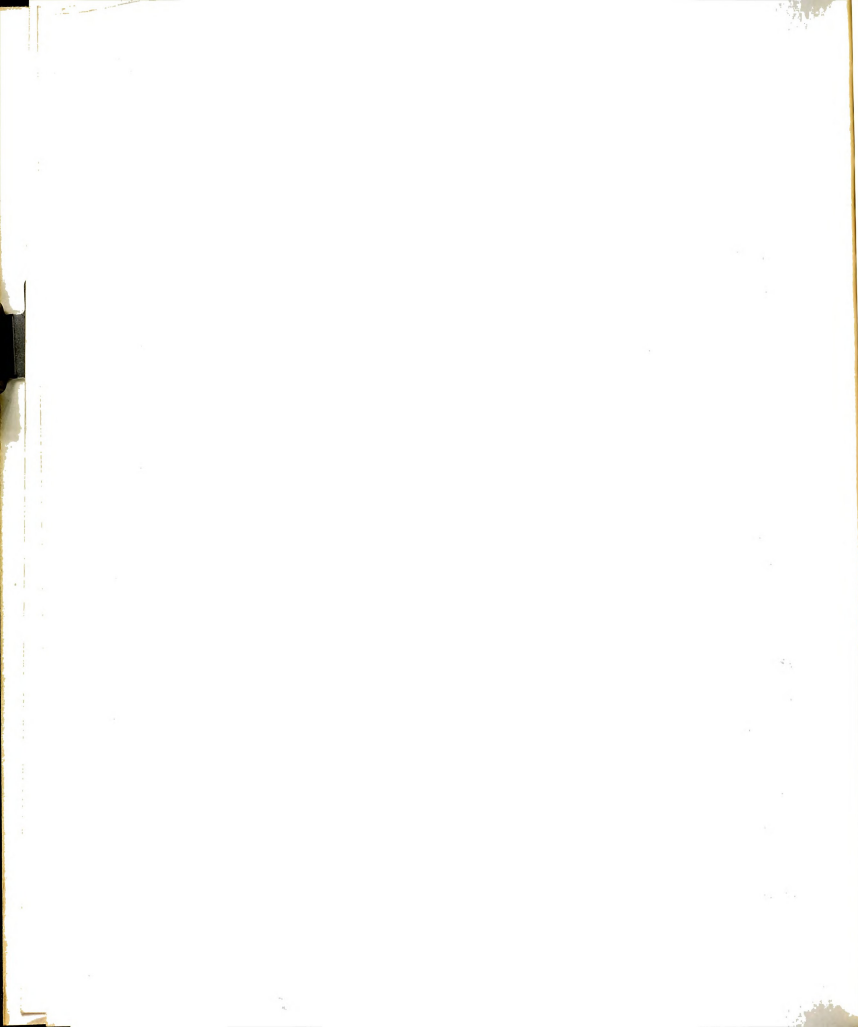


CHAPTER 6

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L. V. RELATIONSHIP OF POD ABSCISSION TO DIFFERENTIAL LEVELS OF CARBOHYDRATES PRODUCED BY VARIATION IN CARBON DIOXIDE CONCENTRATION

Abstract

Levels of free sugar, starch and total non-structural carbohydrates were determined in two dry bean (Phaseolus vulgaris L.) cultivars grown under ambient (≈ 300 ppm) and enriched (≈ 800 ppm) level of carbon dioxide. Free sugars were higher in both vegetative (root, stem, and leaf) and reproductive (seed and pod wall) tissues in both cultivars grown under high carbon dioxide, while starch concentration was higher only in the vegetative tissues. Black Turtle Soup (indeterminate) contained significantly more starch in the vegetative tissues, but not in the seed, than did Seafarer (determinate). Free sugar and starch decreased at maturity in the vegetative tissues, but not in seed, where most of the carbohydrate was stored as starch. A shift of available carbohydrates from the vegetative tissues and the pod wall to the seed



occurred with maturation. The role of available carbohydrates in pod abscission, seed yield, and vegetative growth is discussed.

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Introduction

An extensive review article by Wittwer and Robb (5), emphasizing tremendous increases in crop production obtained by carbon dioxide enrichment of greenhouse atmospheres, aroused the attention of crop physiologists in the early sixties. Carbon dioxide enrichment has since been reported to increase yield in soybean (1, 3), wheat (4) and cotton (2).

Our previous studies with Phaseolus vulgaris L. showed that growth rate, seed yield, and pod retention could be increased by raising the ambient carbon dioxide concentration (see Chapter 5). The objective of the present study was to determine the effects of such treatment on carbohydrate concentration of various tissues.

Materials and Methods

Sample Preparation

Two dry bean cultivars, "Black Turtle Soup" (indeterminate) and "Seafarer" (determinate), were grown and treated with two carbon dioxide levels as previously described (see Chapter 5).

Harvesting times, handling of samples during harvesting, preparation of samples, and analysis of free sugars and total nonstructural carbohydrate has been described elsewhere (Chapter 4). Free sugar, starch, and total nonstructural carbohydrate concentrations are expressed as mg glucose equivalent per g of dry tissues.

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The data were analyzed factorially, using 10 replications (plants) per treatment.

Results and Discussion

Free Sugar

Increasing the carbon dioxide level increased the free sugar concentration in all tissues analyzed for both cultivars (Table 1). Black Turtle Soup retained more free sugars in the root, stem, and leaf than did Seafarer; however, the reverse occurred in seeds and pods, although the difference was not significant (1%) in pods (Table 1). These data indicate a stronger sink effect of seeds in Seafarer than in Black Turtle Soup.

No interaction was observed between cultivar and carbon dioxide level except in the leaf. Black Turtle Soup leaves contained more sugar at 300 ppm carbon dioxide, but no difference was evident at 800 ppm (data not shown).

The free sugar levels in all tissues were high at peak flowering and decreased as the pods developed, as was seen in a previous study (Chapter 4). Several interactions were noted between carbon dioxide level and growth stage. As the pods matured, the free sugar level in the stem and leaves decreased at a faster rate at the low carbon dioxide level than at the high carbon dioxide (Fig. 1A and 1B). These results are consistent with the hypothesis that available free sugars are limiting during pod formation and filling. The free sugar level in the

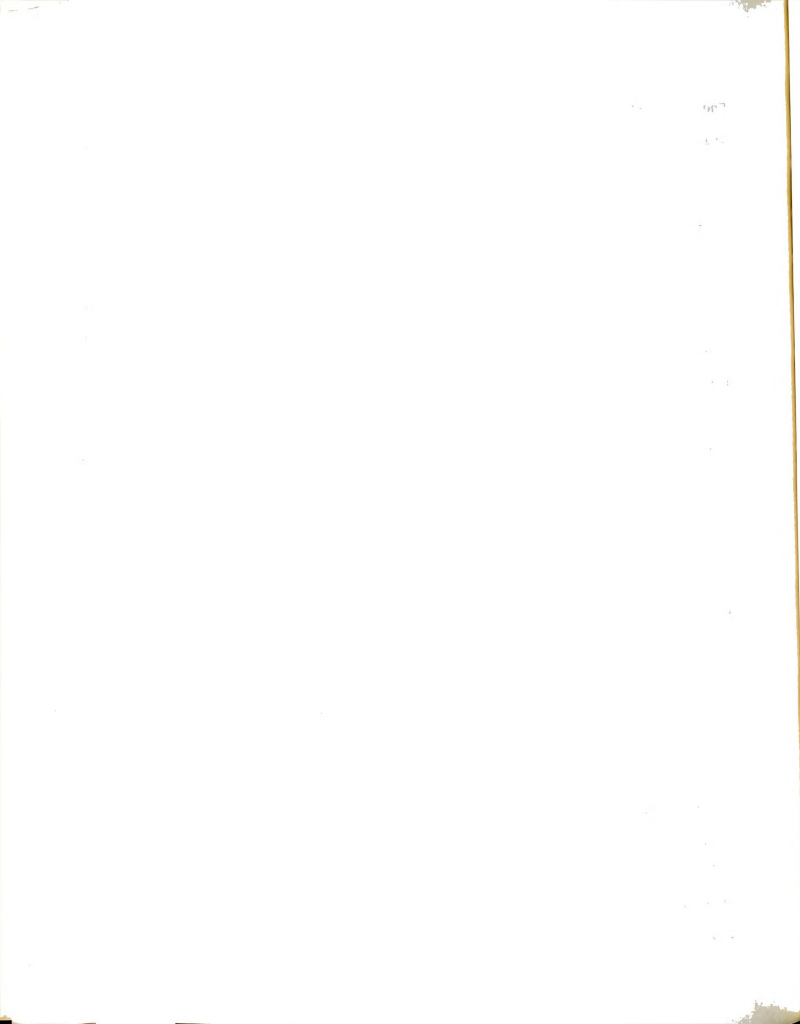
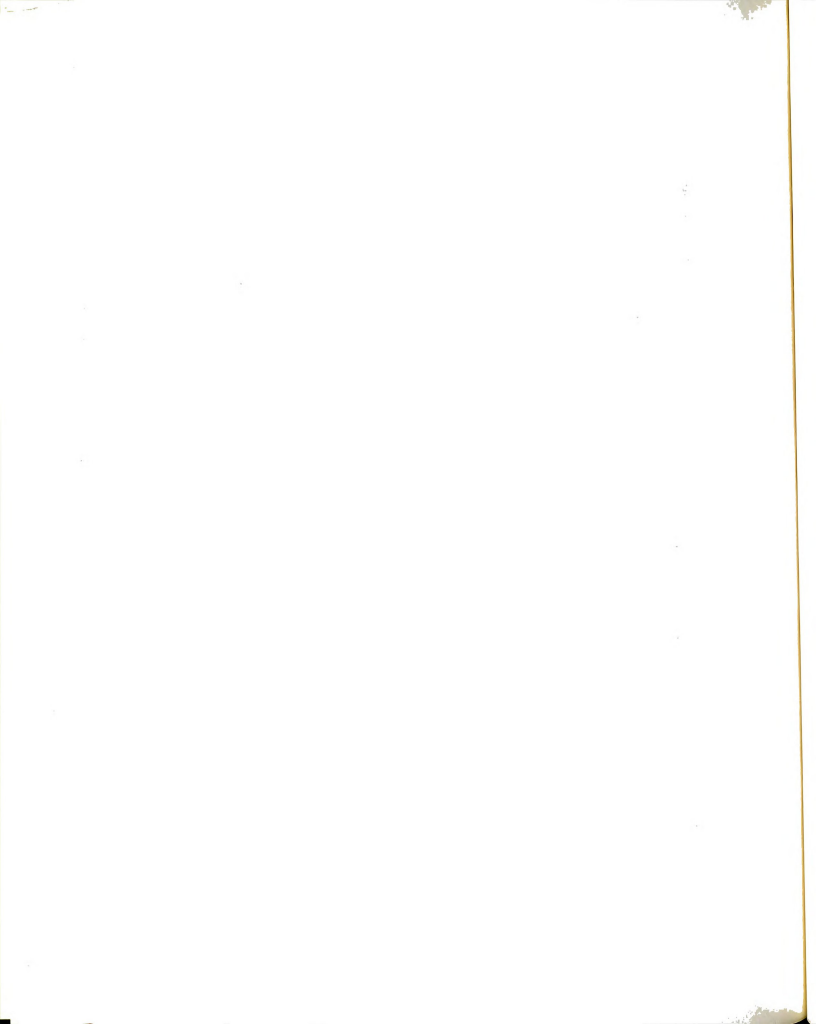


Table 1
The Effects of Developmental Stage and Carbon Dioxide Levels on Free Sugar Concentration in Various Plant Parts of the Two Bean Cultivars^a

	Mg Glucose per g Dry Weight				
	Root	Stem	Leaf	Seed	Pod
I. Time					
Peak flowering	23.9 b	65.7 c	69.7 a	-	267.7 c ^b
Pod filling	18.9 a	56.2 b	73.2 a	90.5 b	117.0 b
Maturity	20.9 a	38.8 a	-	80.6 a	37.7 a
II. Cultivars					
Black Turtle Soup	24.2 n	62.3 n	76.4 n	84 m	137 m
Seafarer	18.2 m	44.8 m	66.6 m	87 n	145 m
III. CO ₂ Level					
300 ppm	18.9 x	42.6 x	58.9 x	68 x	125 x
800 ppm	23.5 y	64.5 y	84.1 y	102 y	157 y
Interactions					
I x II	n.s.	n.s.	n.s.	n.s.	n.s.
I x III	n.s.	**	**	**	*
II x III	n.s.	n.s.	**	n.s.	n.s.
I x II x III	n.s.	**	n.s.	*	**

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.



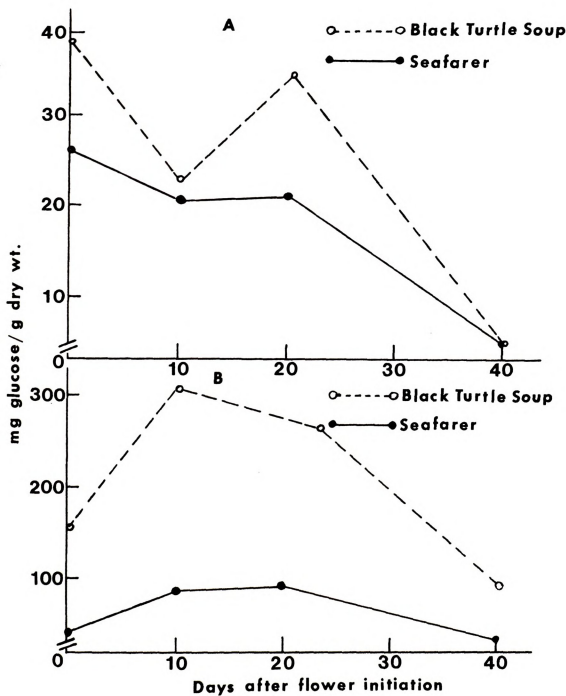
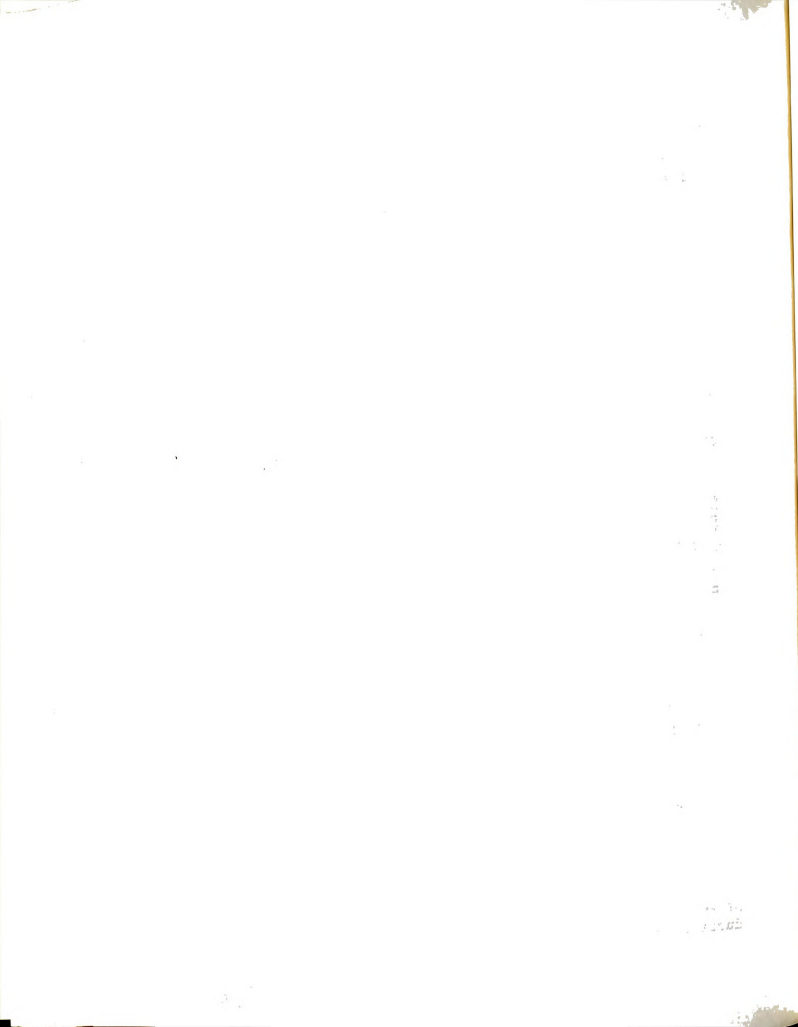


Fig. 1. Levels of starch in A. root; and B. stem; of two *Phaseolus vulgaris* L. cultivars during their reproductive phase, averaged from the two carbon dioxide levels.



leaves of plants exposed to 800 ppm carbon dioxide increased between peak flowering and pod filling (Table 2).

The level of free sugar in flowers and newly set pods (seed could not be separated at this stage) was high under both the high and low carbon dioxide treatment at peak flowering but decreased sharply with maturation (Table 2). High carbon dioxide significantly increased seed free sugar concentration at all developmental stages. Free sugars in seeds dropped between pod filling and maturity under the high carbon dioxide treatment, but increased slightly during the same period at the ambient carbon dioxide level (Table 2). Greater pod retention in the high carbon dioxide treatment (Chapter 5) probably created greater competition for sugar among seeds, resulting in a decline in free sugar level from pod filling to maturity. Much pod abscission occurred under the ambient carbon dioxide level and fewer pods and seeds were retained (Chapter 5). This reduced competition and prevented a decline in concentration in the seeds. Free sugar content of pod walls decreased with maturation under both carbon dioxide levels (Table 2).

Starch

High carbon dioxide increased starch concentrations in vegetative tissues (root, stem and leaf), but decreased them in the seed and pod wall (Table 3). Starch

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Table 2
Effects of Carbon Dioxide and Time of Sampling on Free Sugar Concentration
(mg glucose/g dry weight) of Bean Tissues^a

Carbon Dioxide Level (ppm)	Time After Flower Initiation (days)	Tissues				
		Root	Stem	Leaf	Seed	Pod
300	0	20.3 ab	79.5 e	82.1 d	-	-
	10	22.7 bc	59.3 c	64.6 b	-	243.8 e ^b
	20	16.4 a	49.8 b	53.3 a	64.5 a	104.7 c
	40	17.7 a	18.7 a	-	72.6 a	26.1 a
800	0	20.3 ab	79.5 e	82.1 d	-	-
	10	25.1 c	72.0 d	74.9 c	-	291.6 f
	20	21.4 b	62.7 c	93.2 e	116.5 c	129.2 d
	40	24.1 bc	58.8 c	-	88.5 b	49.2 b

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.

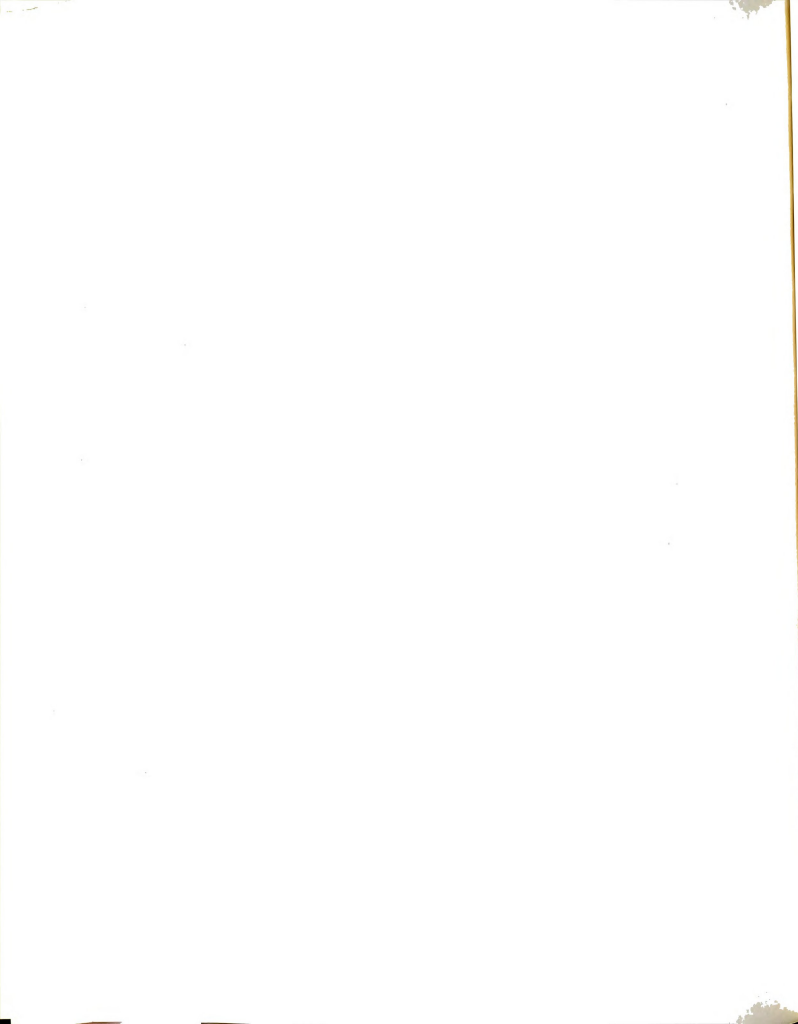
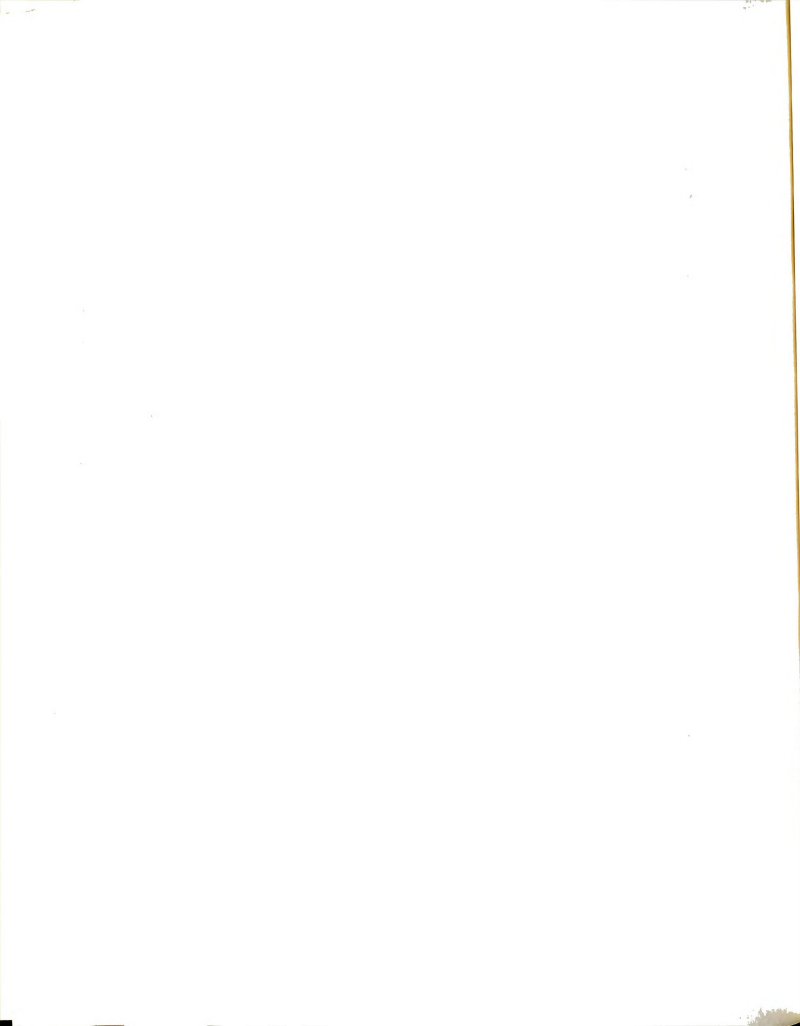


Table 3
Effects of Developmental Stages and Carbon Dioxide Levels on Starch Concentration in Various Plant Parts of the Two Dry Bean Cultivars^a

Mg Glucose Equivalent per g Dry Weight						
	Root	Stem	Leaf	Seed	Pod	
I. Time						
Peak flowering	21.5 b	194 b	355 b	-	150 b ^b	
Pod filling	38.0 c	178 b	206 c		406 c	
Maturity	4.7 a	67.2 a	-	348 b	35.0 a	
				269 a		
II. Cultivars						
Black Turtle Soup	20.8 n	223 n	342 n	307 m	205 n	
Seafarer	15.3 m	70.5 m	218 m	309 m	190 m	
III. CO ₂ Level						
300 ppm	12.1 x	123 x	139 x	340 y	210 y	
800 ppm	24.1 y	170 y	422 y	277 x	184 x	
Interactions						
I x II	**	**	n.s.	*	n.s.	
I x III	*	**	**	**	**	
II x III	n.s.	**	**	n.s.	*	
I x II x III	n.s.	*	**	n.s.	n.s.	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

^bSeed not separate from pod.



accumulation was greater in the vegetative organs and pods in Black Turtle Soup than in Seafarer, however, no differences were evident in seed (Table 3). No interaction was seen between carbon dioxide levels and cultivars in root starch concentration (Table 3). Although starch concentration in the stems increased significantly with increasing carbon dioxide concentration in both cultivars (Table 3), the increase was not significant in Seafarer (Table 4). Starch concentration was consistently low in Seafarer stems even under field conditions; this may be characteristic of the determinate growth habit. Carbon dioxide enrichment markedly increased starch accumulation in leaves of both cultivars (Table 4). Interaction was again significant (Table 3), with a 4-fold increase in Seafarer as compared with a 3-fold increase in Black Turtle Soup (Table 4). Carbon dioxide-cultivar interaction in seed starch concentration was nonsignificant (Table 3).

