

AN ABSTRACT OF THE THESIS OF

CRAIGHTON STILES MAUK for the degree of DOCTOR OF PHILOSOPHY

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Title: INFLUENCE OF IRRIGATION AND PLANT POPULATION ON YIELD PAR-  
METERS, FLOWER AND POD ABSCISSION, AND PHOTOSYNTHATE DIS-  
TRIBUTION IN SNAP BEANS, *Phaseolus vulgaris* L. VAR. 'OREGON  
1604'

Abstract approved: \_\_\_\_\_  
Patrick J. Breen

During 2 seasons effects of high and low irrigation (water applied at -0.6 and -2.5 bars soil water potential, respectively) and density were evaluated on yield parameters and flower/pod development at mainstem nodes 2 and 6 (terminal) of 'Oregon 1604', a determinate snap bean. High and low plant densities were 45 vs. 13 and 54 vs. 33 plants/m<sup>2</sup> in 1978 and 1979, respectively.

Yield/unit area was increased under high irrigation and/or high density. Yield/plant was increased 121% by high irrigation, and was 67% greater under low than high density in the more stressful year of 1978, (no density effect in 1979). High irrigation increased number of pods formed (1978, 1979), and percent set and total pod fresh weight (1978) at node 6, as well as, percent set (1978, 1979) and pods formed (1978) at node 2. Density had no effect at node 6, however, low density increased number of flowers and all other yield parameters at node 2. Nodes 2 and 6 combined were responsible for

over 80% of the total yield per plant.

The flowering period was prolonged for organs at more distal raceme nodes (RN) within an inflorescence. There was an acropetal decline in yield parameters, which was reduced by high irrigation at both the terminal (6-T) and main lateral (2-A) inflorescences at nodes 6 and 2, respectively, whereas, low density only limited the decrease at 2-A (1978). The most proximal raceme node (RN-1) accounted for 65-80% of the total yield per inflorescence.

High irrigation reduced flower/pod abscission at both nodes, but low density only decreased abscission at node 2. A large fraction of abscised organs were shed the day after anthesis, and this proportion increased under low irrigation (6-T, 2-A), and high density (2-A). Abscission increased acropetally within both 6-T and 2-A.

Organs at RN-1 and RN-2 of 6-T received a larger percentage of tranlocated  $^{14}\text{C}$ -assimilate (12-19%) from 7-8 days after their anthesis than those at RN-3 (2-3%). Flowers/pods at 2-A showed a similar acropetal decline in  $^{14}\text{C}$ -activity, but less pronounced. Low density increased percent  $^{14}\text{C}$ -activity recovered in RN-1 and RN-2 pods of 2-A at 7-8 days after their anthesis, however, irrigation (6-T, 2-A) and density (6-T) effects were slight.

INFLUENCE OF IRRIGATION AND PLANT POPULATION ON YIELD  
PARAMETERS, FLOWER AND POD ABSCISSION, AND PHOTOSYNTHATE  
DISTRIBUTION IN SNAP BEANS, PHASEOLUS VULGARIS L.

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Typed by Karla Sorenson and Kent Kobayashi for Craighton S. Mauk

This thesis is dedicated to Adrienne L. Mauk, whom left this world on March 22, 1979 for another reserved only for those of her caliber. A woman of such grace, compassion, and wisdom should of been allowed to live forever. Words are so inadequate in describing my feelings and love for her. Let it suffice to say that among all the titles that I may receive in my lifetime, none will equal the honor of having been her son.

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### CONTRIBUTION OF AUTHORS

Patrick J. Breen was the head of the research project with which I was affiliated and served as the major advisor for my graduate program. He provided technical assistance and consultation during the experimental period and assumed a major role in the preparation and review of the thesis.

Harry J. Mack provided and maintained field plots at the OSU Vegetable Research Farm where the research was conducted and furnished work-study labor during the 1978 season.

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The author was born on March 15, 1952 in Altoona, Pennsylvania where he attended Altoona Area High School and was graduated in June, 1970. In September of 1970 he continued his education at Juniata College in Huntingdon, Pennsylvania and received a B. S. in Biology in June, 1974. The following September he accepted a graduate research assistantship at the University of Maine at Orono where he obtained his M. S. in Horticulture from the Department of Plant and Soil Sciences in May, 1977. Three months later he was the recipient of a graduate research assistantship in the Department of Horticulture at Oregon State University in Corvallis and embarked on a Ph.D. program.

The author is a member of the American Society of Plant Physiologists, American Society for Horticultural Science, and Sigma Xi Scientific Research Society.

## PREFACE

This dissertation is presented as a series of four papers written in the format required by the Journal of the American Society for Horticultural Science

INFLUENCE OF IRRIGATION AND PLANT POPULATION ON YIELD  
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INTRODUCTION

Legume crops such as dry beans, peas, lentils, field beans, chickpeas, and soybeans are important sources of protein and play a significant role in fulfilling nutritional requirements on a global basis (192). To meet the rising demands of an expanding world population, increased yields of legumes will be needed.

The snap bean (Phaseolus vulgaris), a non-seed legume, is a popular vegetable in the diet of more developed, Western nations where it is a vitamin and mineral source, in addition to being prized for its flavor. Annual snap bean production in the United States alone (fresh market and processed combined) is over  $8.1 \times 10^5$  metric tons with a market value exceeding 200 million dollars (31). Yields of snap beans (and legumes in general) appear to be limited by premature shedding of flowers and young pods, often in excess of 80% of the total reproductive organs formed (195). Abscission rates are markedly influenced by water availability and plant population. Yields on an area and per plant basis, for example, can be increased 20-40% by improved irrigation practices which coincide with greater pod set and reduced flower and pod abscission (54,55). Per area yield can increase by as much as 50% by high plant populations, largely because the increase in flower and pod abscission per plant is offset by a higher number of plants per area. To continue to improve yield under such cultural practices, more detailed knowledge on the integrated effects of irrigation and plant

population is needed. It is not yet known where the major proportion of abscission takes place in the snap bean plant and how irrigation-density treatment influences abscission patterns and relative yield contributions of the major pod-bearing nodes.

In addition to the effects of cultural practices, the influence of certain physiological factors deserves much more attention. As plants are moved closer together (increasing density), greater inter-plant competition for light, soil nutrients, and water develops. This competition can even occur between reproductive organs within the same plant and/or inflorescence. Proximal reproductive organs usually possess a greater chance of developing and being retained than more distal ones (2). Exposures to higher CO<sub>2</sub> concentrations, however, can greatly increase growth and retention of more distal fruit (116). Removal of proximal organs as they reach anthesis also increases survival of those at higher raceme nodes in the same inflorescence (93, 212). These effects suggest that photosynthate may be limiting to reproductive organ development, especially at more distal raceme nodes. Flowers and pods at the base of an inflorescence might monopolize a limited photosynthate supply that could result from water stress (reduced irrigation) and/or increased plant competition (higher density).

The following studies were initiated to evaluate the effects of irrigation level and plant population density on yield parameters and reproductive development in snap beans. A <sup>14</sup>C-translocation experiment was also performed to investigate the relationship between photosynthate distribution patterns and reproductive organ growth and/or abscission. Information gained from these studies could result in improved

understanding of flower-pod abscission in legumes and could also be beneficial towards development of high yielding cultivars (particularly under increased plant population). Such knowledge would aid in the design of crop management systems for utilizing the genetic potential of existing and newly developed cultivars.

## REVIEW OF THE LITERATURE

### I. Plant Population Density and Arrangement

#### A. General Plant Population Effects

Yield of beans, on a unit area basis, has been static over the past decade in comparison to marked increases in cereal crops such as rice and wheat. These higher cereal yields have been primarily due to an improved plant architecture and increased response to high density plantings. Such advances are exemplified by significantly greater yields obtained from semidwarf cultivars morphologically suited to sowing at high densities and fertility. Beans, on the other hand, have been conventionally grown in widely separated rows (75-90 cm) to permit cultivation by mechanical harvesters that were originally designed for maize culture (60). Lower densities (160,000-320,000 plants/ha) also facilitate the effective use of herbicides for weed control. In the late 1960's new developments in herbicide technology and production of better adapted harvesting machinery lead to new investigations into yield response under varying densities. Atkin (4), for instance, found increased yields of snap beans and dry beans at 23-46 cm rows in comparison to conventional 92 cm rows. Cutcliffe (33) discovered that 'Tender-crop' snap beans seeded 2.5 cm apart in 76 cm rows consistently resulted in greater yields compared to those at the more common 4-5 cm within-row spacing. Goulden (60) reported that yield per hectare generally increased with increased plant density, especially with a decrease in row width. Greater yields under higher plant densities have been reported for other leguminous crops such as soybean (26,

125,232), broad beans, Vicia faba L. (87,202), and in lupins (76,77, 79).

Response to plant density is greatly dependent on the cultivar and its growth habit. Seed yield/area, for example, was relatively constant over a wide range of plant populations for indeterminate cultivars, but decreased at lower populations for determinate genotypes (236). This suggests that greater seed yield potential exists in determinate cultivars grown under increased density. In another study involving different indeterminate cultivars, greater seed yields (kg/ha) were obtained at higher (740,700 plants/ha) than lower (240,100, 370,400 plants/ha) plant densities (44,45). In addition to cultivar differences, the latter study also employed varying rates of fertilizer which probably were partially responsible for the yield response under increasing density. Evaluation of several different growth habits of bean genotypes by Kueneman et al (112) proved that narrow between-row spacings of 50 cm outyielded wider 75 cm spacings. There are, however, upper limits for planting density based upon the response of the genotype to interplant competition beyond which yield/area declines (14,15,20,114,126).

#### B. Individual Plant Response and Effects on Specific Yield Components

Although greater plant population density affords increased yield on a per unit area basis, inter- and intraplant competition result in dramatic changes in the response of individual plants. Increased density led to a decrease in number of branches per plant as observed by Lucas and Milbourn (126) in Phaseolus and in soybean cultivars by

Weber et al (232). Soybean plants at excessively high density also lodge more and have less structural support than those at lower densities (26,125,232). Hinsen and Hansen (83) reported that reduced spacing in soybean decreased plant height, number of nodes, and yield. Bennet et al (75) reported that higher density plantings of several bean varieties significantly reduced racemes per node and the degree of branching. Increased density in broad beans, Vicia faba L., resulted in lengthened mainstem internodes (87) in the upper part of the shoot and a lesser number of inflorescences per node lower in the canopy. Atkin (4) and Edje et al (45) reported that closer spacing in snap beans produced more upright plants which held their pods farther off the ground. Analogous results were found in broad beans (87) and soybeans (125) under higher plant populations.

An increase in plant population per unit area also produces greater leaf area indices for lupins (61), soybeans (232), and snap beans (129). Leaf area and number of leaves per plant have been reported as being inversely related to plant density of beans (14,15). Although many general trends attributable to increasing density can be identified, specific effects are decidedly influenced by genotype as evidenced by the variable responses in several studies (14,15,44, 45,114,151,236).

Yield components on a per plant basis generally decline with increasing plant density. Adams (2) listed the order of stress responsiveness in dry beans as pods per plant, seeds per pod, and average weight per seed. Analogous findings were reported for snap beans (6,131), soybeans (125,230,237), broad beans (87,202), and

lupin (77). In general, pods per plant are inversely related with density (20,114,126,129). Bennet et al (6) stated that stress due to plant density manifested itself during the period of maximum leaf area which coincided with early reproductive phases in bean plants. Other bean yield components which show a reduction with an increase in plant population include racemes per node (6,113), number of branches (6,126), seed yield per plant (114,236), and seeds per pod as well as weight per seed (20,236). Similar responses to increased density were demonstrated in soybeans (125,230), and lupins (76). The percent of total yield in snap beans (pods of size suitable for processing) is not affected by increasing plant population (4,33,131). Although higher plant density may restrict the performance of individual plants within a population, production on an area basis can be maximized through increased plant numbers and yield component compensation (2).