The concentration of starch in the vegetative tissues decreased with maturity (Table 3). This decrease, especially in stems and leaves coincided with an increase in starch concentration in seeds and pod walls. Starch concentration in all tissues was lower at maturity than at pod filling (Table 3), possibly due to hydrolysis.

Significant interactions occurred between cultivars and starch concentration in roots, stems and seeds

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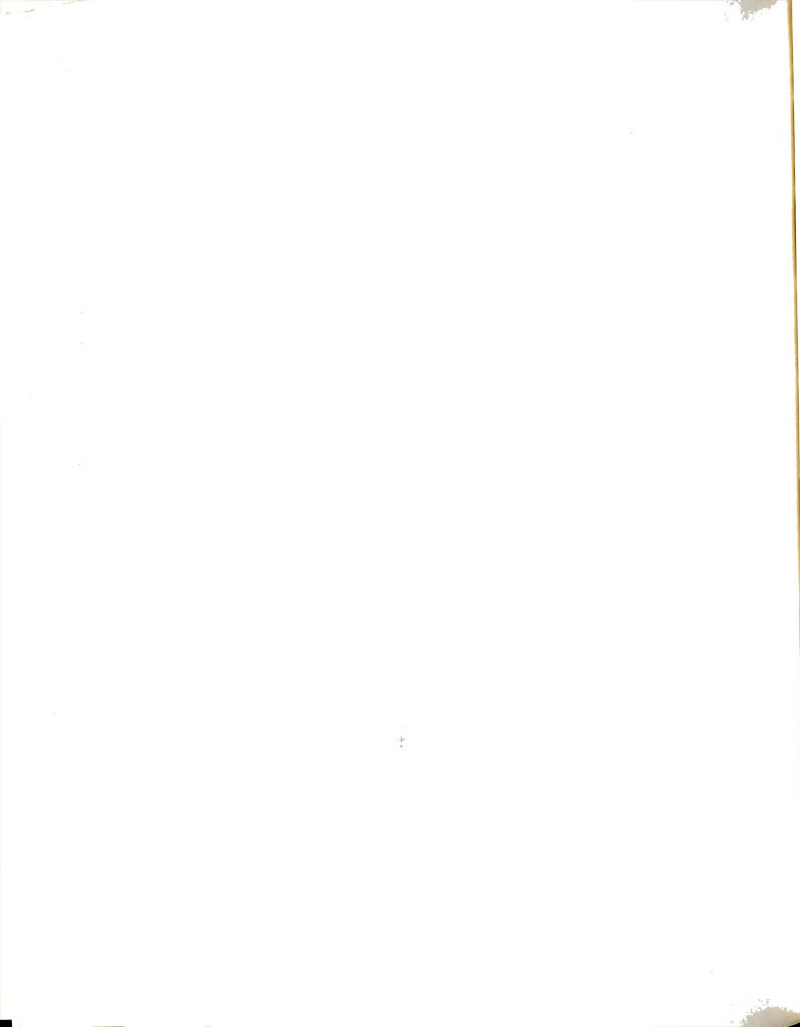
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Table 4
Effects of CO₂ and Cultivar on Starch Concentration (mg glucose/g dry weight) in
Bean Tissues^a

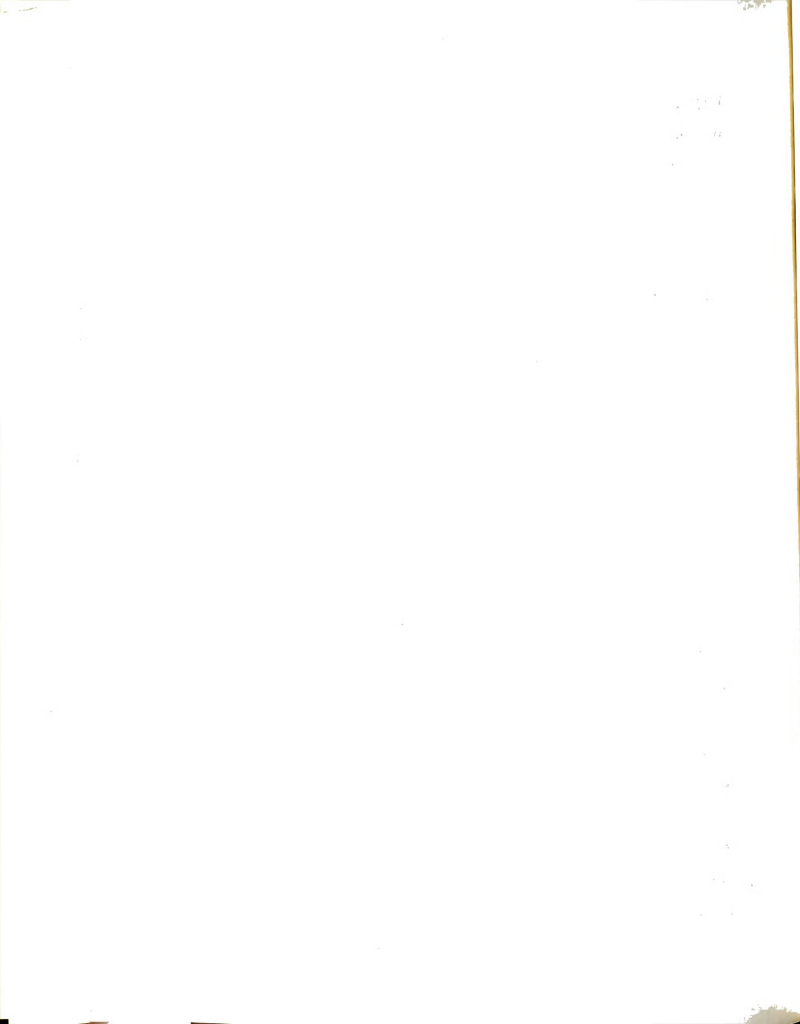
Carbon Dioxide Level (ppm)	Cultivar	Tissue			
		Root	Stem	Leaf	Seed
300	Black Turtle Soup	13.1 a	182.2 b	186.6 b	295.0 b
	Seafarer	11.1 a	63.5 a	92.1 a	292.2 b
	Mean	12.1 x	122.8 x	139.3 x	293.6 y
800	Black Turtle Soup	28.5 c	263.0 c	498.4 d	221.0 a
	Seafarer	19.6 b	77.4 a	344.9 c	216.2 a
	Mean	24.0 y	170.2 y	421.6 y	218.6 x

^aMeans within columns and sets (abc, xyz) with similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



during the reproductive phase (Table 3). In roots, the starch concentration was higher in Black Turtle Soup at all developmental stages except maturity (Fig. 1A), but the difference was minimal at peak flowering. On the other hand, the difference was maximal at this time in the stem (Fig. 1B). In both cultivars, the starch levels in roots and stems decreased as the seeds matured (Table 3). In leaves there was no interaction between cultivar and growth stage during pod development (Table 3). As the pods developed, the starch concentration in leaves decreased (Table 3). Cultivar-developmental stage interaction on seed starch was shown in Figure 2, where starch concentration in seeds of both cultivars increased from peak flowering to pod filling, then decreased at maturity (Fig. 2).

Interaction between carbon dioxide levels and stage of pod development on starch concentration was noted (Table 3). In root, stem and leaf, carbon dioxide enrichment increased starch accumulation (Table 5), but response varied considerably with time. However, in seed, carbon dioxide enrichment decreased starch concentration regardless of the stage of pod development (Table 5). The greater number of seeds produced apparently reduced the starch available for storage in each seed. The rapid decline in starch concentration in the pod wall at maturity (Table 5) paralleled data obtained in a previous



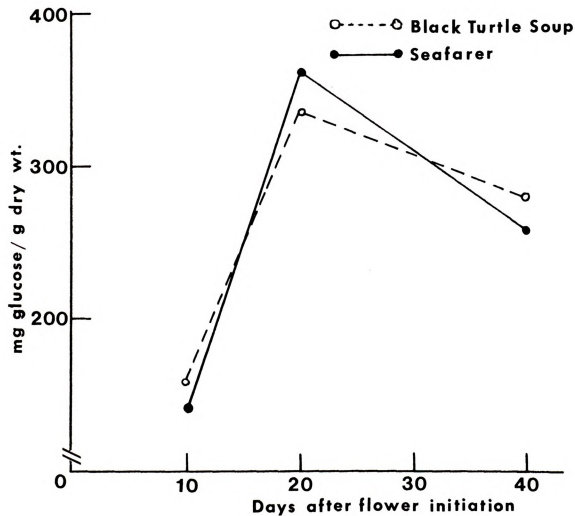


Fig. 2. Levels of starch in seed of two *Phaseolus vulgaris* L. cultivars during their reproductive phase, averaged from the two carbon dioxide levels.

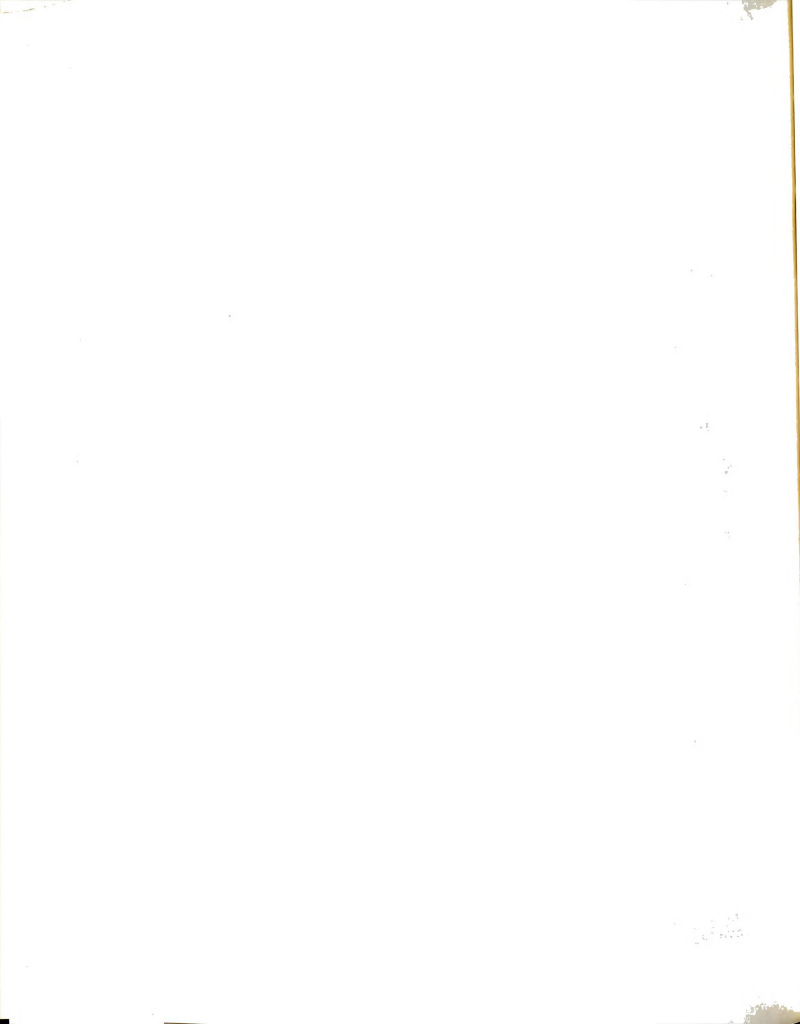
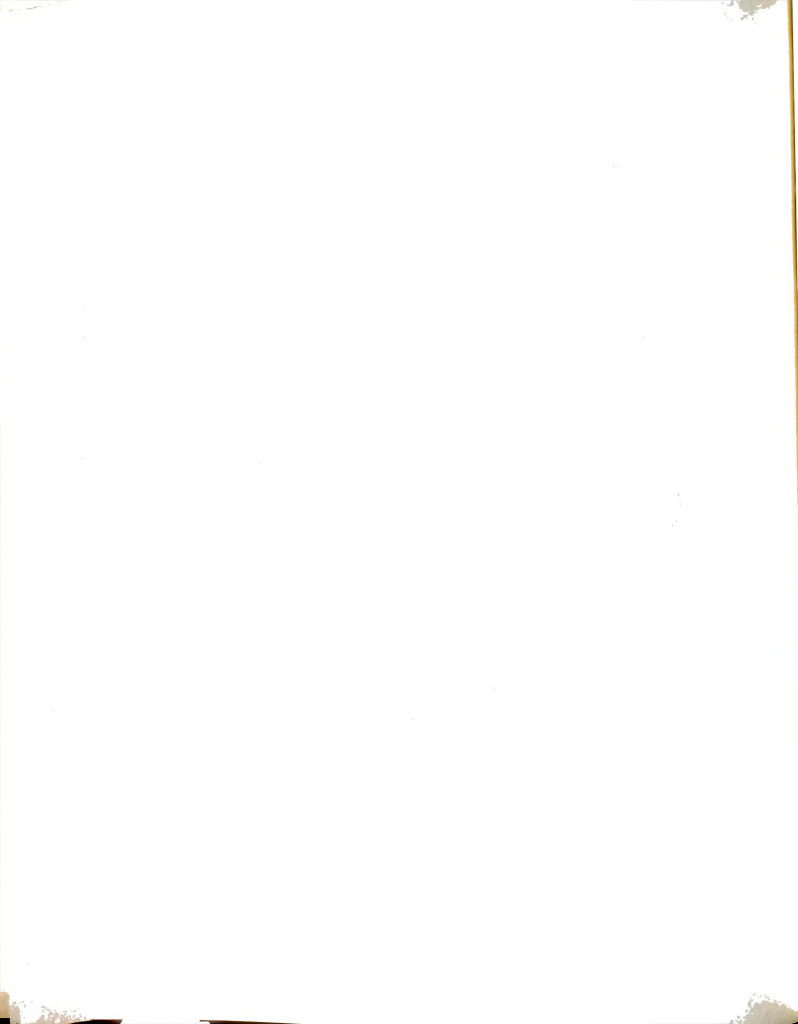


Table 5
Effects of Carbon Dioxide and Time of Sampling on Starch Concentration
(mg glucose/g dry weight) of Bean Tissues^a

Carbon Dioxide Level (ppm)	Time After Flower Initiation (Days)	Tissues			
		Root	Stem	Leaf	Seed
300	0	32.3 d	97.4 b	166.7 b	-
	10	12.0 b	197.9 d	225.4 c	-
	20	22.2 c	139.8 c	53.3 a	405.1 c
	40	2.0 a	30.8 a	-	200.7 c
800	0	32.3 d	97.4 b	166.7 b	-
	10	31.1 d	189.7 d	484.9 e	-
	20	33.7 d	217.3 d	358.3 d	291.8 b
	40	7.4 ab	103.6 b	-	412.1 d
					263.6 a
					40.5 a

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



experiment (Chapter 4), and suggests rapid utilization of starch from the pod wall by the growing seeds.

Relation of Pod Abscission to
Available Carbohydrates

The data presented in Chapter 5 showed that carbon dioxide enrichment during the reproductive phase increased plant size, seed yield, and pod retention. In this study, using the same growing conditions, increasing the carbon dioxide concentration increased free sugar and starch in root, stem, and leaf. Available carbohydrate concentration paralleled vegetative growth, seed yield, and pod retention, suggesting a direct influence of carbohydrate in limiting abscission. However, correlation coefficients between percentage of pod abscission and free sugar and starch levels under the two carbon dioxide levels did not reveal any significant relationships (Table 6). Non-significant negative correlations were observed between abscission rates and levels of available carbohydrate. Starch concentration of stems was negatively correlated with percentage of abscission in both cultivars at least at pod filling (Table 6). This may indicate that the carbohydrates temporarily stored in stems are used to retain pods. No significant correlations were evident between available carbohydrate in vegetative tissues or stem weight and seed yield (Table 7 and 8). Abscission is a complex process whose mechanism is not fully

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Table 6

Correlation Coefficients Between Percentage of Pod Abscission and Available Carbohydrate Fractions in Vegetative Tissues in Two Dry Bean Cultivars Under Two Levels of Carbon Dioxide

Characters	Black Turtle Soup		Seafarer	
	300 ppm CO ₂	800 ppm CO ₂	300 ppm CO ₂	800 ppm CO ₂
I. At Pod Filling Stage				
Free sugar in root	-.78 ^b	.17	.29	.05
Free sugar in stem	.66 ^a	.51	-.11	-.33
Free sugar in leaf	.02	-.09	.41	-.12
Starch in root	-.26	.35	-.59	-.12
Starch in stem	-.68 ^a	-.20	-.21	-.75 ^b
Starch in leaf	-.44	.19	-.47	-.09
II. At Maturity				
Free sugar in root	.59	-.41	.19	.21
Free sugar in stem	.02	-.34	-.31	.24
Starch in root	-.22	.12	-.14	-.30
Starch in stem	.17	-.09	.03	-.40

^aSignificant at 5% level.

^bSignificant at 1% level.

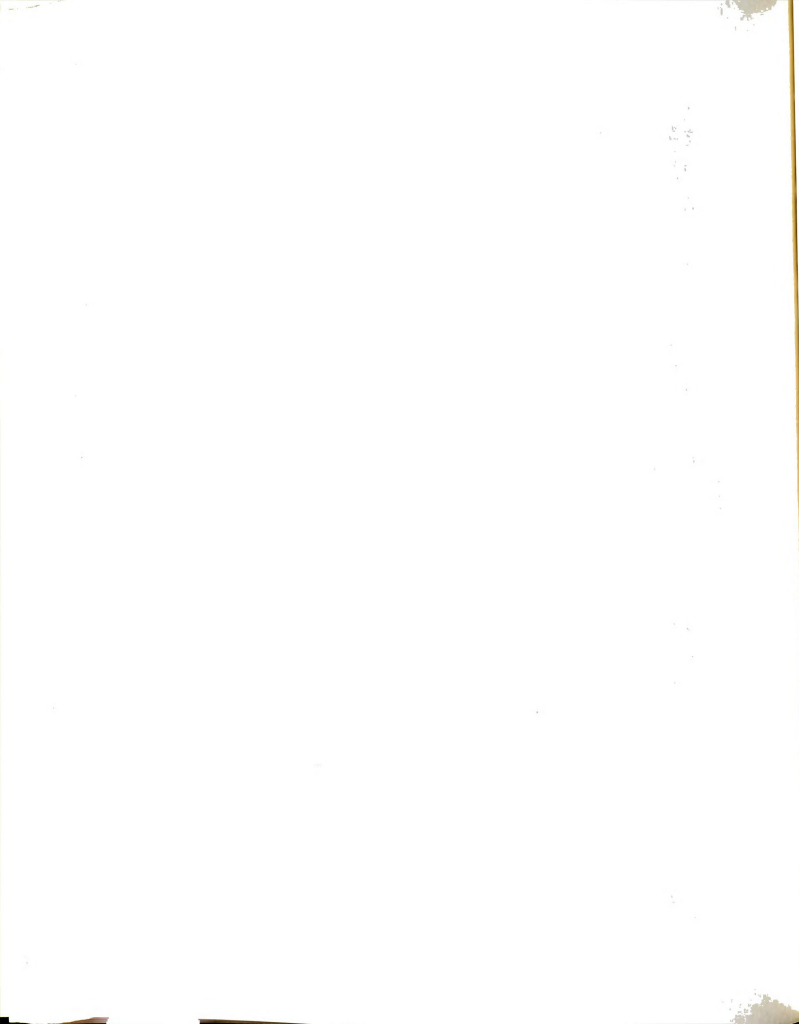


Table 7

Correlation Coefficients Between Seed Weight Per Plant and Available Carbohydrate Fractions in Vegetative Tissues in Two Dry Bean Cultivars Under Two Levels of Carbon Dioxide

Characters	Black Turtle Soup		Seafarer	
	300 ppm CO ₂	800 ppm CO ₂	300 ppm CO ₂	800 ppm CO ₂
I. At Pod Filling Stage				
Free sugar in root	-.66 ^a	-.20	-.10	-.45
Free sugar in stem	.41	.67 ^a	.27	.16
Free sugar in leaf	.12	.04	.48	.16
Starch in root	-.06	-.21	-.45	-.43
Starch in stem	-.59	-.70 ^a	.30	-.62 ^a
Starch in leaf	-.57	.21	.30	-.14
II. At Maturity				
Free sugar in root	.38	.22	.09	-.20
Free sugar in stem	-.06	.12	.15	-.02
Starch in root	.09	-.51	.26	.18
Starch in leaf	.52	-.25	.13	.41

^aSignificant at 5% level.

^bSignificant at 1% level.

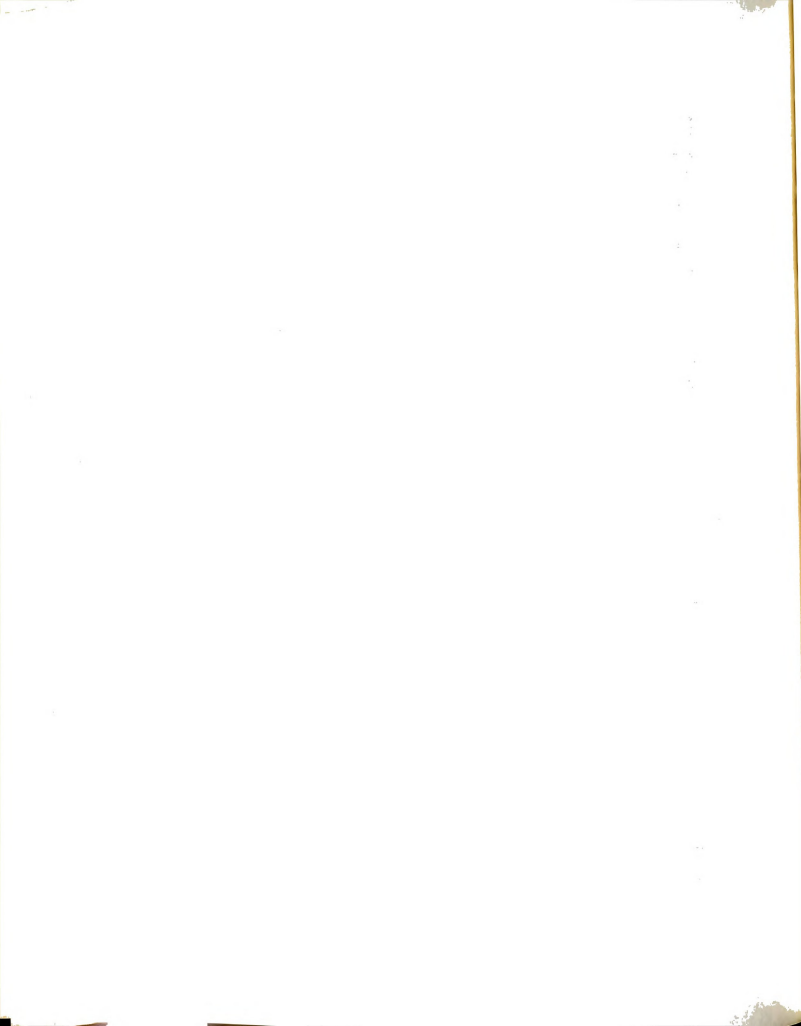


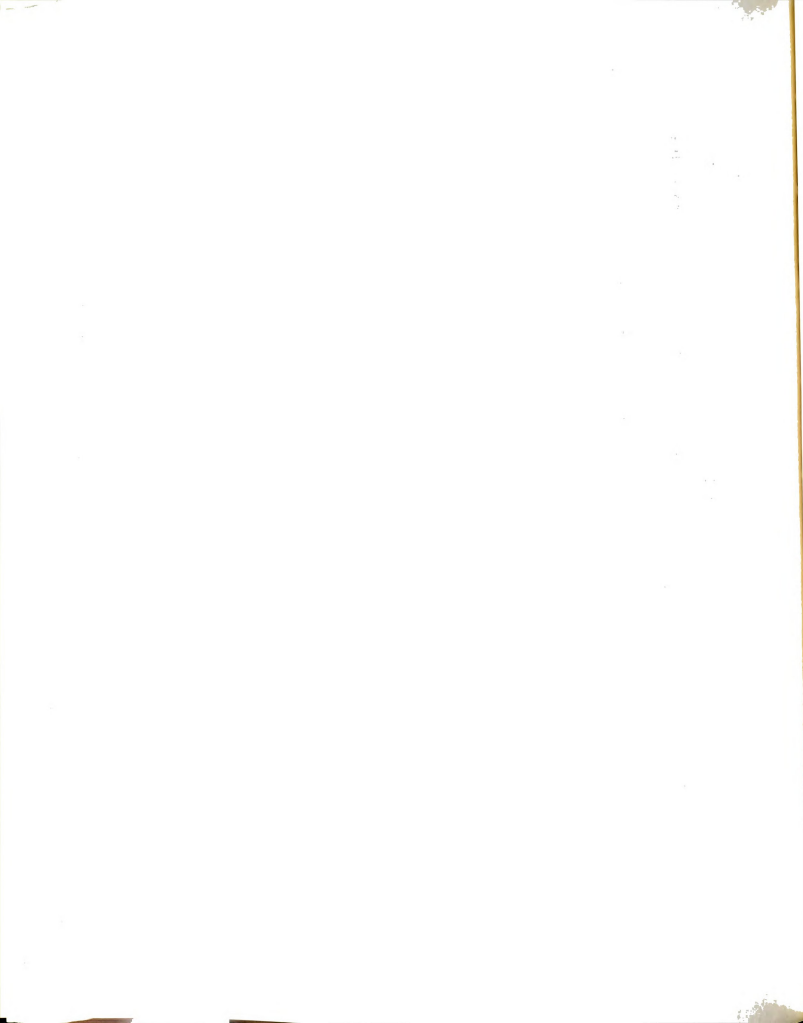
Table 8

Correlation Coefficients Between Stem Weight Per Plant and Available Carbohydrate Fractions in Vegetative Tissues in Two Dry Bean Cultivars Under Two Levels of Carbon Dioxide

Characters	Black Turtle Soup		Seafarer	
	300 ppm CO ₂	800 ppm CO ₂	300 ppm CO ₂	800 ppm CO ₂
I. At Pod Filling Stage				
Free sugar in root	.14	-.16	-.47	.04
Free sugar in stem	-.49	-.53	.44	.29
Free sugar in leaf	.08	-.07	.41	-.15
Starch in root	.31	-.53	-.15	.51
Starch in stem	.57	-.16	.23	.32
Starch in leaf	-.15	-.19	.06	.31
II. At Maturity				
Free sugar in root	.32	.64 ^a	.25	-.26
Free sugar in stem	.23	.64 ^a	-.15	.17
Starch in root	.35	.48	-.09	.55
Starch in stem	.33	.43	-.17	-.41

^aSignificant at 5% level.

^bSignificant at 1% level.



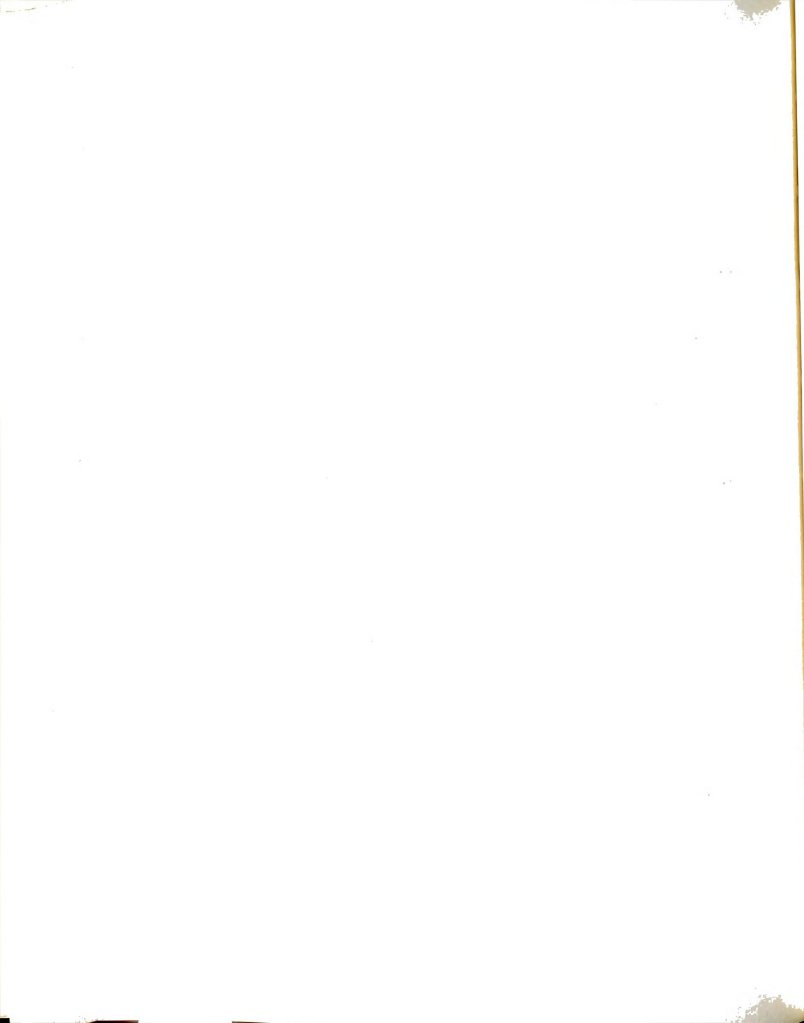
understood. Available carbohydrate probably plays only an indirect role in the phenomenon.

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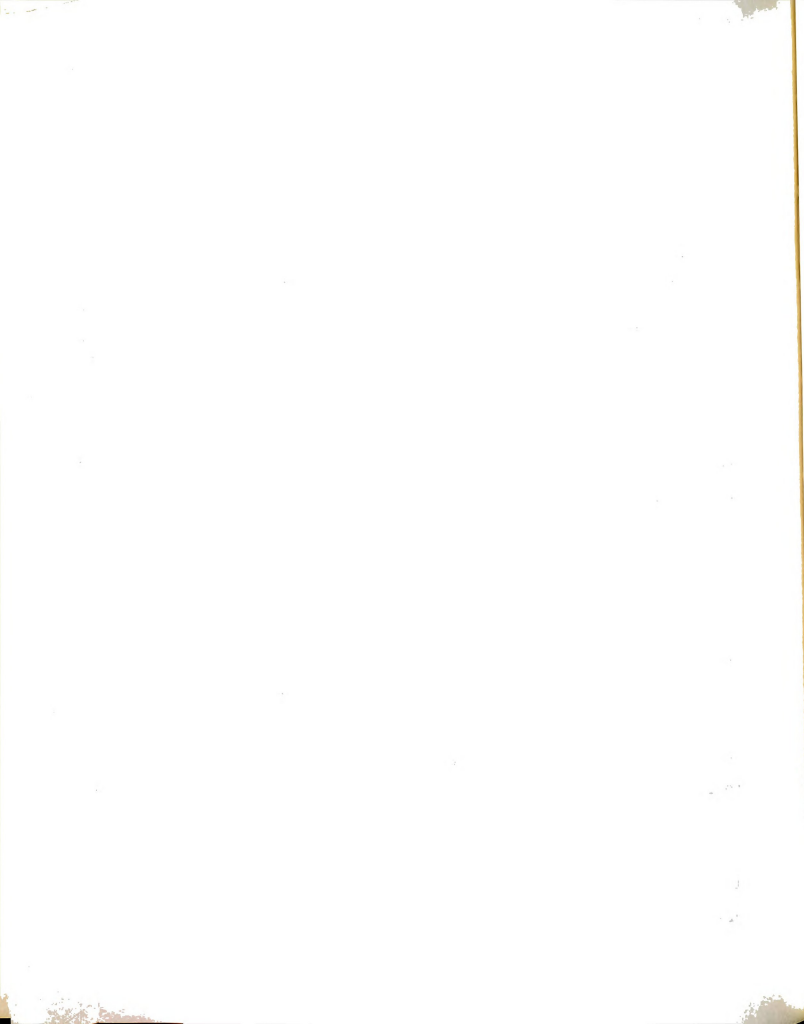
CHAPTER 7

ABSCISSION OF FLOWERS AND FRUITS IN PHASEOLUS VULGARIS L.

VI. THE RELATIONSHIP BETWEEN POD ABSCISSION AND ENDOGENOUS ABSCISIC, PHASEIC, AND DIHYDRO- PHASEIC ACIDS IN THE PEDICELS AND FRUITS

Abstract

In two cultivars of dry bean, populations of fruits having low vs. high abscission potential were established by removing early-opening flowers from half the plants. Fruits were harvested 4 to 5 days after anthesis and separated according to length, which was negatively correlated with abscission potential. Absciscic acid (ABA), phaseic acid (PA), and dihydrophaseic acid (DPA) contents were determined in methanol extracts of both pods and pedicels, using electron capture gas liquid chromatography (GLC). None of the treatments affected the content of these 3 compounds in pedicels. ABA content of pods was positively correlated with abscission potential of the 2 cultivars and with fruit load, but was unaffected by fruit size. PA content increased with fruit size and with fruit load, but was not affected by cultivar. DPA content was greater in the cultivar exhibiting the higher rate of



abscission, but was unaffected by pod size or fruit load. I conclude that levels of extractable ABA, PA, and DPA do not regulate fruit abscission in bean.

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Introduction

During fruit abscission, both persisting (actively growing) and abscising fruits occur in the same population (3, 7). In order to make valid comparisons, one must be able to recognize and separate persisting and abscising fruits. Earlier attempts to do so were based on criteria such as fruit size, color, or loosening (2, 3, 5), which are useful only in the terminal stages of abscission (7), well after induction has occurred.

Growth inhibitors have been frequently viewed as potential abscission-regulation hormones (2, 4). Absciscic acid has been identified and believed to have this abscission regulating property (7). In peach, greater levels of absciscic acid was found in abscising (i.e. loose) than in persisting (i.e. tight) fruits (5). A strong correlation between absciscic acid content and abscission was reported in cotton fruit (2). However, the absciscic acid data presented in that paper could also be interpreted to be correlated with fruit growth. The evidence of absciscic acid levels correlated with growth rates was presented in soybean pods (9). Studying abscission in peach fruit, Zucconi (12) found levels of absciscic acid to be negatively correlated with abscission.

My purpose was to test the hypothesis that ABA content controls fruit abscission in bean. Differential treatments, which had previously been shown to result in

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different rates of abscission, were applied, and pods were sampled during the induction phase for subsequent analysis. PA and DPA, previously shown to be metabolites of ABA (6), were also measured.

Materials and Methods

Plant Culture

Two Phaseolus vulgaris L. cultivars, "Black Turtle Soup" and "Seafarer," were selected for their contrasting growth habits and abscission potentials. Seeds were planted in soil mixture (1:1:1 ratio of sand: sandy loam and peat) in 25 cm. pots in a greenhouse maintained at $24 \pm 3^{\circ}\text{C}$ on February 16, 1976 for Black Turtle Soup and February 21, 1976 for Seafarer. The reason for sowing at different times is to get the two cultivars flowering at the same time. On emergence, the seedlings were thinned to one per pot. When the plants reached flowering stage on March 26, 1976, they were divided into two groups of 150 plants of each cultivar and differential treatments applied.

Flowers opening six days or later after the first flower on the same plant have a high abscission potential in comparison with those opening earlier (Chapter 2). In the control treatment, flowers borne on the first five days were left on the plant. In the second group of plants, all flowers opening during the first five days were removed. Flowers opening the sixth day and thereafter

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were tagged with color-coded wire, and the pods from these tagged flowers were harvested at 2-day intervals, immediately frozen on dry ice and stored at -10°C .

Eighty plants of each cultivar and treatment were used to record the rate of abscission. For each cultivar and treatment, 40 flowers that were borne on day six were tagged and individually numbered. Pods from these tagged flowers were measured every day and abscission was recorded.

After freeze-drying, pods sampled on day 4 and 5 were divided into 3 groups: small (< 1.5 cm), medium ($1.5\text{--}3.0$ cm) and large (> 3.0 cm). An abscission potential was assigned to each subgroup based on the relationship between pod length and abscission probability determined experimentally from comparable pods monitored (in vivo) throughout their development.

Extraction

Pedicels (20 mg) and fruits (100 mg) were homogenized in 10 ml methanol, following the addition of 100 ng t, t-ABA to correct for losses. No t, t-ABA was recovered from nonspiked samples, and the amount of c, t-ABA recovered from blanks containing 5'-ABA alone was negligible. The homogenates were left for 6 to 12 hours at 2°C in the refrigerator, then filtered, and the tissue was rinsed with methanol. The filtrate was reduced to

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dryness in a flash evaporator at 40°C and resuspended in 20 ml distilled water.

Fractionation

The extract was adjusted to pH 8.0 with 0.1 N NH_4OH and washed 3 times with 10 ml methylene chloride (CH_2Cl_2). The CH_2Cl_2 fraction was discarded. The water phase was adjusted to pH 3.0 with 0.1 N formic acid and partitioned 3 times with 15 ml ethyl acetate (EtAc) to obtain the acidic fraction, which was evaporated and stored at -10°C until analyzed.

Analysis

The samples were resuspended in 0.5 ml methanol and methylated with diazomethane according to Schlenk and Gellerman (8). The methylated samples were evaporated under nitrogen, the residues resuspended in 2 and 1 ml ethyl acetate for the pod and pedicel samples, respectively, and 2 μl of each sample was injected into a Packard 7300 Gas-Liquid Chromatograph equipped with a 63 Ni electron capture detector operated at 5v. The column was 2 mm i.d X 1.83 m, packed with 1% XE-60, 12,500 Centistrokes (CS or CSTK - the viscosity rating), on Gaschrome Q 80/100 mesh. Column, inlet and detector temperatures were 200°, 240°, and 240°C, respectively. The carrier gas was N_2 at a flow rate of 40 ml/min at 40 psi. Nitrogen scavenger gas was supplied to the detector at 90 ml/min.

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Data were quantified by measuring peak heights and comparing with a standard curve (semi-log) for each compound measured. Peak heights were linear over a range of 0.05 to 1.0 ng/ μ l ABA, 0.10 to 2.0 ng/ μ l PA and 0.05 to 2.0 ng/ μ l DPA. Data were corrected for losses during extraction and fractionation from the percentage of recovery of the standard t,t-ABA, assuming parallel losses, in c,t-ABA, PA and DPA.

Results

Pod Growth vs. Abscission

Persisting and abscising pods could not be distinguished on the basis of length during the first three days after pod setting. However, the growth rate of abscising pods began to decrease thereafter, and the differences in pod size increased until the pods abscised from the plants (Fig. 1A and B).

Control vs. deflowered plants differed markedly in percentage of pod abscission. Only 30 and 20% of the pods abscised in the latter vs. 55 and 75% in the former for "Black Turtle Soup" and "Seafarer" respectively. Within treatments and cultivars, the degree of abscission was strongly correlated with pod size on days 4 and 5, smaller pods having a much greater tendency to abscise (Table 1).

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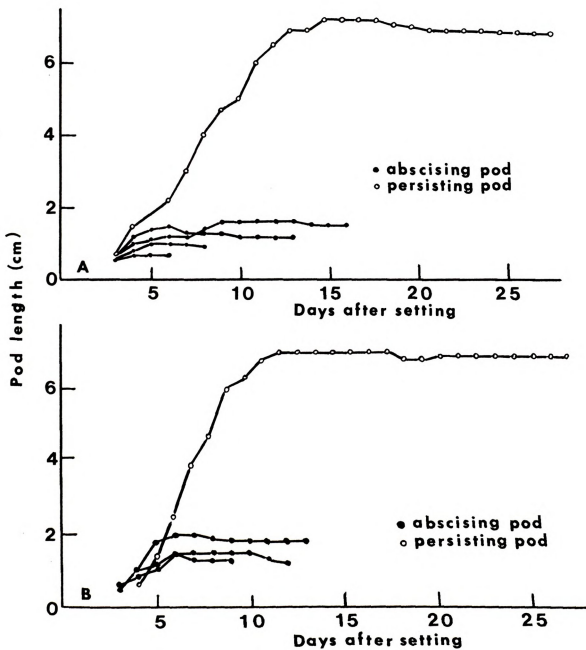


Fig. 1. Growth curves of abscising and persisting pods. A. Black Turtle Soup; B. Seafarer.

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Hormone Content vs. Abscission

ABA. ABA content of "Seafarer" pods was higher than that of "Black Turtle Soup" pods, particularly in the control treatment (Table 1). Deflowering reduced ABA content in all cases. However, the effect of pod size was inconsistent. Thus, ABA content paralleled abscission in the case of cultivar and treatment effects, but not in size effect. None of the treatments affected ABA content of the pedicels.

PA. Low levels of PA were detected in both pod and pedicel. PA was higher in pods from control plants than in those from deflowered plants in all but one case (Table 1). However, large pods contained more PA than medium or small pods, indicating no correlation with abscission. Cultivar did not affect PA content. PA levels in the pedicels were not affected by any of the treatments.

DPA. "Seafarer" pods contained significantly more DPA than did "Black Turtle Soup" pods (Table 1). However, neither deflowering nor pod size affected DPA content of the pedicels.

Discussion

Although the work of both Martin and Nishijima (5) and Davis and Addicott (2) suggests a positive relationship between the content of ABA or ABA-like

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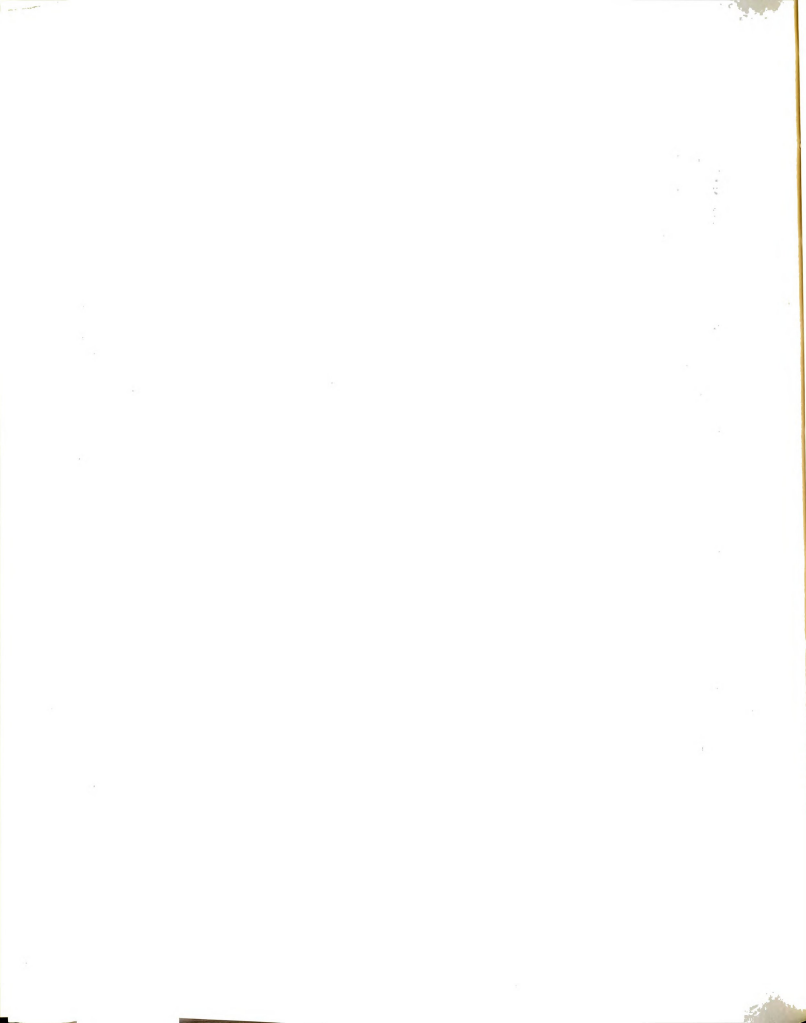
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Table 1
Levels of ABA, PA and DPA in Relation to Percentage of Abscission of the Two Bean Cultivars^a

Variety	Pod Size	Abscission	Abscission ^a	µg/g Dry Wt.					
				ABA		PA		DPA	
				Pod	Pedicel	Pod	Pedicel	Pod	Pedicel
BTS	Small	Low	46	10.0	19.3	0	2.3	4.2	7.8
		High	56	65.0	24.0	0	0.7	25.3	8.1
	Medium	Low	0	10.4	17.5	0	0	0.8	5.0
		High	33	73.0	16.7	6.6	1.7	22.6	6.4
Seafarer	Large	Low	0	8.0	18.0	0	0	1.0	3.9
		High	0	99.0	32.8	64.7	0	13.4	4.7
	Small	Low	17	101.0	23.9	0	2.5	52.9	5.6
		High	88	159.0	19.7	11.8	1.3	36.0	2.6
Seafarer	Medium	Low	0	68.0	22.9	0	0	41.6	3.5
		High	33	101.0	17.7	4.0	1.8	31.0	4.7
	Large	Low	0	81.0	24.1	16.4	2.8	48.6	6.9
		High	0	89.0	14.4	61.8	0	49.0	2.4
Means for:									
BTS			22 a	44.2 a	21.4 a	11.9 a	0.8 a	11.4 a	6.0 a
			23 a	99.8 b	20.4 a	15.4 a	1.4 a	43.2 b	4.3 a
Seafarer	Small		52 b	83.7 x	21.7 x	2.9 x	1.7 x	29.8 x	6.0 x
			16 a	63.1 x	18.7 x	2.6 x	0.9 x	24.0 x	4.9 x
Seafarer	Medium		0 a	69.2 x	22.3 x	35.7 y	0.7 x	28.0 x	4.5 x
			10 a	46.4 m	20.9 m	2.7 m	1.3 m	24.8 m	5.4 m
Seafarer	Large		35 b	97.7 n	20.9 m	24.8 n	0.9 m	29.7 m	4.8 m

^a - followed by similar letters are not significantly different

^aMeans within the same parameter followed by similar letters are not significantly different at the 5% level by Duncan's Multiple Range Test.



inhibitors in fruits and their abscission, Zucconi (12) has pointed out the fallacy of measuring ABA content of abscising fruits, viz., that one is measuring the result of abscission rather than its cause. ABA content should be measured during induction. Zucconi (12) actually demonstrated a negative correlation between content of an ABA-like inhibitor and the induction of abscission in peach fruits.

In the present study, ABA content of the fruits paralleled relative abscission potential as affected by cultivar and treatment (deflowering), but fruit size, which greatly affected abscission, had little effect on ABA content. I conclude from this that the cultivar and treatment effects on ABA content were fortuitous, rather than being causally related to abscission. If ABA content were in fact responsible for abscission, one would expect differences to be apparent in the pedicel, where abscission actually occurs. However, this was not the case.

PA and DPA have not been implicated directly in abscission, and their levels appear to bear little relationship to fruit retention. There was no correlation between relative levels of PA vs. DPA in the pods; PA levels were significantly affected by deflowering and by pod size, while DPA content varied only with cultivar.

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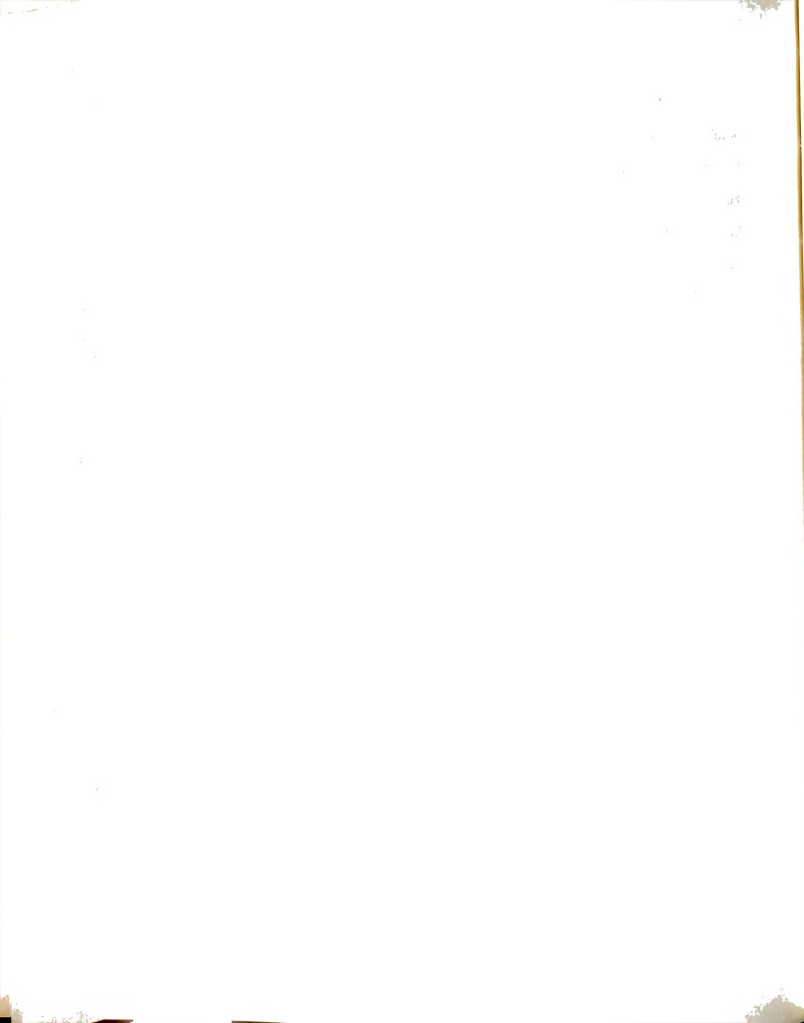
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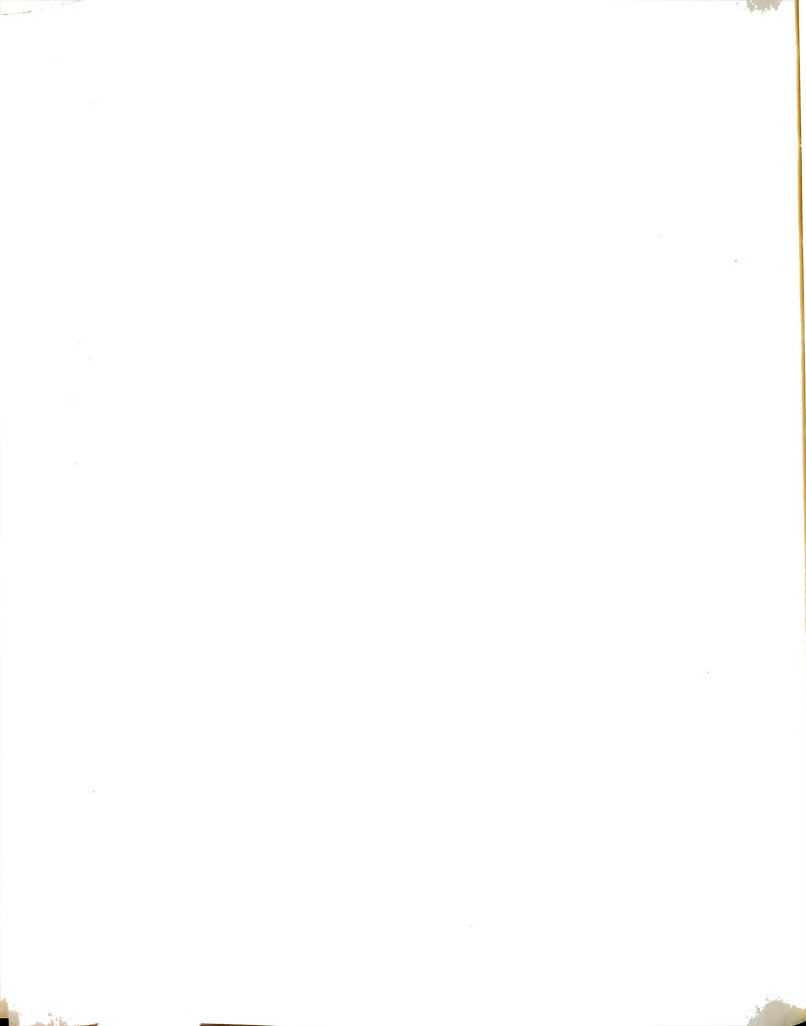
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If ABA regulates abscission, it must do so independently of concentration in the tissue as a whole. Concentrations might be very different in the cells of the abscission zone itself, for example. On the other hand, diffusible ABA could control abscission independently of the size of the pool of extractable ABA.