Key factors influencing legume yield components under increased population density are cultivar growth habit and genotypic response. For example, Lucas and Milbourne in England (126) determined optimum densities for yield of 2 dry bean varieties, however, there was no significant effect of density on number of nodes per plant, which was verified by the data of Scarsibrick et al (189). Even though one cultivar had double the number of mature pods of the other, it was out-yielded on the basis of seeds per pod and greater mean seed weight. Although narrow between row spacings resulted in higher yields regardless of growth habit in tropical dry bean cultivars, determinate cultivars were less responsive than indeterminate types (112). This

was later attributed to a decrease in harvest index (ratio of seed weight to total plant dry weight) of determinate cultivars in response to increased row spacing (114). Carothers and Westerman (20) on the other hand, found that determinate snap bean cultivars, in comparison to semi-vining indeterminate types, had greater seed yields in more equidistant than conventional spacing arrangements. Snap bean yields in general are higher when plants are in a square arrangement compared to 30, 61, or 91 cm rows (113,131,180).

In addition to growth habit and variation due to cultivar selection, environmental and seasonal variables greatly influence the effect of plant density. Brandes et al (14,15) reported variation in yield components in wet compared to dry seasons under several planting densities. Earlier maturing varieties of soybean (26) and lupin (76) were shown to outyield later varieties under high density spacing due to a lesser period of stressful interplant competition. Plant maturity was also advanced in beans grown under higher densities (14,20), as well as in broad beans (76) and lupins (79,202).

### C. Influence on Formation and Abscission of Reproductive Organs

The effect of plant population on reproductive organ growth is variable depending on the crop, specific cultivar, and environmental conditions. Number of pods per plant was identified as the yield component most sensitive to stress during reproductive development in beans (2,131). Results with beans range from a strong inverse correlation between number of pods/plant and density (45) to no significant effect of density on number of pods/plant (6,60,189). This is partially

due to the variation in cultivars used in each study, and the response of specific pod-bearing mainstem nodes within a particular cultivar (203,213). For example, high density generally reduces the number of pods formed at mainstem nodes lower in the canopy, but can increase the number of pods at higher nodes on the plant as in the cases of 'Tashio-Kintoki' (213) and 'Oregon-58' (203). In certain instances, this may result in no net density effect on pod number/plant and possibly account for the variable results of previous studies (6,60).

Number of pods/plant is highly correlated with the number of potential reproductive sites (i.e. nodes and branches), which decrease in number in response to higher densities. Even with a reduction in the number of potential pod forming sites, abscission rates increase under higher densities. Lucas and Milbourne (126) observed less pod retention in high density bean plantings, yet the reduction in numbers of pods at maturity was offset by the higher plant number per unit area. Increased densities in broad beans depressed the number of nodes on the lower half of the mainstem that produced mature pods and resulted in only 14% of the flowers formed setting pods (87). At the top of the shoots, flowers were infertile, while above the middle node, most of the pods formed were shed at an immature stage of development.

Reductions in numbers of reproductive organs due to abscission range from 40-80% in soybeans (195) with greater losses at lower nodes and branches where effects of density are quite pronounced (237). Oba et al (152) also observed decreased pod set on branches and lower nodes under high (84,681 plants/ha) compared to low (42,340 plants/ha) density in soybeans. Regardless of density, only 23% of the flowers

formed in lupins may set pods due to high abscission rates (61). The number of floral buds is less at higher densities and depends on the relative position of the flower or pod, i.e. whether on mainstem or lateral branches. Competition between vegetative and reproductive organs has been forwarded as an explanation for the high rates of lupin floral abscission (77). Herbert and Hill (79) evaluated floral abscission as the greatest limitation to yield in lupins. They observed that floral development was more advanced at a greater density ( $1.56 \times 10^6$  plants/ha), however, the flowers attained a lower maximum dry weight and aborted at earlier stages of development than those in low density plantings ( $0.27 \times 10^6$  plants/ha).

Seldom have studies been done on the pattern of flowering and pod development and/or abscission within individual inflorescences (100, 155). The influence of plant density and competitive, neighboring inflorescences on these processes has received even less attention. Such information would be very beneficial in attempting to understand the relationship between plant density and yield parameters in legumes.

## II. Irrigation - Water Stress Effects

### A. General Overview of Water as an Agricultural Resource

The manipulation of plant-water relations is potentially one of the most influential aspects for augmenting crop productivity. Currently 22% of the world's ice free land surface is capable of supporting crops without irrigation (178). This constitutes approximately  $2.84 \times 10^9$  hectares. Potentially arable land that could be added to this figure by irrigation practices totals  $1.08 \times 10^9$  hectares. The

demand for irrigation, its limited availability in general, and economic considerations of its utilization place an enormous emphasis on understanding plant response to irrigation.

The importance of water in mediating a myriad of plant processes cannot be overemphasized. Depending on which part of the plant is analyzed, water comprises 70-95% of the organ's weight. Although it is a chemical substrate in photosynthesis and other processes, it is utilized primarily in terrestrial plants for cooling and as a medium for transport of substances within the plant complex. Crop growth sensitivity to water stress is primarily manifested through physiological effects on production and maintenance of photosynthetic tissue. Crop yield response to water stress varies with the harvested organ and origin of its constituents (49). The problem of agriculture today rests on the ability to avoid water stress during critical periods in plant development and how to manipulate existing supplies of available water to improve yield and water use efficiency. For crop plants in general, this translates into relating basic plant water physiology to the effects of water stress on various components of yield.

#### B. Effects of Water Stress in General and at Different Growth Stages

Variations in soil moisture and plant water content can have quite an impact during specific phases of plant development leading to marked effects on several growth parameters and subsequent yield. Rate of crop growth, (numerical product of leaf area and net assimilation rate), for example, is very sensitive to water supply. In general, the rate of photosynthesis is moderately sensitive to de-

creases in water potential (49,160). Light interception and efficiency of radiant energy conversion also decline with increased water deficits (15). Leaf expansion growth is perhaps the most sensitive indicator of water stress in plants (91). It has been observed in several legumes such as beans (54), cowpeas (218), broad beans (202), lupins (79), and soybeans (40) that a reduction in leaf area results in decreased crop growth and total yield under water stress situations in the field. Although water stress was shown to decrease individual leaf size and hastened senescence of pre-existing leaves, it did not strongly affect the rate of leaf initiation (49,93). Considering all factors, crop growth was judged to be sensitive to water stress primarily due to the reduction in leaf area.

Considerable evidence has been compiled to indicate that legumes are particularly sensitive to water stress at specific stages in their reproductive development (9,32,43,54,218). Several comprehensive reviews have been written on the subject of water stress effects in relation to development of crop plants (93,184). Effects of irrigation at one or a combination of several developmental stages have been studied in snap beans (43,54,55). These stages were (a) planting until floral initiation, (b) flowering, and (c) the period of pod growth until harvest. In general, irrigation during pre-flowering, vegetative stages only slightly increased yields, which indicates that water stress during this stage was not as detrimental to yield compared to water stress at later stages of development. Plants were very sensitive to water stress, however, during the period of flowering, as well as at the stages of pod and seed development. Irrigation

during flowering results in maximum yield increases in legumes such as peas (184), soybeans (243), lupins (9,79), cowpeas (82,218), lima beans (223), and snap or dry beans (32,43). Beneficial effects of irrigation during post-flowering periods as well as at anthesis were also noted in beans (139) and soybeans (40,200). McKay and Eaves (132) found that corn and snap beans both responded to irrigation during flowering until harvest, but beans benefited slightly more than corn when irrigation was applied prior to flowering. Robins and Domingo (179) and Mack (129,130) found that frequent irrigation at all stages resulted in yield increases from 20-40% over non-irrigated controls. Few cases have been recorded where irrigation of legumes during pre- or post-flowering stages resulted in greater yields than that during flowering, with the exception of a study with broad beans (202). Much of the discrepancy between studies and the relative sensitivity of one stage of development compared to another could possibly be explained on the basis of environmental conditions (i.e. temperature, humidity, rainfall) during each stage, which were seldom addressed in the studies listed above.

In terms of indirect beneficial effects of irrigation, added resistance to disease, cold tolerance, increased vigor, and easier access of nutrients were reported (49,184). In addition, several desirable effects of controlled plant water stress have been demonstrated. Water stress increased floral initiation in cotton (206), hastened maturity in beans (139) and lupins (79), and reduced plant height and lodging susceptibility in soybean during early stand establishment (146). Water stress applied at strategic intervals also en-

hanced genotypic response and variation in soybean cultivars in selection trials (141). Excessive irrigation, on the other hand, during and shortly after flowering in beans (32,139) and cotton (206) results in a yield reduction.

### C. Response of Yield Components and Individual Plant Variables

As stated in previous sections, yield components in seed legumes basically involve number of pods per plant, average number of seeds per pod, and average seed size (2). Other important yield parameters are racemes per node, nodes per branch, and branches per plant, all of which profoundly influence the number of sites for reproductive organs (6). Admas (2) reported that the order of yield component response to stress was analogous to the developmental succession. In bean, the most sensitive yield component to water stress is the number of pods produced per plant (43,54,129,130,139,223). The same situation exists in soybeans (40,146,200), lupins (79), and cowpeas (111,218). The number of pods per plant and pods/m<sup>2</sup> increase substantially under improved irrigation for each crop.

Further analysis of yield components in Phaseolus vulgaris L. reveals beneficial irrigation effects on the number of seeds per pod and average seed weight (54,179,223). Irrigation at floral initiation in comparison to other growth stages has the most influence on number of pods per plant and number of seeds per pod. Reports on average bean seed weight have ranged from significant decreases (54,55,179), to increases under low irrigation regimes (32,59). The same situation exists in cowpeas where average seed weight is not affected by irriga-

tion (111), or sufficient irrigation results in an increased weight (218). Irrigation decreased average seed weight in lupins (80), whereas with soybeans, results were variable and dependent upon the cultivar used (40,146). Thus, the response of average seed weight varies with species, variety, degree of water stress, (moderate versus severe), and developmental stage of the crop during irrigation. Increase in average seed weight due to reduced irrigation may be due to a lesser number of developing seeds (resulting from increased ovule abortion) which exhibit greater gains in weight due to less competition among fewer surviving ovules.

In regards to individual plant parameters, limited water supply affects crop performance by reducing plant height, size of assimilating leaf area, and number of potential sites for reproductive organs, (i.e. branches, racemes). Water stress reduces nodes/inflorescence in soybeans (146), lupins (9) and beans (129). Turk and Hall (218) found that increased levels of drought in cowpeas resulted in progressively less leaf area, shoot dry matter, number of leaflets, and average leaflet area, the latter exhibited the greatest sensitivity to water stress. Biddescombe (9) stated that drought during flowering in lupin cultivars manifested itself most dramatically through reduction in plant size, number of nodes, and potential flower number. In terms of snap bean pod quality, water stress at the time of flowering and pod development altered the sieve size distribution which resulted in a greater proportion of larger pods (32,59,129,130). Whereas cultivar differences were noticed in regard to pod length, pigmentation, and fiber content, water stress generally increased bean pod toughness, frequency of

misshapen pods, and hastened development (32,54,59,129).

In addition to the array of responses to water availability on a whole plant basis, inadequate water supply expresses itself at the organ, cellular, and subcellular level (91). Water deficits in Phaseolus result in loss of turgor and visible signs of wilting, closure of stomates, and a myriad of biochemical and physiological alteration that include the inhibition of photosynthesis and changes in respiration rates (98,101,160,205). Due to the multiplicity of the factors affected by water availability at various levels of plant development, a strong case can be made for water as the single most critical aspect that influences plant growth, distribution, and biomass production.

D. Effects of Water Stress on Reproductive Organ Development and/or Abscission

One of the major limitations to achieving higher yields in legumes is the premature abscission of reproductive structures. This loss is intensified by water stress and rates of abscission under such conditions range from 20-55% in snap beans (54,179), 36-47% in lupins (9), and as great as 80% in soybean (195). Gabelman and Williams (54) noted that most of the yield increase under optimum irrigation was due to a reduction in abscission of reproductive organs, whereas, only 20% of the increase was attributable to greater pod size. An increased number of flowers which set and developed into harvestable pods was noted by Vittum et al (223) when lima beans were irrigated during flowering. Sufficiently high temperatures, in addition to adequate

irrigation was required for pod set and reduced abscission.