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CHAPTER 8

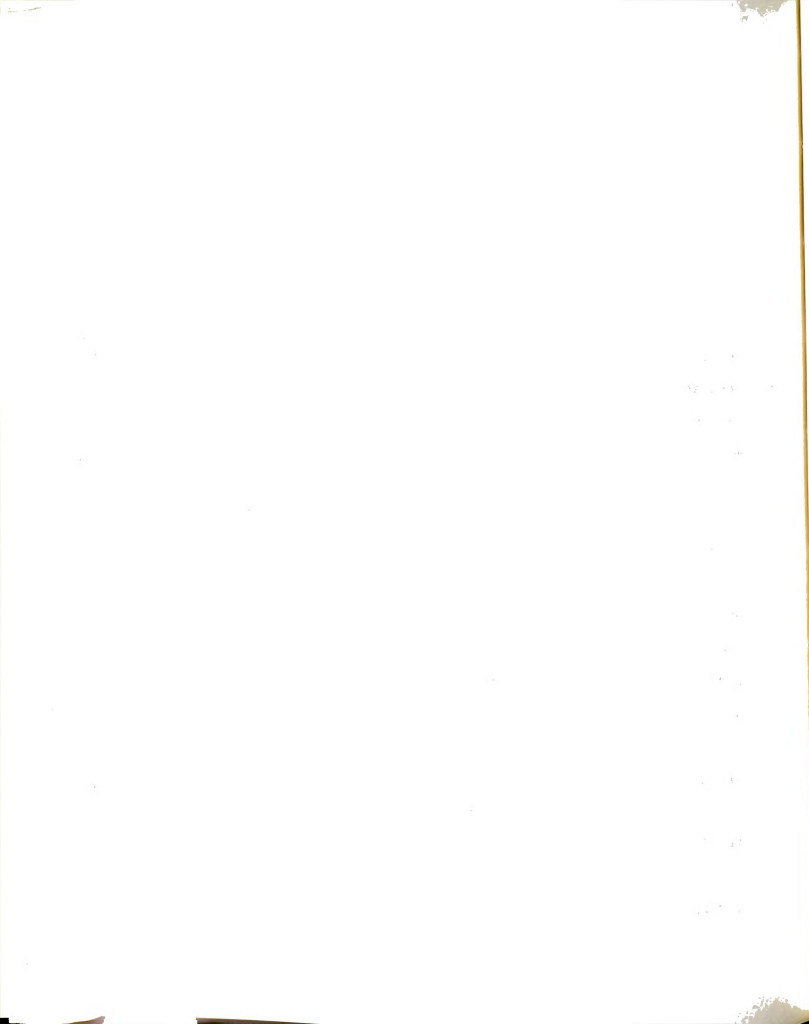
SUMMARY AND CONCLUSIONS

Elucidation of the causes of physiological processes is difficult, especially in an area as complex as abscission. However, an effort must be made to generate reasonable hypotheses, and to design appropriate experiments to test them, if progress is to be made.

In this work, differences were established in abscission potential of reproductive structures in dry bean cultivars.

Among the bean cultivars studied, Black Turtle Soup and Seafarer were selected for their contrasting growth habits and abscission rates. Black Turtle Soup, an indeterminate type, had a lower pod abscission rate than Seafarer, a determinate bush bean.

Exposure of either cultivar to long photoperiods or high carbon dioxide levels after the onset of flowering increased vegetative growth and leaf area, reduced pod abscission and consequently resulted in higher seed number and greater seed yield. Black Turtle Soup was more responsive to both factors than was Seafarer.



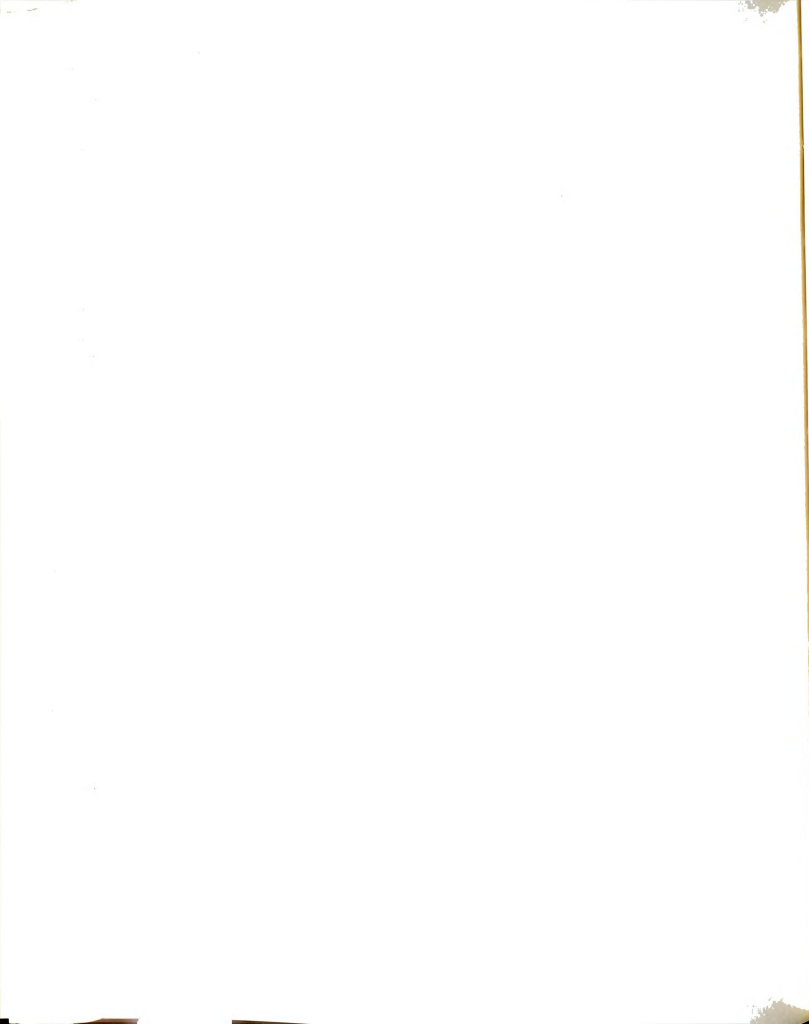
Levels of free sugar and starch in root, stem and leaf increased with photoperiod and carbon dioxide level. Available carbohydrate concentration in vegetative tissues was higher in the Black Turtle Soup cultivar, consistent with larger plants, greater leaf area and a lower abscission rate. However, the results provide only correlative evidence in support of the carbohydrate hypothesis.

Levels of abscisic acid and its related compounds in pod and pedicel were not related to the role of abscission in either cultivar. Young pods of Seafarer contained more abscisic acid and dihydrophaseic acid than did those of Black Turtle Soup. Levels in the pedicel were not affected by cultivar.

In conclusion, pod abscission in dry bean is not totally dependent on available carbohydrate levels. Many nutritional factors such as nitrogen, or carbohydrate/nitrogen ratio could regulate abscission. Although endogenous abscisic acid content was not correlated with abscission, other naturally occurring growth regulators, such as ethylene, cytokinin and auxin could play a role. The interplay between the nutritional and hormonal levels at a particular stage of development may control pod abscission. Since abscission is a complex process influenced by many environmental factors, care must be taken to design critical experiments to test available hypotheses.



APPENDICES



APPENDIX A

GROWTH AND POD ABSCISSION AS AFFECTED
BY DIFFERENT DAYLENGTHS

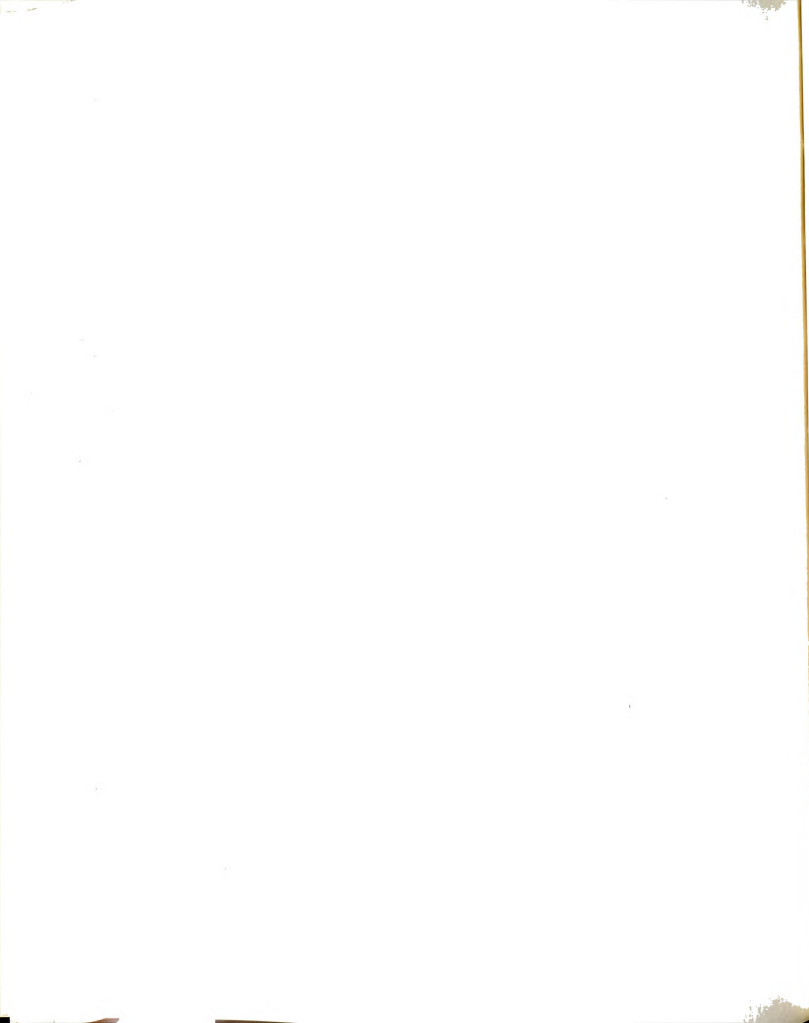


Table A-1

Effects of Daylengths on Number of Flowers, Number of Pods and Percentage of Pod Abscission at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1975a

Dev. Stages	Cultivar	No. of Flowers					No. of Pods					% Pod Abscission				
		Daylengths					Daylengths					Daylengths				
		8	13	18	Mean		8	13	18	Mean		8	13	18	Mean	
Peak Flowering	Black Turtle Soup	7	8	17	10		7	8	16	10		-	-	-	-	
	Seafarer	12	29	31	24		12	27	30	23		-	-	-	-	
	Mean	10	18	24	17a		9	17	23	16c		-	-	-	-	
Pod Filling	Black Turtle Soup	8	9	17	11		5	7	16	9		29.6	21.1	9.3	20.0	
	Seafarer	12	27	32	24		5	9	19	11		48.5	66.5	42.1	52.3	
	Mean	9	18	25	17a		5	8	17	10b		39.0	43.8	25.7	36.2a	
Maturity	Black Turtle Soup	9	8	17	11		3	5	12	7		63.0	30.1	29.7	40.9	
	Seafarer	14	29	35	26		3	7	16	8		73.8	71.8	53.6	66.4	
	Mean	11	18	26	19a		3	6	14	8a		68.4	50.9	41.7	53.7b	
	Mean	10x	18y	25z			6x	10y	18z			53.7z	47.4y	33.7x		
Mean cultivar	BTS	11 m					9 m					30.5 m				
	Seafarer	25 n					14 n					59.4 n				
Interactions																
1) Dev. stage x cultivar		n.s.					**					n.s.				
2) Dev. stage x photoperiod		n.s.					*					**				
3) Cultivar x photoperiod		**					**					**				
4) Dev. stage x cultivar x photoperiod		n.s.					**					n.s.				

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

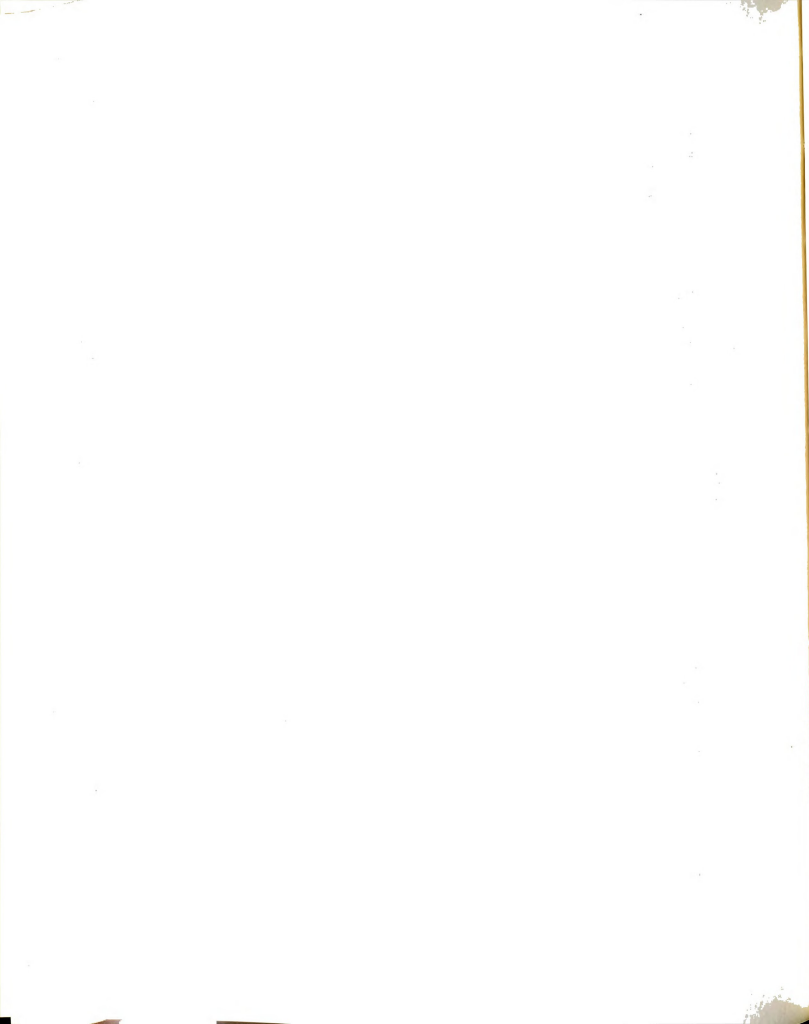


Table A-2
Effects of Daylengths on Number of Flowers, Number of Pods and Percentage of Pod Abscission at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1976a

Dev. Stages	Cultivar	No. of Flowers					No. of Pods					% Pod Abscission				
		Daylengths					Daylengths					Daylengths				
		8	13	16	Mean		8	13	16	Mean		8	13	18	Mean	
Peak Flowering	Black Turtle Soup	6	6	9	7		6	6	9	7		-	-	-	-	
	Seafarer	14	18	15	10		13	16	13	14		-	-	-	-	
	Mean	10	12	12	11a		9	11	11	10c						
		7	8	12	9		5	5	10	7		37.6	27.3	14.0	26.3	
Pod Filling	Black Turtle Soup	16	18	22	18		5	8	11	8		67.3	56.5	50.0	57.9	
	Seafarer	11	13	17	14a		5	7	10	7b		67.3	41.9	32.0	42.1a	
	Mean	5	9	11	9		2	5	7	5		52.0	40.6	33.6	42.1	
		13	15	22	17		4	6	8	6		74.6	62.7	61.1	66.2	
Maturity	Black Turtle Soup	9	12	17	13a		3	6	8	5a		63.3	51.6	47.3	54.1b	
	Seafarer															
	Mean	10x	12y	15z			6x	8y	10z			57.9z	46.8y	39.7x		
Mean	BTS	8 m					6 m					34.18 m				
cultivar	Seafarer	17 n					9 n					62.02 n				
Interactions																
1) Dev. stage x cultivar		n.s.					**					n.s.				
2) Dev. stage x photoperiod		n.s.					*					n.s.				
3) Cultivar x photoperiod		n.s.					n.s.					n.s.				
4) Dev. stage x cultivar x photoperiod		n.s.					n.s.					n.s.				

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

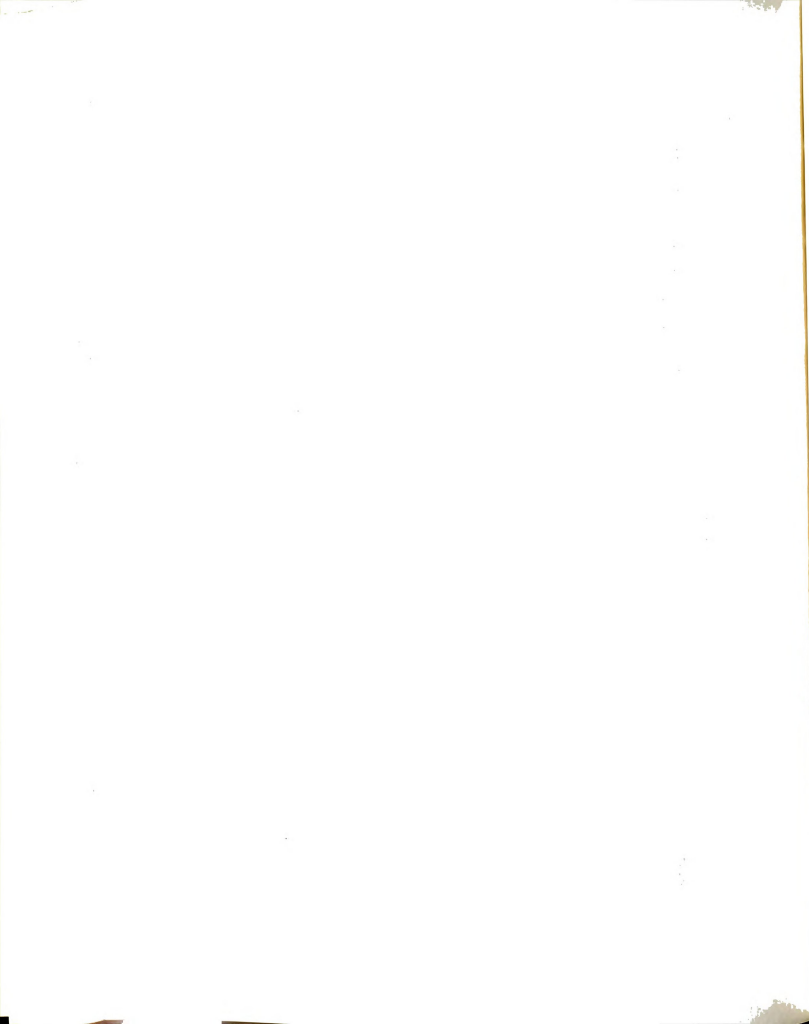


Table A-3
Effects of Daylengths on Leaf Area Per Plant, Number of Leaf Per Plant and Leaf Weight Per Plant at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1972a

Dev. Stage	Cultivar	Leaf Area/Plant				No. Leaf/Plant				Leaf Weight/Plant (g)			
		Daylengths				Daylengths				Daylengths			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	1282	1478	1903	1554	14	16	21	17	2.5	3.3	7.1	4.3
	Seafarer	1135	1271	1297	1234	17	16	17	17	2.3	2.8	4.1	3.1
	Mean	1208	1374	1600	1394a	15	16	19	17a	2.4	3.1	5.6	3.7a
Pod Filling	Black Turtle Soup	1229	1742	2111	1694	13	15	20	16	3.5	5.0	6.5	5.0
	Seafarer	1041	1350	1357	1250	14	17	19	17	3.3	4.1	4.9	4.1
	Mean	1135	1546	1734	1472a	13	16	20	16a	3.4	4.6	5.7	4.6b
	Mean	1172x	1460y	1667z		14x	16y	19z		2.9x	3.8y	5.7x	
Mean cultivar	BTS	1624 n				16 m				4.7 n			
	Seafarer	1242 m				17 m				3.6 m			
Interactions													
1) Dev. stage x cultivar		n.s.				n.s.				n.s.			
2) Dev. stage x photoperiod		n.s.				n.s.				n.s.			
3) Cultivar x photoperiod		**				*				**			
4) Dev. stage x cultivar x photoperiod		n.s.				n.s.				n.s.			

a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range test.

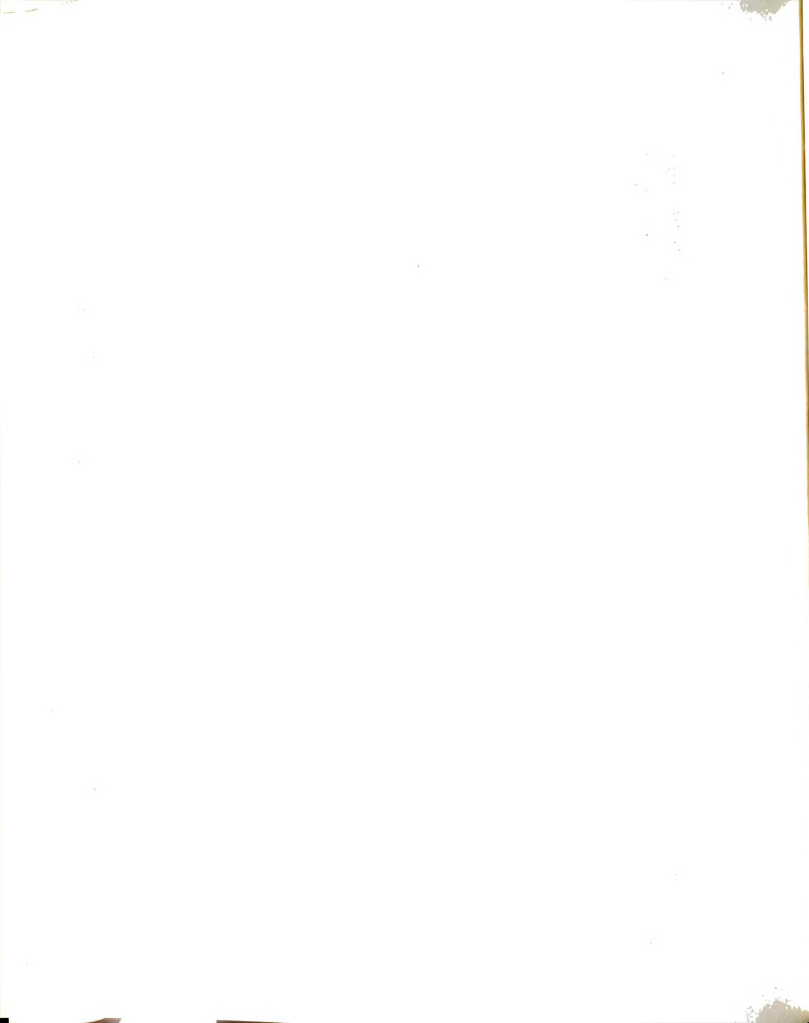


Table A-4
Effects of Daylengths on Leaf Area Per Plant, Number of Leaf Per Plant and Leaf Weight Per Plant at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1976a

Dev. Stage	Cultivar	Leaf Area/Plant				No. Leaf/Plant				Leaf Weight/Plant (g)			
		Daylengths				Daylengths				Daylengths			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	903	1071	1279	1084	10	11	13	12	1.9	2.0	3.0	2.3
	Seafarer	681	907	1108	899	10	11	15	12	1.5	2.2	3.1	2.3
	Mean	792	989	1194	991a	10	11	14	12a	1.7	2.1	3.1	2.3a
Pod Filling	Black Turtle Soup	868	1121	1651	1214	9	12	15	12	1.6	2.3	4.4	2.7
	Seafarer	903	1003	1241	1049	11	14	16	14	1.5	2.0	3.5	2.3
	Mean	886	1062	1446	1131b	10	13	15	13b	1.5	2.2	3.9	2.5a
Mean		839x	1026y	1320z		10x	12y	15z		1.6x	2.1y	3.5z	
Mean cultivar	BFS	1149 n				12 m				2.5 m			
	Seafarer	974 m				13 m				2.3 m			
Interactions													
1) Dev. stage x cultivar		n.s.				n.s.				n.s.			
2) Dev. stage x photoperiod		n.s.				n.s.				*			
3) Cultivar x photoperiod		n.s.				n.s.				n.s.			
4) Dev. stage x cultivar		n.s.				n.s.				n.s.			
x photoperiod		n.s.				n.s.				n.s.			

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

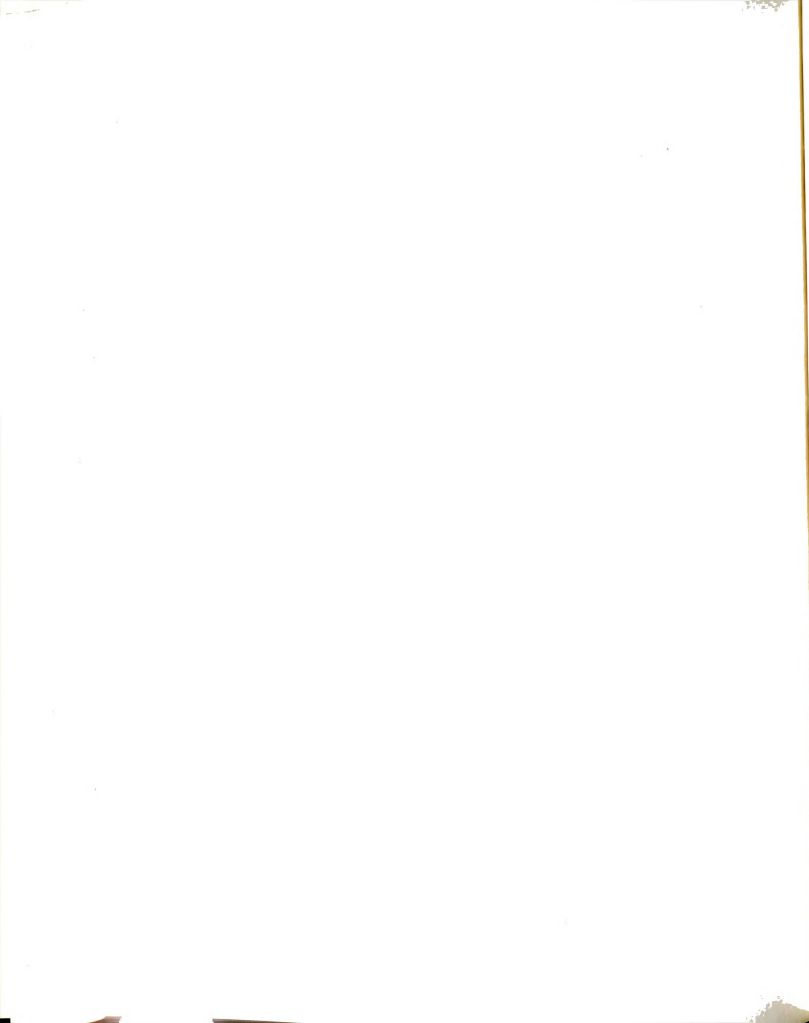


Table A-5
Effects of Daylengths Effects on Root Weight Per Plant, Stem Weight Per Plant and Total Plant Weight at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1975a

Dev. Stage	Cultivar	Root Weight (g)/Plant				Stem Weight (g)/Plant				Total Plant Wt. (g)			
		Daylengths				Daylengths				Daylengths			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	1.1	1.8	3.4	2.1	1.3	1.6	3.6	2.2	5.2	6.4	13.1	8.2
	Seafarer	1.1	1.2	2.7	1.7	1.3	1.7	3.2	1.7	4.7	5.3	8.2	6.1
	Mean	1.1	1.5	3.0	1.9c	1.3	1.6	2.9	2.0b	4.9	5.9	10.7	7.2a
Pod Filling	Black Turtle Soup	0.7	1.0	2.0	1.2	1.2	1.8	3.3	2.1	7.2	12.6	18.2	12.7
	Seafarer	0.5	0.8	1.6	1.0	1.3	1.6	2.6	1.8	5.4	12.8	19.0	12.4
	Mean	0.6	0.9	1.8	1.1b	1.2	1.7	2.9	2.0b	6.3	12.7	18.6	12.5c
Maturity	Black Turtle Soup	0.7	0.9	1.4	1.0	1.1	1.3	2.3	1.6	5.9	10.0	20.6	12.2
	Seafarer	0.6	0.6	1.0	0.7	1.5	1.4	2.0	1.6	5.9	8.0	17.1	10.4
	Mean	0.7	0.7	1.2	0.9a	1.3	1.3	2.2	1.6a	5.9	9.0	18.9	11.3b
	Mean	0.8x	1.0y	2.0z		1.3x	1.6y	2.7z		5.7x	9.2y	16.0z	
Mean cultivar	BTS	1.4 n				1.9 n				11.0 n			
	Seafarer	1.1 m				1.7 m				9.6 m			
Interactions													
1)	Dev. stage x cultivar	n.s.				*				n.s.			
2)	Dev. stage x photoperiod	**				**				**			
3)	Cultivar x photoperiod	n.s.				**				n.s.			
4)	Dev. stage x cultivar x photoperiod	n.s.				n.s.				*			

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

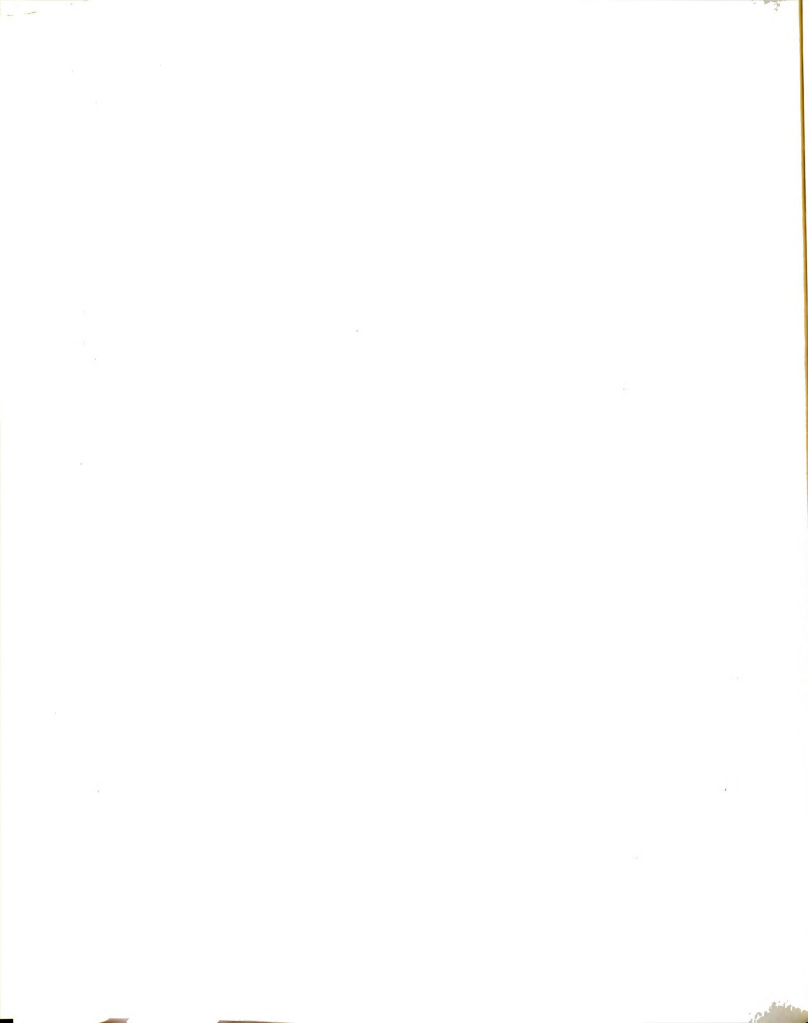
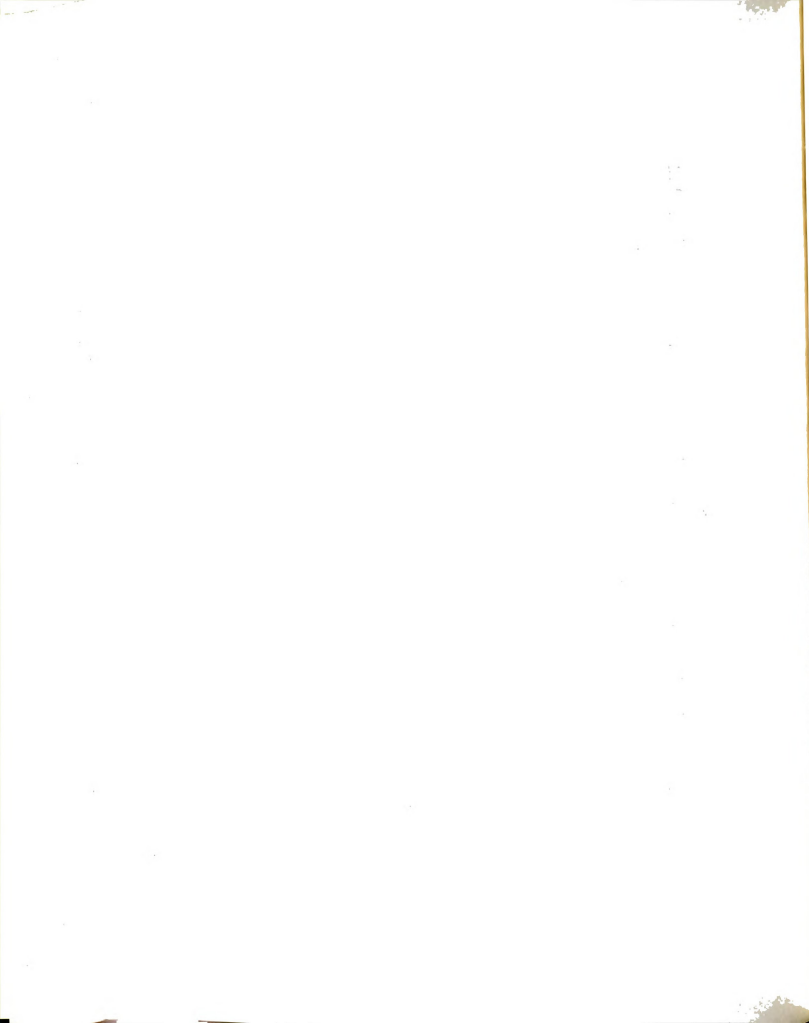


Table A-6
Effects of Daylengths on Root Weight Per Plant, Stem Weight Per Plant and Total Plant Weight at 3 Stages of Development of Two Dry Bean Cultivars Grown Under Greenhouse Conditions in 1976a

Dev. Stage	Cultivar	Root Weight (g)/Plant				Stem Weight (g)/Plant				Total Plant Wt. (g)			
		Daylengths				Daylengths				Daylengths			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	0.7	0.8	1.1	0.9	0.9	0.9	1.3	1.0	3.6	3.8	5.9	4.5
	Seafarer	0.7	1.0	1.4	1.0	0.9	1.3	1.7	1.3	3.5	5.2	6.7	5.1
	Mean	0.7	0.9	1.3	1.0a	0.9	1.1	1.5	1.2a	3.6	4.5	6.3	4.8a
Pod Filling	Black Turtle Soup	0.5	0.8	1.5	0.9	0.8	1.3	2.4	1.5	4.0	6.7	12.7	7.8
	Seafarer	0.5	0.9	1.8	1.1	1.0	1.3	2.2	1.5	4.0	7.6	13.7	8.8
	Mean	0.5	0.9	1.6	1.0a	0.9	1.3	2.3	1.5b	4.5	7.1	13.2	8.3b
Maturity	Black Turtle Soup	0.3	0.8	1.1	0.7	0.5	1.0	1.5	1.0	2.6	7.7	10.5	6.9
	Seafarer	0.5	0.7	1.8	1.0	1.0	1.1	2.1	1.4	4.6	7.4	12.5	8.1
	Mean	0.4	0.7	1.5	0.9a	0.8	1.1	1.8	1.2a	3.6	7.5	11.5	7.5b
	Mean	0.5x 0.8y 1.5z				0.9x 1.1y 1.9z				3.9x 6.4y 10.3z			
Mean cultivar	BTS	0.86 m				1.2 m				6.4 m			
	Seafarer	1.04 n				1.4 n				7.3 m			
Interactions													
1) Dev. stage x cultivar		n.s.				n.s.				n.s.			
2) Dev. stage x photoperiod		**				*				**			
3) Cultivar x photoperiod		*				n.s.				n.s.			
4) Dev. stage x cultivar x photoperiod		n.s.				n.s.				n.s.			

^a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



APPENDIX B

RELATIONSHIP OF POD ABSCISSION TO DIFFERENTIAL LEVELS
OF CARBOHYDRATES PRODUCED BY VARIATION
IN DAYLENGTH

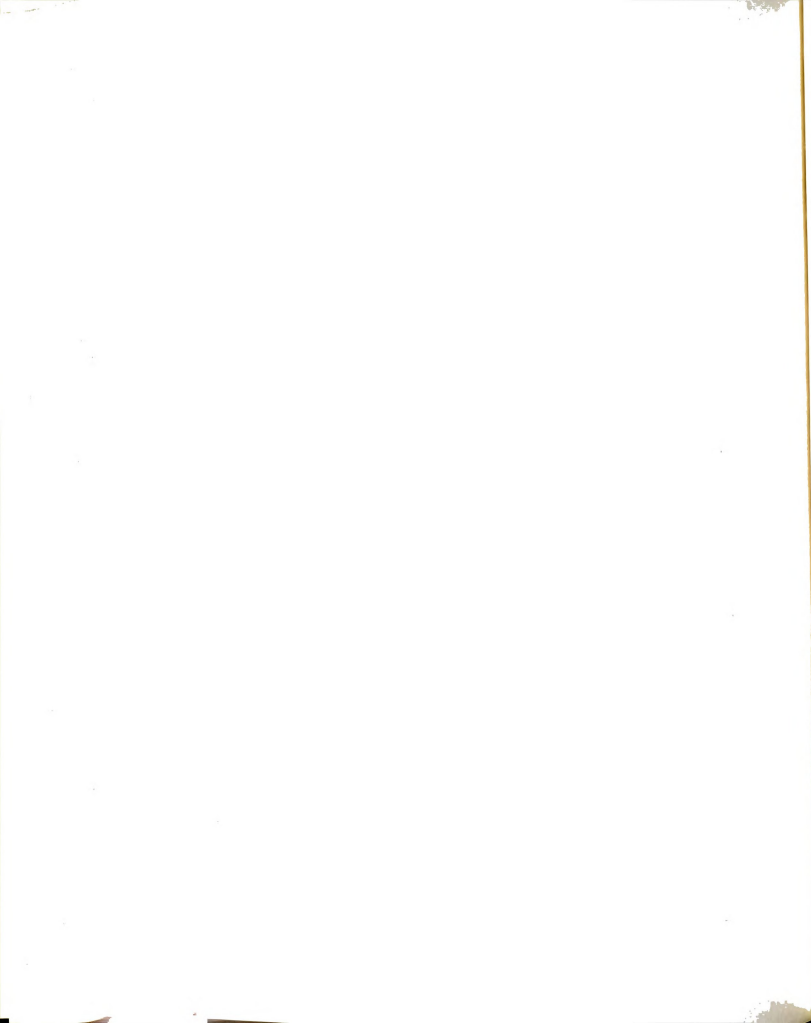


Table B-1
Effects of Developmental Stages and Daylength on Free Sugar Levels in Vegetative Tissues of Two *Phaseolus vulgaris* L. Cultivars (data in mg glucose per gram dry weight)^a

Dev. Stage	Cultivars	Root			Stem			Leaf		
		Daylength (hrs)			Daylength (hrs)			Daylength (hrs)		
		8	13	18	8	13	18	8	13	18
Peak Flowering	Black Turtle Soup	11.8	16.0	17.0	14.9	81.4	95.2	88.6	88.4	49.3
	Seafarer	9.0	11.2	9.4	9.9	53.9	67.6	61.3	60.9	38.9
	Mean	10.4	13.6	13.2	12.4a	67.6	81.4	74.9	74.5c	44.1
Pod Filling	Black Turtle Soup	16.2	21.9	22.7	20.3	57.8	83.7	88.9	76.8	67.2
	Seafarer	13.6	15.1	13.3	14.0	36.8	49.9	59.2	48.6	55.9
	Mean	14.9	18.5	18.0	17.1c	47.3	66.8	74.0	62.7b	61.5
Maturity	Black Turtle Soup	9.0	11.2	19.8	13.3	21.6	35.7	58.5	38.6	-
	Seafarer	13.2	13.9	15.3	14.1	21.0	34.9	38.0	31.3	-
	Mean	11.1	12.5	17.5	13.7b	21.3	35.3	48.2	34.9a	-
Mean: Daylength		12.1x	14.9y	16.3z		45.4x	61.2y	65.7z	52.8x	67.2z
Mean cultivar	BTS	16.2 n				67.9 n			68.8 n	
	Seafarer	12.7 m				47.0 m			52.8 m	
Interactions										
1) Dev. stage x cultivar		**			**				*	*
2) Dev. stage x daylength		**			**				**	*
3) Cultivar x daylength		**			*				*	*
4) Dev. stage x cultivar x daylength		n.s.			*				**	*

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

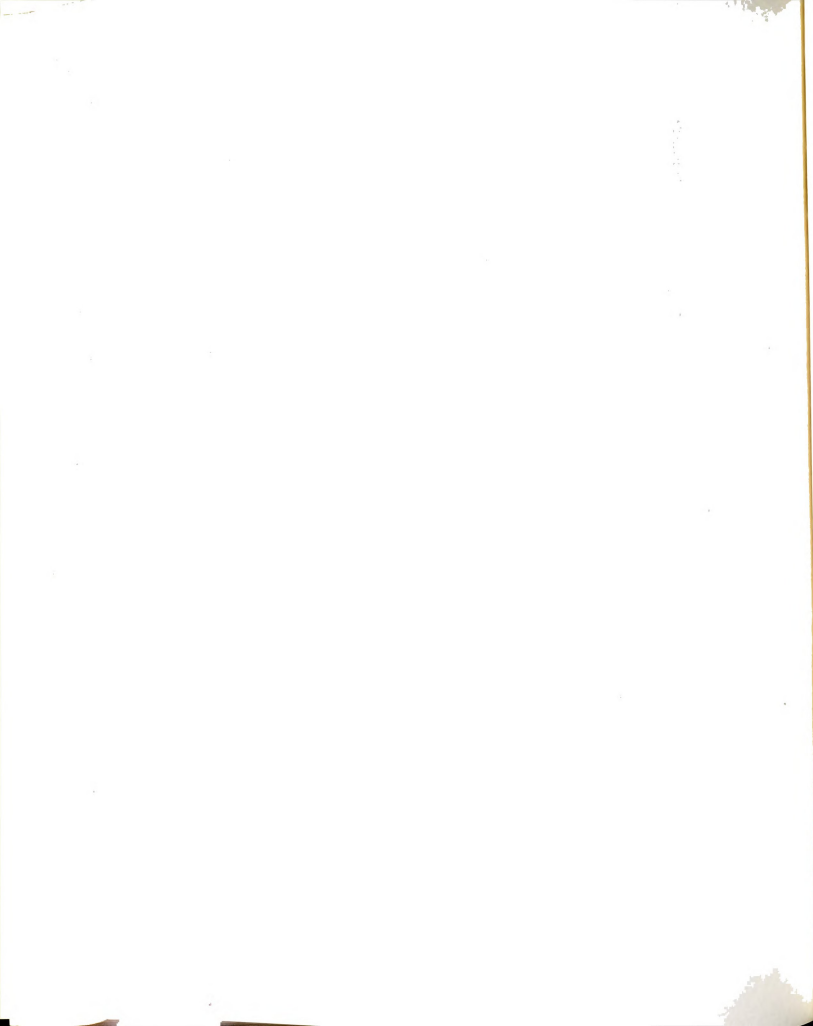


Table B-2
Effects of Developmental Stages and Daylength on Free Sugar Levels in Reproductive tissues of
Two *Phaseolus vulgaris* L. (data in mg glucose per gram dry weight)^a

Dev. Stage	Cultivars	Seed				Pod Wall			
		Daylength (hrs)				Daylength (hrs)			
		8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	-	-	-	-	173	178	208	187
	Seafarer	-	-	-	-	146	170	183	166
	Mean	-	-	-	-	159	174	195	176c
Pod Filling	Black Turtle Soup	52.3	63.7	103.8	73.3	151	130	192	158
	Seafarer	46.1	58.4	75.2	59.9	140	113	120	124
	Mean	49.2	61.0	89.5	66.6a	145	122	156	141b
Maturity	Black Turtle Soup	57.8	69.4	74.2	67.1	21.4	21.2	25.4	22.7
	Seafarer	70.8	76.4	80.1	75.8	32.2	27.3	29.1	29.5
	Mean	64.3	72.9	77.1	71.5a	26.8	24.2	27.2	26.1a
Mean: daylength		56.7x	66.9y	83.3z		110.7x	106.7x	126.4y	
Mean cultivar	BFS		70.2 m					122.4 n	
	Seafarer		67.8 m					106.8 m	
Interactions									
1) Dev. stage x cultivar			**					**	
2) Dev. stage x daylength			*					**	
3) Cultivar x daylength			n.s.					**	
4) Dev. stage x cultivar x daylength			n.s.					*	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

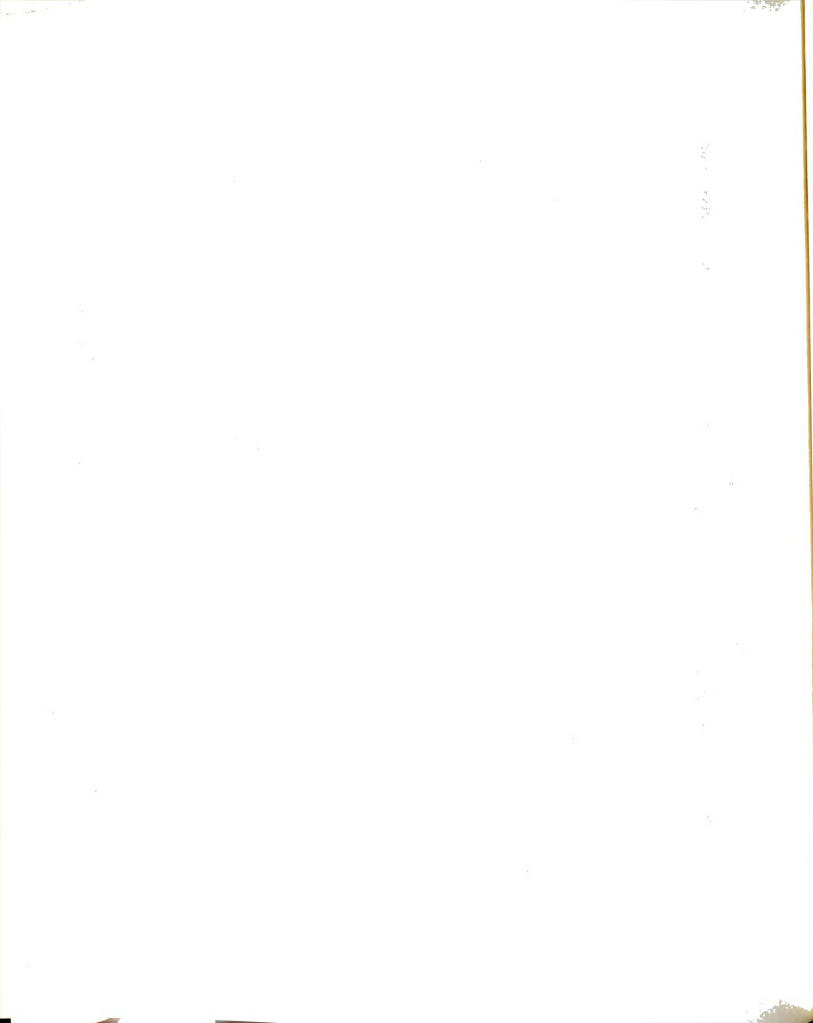


Table B-3
Effects of Developmental Stages and Daylength on Starch Levels in Vegetative Tissues of Two *Phaseolus vulgaris* L. Cultivars (data in mg glucose equivalent per gram dry weight)^a

Dev. Stage	Cultivars	Root				Stem				Leaf			
		Daylength (hrs)				Daylength (hrs)				Daylength (hrs)			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle	28.9	30.7	9.3	23.0	110.6	121.0	197.1	142.9	83.3	63.4	217.5	121.4
	Soup	22.1	25.4	6.2	17.9	55.6	69.9	137.0	87.5	67.7	31.1	76.2	58.3
	Seafarer	25.5	28.1	7.8	20.4b	83.1	95.5	167.1	115.2b	75.5	47.3	146.8	89.9b
	Mean												
Pod Filling	Black Turtle	5.0	15.7	25.0	15.2	65.9	162.0	242.2	156.7	15.2	53.6	30.2	33.0
	Soup	19.9	19.3	13.1	17.5	72.7	84.2	107.3	78.0	18.8	39.5	14.5	24.3
	Seafarer	12.5	17.5	19.0	16.4a	69.3	108.1	174.7	117.4b	17.0	46.6	22.4	28.7a
	Mean												
Maturity	Black Turtle	19.5	26.6	18.7	21.6	11.3	25.5	39.3	25.4	-	-	-	-
	Soup	17.0	25.8	23.2	22.0	13.5	41.6	20.5	25.2	-	-	-	-
	Seafarer	18.3	26.2	20.9	21.8b	12.4	33.5	29.9	25.3a	-	-	-	-
	Mean												
Mean: daylength		18.8x	23.9y	15.9x		54.9x	79.0y	123.9z		46.3x	46.9x	84.6y	
Mean cultivar	BTS	19.9 m				108.3 n				77.2 n			
	Seafarer	19.1 m				63.6 m				41.3 m			
Interactions													
1) Dev. stage x cultivar		*				**				**			
2) Dev. stage x daylength		**				**				**			
3) Cultivar x daylength		n.s.				**				**			
4) Dev. stage x cultivar x daylength		**				**				**			

^a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range test.