Floral abscission was reportedly greater than pod abscission under drought conditions as evidenced by relatively higher numbers of abscised flowers than pods in water-stressed lupins (9,221), soybeans (104,243), cowpeas (218), and snap beans (32,54,207). Turk et al (218) observed that irrigation resulted in partial yield recovery in cowpeas after severe drought had caused severe floral abscission. Resumption of irrigation permitted a new flush of flowers to produce pods later in the season. Ojehomon (154) observed compensation for losses of early formed flowers in cowpeas by initiation of flowers later in the season at other raceme nodes. This ability to partially compensate for early losses of flowers was also demonstrated in lupins (80,81) however, this response generally is not expressed in determinate bean and soybean cultivars (207,237).

Differences in response of field grown versus potted greenhouse plants to moisture stress have been noted by Gabelman and Williams (54) for snap bean cultivars. In potted plants subjected to water stress, young pods ceased development when they were approximately 5 cm in length, yet were still retained, whereas smaller pods ( 5 cm) usually abscised. The authors attributed these findings to more gradual soil moisture changes in the field as compared to more rapid changes in containers. It was judged that field grown plants shed all the small fruit they cannot nutritionally support, whereas, water stress forces the drop of more mature pods. In another study, Gabelman and Williams (55) stated that increased abscission under water stress conditions was accompanied by increased ovule and seed abortion. They also re-

ported that the ovular abortion increased towards the proximal end of the pod, but as described by others (1,65a) this is not due to a lack of fertilization. Embryos which most often abort are actually nearest the source of metabolites and water. Similar cases were noted in soybean pods (103,104,105) where water stress increases the incidence of ovular abortion, particularly at the proximal end of the pod. In some cases (93) soybean ovary growth was enhanced by direct application of water droplets into the calyx cup. Increase in the incidence of abortion at the proximal position may be due to competition between distal ovules which develop first and produce larger embryos with more activity and higher auxin production.

### III. Hormonal Influence on Abscission of Reproductive Organs

#### A. Role of Absciscic Acid

Absciscic acid (ABA) has been involved in the regulation of numerous physiological processes in plants. These have been covered in reviews by Addicott and Lyon (3) and Milborrow (142). The last decade produced several hundred publications specifically dealing with ABA's role in the regulation of reproductive organ abscission. This has been partially due to the advances in hormone extraction, isolation identification, and quantification (22,34,176,201). ABA has been implicated in fruit abscission of legumes ever since it was identified by Van Steveninck (221,222) as the compound in lupin tissue which induced abscission in explants. Results with cotton fruit (39), peaches (136), soybean (176), and beans (7,212) demonstrated the abscission accelerating capabilities of ABA. Davis and Addicott (39)

measured high levels of ABA in intact cotton fruit that coincided with the period of self thinning. Aborted fruitlets at this time contained significantly larger ABA levels than attached ones. Similar results were recorded in abscising as compared to persisting peach fruits (136).

Contradicting evidence which refuted the intimacy of ABA levels and abscission of reproductive organs has been published. Subhadrabandhu et al (207) concluded from the levels of extractable ABA and its metabolites that it did not regulate abscission in dry beans. Although they found that ABA content was highly inversely related with pod abscission in one particular cultivar, ('Seafarer') it was directly related with shedding of reproductive organs in another ('Black Turtle Soup'). Porter (174) also questioned the role of ABA in the control of reproductive organ abscission in lupin. He was only able to induce floral abscission exogenously through application of ABA to leaves. Injection of ABA into the flower-bearing nodes and saturation of the root zone with an ABA solution failed to significantly increase abscission in comparison to non-treated controls. Experimental results of this nature should be judged more inconclusive than negative since it is unclear to what degree ABA was transported, or metabolized by plant tissue. Results from experiments with ABA and reproductive organ abscission may also be confounded by the possibility that ABA induces abscission indirectly through other hormones such as ethylene (183).

Additional experiments which support the role of ABA in fruit abscission specifically deal with the effects of removing early developing flowers and pods on the response of those that formed later. Studies with soybean (170), yellow lupins (220), and snap beans (12,

56,213) illustrated that manual removal of the earliest formed flowers results in the subsequent development and retention of reproductive structures which normally abscise. These findings suggest that older fruit have a profound influence on the growth of more immature ones through competitive inhibition. Tamas et al (212) observed that when older bean pods (which formed at the basal portion of a raceme), were removed, not only was the abscission rate of the remaining fruits reduced, but their endogenous ABA levels were significantly lowered. Subhadrabandhu et al (208) found that the ABA levels in pods of non-deflorated plants of the bean cultivar 'Black Turtle Soup' were 6-10 times greater than in pods of plants in which flowers were removed for the first 5 days after initial anthesis. Percent abscission was also reduced in these deflorated plants.

Abscission of reproductive organs increases under high temperature stress and long day photoperiods in soybeans (195,221) and several varieties of beans (9,134,157). Makus and Shannon (134) found higher ABA levels in snap bean seeds of plants exposed to high temperature stress (46°C) as compared to lower temperatures (35°C), and in seeds from plants exposed to 16 hr versus 10 hr days. High ABA levels were also measured in soybean seeds (176). Hsu (92) found low levels of ABA in bean pods throughout their development, but noted two peaks of ABA levels in the seed. Other than restricting precocious germination, the role of ABA in seeds still remains unclear. Zehni et al (249) suggest that an inhibitor is formed in lower leaves under long day conditions and transported acropetally. Bentley et al (7) reported results that provide strong evidence for the role of ABA in mediating long day

effects on flower bud development in beans. Bentley et al (7) did find greater ABA production in leaves under long days and its accumulation in floral buds that subsequently abscised. These abscised floral buds contained significantly more free and bound ABA than they did 6 days previous. Application of exogenous ABA to differentiating flower buds of plants exposed to short days resulted in inhibition of growth and abscission of reproductive structures at later stages. It was reported, however, (150,248) that applied ABA is not metabolized in a manner analogous to that of endogenous ABA. Such results offer a note of caution in interpreting results obtained with exogenous versus endogenous ABA. Bentley et al (7) reported that ABA-induced inhibition of bean floral bud differentiation was most pronounced in the terminal inflorescence. Huff and Dybing (93) extracted unidentified substances from young soybean pods and discovered that these compounds produced the same effect as proximal flowers in inducing the shedding of more distal reproductive structures.

In terms of other plant responses, ABA is also reported to regulate stomatal aperture and leaf senescence (3,25,42,71,84,186). Levels of ABA in water-stressed leaves of soybean (187), wheat (5), xanthium (42,247), lupin (85), Phaseolus coccineus L. (73), and Phaseolus vulgaris L. (25,71) increase significantly more than non-stressed plants.

Water stress not only affects endogenous levels of ABA in plant tissue, but also influences ABA translocation. In Phaseolus coccineus L., Hartung (73) observed negligible transport of 2-<sup>14</sup>C-ABA which was applied to a primary leaf of water stressed plants in comparison to non-

stressed controls. He concluded that water stress can promote ABA increase in leaves by enhancement of ABA synthesis or inhibition of ABA transport. Setter et al (187), Loveys et al (123), and Hocking et al (86) induced significant increases in ABA in soybean, grape, and bean leaves, respectively after obstruction of the transport pathway by girdling. Goldbach and Goldbach (58) achieved significantly higher levels of ABA in the ears of barley plants by treating leaves with warm air at 36°C. These results suggest that increased levels of ABA in one part of the plant could also be attributed to translocation from another plant portion.

Recent observations by Hoad (85) and Setter et al (185) reaffirmed the fact that pods were the recipients for a major proportion of the ABA produced in leaves. Utilization of  $^{14}\text{C}$ -ABA by Setter et al (186) and Hocking et al (86) proved that either petiole girdling or pod removal increased leaf ABA levels in soybean and snap bean respectively.

Research suggests that ABA is more than likely involved in reproductive organ development and abscission in legumes, however, the mechanism of action and synergistic effect with other hormones need more intensive study.

#### B. Involvement of Other Hormones

Hormonal control of plant water status was covered by several reviews (91,121). Other reviews (3,28) on the other hand specifically deal with the relation of hormones and control of abscission in agricultural crops. In general, auxins (including synthetic naphthalene and

phenoxy derivatives) and cytokinins are utilized in the prevention of abscission, whereas growth inhibitors such as ABA, TIBA, ethylene, and ethylene releasing agents accelerate fruit drop. Effects of these hormone groups on abscission are quite complex and variable due to application dosage, stage of development of the plant at the time of application, particular tissue treated, plant species, and differential response of cultivars of a crop. For example, naphthalene and phenoxy auxin derivative prevent preharvest drop in apples, pears, and citrus (28). However, NAA sprays on apple tree foliage and fruit at other times reduce fruit retention and  $^{14}\text{C}$ -assimilate translocation, whereas, if NAA is applied to only the apple fruit, there is no observable effect on retention (191). The reduction of auxin transport apparently is a prerequisite for abscission zone formation in advance of organ abscission (66,73,188). It is noteworthy to mention that supraoptimal concentrations of IAA induced formation of ethylene, an abscission accelerating agent.

Ethylene has long been acknowledged for its promotion of abscission. Data reviewed by Burg (18) and Pratt and Goeschl (175) suggests that ethylene induces abscission both indirectly through inhibition of auxin synthesis, transport, and destruction, as well as directly through its action on plant wall structure. Jackson and Osborne (97) presented data that correlated abscission with the concentration of ethylene in the cells of the abscission zone in the petioles of primary bean leaves. McMichael et al (140) reported marked increases in ethylene synthesis in petioles of water stressed cotton leaves which subsequently abscised. Rewatering led to a reduction of ethylene

to pre-stress levels. It was shown that abscission in Ecballium elaterium (242) cannot take place until specific ethylene target cells are first differentiated in the abscission zone. Once such cells were identified, ethylene-induced enlargement takes place which eventually results in ovary - pedicel separation. Webster (233) had previously observed ethylene-induced changes in cells of the abscission zone in Phaseolus explants. Exogenous application of ethylene-generating compounds, such as ethephon, caused fruit drop in apple (122) and abscission of reproductive structures in Phaseolus when applied in large concentrations (234). Bud and flower abscission in bean were more sensitive to ethephon treatment than pod abscission. Although low levels of ethephon (250 ppm) controlled abscission, higher levels (1000-2000 ppm) actually accelerated the response.

Reviews on the physiology of cytokinins (63,107) state the importance of their role in retarding senescence, mobilization of metabolites, regulation of nucleic acid synthesis, and control of growth in general. An additional role involves the retention of reproductive structures. Davey and Van Staden (35,36,37) studied cytokinin metabolism in white lupin where cytokinin levels were found to fluctuate throughout development of seeds and pod walls. Leopold and Kawase (120) showed that the exogenous application of cytokinins to one or more leaves induced senescence in other leaves which mimicked effects as those normally induced in senescing flowers and fruits. Peterson (169) was able to increase retention of soybean pods with application of  $10^{-3}$  M benzyladenine. He also observed swelling of the pod's peduncle, as well as maintenance of chlorophyll synthesis. Bentley et al (7)

stimulated development and retention of flower buds on bean plants with the application of cytokinins. These reproductive organs would have otherwise dropped under exposure of the plants to long day conditions. In addition to exogenous results, abscission was negatively correlated with endogenous cytokinin concentration in cotton fruit (182).

#### IV. Translocation and Partitioning of Photosynthate

##### A. Introduction

Equally as important as photosynthate production is its distribution to the metabolic sinks of the plant. Patterns of assimilate distribution are very complex and extremely variable. Alterations in photosynthate partitioning were largely responsible for the higher yield of contemporary cereal crops in comparison to their less yielding wild type ancestors. Unfortunately advances in corn and wheat yields, for instance, have not been accompanied by concomitant developments in the legume crops. Increased understanding in the area of photosynthate distribution was judged essential for future improvement of agricultural productivity in legumes (195). Research over the last 20 years added to comprehension of transport system structure and function. Advent of radioisotopes in particular, enhanced our knowledge of translocation patterns enabling researchers to distinguish between molecules of diverse origin. The principles governing photosynthate distribution, however, have still remained very speculative. The relationship of source-sink, i.e. supply and demand, has been extensively investigated, yet mechanisms of control and regulation are still not adequately explained. Until factors such as these are more fully

understood, and then manipulated, prospective yield increases of legumes will not be fully realized.