Table B-4

Effects of Developmental Stages and Daylength on Starch Levels in Reproductive Tissues of Two *Phaseolus vulgaris* L. Cultivars (data in mg glucose equivalent per gram dry weight)^a

Dev. Stage	Cultivars	Seed			Pod Wall			
		Daylength (hrs)		Mean	Daylength (hrs)			Mean
		8	13	18	8	13	18	
Peak Flowering	Black Turtle Soup	-	-	-	36.3	58.8	69.6	54.9
	Seafarer	-	-	-	68.4	53.7	52.5	58.2
	Mean	-	-	-	52.4	56.3	61.0	56.6b
Pod Filling	Black Turtle Soup	362.6	428.0	348.6	379.8	276.7	412.0	325.4
	Seafarer	372.1	456.7	366.0	398.3	341.8	424.3	366.6
	Mean	367.4	442.4	357.3	389.0c	309.2	418.1	346.0
Maturity	Black Turtle Soup	283.7	371.1	386.3	347.0	8.4	30.3	64.2
	Seafarer	310.9	351.8	356.0	339.5	24.4	26.1	76.9
	Mean	297.3	361.4	371.2	343.3b	16.4	28.2	70.5
Mean: daylength		332.3x	401.9z	364.2y	126x	167y	159y	
Mean cultivar	BTS		363.4 m			142 m		
	Seafarer		368.9 m			159 n		
<u>Interactions</u>								
1) Dev. stage x cultivar			n.s.					**
2) Dev. stage x daylength			**					**
3) Cultivar x daylength			*					*
4) Dev. stage x cultivar								
x daylength				n.s.				n.s.

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

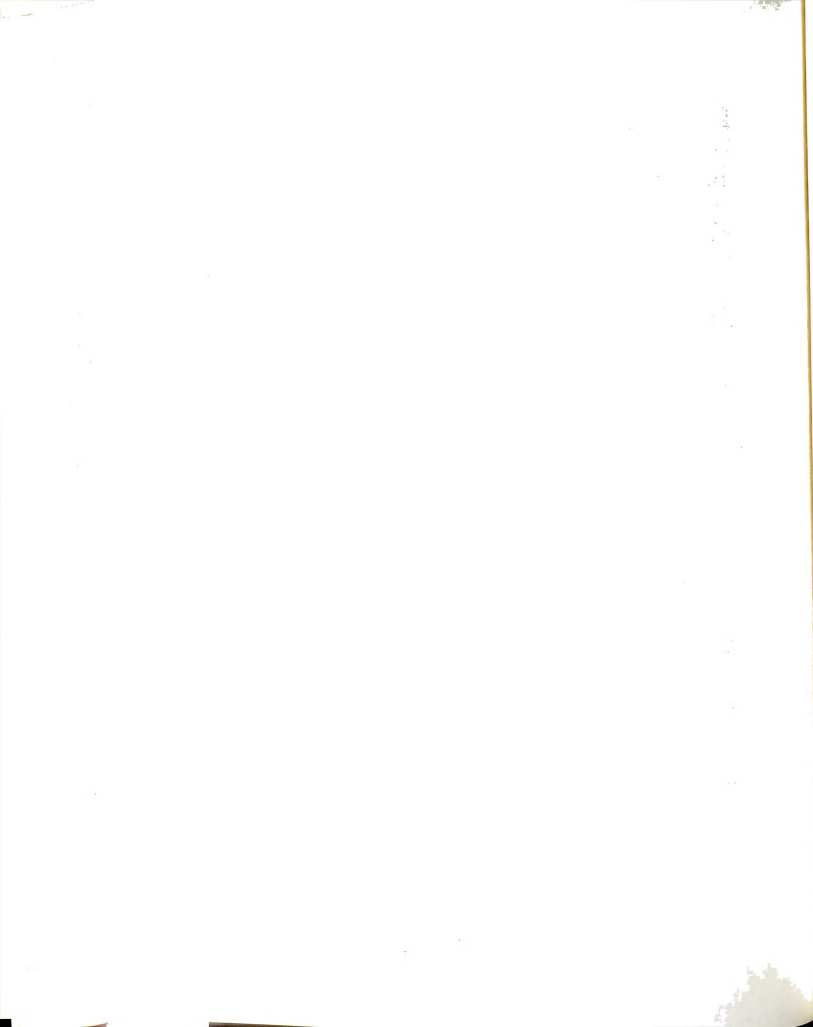


Table B-5
Effects of Developmental Stages and Daylength on Total Nonstructural Carbohydrate Levels in Vegetative Tissues of Two *Phaseolus vulgaris* L. Cultivars (data in mg glucose per gram dry weight)^a

Dev. Stage	Cultivars	Root				Stem				Leaf			
		Daylength (hrs)				Daylength (hrs)				Daylength (hrs)			
		8	13	18	Mean	8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle	189.7	223.1	285.9	232.9	40.4	46.5	20.9	35.9	132.7	126.5	290.1	183.1
	Soup	110.4	135.6	198.2	148.0	31.1	34.2	13.6	26.3	106.6	85.1	126.5	106.9
	Seafarer	150.0	179.4	242.0	190.5b	35.8	40.3	17.2	31.1a	119.6	105.8	208.3	144.5b
Pod Filling	Black Turtle	123.8	255.7	321.1	236.9	22.4	36.8	43.5	34.2	81.7	144.4	94.8	106.1
	Soup	109.4	104.2	166.5	126.7	30.1	31.2	26.1	29.1	71.3	95.8	65.7	77.6
	Seafarer	116.6	179.9	249.0	181.8b	26.3	34.0	34.8	31.7a	76.5	120.1	80.2	92.3a
Maturity	Black Turtle	30.9	53.2	86.5	56.9	27.9	37.3	36.9	34.1	-	-	-	-
	Soup	57.0	61.5	52.3	57.0	26.9	37.9	39.5	34.8	-	-	-	-
	Seafarer	44.0	57.3	69.4	56.9a	27.4	37.6	38.2	34.4a	-	-	-	-
Mean		103.6x	138.3y	186.7z		29.8x	37.3y	30.1x		98.0x	112.9x	144.3y	
Mean	BTS	175.5 n				34.7 n				145.0 n			
Mean	Seafarer	110.6 m				30.1 m				91.8 m			
Interactions													
1) Dev. stage x cultivar			**				**				**		**
2) Dev. stage x daylength			**				**				**		**
3) Cultivar x daylength			**				n.s.				**		**
4) Dev. stage x cultivar x daylength			**				**				**		**

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

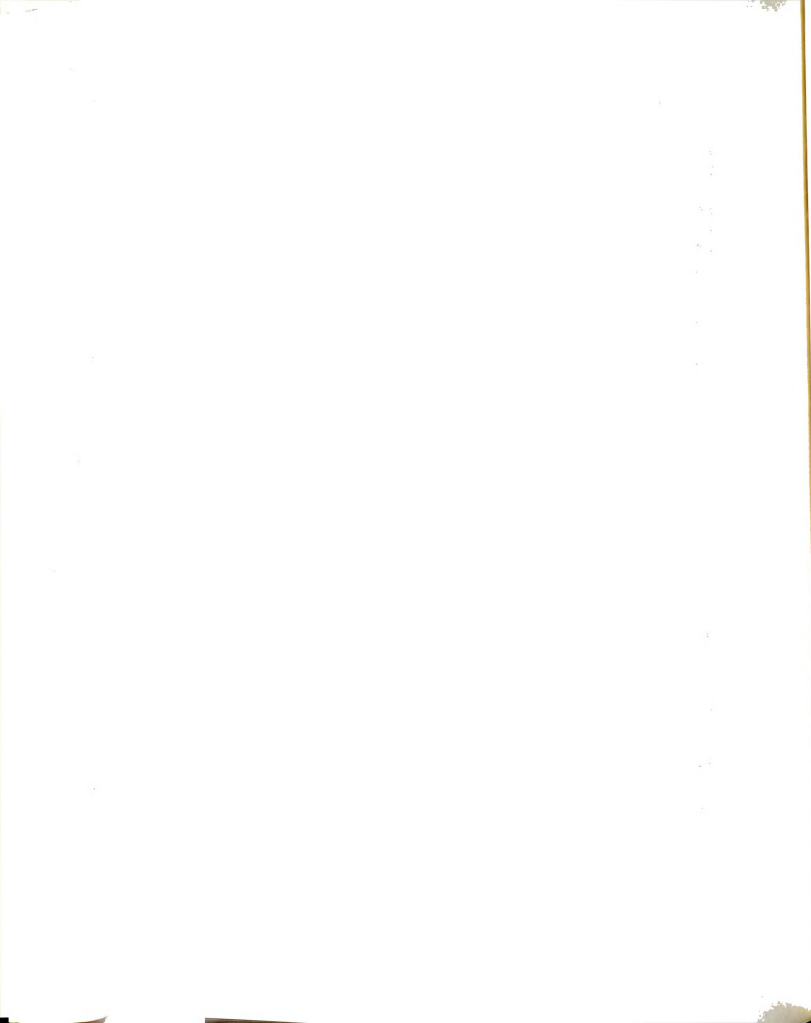
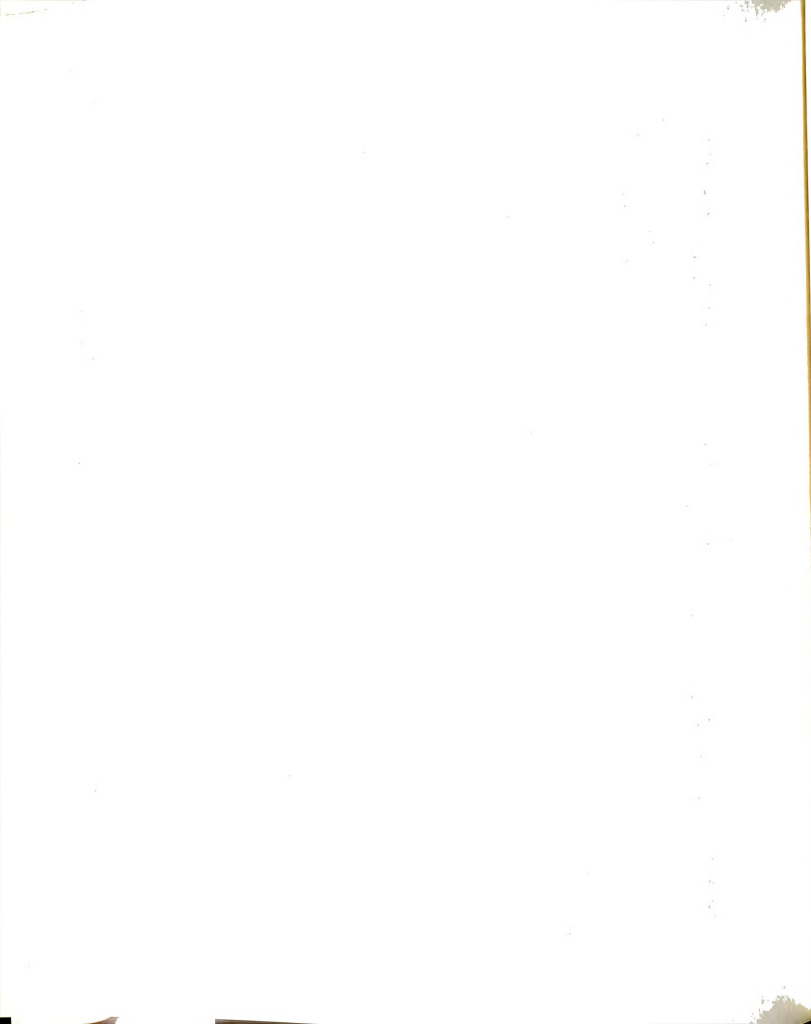


Table B-6
Developmental Stages and Daylength Effects on Total Nonstructural Carbohydrate Levels in Reproductive
Tissues of Two *Phaseolus vulgaris* L. Cultivars (data are means of 10 plants,
expressed as mg glucose per gram dry weight)^a

Dev. Stage	Cultivars	Seeds				Pod Wall			
		Daylength (hrs)				Daylength (hrs)			
		8	13	18	Mean	8	13	18	Mean
Peak Flowering	Black Turtle Soup	-	-	-	-	219	238	271	243
	Seafarer	-	-	-	-	206	221	244	224
	Mean	-	-	-	-	212	229	258	233b
Pod Filling	Black Turtle Soup	435	491	445	457	426	541	510	492
	Seafarer	409	514	463	462	485	536	499	507
	Mean	422	503	454	459c	455	538	504	499c
Maturity	Black Turtle Soup	341	438	458	412	29	51	88	56
	Seafarer	380	428	434	414	64	53	106	74
	Mean	361	433	446	413b	46	52	97	65a
Mean: daylength		391x	468y	450y		238x	273y	286y	
Mean cultivar	BTS	434 m				264 m			
	Seafarer	439 m				268 m			
Interactions									
1)	Dev. stage x cultivar							*	
2)	Dev. stage x daylength							**	
3)	Cultivar x daylength							*	
4)	Dev. stage x cultivar x daylength							n.s.	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



APPENDIX C

GROWTH AND POD ABSCISSION AS AFFECTED BY
CARBON DIOXIDE LEVELS

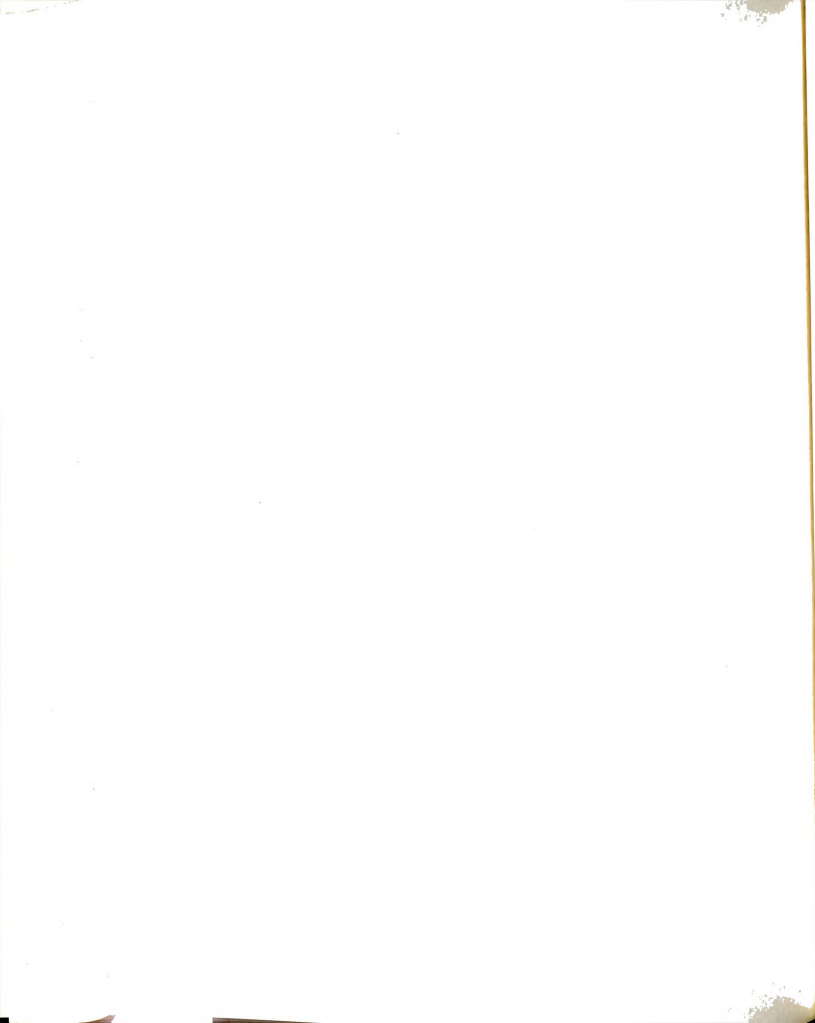


Table C-1

Effects of Carbon Dioxide Levels on Number of Flowers, Number of Pods and Percentage of Pod Abscission at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1975^a

Dev. Stages	Cultivars	No. of Flowers			No. of Pods			% Pod Abscission		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	9	11	10	8	8	8	-	-	-
	Seafarer	24	24	24	19	22	20	-	-	-
	Mean	16	17	17a	14	15	14c	-	-	-
Pod Filling	Black Turtle Soup	8	13	11	6	13	10	24.8	4.0	14.4
	Seafarer	20	21	21	11	16	13	43.8	27.6	35.7
	Mean	14	17	16a	9	14	11b	34.3	15.8	25.1a
Maturity	Black Turtle Soup	10	12	11	5	11	8	44.1	14.6	29.3
	Seafarer	16	24	20	6	13	9	63.9	41.8	52.3
	Mean	13	18	16a	5	12	9a	54.0	28.2	41.1b
	Mean	15x	17y		9x	14y		44.2y	22.0x	
Mean cultivar	BTS	10 m			9 m			21.9 m		
	Seafarer	22 n			14 n			44.3 n		
Interactions										
1) Dev. stage x cultivar		*			**			n.s.		
2) Dev. stage x CO ₂ level		n.s.			**			n.s.		
3) Cultivar x CO ₂ level		n.s.			n.s.			n.s.		
4) Dev. stage x cultivar x CO ₂ level		n.s.			n.s.			n.s.		

^aMeans within a given parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

Table C-2
Effects of Carbon Dioxide Levels on Number of Flowers, Number of Pods and Percentage of Pod Abscission at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1976a

Dev. Stages	Cultivar	No. of Flowers			No. of Pods			% Pod Abscission		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	5	9	7	5	8	7	-	-	-
	Seafarer	15	20	18	12	18	15	-	-	-
	Mean	10	14	12a(*)	8	13	11b	-	-	-
Pod Filling	Black Turtle Soup	5	9	7	4	9	6	15.5	5.4	10.4
	Seafarer	15	22	18	4	15	10	52.5	33.2	46.4
	Mean	10	16	13a	5	12	8a	37.5	19.3	28.4a
Maturity	Black Turtle Soup	6	16	11	4	10	7	36.7	24.4	30.5
	Seafarer	16	24	20	6	10	8	74.2	53.9	64.1
	Mean	11	20	15b	5	10	7a	55.5	39.1	47.3b
Mean		10x	17y		6x	11y		46.5y	29.2x	
Mean cultivar	BTS		8 m		6 m			20.5 m		
	Seafarer		19 n		11 n			55.2 n		
Interactions										
1) Dev. stage x cultivar			n.s.			**		n.s.	n.s.	
2) Dev. stage x CO ₂ level			n.s.			n.s.		n.s.	n.s.	
3) Cultivar x CO ₂ level			n.s.			n.s.		n.s.	*	
4) Dev. stage x cultivar x CO ₂ level			n.s.			n.s.		n.s.	n.s.	

*Means within a given parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



Table C-3
Effects of Carbon Dioxide Levels on Root Weight Per Plant, Stem Weight Per Plant and Total Plant Weight at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1975a

Dev. Stage	Cultivar	Root Wt/Plant (g)			Stem Wt/Plant (g)			Total Plant Wt (g)		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	1.3	1.7	1.5	1.6	2.0	1.8	6.4	9.0	7.7
	Seafarer	1.3	1.5	1.4	1.6	1.9	1.8	6.8	8.3	7.6
	Mean	1.3	1.6	1.4b	1.6	1.9	1.8b	6.6	8.6	7.6a
Pod Filling	Black Turtle Soup	0.9	1.5	1.2	1.4	2.8	2.1	7.8	15.4	11.6
	Seafarer	0.9	1.2	1.0	1.5	1.8	1.7	8.2	12.5	10.4
	Mean	0.9	1.3	1.1a	1.4	2.3	1.9b	8.0	14.0	11.0b
Maturity	Black Turtle Soup	0.7	1.5	1.1	0.9	2.1	1.5	6.8	15.7	11.2
	Seafarer	0.9	1.6	1.3	1.0	2.0	1.5	5.5	13.8	9.7
	Mean	0.8	1.6	1.2a	0.9	2.1	1.5a	6.2	14.8	10.5b
	Mean	1.0x	1.5y		1.3x	2.1y		6.9x	12.5y	
Mean cultivar	BTS	1.3 m			1.8 n			10.2 n		
	Seafarer	1.2 m			1.6 m			9.2 m		
Interactions										
1) Dev. stage x cultivars		**			**			n.s.		
2) Dev. stage x CO ₂ level		**			**			**		
3) Cultivar x CO ₂ level		**			**			**		
4) Dev. stage x cultivar x CO ₂ level		n.s.			**			n.s.		

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

Table C-4
Effect of Carbon Dioxide Levels on Root Weight Per Plant, Stem Weight Per Plant and Total Plant Weight
at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1976a

Dev. Stage	Cultivars	Root Wt./Plant (g)			Stem Wt./Plant (g)			Total Plant Wt (g)		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	1.0	1.4	1.2	0.9	1.6	1.2	4.0	7.0	5.5
	Seafarer	0.6	0.9	0.8	0.6	0.9	0.7	2.5	3.9	3.1
	Mean	0.8	1.2	1.0a	0.7	1.2	1.0a	3.2	5.5	4.3a
Pod Filling	Black Turtle Soup	1.2	2.2	1.7	1.3	2.3	1.8	6.4	8.9	7.6
	Seafarer	0.8	1.4	1.1	0.8	1.9	1.4	4.0	8.0	6.0
	Mean	1.0	1.8	1.4b	1.0	2.1	1.6b	5.2	8.5	6.8b
Maturity	Black Turtle Soup	1.2	2.7	2.0	0.9	2.7	1.8	7.4	14.0	10.9
	Seafarer	0.7	1.9	1.3	1.1	2.9	2.0	5.3	11.0	8.2
	Mean	1.0	2.3	1.6c	1.0	2.8	1.9c	6.4	12.7	9.5c
	Mean	0.9x	1.7y		0.9x	2.0y		4.9x	8.9y	
Mean cultivar	BTS	1.6 n			1.6 n			8.0 n		
	Seafarer	1.1 m			1.4 m			5.8 m		
Interactions										
1) Dev. stage x cultivars		n.s.			**			n.s.		
2) Dev. stage x CO ₂ level		**			**			*		
3) Cultivar x CO ₂ level		n.s.			n.s.			n.s.		
4) Dev. stage x cultivar		n.s.			n.s.			n.s.		
x CO ₂ level		n.s.			n.s.			n.s.		

a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



Table C-5

Effects of Carbon Dioxide Levels on Leaf Area Per Plant, Number of Leaf Per Plant and Leaf Weight Per Plant at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1973^a

Dev. Stage	Cultivar	Leaf Area/Plant (cm ²)			Number of Leaf/Plant			Leaf Wt./Plant (g)		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	715	802	758	12	24	18	2.9	4.5	3.7
	Seafarer	710	740	725	14	13	14	2.0	3.5	2.7
	Mean	713	771	742a	13	18	16b	2.4	4.0	3.2a
Pod Filling	Black Turtle Soup	620	1058	839	10	15	12	1.9	5.5	3.7
	Seafarer	708	738	723	13	13	13	1.9	3.2	2.6
	Mean	614	898	756a	11	14	13a	1.9	4.4	3.2a
Mean		663x	835y		12x	16y		2.2x	4.2y	
Mean cultivar	BTS	799 n			15 m			3.7 n		
	Seafarer	699 m			13 m			2.7 m		
Interactions										
1) Dev. stage x cultivar		n.s.			*			n.s.		
2) Dev. stage x CO ₂ level		**			n.s.			**		
3) Cultivar x CO ₂ level		**			**			**		
4) Dev. stage x cultivar x CO ₂ level		n.s.			*			**		

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



Table C-6
Effects of Carbon Dioxide Levels Leaf Area Per Plant, Number of Leaf Per Plant and Leaf Weight Per Plant
at 3 Stages of Development of Two Dry Bean Cultivars Grown in 1976a

Dev. Stage	Cultivar	Leaf Area/Plant (cm ²)			No. Leaf/Plant			Leaf Wt/Plant (g)		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	418	834	626	10	12	11	2.0	4.1	3.0
	Seafarer	322	621	471	10	11	11	1.3	2.1	1.7
	Mean	370	727	549a	10	12	11a	1.6	3.1	2.4a
Pod Filling	Black Turtle Soup	423	1252	837	11	17	14	3.1	8.4	5.8
	Seafarer	363	825	594	10	13	12	2.0	4.3	3.1
	Mean	393	1039	716b	11	15	13b	2.5	6.4	4.4b
Mean		381x	883y		10x	13y		2.1x	4.7y	
Mean cultivar	BTS	732 n			12 n			4.4 n		
	Seafarer	533 m			11 m			2.4 m		
Interactions										
1) Dev. stage x cultivar		n.s.			**			**		
2) Dev. stage x CO ₂ level		**			**			**		
3) Cultivar x CO ₂ level		**			*			**		
4) Dev. stage x cultivar x CO ₂ level		n.s.			n.s.			**		

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.



APPENDIX D

RELATIONSHIP OF POD ABSCISSION TO DIFFERENTIAL LEVELS
OF CARBOHYDRATES PRODUCED BY VARIATION IN
CARBON DIOXIDE CONCENTRATION

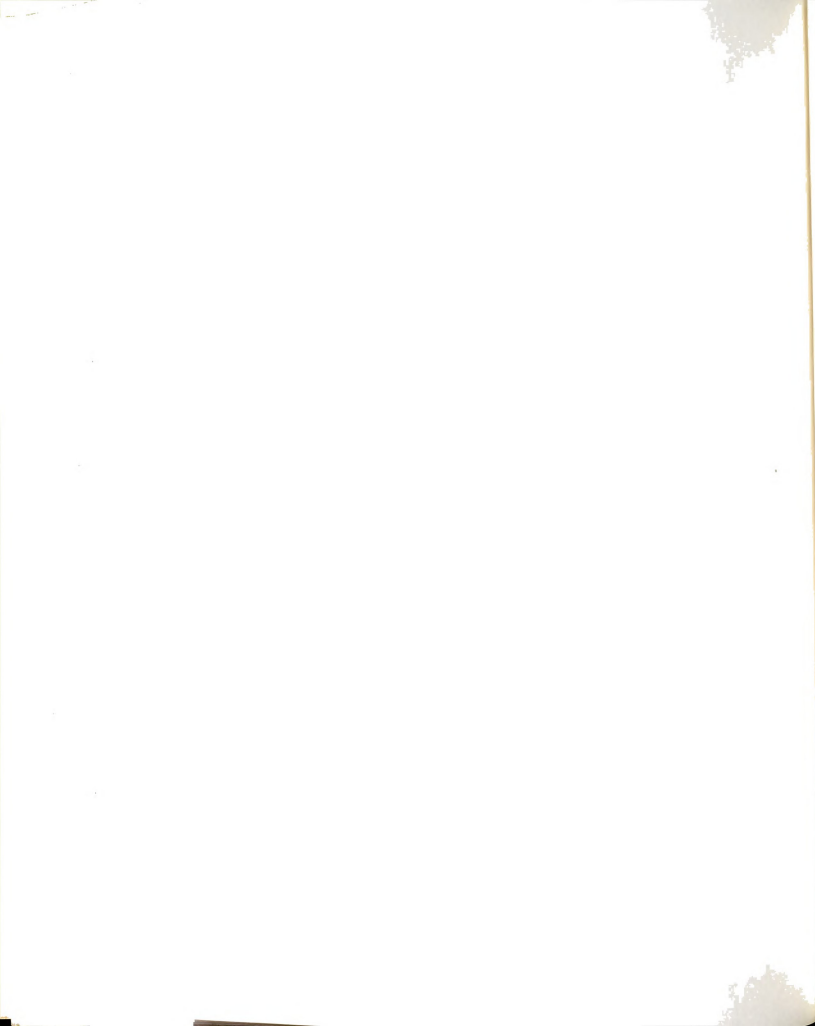


Table D-1
Effects of Stages of Pod Development and Carbon Dioxide Levels on Free Sugar Concentration in Root,
Stem and Leaf of the Two Dry Bean Cultivars (mg glucose per g dry weight)^a

Dev. Stage	Cultivar	Root			Stem			Leaf		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	24.7	26.9	25.8	69.0	82.6	75.8	72.3	79.3	75.8
	Seafarer	20.6	23.4	22.0	49.7	61.4	55.5	56.9	70.5	63.7
	Mean	22.7	25.1	23.9b	59.3	72.0	65.7c	64.6	74.9	69.7a
Pod Filling	Black Turtle Soup	19.8	26.4	23.1	63.4	64.3	63.9	61.8	92.2	77.0
	Seafarer	13.1	16.4	14.7	36.2	61.0	48.6	44.7	94.3	69.5
	Mean	16.4	21.4	18.9a	49.8	62.7	56.2b	53.3	93.2	73.2a
Maturity	Black Turtle Soup	22.0	25.6	23.8	21.3	73.5	47.4	-	-	-
	Seafarer	13.4	22.6	18.0	16.2	44.2	30.2	-	-	-
	Mean	17.7	24.1	20.9a	18.7	58.8	38.8a	-	-	-
Mean: CO ₂ Level		18.9x	23.5y		42.6x	64.5y		58.9x	84.1y	
Mean cultivar	BTS		24.2 n			62.3 n			76.4 n	
	Seafarer		18.2 m			44.8 m			66.6 m	
Interactions										
1)	Dev. stage x cultivar		n.s.			n.s.			n.s.	
2)	Dev. stage x CO ₂ level		n.s.			**			**	
3)	Cultivar x CO ₂ level		n.s.			n.s.			n.s.	
4)	Dev. stage x cultivar x CO ₂ level		n.s.			**			n.s.	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

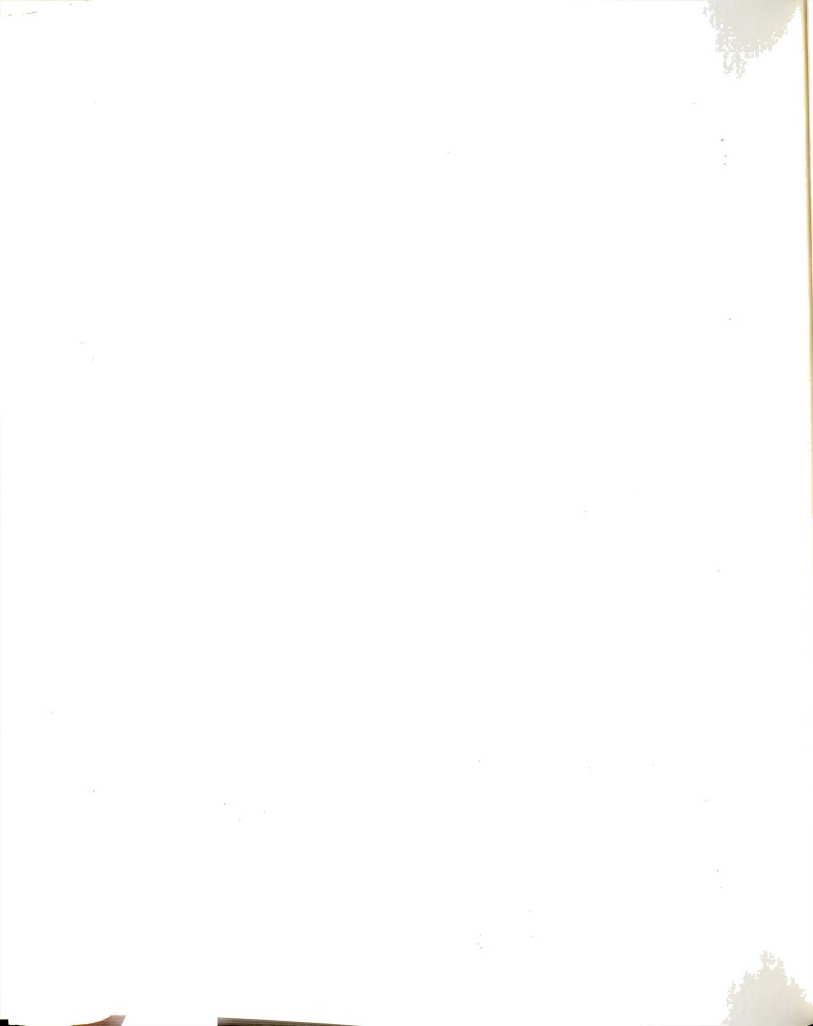


Table D-2
Effects of Stages of Pod Development and Carbon Dioxide Levels on Free Sugar Concentration in Seed
and Pod Wall of the Two Dry Bean Cultivars (mg glucose per g dry weight)^a

Dev. Stage	Cultivar	Seed			Pod Wall		
		CO ₂ Level (ppm)		Mean	CO ₂ Level (ppm)		Mean
		300	800		300	800	
Peak Flowering	Black Turtle Soup Seafarer Mean	-	-	-	226 262 244	293 291 292	259 276 268c
Pod Filling	Black Turtle Soup Seafarer Mean	68 60 64	115 118 116	92 89 90b	108 102 105	118 140 129	113 121 117b
Maturity	Black Turtle Soup Seafarer Mean	69 76 73	82 94 88	76 85 80a	20 32 26	56 42 49	38 37 38a
Mean: CO ₂ Level		68x	102y		125x	157y	
Mean Cultivar	BTS Seafarer		84 m 87 m			137 m 145 m	
Interactions							
1) Dev. stage x cultivar			n.s.			n.s.	
2) Dev. stage x CO ₂ level			**			*	
3) Cultivar x CO ₂ level			n.s.			n.s.	
4) Dev. stage x cultivar x CO ₂ level			*			**	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

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Table D-3

Effects of Stages of Pod Development and Carbon Dioxide Levels on Starch Concentration in Root, Stem and Leaf of the Two Dry Bean Cultivars (mg glucose per g dry weight)^a

Dev. Stage	Cultivar	Root			Stem			Leaf		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	10.1	34.9	22.5	304	298	301	304	540	422
	Seafarer	13.8	27.3	20.6	91	82	87	146	430	288
	Mean	12.0	31.1	21.5 ^b	198	190	194 ^b	225	485	355 ^b
Pod Filling	Black Turtle Soup	28.9	41.2	35.1	214	321	268	69	457	263
	Seafarer	15.6	26.2	20.9	65	113	89	38	260	149
	Mean	22.2	33.7	28.0 ^c	140	217	178 ^b	53	358	206 ^a
Maturity	Black Turtle Soup	0.3	9.4	4.8	28	170	99	-	-	-
	Seafarer	3.8	5.4	4.6	33	37	35	-	-	-
	Mean	2.0	7.4	4.7 ^a	31	103	67 ^a	-	-	-
Mean: CO ₂ Level		12.1 ^x	24.1 ^y		123 ^x	170 ^y		139 ^x	422 ^y	
Mean cultivar	BTS	20.8 n			223 n			342 n		
	Seafarer	15.3 m			70 m			218 m		
Interactions										
1) Dev. stage x cultivar			**			**			n.s.	
2) Dev. stage x CO ₂ level			*			**			**	
3) Cultivar x CO ₂ level			n.s.			**			**	
4) Dev. stage x cultivar x CO ₂ level			n.s.			*			**	

^a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

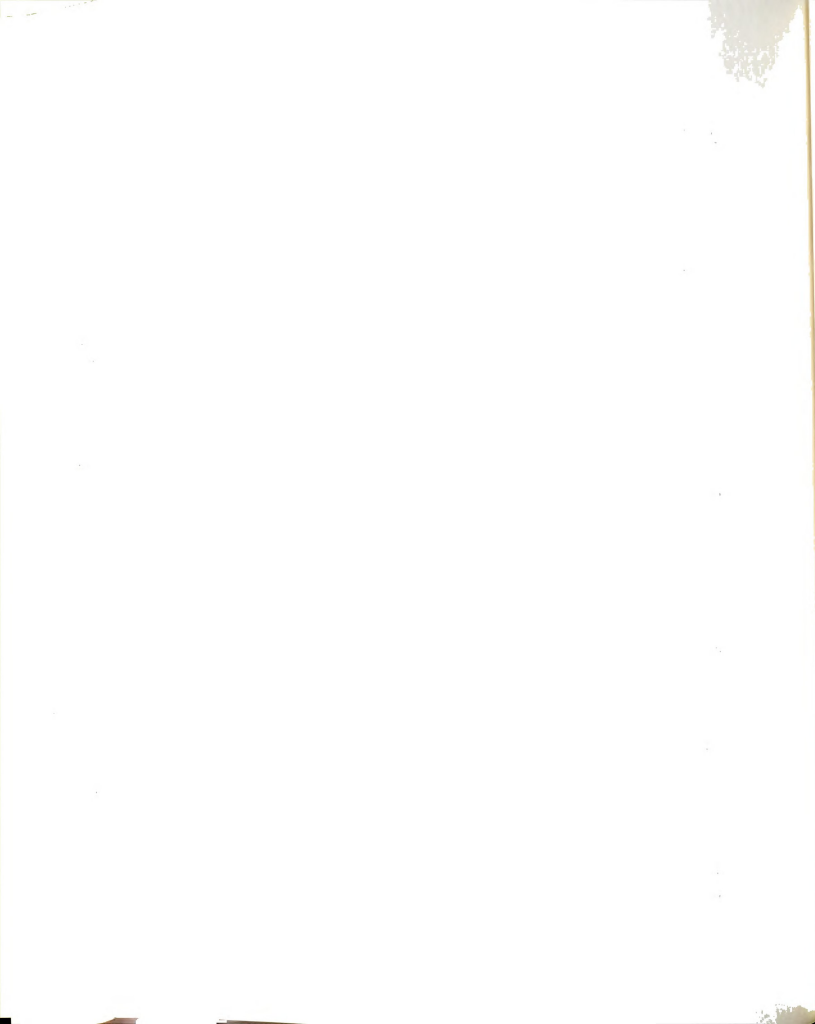


Table D-4

Effects of Stages of Pod Development and Carbon Dioxide Levels on Starch Concentration in Seed and Pod Wall of the Two Dry Bean Cultivars (mg glucose per g dry weight)^a

Dev. Stage	Cultivar	Seed			Pod Wall		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	-	-	-	200	117	158
	Seafarer	-	-	-	201	84	142
	Mean	-	-	-	201	100	150b
Pod Filling	Black Turtle Soup	399	271	335	403	416	409
	Seafarer	411	312	361	398	408	403
	Mean	405	292	348c	401	412	406c
Maturity	Black Turtle Soup	285	275	280	32	60	46
	Seafarer	265	252	258	27	21	24
	Mean	276	263	269b	29	40	35a
Mean: CO ₂ Level		340y	277x		210y	184x	
Mean cultivar	BTS	307 m			205 n		
	Seafarer	209 m			190 m		
Interactions							
1) Dev. stage x cultivar			*			n.s.	
2) Dev. stage x CO ₂ level			**			**	
3) Cultivar x CO ₂ level			n.s.			*	
4) Dev. stage x cultivar x CO ₂ level			n.s.			n.s.	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

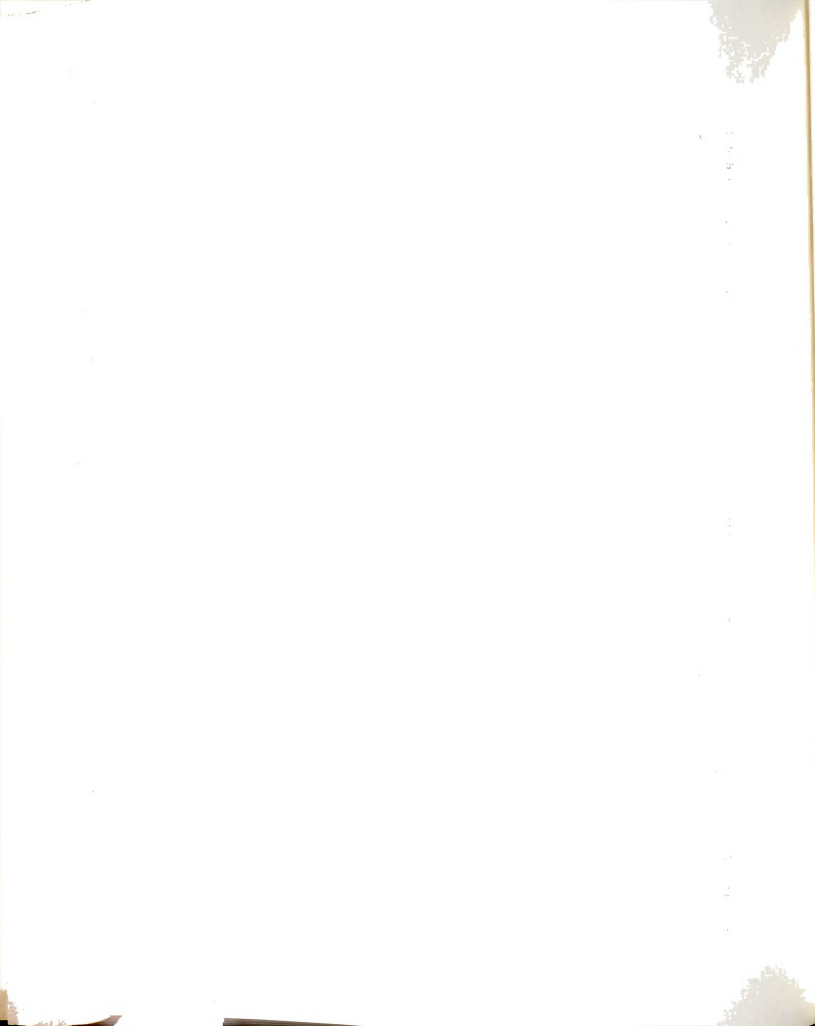


Table D-5

Effects of Stages of Pod Development and Carbon Dioxide Levels on Total Nonstructural Carbohydrate Concentration in Root, Stem and Leaf of the Two Dry Bean Cultivars (mg glucose per g dry weight)^a

Dev. Stage	Cultivar	Root			Stem			Leaf		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	30	61	46	373	380	377	378	614	496
	Seafarer	24	44	34	141	153	147	206	499	352
	Mean	27	53	40 ^c	257	267	262 ^b	292	556	424 ^b
Pod Filling	Black Turtle Soup	48	67	58	286	386	336	133	545	339
	Seafarer	30	42	36	102	194	148	85	347	216
	Mean	39	54	47 ^b	194	290	242 ^b	109	446	278 ^a
Maturity	Black Turtle Soup	21	35	28	49	218	134	-	-	-
	Seafarer	17	29	23	50	84	67	-	-	-
	Mean	19	32	25 ^a	49	151	100 ^a	-	-	-
Mean: CO ₂ Level		28x	46y		167x	236y		200x	501y	
Mean cultivar	BTS	44 n			282 n			418 n		
	Seafarer	31 m			121 m			284 m		
Interactions										
1) Dev. stage x cultivar			**			**			n.s.	
2) Dev. stage x CO ₂ level			*			**			**	
3) Cultivar x CO ₂ level			n.s.			*			**	
4) Dev. stage x cultivar x CO ₂ level			n.s.			*			**	

^aMeans within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

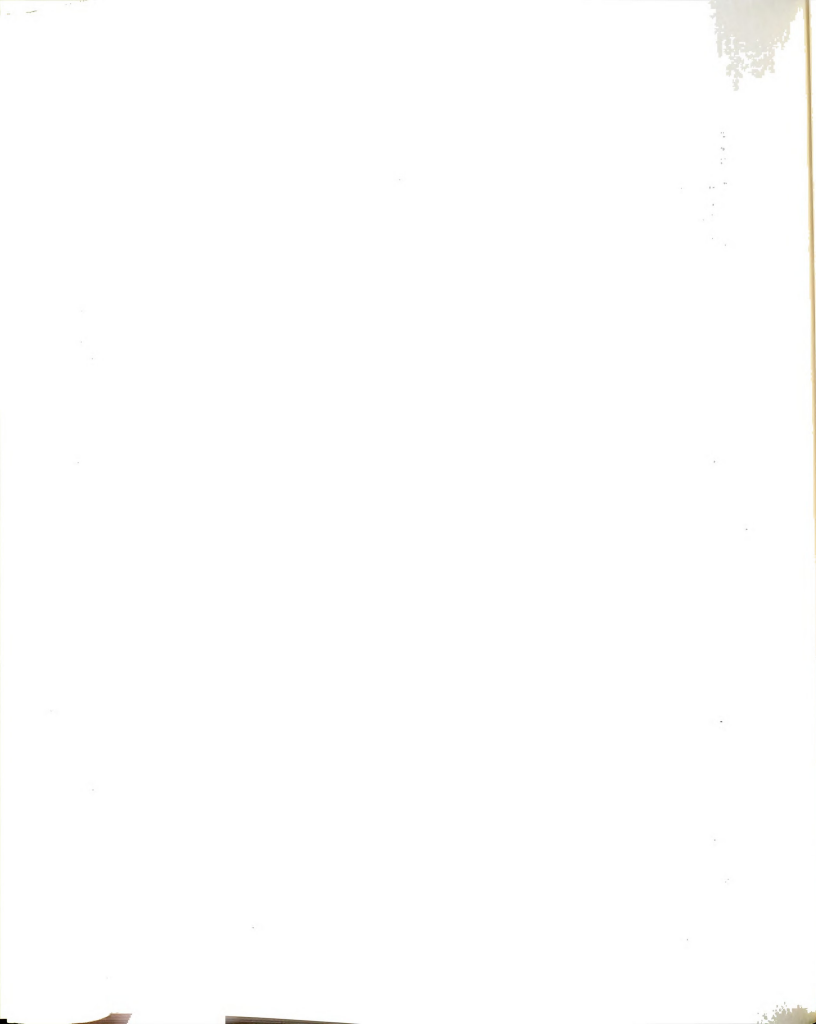
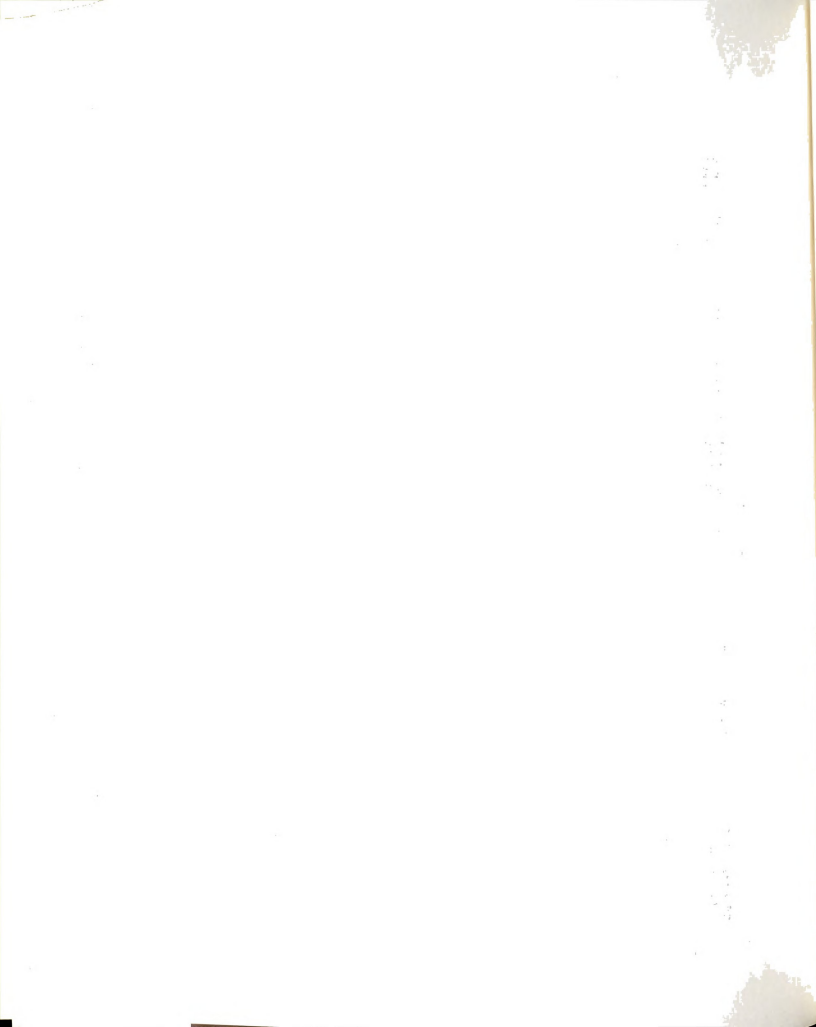


Table D-6

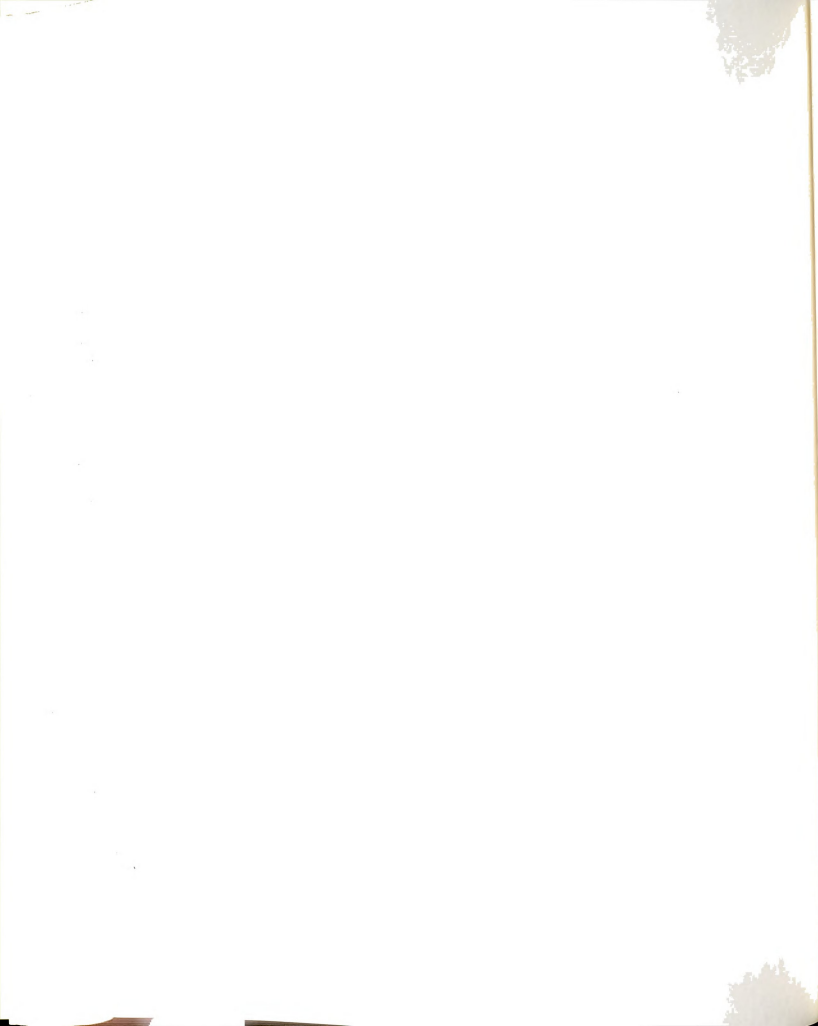
Effects of Stages of Pod Development and Carbon Dioxide Levels on Total Nonstructural Carbohydrate Concentration in Seed and Pod Wall of the Two Dry Bean Cultivars (mg glucose per g dry weight) a

Dev. Stage	Cultivar	Seed			Pod Wall		
		CO ₂ Level (ppm)			CO ₂ Level (ppm)		
		300	800	Mean	300	800	Mean
Peak Flowering	Black Turtle Soup	-	-	-	433	406	420
	Seafarer	-	-	-	429	372	401
	Mean	-	-	-	431	389	410b
Pod Filling	Black Turtle Soup	450	363	407	515	532	524
	Seafarer	457	412	434	501	542	522
	Mean	453	387	420b	508	537	523c
Maturity	Black Turtle Soup	355	371	363	52	112	82
	Seafarer	328	342	335	59	91	75
	Mean	341	357	349a	55	101	78a
Mean: CO ₂ Level		397y	372x		331x	343x	
Mean cultivar	BTS		385 m			342 m	
	Seafarer		384 m			332 m	
Interactions							
1) Dev. stage x cultivar			**			n.s.	
2) Dev. stage x CO ₂ level			**			**	
3) Cultivar x CO ₂ level			n.s.			n.s.	
4) Dev. stage x cultivar x CO ₂ level			n.s.			n.s.	

a Means within the same parameter followed by similar letters are not significantly different at the 1% level by Duncan's Multiple Range Test.