## B. Photosynthate Distribution Patterns in General

### 1. Feature of the Transport System

Transport of photosynthate primarily occurs in phloem tissue of the vascular system composed of conducting sieve tubes which consist of a network of specialized sieve cells. Esau (46) and Canney (19) characterized phloem cell types and vascular anatomy in more depth. The vascular system can be described as an extremely intricate and highly branched complex which interconnects plant tissue from root to shoot apices. The vascular network in Phaseolus vulgaris L. was defined with (10,150) and without (41) the use of radiotracers and autoradiography. Douth (41) extensively studied the vascular system of the bean cultivar 'Black Valentine' and characterized development of vascular bundles at each node throughout growth. She specifically traced developmental changes in vascular anatomy from embryonic tissue (hypocotyl and radicle) to the initiation of embryos within ovaries of individual flowers and pods. Mullins (150) utilized  $^{14}\text{CO}_2$  in his studies of photosynthate translocation patterns in Phaseolus seedlings. He observed that  $^{14}\text{C}$ -photosynthate from primary leaves travels basipetally one node down the stem prior to entering a pathway where it begins an acropetal ascent. Biddulph and Cory (10) reached the conclusion from their work that photosynthate distribution was not random but directional, i.e. assimilate produced in one area travelled to a particular metabolic sink. During the course of such transport, Biddulph and Cory witnessed little, if any detectable signs of lateral transport from one source-sink

channel to another.

Eventhough the major translocatable organic component in soybean (23) and several other legumes is sucrose or an alpha-galactoside derivative (19), fruiting plants of lupin utilize a larger proportion of amino acids, specifically asparagine (159). Housely (90) and Peterson (170) determined selectivity of amino acid translocation in soybean and oat and found that the amount of amino acids which enters the vascular system is far less than that of sucrose. Apples, on the other hand, were reported to translocate sorbitol instead of sucrose (67). Organic acids such as malate and citrate were quantified in soybean exudate where they comprised 1-10% of the  $^{14}\text{C}$  transported assimilate, the fraction being dependent on the stage of plant growth (110).

## 2. Relationship between Leaf Position, Ontogeny, and Assimilate Distribution

Certain phyllotactic generalities of assimilate distribution were noted in plants based on results obtained through exposing leaves to  $^{14}\text{CO}_2$  and assaying for radioactivity some time later at initially unlabeled sites. In the broadest sense, lower leaves are the source for the root sink, whereas upper leaves supply the shoot apex with foliage in the centralized portion of the plant transporting photosynthate in both directions. These trends were observed in soybeans (204,215,217), wheat (177), corn (161) and bush beans, Phaseolus vulgaris L. (213,231, 238). Tomato plants, however, were proven by Khan and Sager (108) to be one of several exceptions to the rules. In this species, phyllotactic effects are extremely diverse, largely because of the complex vascular system which possesses both internal and external phloem. Due to the

highly vegetative nature of the tomato plant, diurnal fluctuations in photosynthesis, growth, and storage influence photosynthate partitioning and even result in reversals of translocation patterns.

Distribution patterns and direction from any supply leaf change with development of the particular plant. The orientation of each leaf position relative to the shoot apex undergoes constant change. This is due to more leaves and increased growth which separate lower supply leaves from the shoot apex. As a result, earlier formed leaves translocate more assimilate to the roots with increased plant development. Young expanding leaves are photosynthate importers (19). Tanaka and Fujita (213) found that young bean leaves were actually the major photosynthate sinks until maximum expansion was reached, accumulating 60-70% of the translocated  $^{14}\text{C}$ -photosynthate. This percentage rose to 80% when leaves were efficiently utilized by neighboring sinks. Soybean leaves changed from net photosynthate importers to exporters at 50-60% full expansion (17). Increased age results in decreased export from older leaves in beans (217), soybeans (197,202). As a rule, older leaves do not import a significant amount of assimilate, but act as sinks for their own photosynthate prior to export of any surplus. Rawson and Hofstra (177) reported that wheat leaves were also photosynthate importers when young (prior to full expansion), and became exporters after full expansion, however their photosynthate export declined towards senescence.

As previously mentioned, the network of vascular anatomy places restrictions on assimilate movement. Translocation displays a propensity for strict longitudinal movement of photosynthate over considerable

distances. For example, older bean leaves are capable of supplying younger ones several nodes away (217). Leaves in corn plants contribute labelled photosynthate to specific portions of developing ears (161), and although soybean leaves support pods mainly in their own axil, they also contribute to pods situated two mainstem nodes above and below (47).

### 3. Assimilate Distribution during Reproductive Development

The onset of reproductive development in plants is characterized by abrupt shifts in photosynthate distribution patterns which favor growth of reproductive organs. The work of Minchin and Pate (145), Pate (163), and Pate et al (165) clearly demonstrate such alterations in carbon translocation budgets. During vegetative growth in Pisum sativum L., Minchin and Pate (145) reported that 74% of the fixed carbon went to the roots where 47% of the total was respired to the soil and 15% was recycled to the stem via the nodules as amino acids. Respective percentages for analogous sources of carbon in lupin (163) were 71%, 4%, and 9%. As new reproductive sinks develop in soybeans, much less labelled assimilate is directed to the roots and nodules (94). Lucas et al (127) treated the uppermost trifoliolate of bean plants with  $^{14}\text{CO}_2$  and monitored the distribution of  $^{14}\text{C}$ -photosynthate. From 10-38 days after anthesis, the proportion of  $^{14}\text{C}$ -photosynthate that was translocated from the treated leaf to the adjacent pods rose by 37%. At day 38, most of the  $^{14}\text{C}$ -labelled material resided in only the treated leaf and pods in its axil. By maturity, 73% of the total translocated labelled photosynthate was absorbed by the seeds within the pods in the treated leaf axil. Wien et al (237) reported similar results in beans from

treating the uppermost trifoliolate with  $^{14}\text{CO}_2$  at different stages in the reproductive period.  $^{14}\text{CO}_2$  feeding experiments with mung beans (115) showed that photosynthate fixed at the time of anthesis largely remained in vegetative tissue, however, greater proportions migrated to reproductive organs at later times. For instance, at 7, 17, and 38 days post anthesis, pods contained 15-26%, 43%, and 70%, respectively of the labelled assimilate translocated out of a treated leaf 24 hours after  $^{14}\text{CO}_2$  treatment. Waters et al (231) also traced the movement of  $^{14}\text{C}$ -photosynthate in Phaseolus vulgaris L. and observed that during pod-fill, over 85% of the labelled assimilate exported by a leaf at the eighth node was found in pods, with only 1% in the roots. Treatment of pea pods with  $^{14}\text{CO}_2$  during pod-fill (124) revealed that virtually all  $^{14}\text{C}$ -labelled assimilate went to the seeds. Removal of seeds prior to  $^{14}\text{CO}_2$  exposure reduced subsequent export to 15% of that previously recorded. Pods at earlier stages of development also display decreased export of photosynthate to seeds. Nitrogen fixation by soybeans decreased during pod-fill and was attributed to competition for available photosynthate between nodules and pods (117).

In general, developing fruit derive the major proportion of their subsistence from subtending leaves or bracts, i.e. nearest sources of photosynthate (19). The intensity and demand for photosynthate by growing fruit varies greatly with the stage of development. An important aspect previously discussed was the position of assimilate demand relative to various supply leaves. Tanaka and Fujita (213) have extensively mapped translocation patterns in bean in relation to leaf position, developmental stage, and general plant growth habit. They

commented on differences in photosynthate distribution patterns between determinate and indeterminate cultivars as have Yoshida and Gotoh (246). Distribution of  $^{14}\text{C}$  into seeds and pods on the mainstem for determinate cultivars demonstrates a strong control exerted by phyllotaxis of the leaves. Although localized distribution of  $^{14}\text{C}$ -labelled photosynthate in determinates exceeded that of indeterminate types at the vegetative stage, the situation was reversed during reproductive stages, particularly that of pod-fill.

#### 4. Water Stress Effects on Photosynthate Distribution

Inhibition of assimilate translocation by water stress occurs in several crops including field corn (16), sugarcane (72), potatoes (193), soybeans (196), wheat (222), lolium (225), and sorghum (209). The effect of water stress on the transport of  $^{14}\text{C}$ -labelled assimilate in *Phaseolus* has produced variable results. Studies by Plaut and Reinhold (171) with  $^{14}\text{C}$ -sucrose have shown that the amount of  $^{14}\text{C}$ -labelled assimilate translocated out of a treated bean leaf was reduced by water stress when the interval between  $^{14}\text{C}$ -application and radioassay for distribution exceeded 45 minutes. During the initial 45 minutes after application of the  $^{14}\text{C}$ -sucrose, however, translocation in stressed plants exceeded that of the controls. They also observed that stressed plants translocated only small amounts of  $^{14}\text{C}$ -assimilate acropetally, and the disparity in acropetal versus basipetal transport in stressed as compared to control plants increased with time. In a later experiment, Plaut and Reinhold (172) found a ten fold decrease in the amount of  $^{14}\text{C}$ -assimilate translocated from an area treated with  $^{14}\text{C}$ -sucrose in stressed versus non-stressed controls. There was, however, a three

fold increase in translocation of  $^3\text{H}_2\text{O}$  away from the treated area in water stressed as compared to non-stressed plants. Hoddinott et al (88), on the other hand, discovered that translocation of  $^{14}\text{C}$ -photosynthate remained virtually constant for several hours following osmotic shock treatment to the base of rooted or rootless cuttings of Phaseolus vulgaris L.

Wardlaw (225,227) has written comprehensive reviews on the external factors regulating translocation and distribution of assimilates in plants. Under extreme water stress, delayed transfer of assimilate from photosynthetic tissue to the phloem in lolium plants was noted (226). Water stress has also been shown to reduce the translocation velocity in wheat (224). Wardlaw suggested that water stress acts indirectly on translocation via effects on growth since the translocation pathway is rather insensitive to water stress and capable of sustaining conductive function even under such circumstances. More specifically, he indicated that the effect of water stress on translocation was mediated through the demand for available photosynthate.

Water stress induces alterations in  $^{14}\text{C}$ -assimilate distribution patterns in several legumes. Water-stressed soybeans, for example, had more  $^{14}\text{C}$ -assimilate in their roots prior to the pod-fill stage than non-stressed controls (196). Under water stress, soybeans usually retain more labelled material in the fed and non-fed portions of their leaves than non-stressed controls (16). Results of water stress studies suggest that assimilate distribution in general is redirected in such a manner as to most efficiently utilize a limited supply of photosynthate.

## C. Relationship of Source-Sink Regulation and Photosynthate Distribution

### 1. General Aspects of Source-Sink Relations

Developing a clear understanding of the roles of source, sink, and translocation pathways within the plant complex is not an easy task for researchers. An alteration in one of these factors results in severe changes in the others. Complications also arise over the degree of hormonal involvement in directing assimilate transport (229) and the role of the transport system as a sink itself (109,166).

Certain generalities are observed in source-sink relations of legumes in particular (47). The basic source-sink 'nutritional' unit in beans is defined by Adams (2) as the trifoliolate leaf on the main axis in conjunction with the floral bearing raceme in its axil and a second smaller trifoliolate leaf borne on the peduncle subtending the basal florets of the raceme. All these structures are served by the same vascular traces that branched off the main strands of the stem (41). Therefore beans can be described as plants which possess several axillary inflorescences; where each inflorescence is generally supported by its subtending leaf. Evans (47) stated that the overall strength and demand for assimilate in fruits is largely responsible for the observed photosynthate distribution patterns. Number, size, proximity to source, and growth rate are listed as potential determinates of sink strength and capacity (47,227).

### 2. Sink Development and Competition

In most legumes, there is no definite separation of vegetative and reproductive growth periods. Since both occur more or less simultane-

ously, constant competition for photosynthate takes place between vegetative growth and flower and fruit development. Competition may be even more intense between racemes and individual fruits within a raceme for a limited quantity of assimilate. The competition between reproductive organs was investigated in beans (2,156), soybeans (104), and cowpeas (155) where it was partially attributed to the sequence of developmental succession both within and between inflorescences. The degree of competition varied between plant types due to differences in growth habit and raceme development. Determinate bean cultivars, for instance, produced anywhere from 1 to 5 flowering nodes per raceme (241), whereas soybeans (104), and lupins (79) usually set only 2 or 3. In beans and soybeans, a triad composed of 3 floral buds normally originates at each raceme node, but usually only 2 of the buds develop into flowers. Basal flowers of a raceme have a distinct advantage over more distal ones since they bloom and set pods at least 1-2 days prior to those at the next higher node. The "pecking order" in terms of relative sink strength within a bean inflorescence ranges from freshly pollinated flowers and developing embryos of young pods (weakest) to rapidly maturing pods (strongest), (2). Sink strength was found to parallel developmental succession of growth from the base to apex of the inflorescence.

Due to the growth habit of legumes, several developing sinks can engage in strong competition for photosynthate with relative sink size and maturity the key factors in determining the amounts of photosynthate obtained. A definite bias in photosynthate partitioning occurs in soybeans (204) and snap beans (213) which is in favor of the largest

sinks. This "winner take all" or "rich get richer" syndrome has not been thoroughly investigate in legumes (47). Especially lacking is information on competition within an inflorescence for a limited supply of photosynthate.

### 3. Responses to Sink and Source Removal

Experiments involving manual removal of plant organs at various stages of growth have increased the knowledge pertaining to source-sink relationships. Temporarily altering major sources and sinks for photosynthate and recording subsequent effects on vegetative and reproductive growth affords the opportunity to study a closely integrated system of supply and demand. Severe defoliation causes a reduction in the majority of yield components in soybeans (138,214), and beans (213). The plant's growth stage at the time of defoliation will determine its yield response afterwards. Source removal in bean plants during anthesis and early pod growth is extremely detrimental, for instance, whereas leaf removal during pod-fill produces far less drastic effects. Such results were interpreted by Tanaka and Fujita (213) as indicative of source limitations which only occurred during anthesis and early pod development.

Much of the response of legumes to defoliation depends on the crop's ability to compensate for such losses of leaf area. Soybeans were able to tolerate 25% defoliation during the reproductive period by an increased number of pods per plant (214). A defoliation rate of 50%, however, significantly reduced seed yield and number of pods per plant. Similar results were found in beans (213), where post-anthesis defoliation enhanced reproductive organ abscission. These findings

further support the essentiality of adequate source activity during the reproductive period. On the other hand, a 2/3 defoliation during pod expansion only had a slight effect on abscission and seed yield.

In comparison to source reduction effects, response to sink removal have been more extensively studied in several crops such as peas (210), broad beans (21), lupins (221), pepper plants (64,65), cowpeas (154), soybeans (93,147,169), and snap beans (53,56,207,239). Sink removal in legumes has received considerable attention. Depodding in soybeans (93,169), lupins (220), broad beans (21), and cowpeas (154) decreased the potential number of pods but significantly reduced abscission of pods not removed. Removal of the first 6 proximal flowers in a soybean inflorescence increased pod set at more distal raceme nodes (169). This deflowering treatment reduced abscission from a value of 96% to that of 74% beyond the sixth raceme node. Peterson (169) attributed this to either a source-sink problem or inhibitor production by older pods at the first five nodes. As previously reviewed, Huff and Dybing (93) extracted unidentified substances from young soybean pods which when applied to racemes, accelerated abscission of distal flowers on the inflorescence. Tamas et al (212) observed similar effects of older bean fruit on the abscission of younger bean pods and flowers. They attributed the rates of abscission to varying endogenous levels of ABA in younger as compared to more mature fruit. Although Subhadrabandhu et al (208) did not find such a relationship between abscission and ABA content of bean pods, they did observe a 24% reduction in abscission rates in plants where flowers formed during the first 5 days of anthesis were removed. Gage (56) showed that floral abscission in

depodded bean plants was strongly governed by the stage of development of the pods that were removed. For example, removal of pods with relatively low rates of cell expansion had no effect on subsequent flower abscission, whereas, removal of pods undergoing rapid cell expansion drastically reduced flower abscission. These results suggest that young, rapidly growing pods compete with newly developed flowers for photosynthate. During pod-fill, nodule activity in bean plants declined which also implies that rapidly growing pods also compete with vegetative plant organs as well for assimilate (8,231). Similar results were also reported between soybean pod growth and nodule activity (117).

Infrequently studied aspects of sink removal effects include plant growth habit and yield component compensation. Turk et al (218) commented on the proliferation of flowering in water-stressed cowpea plants later in the season after an initial period of flower drop. They stated that this second "wave" of flowering partially offsets losses due to early floral abscission. Ojehomon (156) showed that although the total number of cowpea flowers produced was increased by early flower removal over the first 12 days of anthesis, most of the extra flowers abscised prematurely. He also noted that increased flower numbers induced by deflowering of greenhouse plants or limiting irrigation in field plots results in greater abscission later in development. The growth habit of the cowpea makes it potentially capable of indefinite flowering. For instance, removal of proximal reproductive organs leads to further growth and extension of inflorescences. Such a process can go on indefinitely since cowpea inflorescence apices do not terminate

with the advent of flowering. A similar situation was observed in Vicia faba L. which also exhibits an indeterminate growth habit (87).

Tanaka and Fujita (213) have investigated responses of indeterminate and determinate bean cultivars to sink removal. Their findings, one of the few reports on the subject, demonstrate a profound influence of growth habit. In general, early removal of branches increased main-stem nodes and pod number per node. Although such increases adequately compensated for reduced pod production on branches in semi-determinate bean cultivars far exceeds that of determinate types.

The effect of sink removal on plant activities other than reproductive organ initiation have frequently been studied. For example, photosynthesis in soybeans (147,218), pepper plants (64,65), and peas (50) declines markedly after sink removal. Net CO<sub>2</sub> exchange and photosynthetic leaf capacity are reportedly affected by the removal of sinks in bean plants (53). Changes in photosynthate distribution and rate of assimilate export after sink removal were observed in wheat (229), and peas (210). McAlister and Krober (138) reported increased levels of sugar, starch, and nitrogen in soybean leaves and stems as a result of sink removal.

#### D. Relationship between Photosynthate Distribution and Reproductive Organ Abscission

One hypothesis put forward to explain the abscission of reproductive structures is that there is insufficient photosynthate to adequately support all these organs and those inadequately supplied subsequently abscise. Though many studies have implicated photosynthate partitioning

as a factor in abscission of reproductive structures, the degree of the relationship is still in question. For instance, it still remains conjecture whether or not reduced availability of photosynthate is an indirect or closely related cause of abscission. Regardless of the relationship, experiments involving source-sink manipulation through various means offer a strong case that photosynthate distribution plays a major role in abscission of reproductive organs. In the previous section, responses to sink removal were reviewed. Studies which dealt with selective removal of sinks in soybean (93,138,169), lupin (220), and beans (12,56,207,213,239) support the viewpoint that photosynthate availability to reproductive structures has a definite effect on their tendency to abscise. Percent abscission in deflorated plants in general are reduced by removal of the earliest formed flowers and fruit. It is rationalized that removal of reproductive organs which under ordinary conditions monopolize a limited supply of photosynthate, subsequently permit normally disadvantaged fruit, those which would have abscised, to develop and mature. Evidence exists that older fruit of soybean (93,195) and bean (211) possibly inhibit development of younger fruit via hormonal regulation. It was not ruled out, however, that such effects could be due to hormonal regulation of assimilate transport and distribution to immature fruit. ABA, for example, may actually be exerting an effect on phloem unloading (245). Experiments with defoliation of bean plants (213), strongly suggests that an intimate relationship between available assimilate and abscission exists. The low photosynthate content in pods which subsequently abscise supplies additional evidence for photosynthate supply as a key factor which

determines the fate of reproductive organs.

Other factors which affect the supply of available photosynthate during the reproductive period profoundly influence abscission and number of fruits at maturity. Light enrichment within the canopy of soybean plants during late flowering and early pod growth increases number of pods per plant by 48% as compared to controls (190). Shading, on the other hand, decrease pods per plant by 30% on the average. Mann and Jaworski (135) reported a 50% abscission rate of soybean pods subjected to shade treatments. Temperatures in excess of 40°C result in severe rates of pod abscission as well. These researchers stated that both heat and shade stress could have acted through a similar mechanism which reduced photosynthate supply. Studies that involve CO<sub>2</sub> enrichment during anthesis significantly increased number of flowers and pod set in soybeans (27,69) and beans (116). Alleviation of competition for photosynthate not only affords increases in various yield components but is also responsible for greater stem and leaf dry weights.

Few studies deal with photosynthate distribution and reproductive abscission per se. The majority of statements on this relationship have been obtained through inference and not direct experimentation. Izquierdo et al (96), however, investigated the relationship of assimilate partitioning to abscission of reproductive structures in dry beans. They found significant differences in abscission characteristics for the three cultivars tested. Abscised pods accounted for 64-81% of all reproductive structures that dropped. Although maximum values of stem starch paralleled periods of maximum pod abscission, no explanation was offered as to the relevance of this relationship. Waters et al

(231) found increased levels of starch in lower stem sections of beans from flowering on, whereas, decreased levels occurred in other plant parts after early pod-fill. However, no mention of a possible association with abscission was made. Research in the area of photosynthate partitioning and its connection with reproductive organ development are sparse. This is rather ironic in lieu of the fact that photosynthate production exhibits the greatest potential to increase pod and seed set in crops such as soybean (195). The same case exists in beans where Adams (2) showed that number of pods per plant is the most limiting and sensitive yield component.

## Chapter I

EFFECTS OF IRRIGATION AND POPULATION DENSITY ON YIELD  
PARAMETERS OF 'OREGON 1604' SNAP BEANS AT THE TWO MAJOR  
POD-BEARING NODES<sup>1</sup>

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Abstract. Yield parameters of the sixth (terminal) and second mainstem nodes were evaluated in irrigation x density field trials in 1978 and 1979. Irrigation was supplied either when the soil water potential reached -0.6 bars (high) or -2.5 (low). High versus low plant population densities were, respectively, 45 vs 18 plants/m<sup>2</sup> (1978) and 54 vs 33 plants/m<sup>2</sup> (1979). At the sixth node, the higher irrigation regime significantly increased number of pods formed (1978, 1979), and percent set and pod yield (1978). Number of pods formed and retained through harvest and pod yield (1978), as well as percent set (1978, 1979), were also significantly greater under high irrigation at the second node. Plant population had no significant effect on yield parameters at the

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sixth node, however, at the lower node high density reduced the number of flowers, number of pods formed and harvested, percent set, and pod yield in both years and number of inflorescences (1978). There were no significant irrigation-density interactions for yield or any yield parameter. When averaged over all treatments, the sixth and second nodes together accounted for about 80% of the total yield/plant in both years. Their relative contribution was greatly increased by low irrigation and reduced by high density. Yield per plant was 16% less in 1979 than 1978 primarily due to a 35% reduction in number of inflorescences produced at the second node. Yield per unit area was significantly increased by high irrigation and high density in both years.

## Introduction

Higher plant populations and more equidistant spacing arrangements of bush snap beans result in substantially greater yields compared to more conventional practices (4, 33, 131, 182). Increased irrigation, especially during the critical periods of flowering and early pod set also enhance yield (43, 105, 106). Studies evaluating the effects of plant density and irrigation (30, 129) reported largest yields per unit area from high irrigation and density regimes. Yield potential and limitations under these crop management conditions, however, have not been fully investigated. One area in need of more research is the distribution of yield within the plant under variation in irrigation-density treatment. Seldom has the canopy distribution of yield been evaluated to determine response of inflorescence position to different plant populations (203, 213) or levels of irrigation (129). More knowledge on the effects of irrigation and plant population density on the major pod-producing inflorescences would be extremely beneficial, especially in snap bean breeding programs as an aid in developing cultivars better adapted to high irrigation-density regimes.

The main objective of the following study was to evaluate the distribution of yield and response of individual yield parameters of the major pod-bearing nodes of a popular snap bean cultivar in the Pacific Northwest under various irrigation-density treatments.

## Materials and Methods

Two irrigation x plant population density studies with the determinate, bush snap bean 'Oregon 1604' were conducted during the summers of 1978 and 1979. This cultivar possesses a compact architecture and demonstrates high productivity at increased plant populations (14).