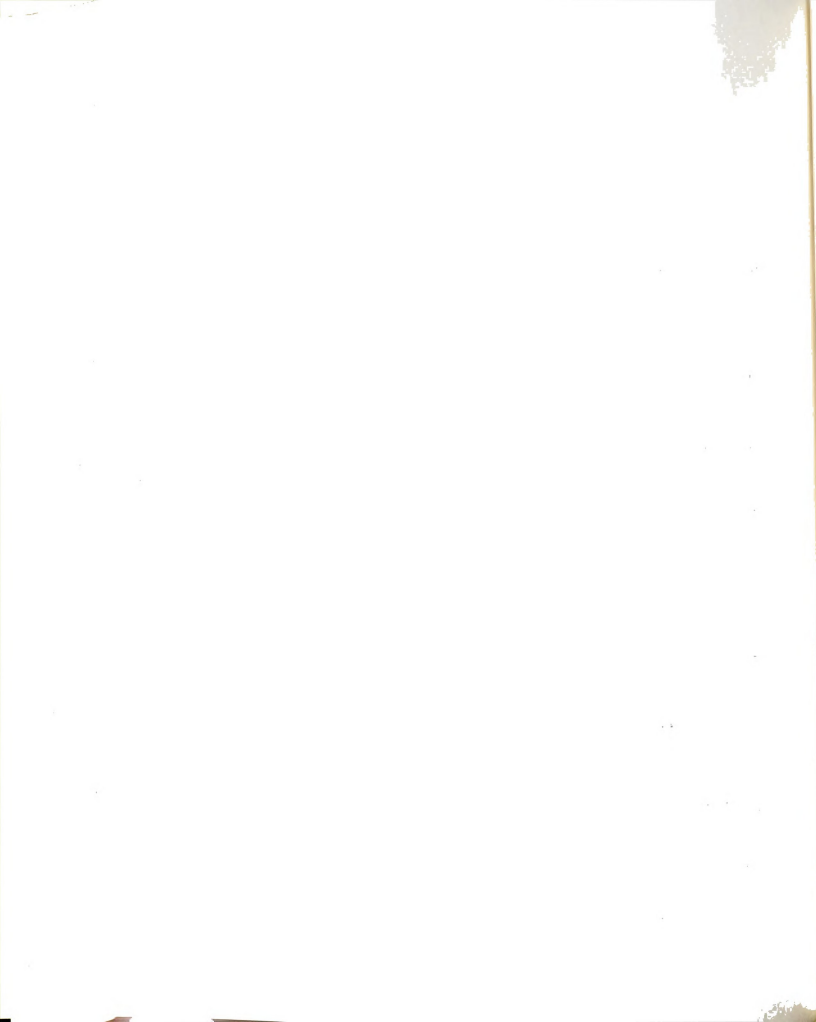


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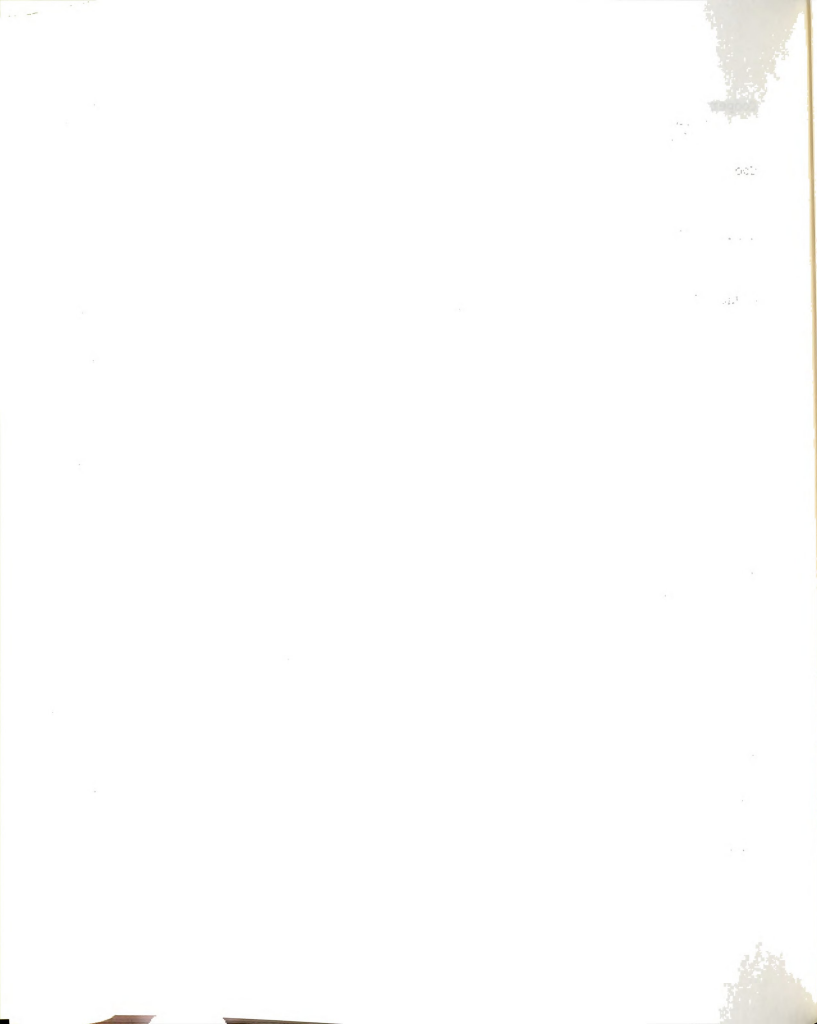
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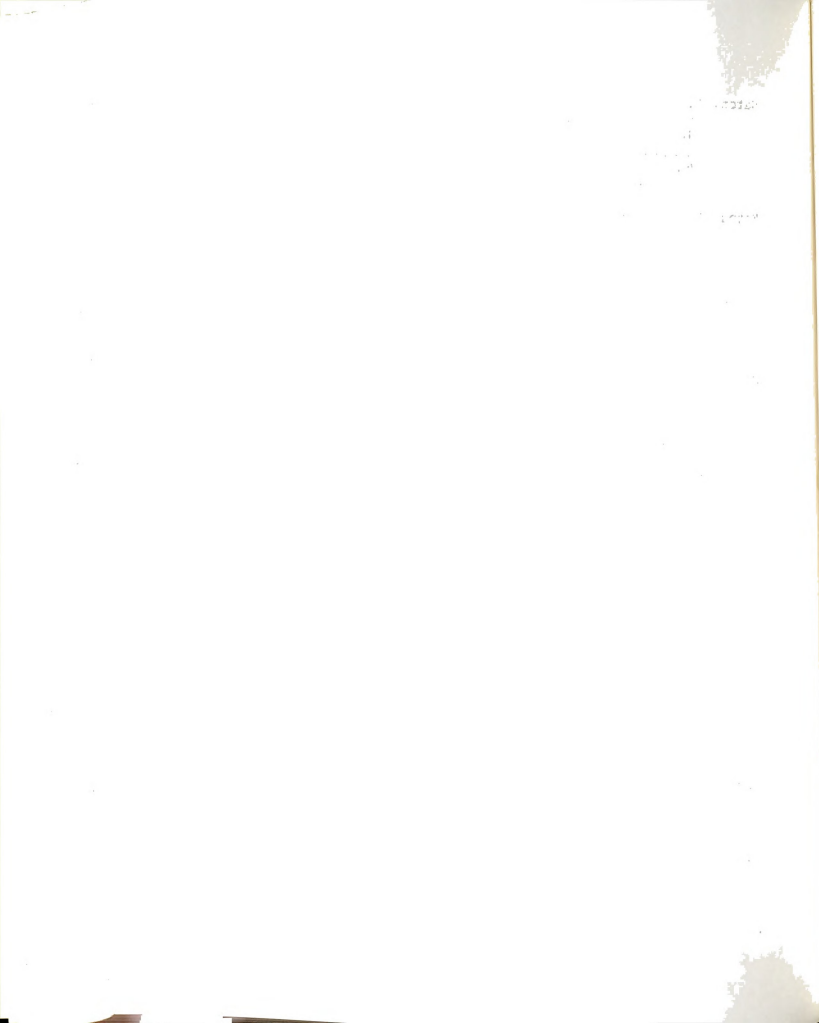


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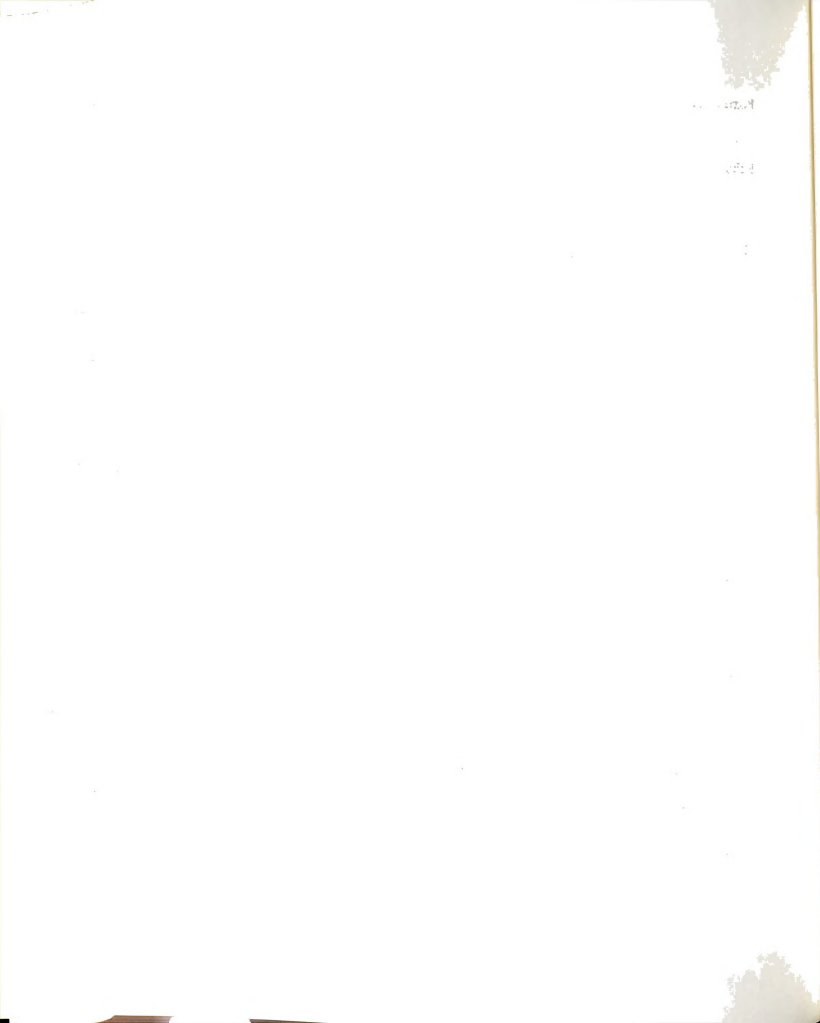
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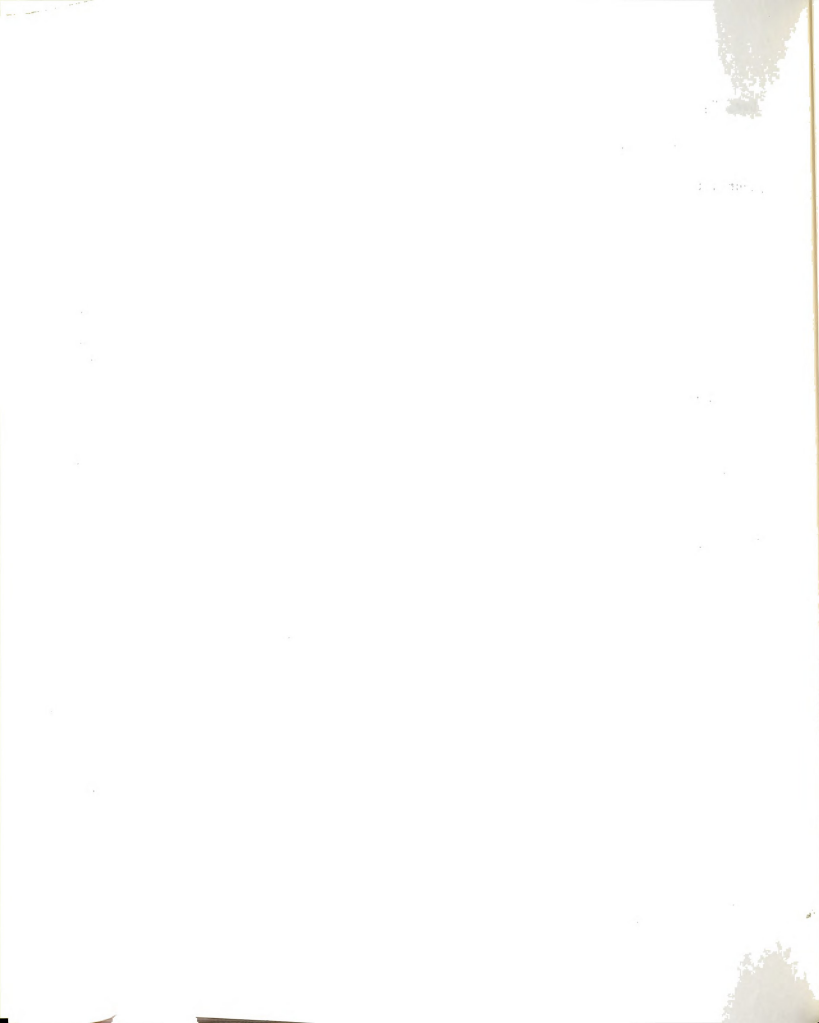
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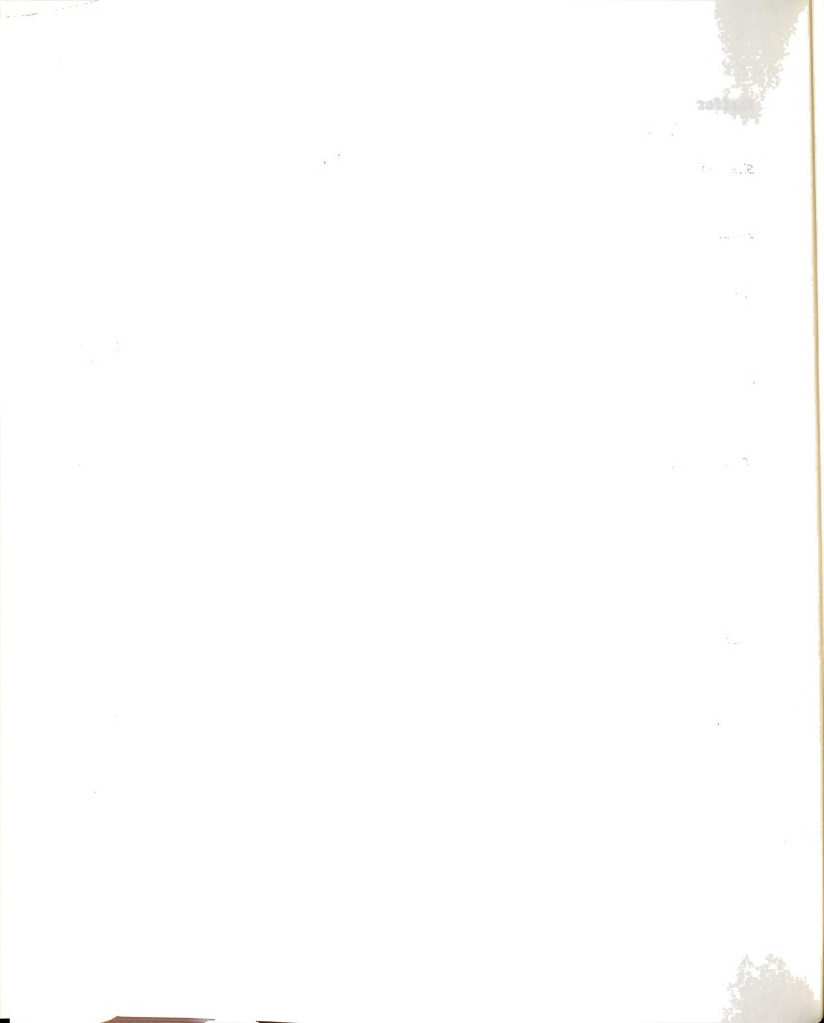
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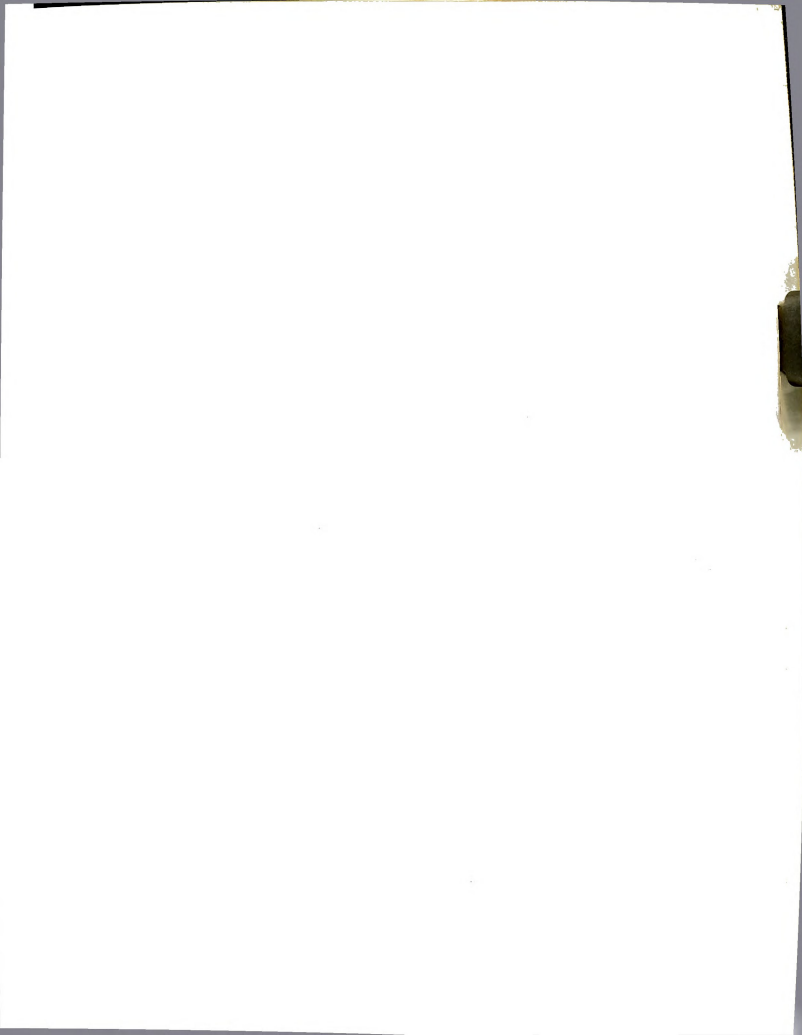
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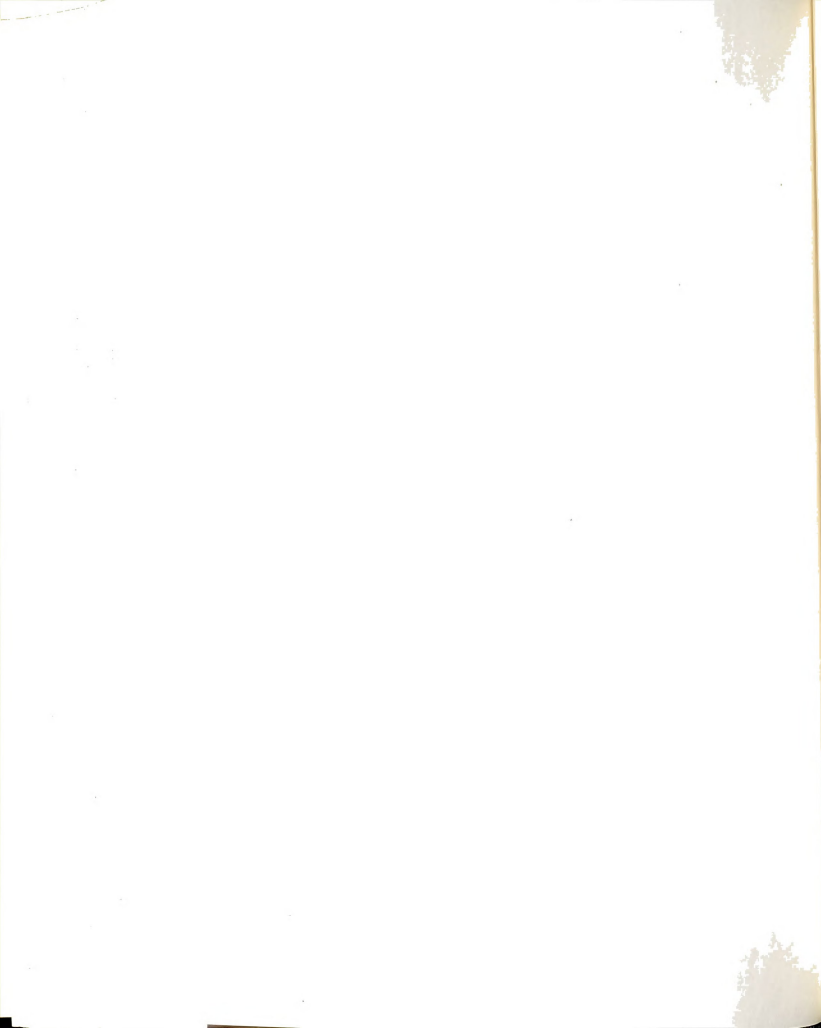
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