A split-plot, with 4 replications, was used with irrigation level (high and low) as the main plot and population density (high and low) as the subplots. Irrigation treatments were randomly assigned and water was supplied by overhead sprinklers when soil water potential fell below -2.5 bars (low) or -0.6 bars (high). These water potential levels reflected available soil moisture removal of 65-70% and 40-45%, respectively, on the Chehalis silty clay loam soil of the experimental site. Irrigation frequency and amount applied were determined from gypsum soil moisture block readings at the 15 cm depth for the initial irrigation and 30 cm depth thereafter. Amounts of water applied were determined by can catchment. In both years, all plots were irrigated at planting and in 1979 again at the time of primary leaf expansion. These irrigations are not reflected in the totals given in Table 1. Rainfall between the start of differential irrigation (June 28, 1978, July 5, 1979) and bloom totalled 0.74 cm in 1978, however, no measurable precipitation occurred during the same period in 1979 or between bloom and harvest in either year.

High and low population densities were obtained by seeding on a 15 x 15 cm spacing or in 91 cm rows with 5 cm within-row spacing. This

Table 1. Irrigation treatments, frequencies, intervals, and total amount of water applied from the start of differential irrigation until harvest for the 1978 and 1979 seasons.

Year	Soil water potential (bars)	Number of irrigations	Irrigation frequency (days)	Water applied (cm)
1978	Low (-2.5)	4	10-14	16.7
	High (-0.6)	9	5-7	26.8
1979	Low (-2.5)	4	9-12	14.6
	High (-0.6)	8	4-7	22.9

resulted in actual plant stands of 45 versus 18 plants/m<sup>2</sup> in 1978 and 54 versus 33 plants/m<sup>2</sup> in 1979. Banded applications of fertilizer were applied at planting at rates of 56 kg N, 74 kg P, and 47 kg K per hectare. Planting dates were June 7, 1978 and June 11, 1979, with corresponding emergence on June 14, and 21, and first bloom on July 20 and 23. First bloom was defined as the day of anthesis for the pair of flowers in the axil of the uppermost trifoliate. These flowers were usually the first to bloom on the plant and most often reached anthesis on the same day (156, 241). In this study, reproductive structures formed at the base of the terminal trifoliate were considered an integral part of the terminal mainstem inflorescence, although they are morphologically distinct from the raceme (156).

One week prior to first-bloom, 4 uniform plants were selected and tagged with each density subplot. A total of 64 plants were monitored each year. Numbering acropetally from the primary leaf node, the terminal or sixth and second mainstem nodes were also identified and tagged for observation as were all individual branches originating from the second node, which develop in succession (241) and were designated 2-A through 2-D (Fig. 1). These 2 mainstem nodes carry a large portion of the plant's reproductive load, and are far enough removed from each other to evaluate the influence of mainstem node position. Flowers at the lowermost raceme node of the branch inflorescence 2-A generally reached anthesis on the first bloom date. Every other day from first bloom, presence, absence, and developmental stage of all reproductive structures were recorded for the singular inflorescence at the terminal node and all inflorescences originating

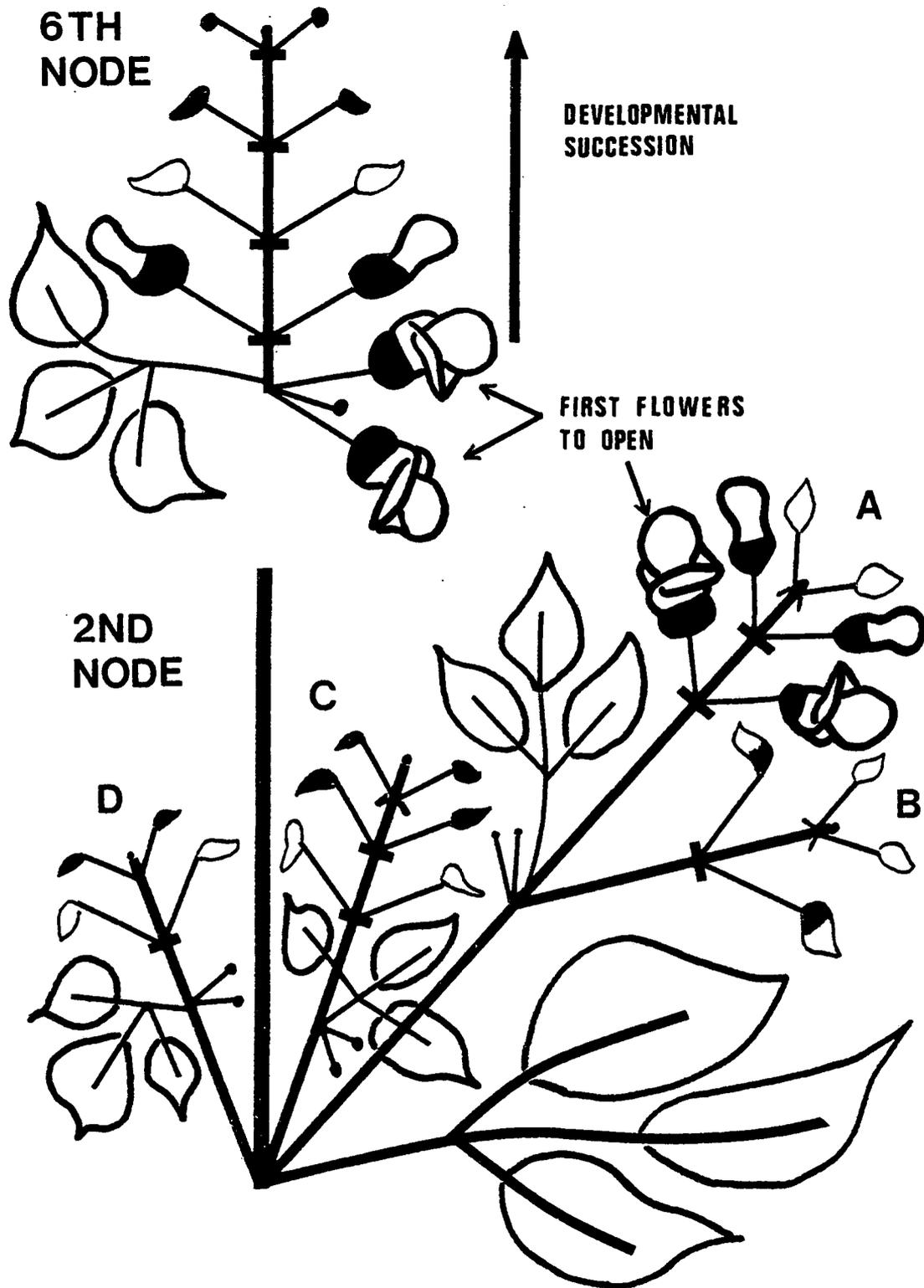


Fig. 1. Inflorescence development in 'Oregon 1604' snap bean at the mainstem terminal (sixth) and second node. The second node is subdivided into its branches; A, B, C and D with branch A the most advanced and D the least.

on lateral branches at the second node. The beginning of pod formation was noted when the enlarging ovary protruded 6-8 mm beyond the calyx tip.

At snap bean maturity, when approximately 50% of the pods formed attained sieve size #1-4 (August 8, 1978, and 11, 1979), plants were harvested, leaf areas measured, and reproductive structures collected and weighed from each tagged inflorescence. Data were analyzed on a plant and per node basis to determine yield parameters such as number of inflorescences, flowers, pods formed and retained through harvest, percent set, and fresh weight per inflorescence. Pod yield was also expressed on a yield/plant and yield/area basis.

During the 1979 season only, the terminal leaflet of the trifoliolate arising from mainstem node 4 was selected for leaf water potential ( $\psi_{1f}$ ) measurement using a pressure bomb (Model 600L - PMS Instrument Co., Corvallis, OR.). Measurements were made on alternate days at about 6:30 PM (PDT) starting the day after first bloom until harvest. At this time of day,  $\psi_{1f}$  readings displayed the greatest response to differential irrigation treatments as evidenced from diurnal water potential curves. At each sampling, 2 terminal leaflets from each density subplot were selected at random from each irrigation-density treatment.

## Results

The 1978 season was extremely warm (Table 2), such that daily max/min temperatures from first bloom through harvest averaged 6.4°

Table 2. Summary of seasonal maximum and minimum temperature data for the 1978 and 1979 seasons during the week before flowering, flowering-pod set, and pod growth.

Year	Stage of development	Dates	Average temperature (°C)		Days over 32°C
			Maximum	Minimum	
1978	Week before flowering	7/13-20	26.0	12.1	1
	Flowering-pod set	7/20-29	33.8	13.0	7
	Pod growth	7/29-8/8	35.4	13.1	10
1979	Week before flowering	7/16-23	34.6	12.0	6
	Flowering-pod set	7/23-8/1	29.4	10.7	2
	Pod growth	8/1-11	28.5	8.5	0

and 3.6°C greater than those in 1979. The warmer 1978 season had 17 days over 32°C, 7 of which occurred during the first 9 days after first bloom, compared to only 8 days over 32°C for the entire 1979 season. One week prior to bloom, however, temperatures exceeded 32°C 6 out of 7 days in 1979.

Irrigation-density treatments markedly affected leaflet water potential readings ( $\psi_{lf}$ ) in 1979 where high irrigation values were generally -7 to -9 bars, compared to -9 to -11 for low irrigation (Appendix I, Fig. A). There was little difference, however, between density treatments within each irrigation level. Differences in  $\psi_{lf}$  between high and low irrigation treatments would likely have been even more pronounced in the more stressful 1978 season.

The pattern of flower formation at the sixth node in 1978 was characterized by a rapid rise at 3 days after first bloom followed by a slow, gradual increase thereafter (Fig. 2A). The cumulative number of flowers reaching at least the white bud stage of development in this year was significantly greater at low than high irrigation (Fig. 2A, Table 3). The greater flowering is largely attributable to a 40% increase in formation of a third flower at the first raceme node late in the season. The influence of irrigation on flower production was less pronounced in 1979 (Appendix I, Fig. B-1).

Whereas low irrigation tended to enhance flower production at the sixth node, the cumulative number of pods formed at this node was significantly less under low irrigation in both years (Fig. 2A and Table 3). Under high irrigation, cumulative number of pods formed during 1978 reached an early plateau compared to the gradual rise

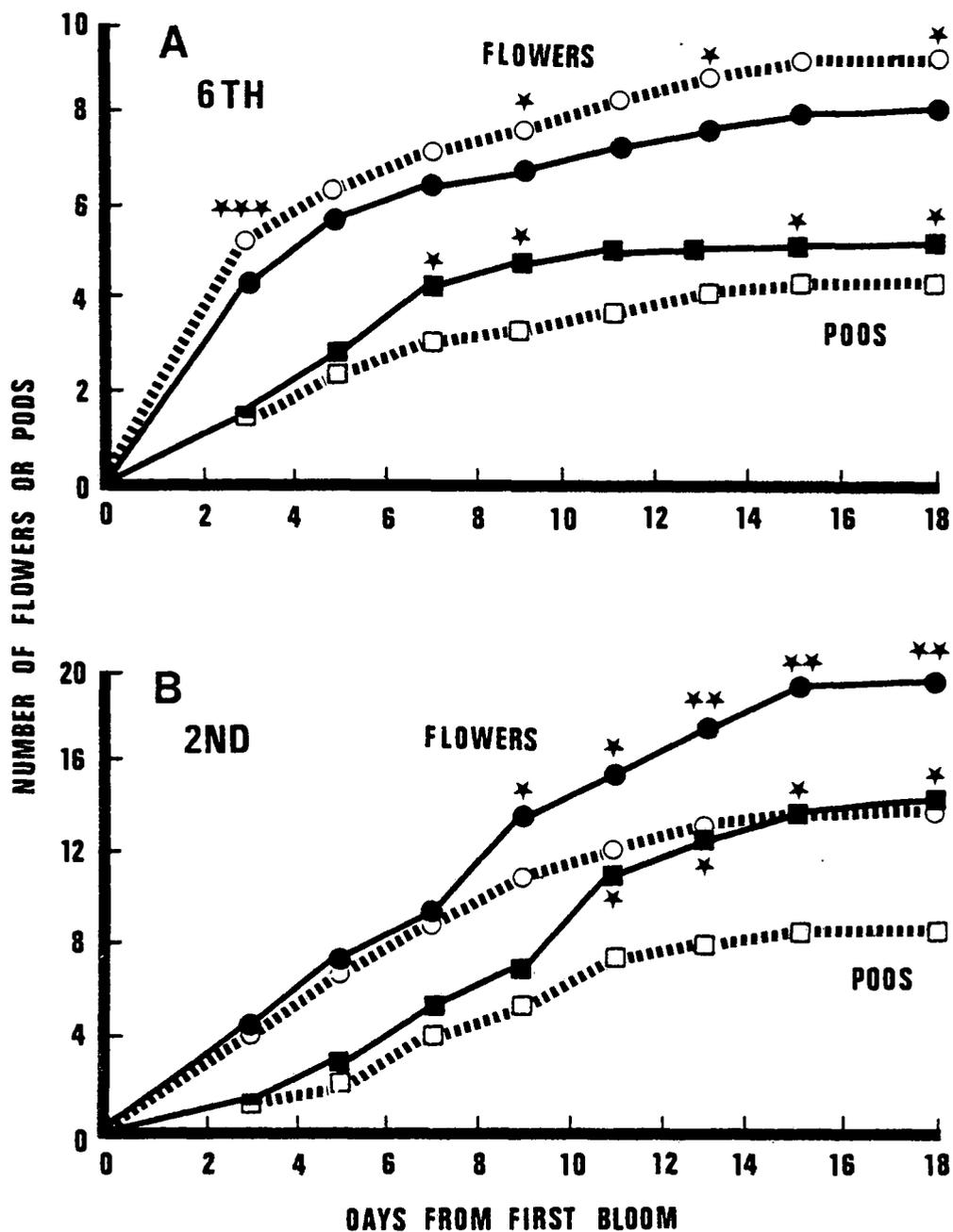


Fig. 2A,B. Effects of irrigation at the sixth mainstem node (A) and population density at the second node for 1978 on cumulative number of flowers or pods produced. Solid lines denote high irrigation (A) or low density (B), whereas, dotted lines represent low irrigation (A) or high density (B). \*, \*\*, \*\*\* Indicate levels of significance at 5%, 1%, and 0.1%, respectively.

Table 3. Per plant yield parameters of 'Oregon 1604' snap bean at the sixth (terminal) and second mainstem nodes as influenced by irrigation and plant density in the 1978 and 1979 seasons.

Yield parameter (per plant.)	Node	1978					1979				
		Irrigation		Density			Irrigation		Density		
		High	Low	Low	High	Avg.	High	Low	Low	High	Avg.
Number of flowers	6	8.58 <sup>*z</sup>	9.53	9.00	9.13	9.05	7.84	8.09	8.25	7.69	7.96
	2	16.5	17.7	20.3 <sup>**</sup>	13.9	17.10	9.13	10.0	11.5 <sup>***</sup>	7.66	9.56
Number of pods formed	6	5.26 <sup>*</sup>	4.28	4.97	4.56	4.77	5.97 <sup>*</sup>	5.28	5.97	5.28	5.63
	2	12.9 <sup>*</sup>	9.53	14.4 <sup>**</sup>	8.41	11.41	6.91	6.25	8.25 <sup>***</sup>	4.91	6.58
Number of harvested pods	6	3.03	2.28	2.77	2.53	2.65	4.00	3.88	4.19	3.69	3.94
	2	9.92 <sup>**</sup>	5.94	10.5 <sup>**</sup>	5.39	7.95	5.66	4.06	6.25 <sup>***</sup>	3.47	4.86
Percent set	6	36.6 <sup>**</sup>	24.7	31.8	29.3	30.6	53.5	49.0	52.1	50.2	51.2
	2	56.3 <sup>***</sup>	31.6	51.6 <sup>**</sup>	36.3	44.0	62.7 <sup>**</sup>	39.4	55.7 <sup>*</sup>	46.5	51.0
Number of inflorescences	6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	2	3.19	3.44	3.75 <sup>*</sup>	2.88	3.22	2.22	2.56	2.69	2.09	2.39
Total pod fresh weight (g)	6	13.3 <sup>*</sup>	9.40	12.2	10.6	11.4	15.4	19.3	17.3	17.4	17.3
	2	27.2 <sup>*</sup>	17.9	30.9 <sup>**</sup>	14.3	22.6	16.2	12.8	19.3 <sup>**</sup>	9.66	14.5

<sup>z</sup> \*, \*\*, \*\*\* Indicate levels of significance at 5%, 1% and 0.1%, respectively, for irrigation or density means at the same mainstem node and year. Each value is the mean of 32 observations.

associated with low irrigation.

As observed at the sixth node, the cumulative number of flowers formed at the second node in 1978 was consistently greater, but usually nonsignificantly so under low irrigation (Table 3). At this node, flower number increased steadily throughout the season and only levelled off after 15 days from first bloom (Fig. 2B). The total number of flowers formed at the second node was twice that of the sixth mainly due to a greater number of inflorescences (Table 3). The cumulative number of pods formed showed a similar, but delayed pattern to that of flowers. High irrigation significantly increased the cumulative number of pods formed from 5 to 18 days after first bloom. Although there were no significant effects of plant density on flower and pod production at the sixth node, a rapid increase in flower formation at the second node occurred under low density at 9 days after first bloom due to increased flowering on branches C and D (Fig. 2B). This change was reflected in an increase in pod formation under low density 2 days later. Flower and pod formation under high density failed to show this rapid increase. Similar significant differences between high and low density were noted for 1979 (Appendix I, Fig. B-2). There was, however, a 67% reduction in total number of flowers and pods formed in 1979 compared to 1978 largely due to a 39% decrease in total number of inflorescences at node 2 (usually C and D failed to form) thus limiting sites for flower production.

In addition to the higher number of pods formed at the sixth node in both years under the higher irrigation regime, percent set and total pod fresh weight in 1978 were also significantly greater (Table 3).

At the second node, percent set was significantly greater under high irrigation in both years as were number of pods formed, number harvested, and total pod fresh weight in 1978.

In contrast to irrigation effects, there were no significant effects of density on yield parameters at the sixth node for either year. At the second node, however, low density significantly increased the number of pods formed and harvested, percent set, and total pod fresh weight for both years (Table 3). Leaf area at harvest, ( $\text{cm}^2/\text{plant}$ ), was also significantly increased by low (1230, 824) compared to high density (698, 525) for 1978 and 1979, respectively.

When averaged over all irrigation-density treatments, total pod fresh weight yield from the entire plant, inclusive of all reproductive mainstem nodes, was 16% greater in 1978 than 1979 (Table 4). The higher yield resulted from the greater response to high irrigation treatment, which outyielded the low by 121% in 1978, but only 43% in 1979. Although pod yield/plant in 1978 was 67% greater under lower density, the effect of density was slight in 1979. This is attributed to a lesser difference (67%) between high and low density plant populations in 1979 compared to 1978 (150%).

As expected, the sixth and second nodes were the major yield contributors, together bearing an average of 78% and 81% of the total yield/plant in 1978 and 1979, respectively (Table 4). Low irrigation increased the proportion of yield contributed by these nodes to over 90%, whereas high density tended to lower their relative yield contribution. Pooling all treatments, the second node in 1978 accounted for more than half the total pod yield, whereas, in 1979 it contributed

Table 4. Per plant summary of 'Oregon 1604' snap bean pod yield and percent yield contribution by the sixth and/or second node for the 1978 and 1979 seasons as affected by irrigation level and plant population density.

Treatment	Total yield (g/plant) <sup>z</sup>		Percent total yield contributed by Sixth plus second node		Pod fresh weight (g/node)			
	1978	1979	1978	1979	Sixth node		Second node	
	1978	1979	1978	1979	1978	1979	1978	1979
<u>Irrigation</u>								
High	65.0	48.0	62.4	65.9	13.3 (20.5) <sup>Y</sup>	15.4 (32.1)	27.2 (41.9)	16.2 (33.8)
Low	29.4	33.4	92.9	96.1	9.4 (32.0)	19.3 (57.8)	17.9 (60.9)	12.8 (38.3)
<u>Density</u>								
Low	59.1	42.0	72.6	87.2	12.1 (20.4)	17.3 (41.2)	30.9 (52.2)	19.3 (46.0)
High	35.3	39.5	70.6	68.7	10.6 (30.0)	17.4 (44.1)	14.3 (40.6)	9.7 (24.6)
<u>Pop. Mean</u>	47.2	40.7	77.6	81.0	26.2	45.0	51.4	36.0

<sup>z</sup>Data for total pod fresh weight represent all mainstem nodes and was obtained from plants harvested only for final yield analysis. Each value is the mean of 80 observations.

<sup>Y</sup>Values in ( ) denote percent contribution of the total yield/plant by the sixth, second or both nodes combined.

less than the sixth node. Although per plant yields were higher in 1978 than 1979, the opposite was the case for per unit area yields (Table 5). In both years per area yields were significantly improved by high irrigation, by 120% (1978) and 40% (1979), and by high density, by 41% (1978) and 54% (1979). Irrigation-density interactions were not significant.

### Discussion

Yield and yield parameters of 'Oregon 1604' snap bean were markedly influenced by irrigation and density treatment, mainstem node position, and season. Yields in the less stressful year of 1979 were somewhat greater than those in 1978 due to higher plant populations and reduced temperatures from bloom to harvest (Table 5). On a per plant basis, however, yield was less in 1979 than 1978 because of higher plant densities in 1979 and possibly the consequence of pre-bloom temperature stress (Table 2) which can disrupt floral bud differentiation and growth in beans (94b, 95a, 205a, 230a). Even though higher plant populations decrease yield per plant, the increased plant number compensates for individual plant losses.

Effects of irrigation and density are discussed separately since there were no significant interactions which implies that those cultural practices can be studied independently. High irrigation and density resulted in significantly greater per unit area yield for both years (Table 5), in contrast to yield per plant which was increased by high irrigation and low density (Table 4). The yield increase under high

Table 5. Yield per unit area of 'Oregon 1604' snap bean as affected by irrigation level and plant population density for the 1978 and 1979 seasons.

Treatment	Pod yield (metric ton/ha)	
	1978	1979
<u>Irrigation</u>		
High	18.7 <sup>*z</sup>	20.5 <sup>*</sup>
Low	8.5	14.6
<u>Density</u>		
High	15.9 <sup>**</sup>	21.3 <sup>**</sup>
Low	11.3	13.8
<u>Pop. Mean</u>	13.6	17.5

<sup>z</sup> \*, \*\* Indicate levels of significance at 5% and 1%, respectively, for irrigation or density means within the same year. Each mean represents the average of 80 observations. Irrigation-density interactions are not presented since none were significant.

irrigation was the result of a greater number of pods formed and harvested, whereas, enhanced yield with low density can also be attributed to less interplant competition resulting in increased branching and hence more reproductive sites. The increase in leaf area per plant under low density and the greater photosynthetic capacity which would most likely occur under high irrigation suggests that those plants had a greater supply of photosynthate to support a greater number of pods.

In regard to individual yield parameters, low irrigation enhanced flowering at the sixth node (Fig. 2A), which during the mid- to late bloom period resulted from the appearance of a third flower at the base of the inflorescence. The earlier rise in flowering from 0 to 3 days after first bloom cannot be explained other than as a hastening of time to flower which can occur in snap beans (139) and lupins (79) when under water stress. Although flower production was greater under low irrigation, number of pods formed and harvested was drastically reduced which suggests that the plant was unable to support a large number of these reproductive organs. Those flowers that formed late in the season would not have contributed to yield since even if they set pods, there was not enough time for them to mature into harvestable fruit.

In contrast to irrigation effects, there was a noticeable lack of a response to density at the sixty node (Table 3), however, low density greatly increased flower production at the second node (Fig. 2B). This was mainly attributed to inflorescences that emerged on later-to-form branches (Fig. 1) during mid-season, 7 to 10 days after first bloom.

High irrigation resulted in a marked increase in pods formed and

harvested, percent pod set, and total pod fresh weight at the sixth node, particularly during the more stressful 1978 season (Fig. 2A, Table 3). It is possible that an increased water supply reduced the detrimental influence of high temperature through a reduction in water stress as indicated by higher leaf water potential measurements with high irrigation (Appendix I - Fig. A). More frequent irrigation may have also directly reduced temperature stress through microclimate modification (30, 32, 177a). The timing of irrigation in 1978 was another factor to consider since the high irrigation plots required and received an irrigation at first bloom which was probably very favorable for pod formation over the following 3-4 days. The high sensitivity of the flowering and pod set period to water and high temperature stress has been frequently reported (2, 43, 105, 137). Both the magnitude and duration of high temperature stress were much less during the flowering and pod set period in 1979 (Table 2), which likely contributed to the reduced irrigation effect. Although the mechanisms by which high temperature adversely affects pod set is unknown, Halterlein et al (65a) concluded that it likely does not result from interference with pollination and fertilization.

Compared to irrigation effects, there was no effect of density on pod formation at the sixth node in either year (Table 3). This would be expected if competition for light was a major density factor since supply leaves for the terminal inflorescence are high in the canopy and much less affected by changes in plant population than those at lower depths.

The relative contribution of the second plus sixth node was

lessened by high irrigation in both years (Table 4). This can be attributed to enhanced pod production at intermediate mainstem nodes derived from total yield/plant (inclusion of all reproductive nodes) obtained from an associated study involving the same plots (129). High density, on the other hand, decreased the relative yield contribution of the second compared to the sixth node (Table 4) by reducing the number of inflorescences produced and decreasing pod set on those that were formed (Table 3). This effect was more pronounced in 1979 when plant population densities were much greater than in 1978. Other studies (203, 213) have shown that the yield contribution of a particular node under different plant densities is very dependent on the cultivar, growth habit, and total number of mainstem nodes.

The results of this study indicate that further yield increases under high irrigation and density could be obtained by utilizing determinate genotypes and selecting for those which a) maintain a multiple number of inflorescences at specific mainstem nodes, and/or b) set and retain more pods per inflorescence. The need exists for further investigation of the plant's capacity to supply or support a greater reproductive load assuming more sites can be made available for flower and pod production.

## Chapter II

A DETAILED ANALYSIS OF SNAP BEAN YIELD PARAMETERS AS  
AFFECTED BY INFLORESCENCE POSITION, RACEME NODE LOCATION, AND  
IRRIGATION-DENSITY TREATMENT<sup>1</sup>

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Abstract. The effects of high (-0.6 bar) and low (-2.5 bars) irrigation and plant population density were evaluated in 2 seasons on yield parameters of individual raceme nodes of the terminal inflorescence (6-T) of the sixth mainstem node and first-formed lateral inflorescence (2-A) at the second mainstem node of 'Oregon 1604' snap beans. A majority of the pod yield is produced by these inflorescences. High and low plant densities were 45 versus 18 plants/m<sup>2</sup> in 1978 and 54 versus 33 plants/m<sup>2</sup> in 1979. The 6-T and 2-A inflorescence formed 4 and 3 raceme nodes respectively, in 1978, whereas each inflorescence had one less raceme node in 1979. The acropetal succession of flowering in each inflorescence was characterized by longer duration of the

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flowering period at more distal raceme nodes. In general, number of flowers and pods formed, percent set, and number of harvested pods decreased acropetally within each inflorescence. There were no significant irrigation-density interactions on yield parameters at any raceme node. However, the acropetal rate of decline for each yield parameter was significantly reduced by high irrigation in both inflorescences in both seasons, whereas, low density lessened the rate of yield decrease only within the 2-A inflorescence. Low irrigation and high density accentuated the difference in yield parameters between the proximal and distal raceme nodes. This effect was more pronounced within the 6-T inflorescence, particularly during the more stressful year of 1978 characterized by temperatures often exceeding 32°C during flowering and pod set. The first raceme node was the major yield contributor accounting for a maximum of 80% of the total inflorescence pod yield in the 6-T (1978) and 67% in 2-A (1979). Over 95% of the total pod yield for either inflorescence and year was attributed to the first 2 raceme nodes which suggests that the most direct route to enhance snap bean yield is to select for genotype with an increased number of inflorescences versus more raceme nodes per inflorescence.

## Introduction

High plant populations (6, 131, 182) and increased irrigation levels (30, 54, 55, 129) can greatly improve yields of snap beans. As plants are moved closer together the plant response at different canopy levels differs appreciably and is characteristically cultivar dependent (203, 213). The yield within individual inflorescences also changes with different plant density treatments (Chapter I). Yield parameters of legumes in general vary considerably with inflorescence position, interplant competition, and availability of soil moisture (87, 93, 100, 213, 237). Response of flowering and pod formation at the raceme node level within an inflorescence, however, has seldom received any attention. More information is needed in regard to the development and persistence of reproductive structures formed at various levels in the canopy to more fully evaluate and interpret snap bean yield effects under diverse irrigation-density regimes.

In an earlier study (Chapter I), the influence of irrigation and plant density on yield parameters of the 2 main pod-bearing nodes of the snap bean 'Oregon 1604' were evaluated. The purpose of this study was to examine reproductive development and yield response in more detail within the terminal inflorescence and main branch inflorescence formed lower in the canopy.

## Materials and Methods

The experimental methodology utilized in this study was previously

outlined (Chapter I). Two irrigation x plant population density field experiments were performed with the determinate bush snap bean cultivar 'Oregon 1604' during the 1978 and 1979 seasons on a Chehalis clay-loam soil. A split-plot experimental design with 4 replications was used in which 2 levels of irrigation (high and low) were the main plot variables and 2 plant densities (high and low) were the subplots. Irrigation was applied by overhead sprinklers when soil water potential determined from gypsum blocks at 30 cm soil depth dropped to -2.5 bars (low) and -0.6 bar (high). Rainfall during the bloom to harvest period was negligible in both years.

High and low population densities were obtained, respectively by seeding at a 15 x 15 cm spacing or in 91 cm rows with 5 cm within-row spacing. This resulted in plant stands of 45 versus 18 plants/m<sup>2</sup> in 1978 and 54 versus 33 plants/m<sup>2</sup> in 1979. Seeding was done June 7, 1978 and June 11, 1979 with first bloom occurring on July 20 and 23, respectively. First bloom was defined as the day in which the majority of flowers in the axil of the terminal trifoliate (sixth mainstem node) reached anthesis. These flowers were considered an integral component of the terminal mainstem inflorescence, although they are morphologically distinct from the remainder of the raceme (156, 241). Both flowers at a raceme node frequently open on the same day, but occasionally their anthesis may be separated by about a day.

A week prior to first bloom, 4 uniform plants were selected and marked from each irrigation-density subplot, totally 64 plants for each observation. Numbering acropetally from the primary leaves at node 1, the terminal or sixth and second mainstem node were identified.

A single terminal inflorescence (denoted 6-T) was produced at the sixth mainstem node, whereas several branches possessing lateral inflorescences originated at the second mainstem node. Of these, only the earliest formed inflorescence (designated 2-A) was used since it was the only inflorescence consistently present under both high and low plant populations that possessed a multiple number of raceme nodes for comparison and statistical analysis. Every other day from first bloom, the presence, absence, and stage of development of all flowers/pods formed at each individual raceme node (RN) of the terminal, 6-T and lateral, 2-A inflorescence were recorded. Stage of development for each reproductive organ was based on days from anthesis, namely the day of anthesis, 1 day before or after, and greater than 1 day after (representing formation of a pod). When the ovary emerged beyond the calyx tip reaching a length of approximately 6-8 mm, it was regarded as an immature pod. On the basis of observed patterns of reproductive development from 2 days before to 2 days after anthesis specific dates of anthesis were determined for flowers which failed to open on an observed day. From the data recorded on observation dates, a seasonal log of flowering was constructed for each raceme node.

Plants were harvested on August 8, 1978 and August 11, 1979 and pods were collected by raceme node at the 6-T and 2-A inflorescences and weighed. Data were subjected to analysis of variance on a raceme node basis to determine the significance of irrigation-density effects on number of flowers produced (those which at least reached a white-bud stage, 1-2 days prior to bloom), number of pods formed and harvested, and percent set (ratio of number of harvested pods to number of

flowers). Data for each year were also pooled across all irrigation-density treatments to evaluate the effect of raceme node position within each inflorescence on the yield parameters listed above, in addition to, average pod fresh weight and distribution of pod yield within each inflorescence.

### Results

Maximum daily temperatures in 1978 were extremely high, frequently exceeding 32°C from 1 day prior to first bloom until harvest (Fig. 1). Cooler temperatures prevailed in 1979, excluding 2 very warm periods 2-7 days before, and 8-9 days after first bloom. Minimum daily temperatures in both years were generally similar with the exception of 2 periods in 1978 when they were considerably higher.

In 1978, inflorescences 6-T and 2-A had 4 and 3 raceme nodes, respectively, whereas, each averaged about 1 less in 1979. This decline may be associated with high temperatures before first bloom the second year. In addition to the seasonal or year effect, plant population also influenced raceme node number. Low density significantly increased the number of raceme nodes per 2-A inflorescence by 30% in 1979 (Appendix II, Table A).

The flowering sequence within a bean inflorescence is acropetal, and in 1978 the majority of flowers at RN-2 and RN-3 of the 6-T inflorescence reached anthesis 1 and 2 days, respectively, after those at RN-1 (Fig. 2A). The peak of flowering at RN-4, however, occurred 5 days after that of RN-1. The flowering period at RN-4 was 10 days

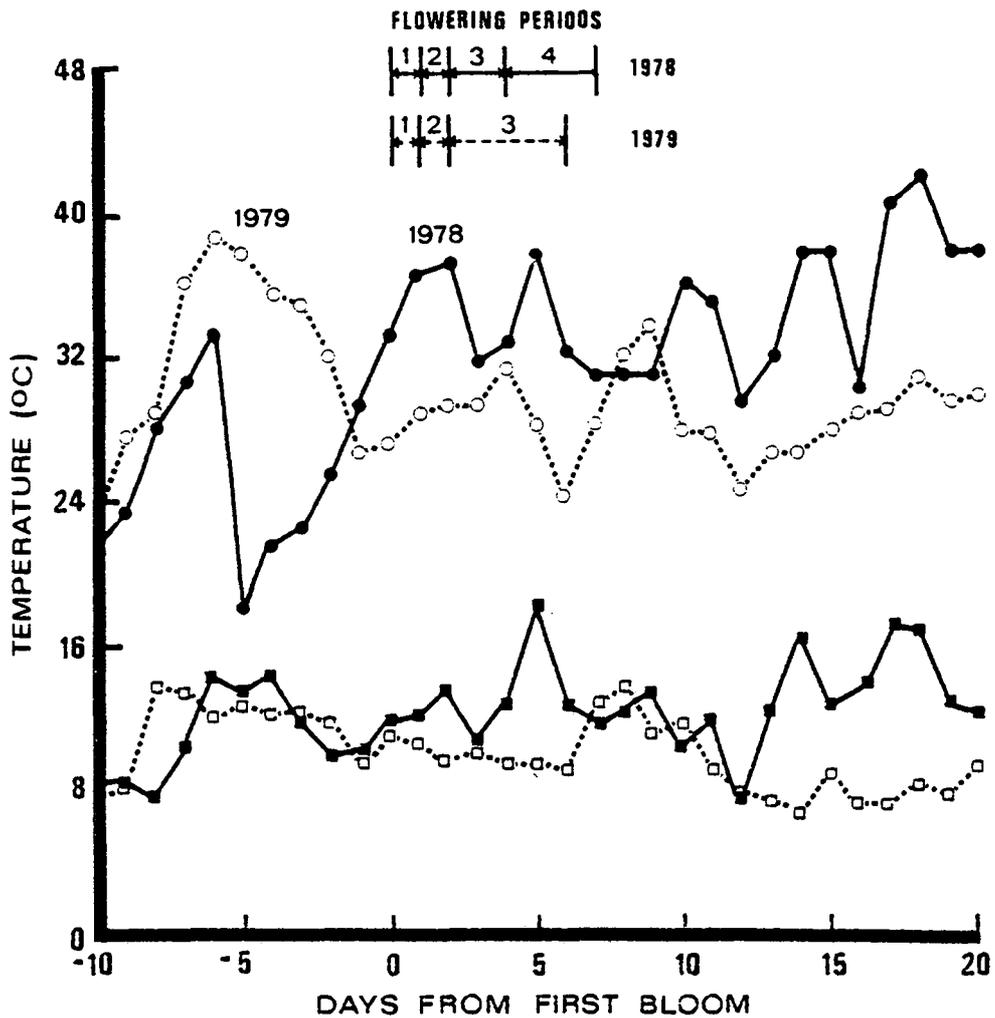


Fig. 1. Seasonal maximum (●,○) and minimum (■,□) air temperatures for 1978 (—) and 1979 (---), respectively. Flowering periods are depicted for reproductive structures at each raceme node (numbered 1-4 acropetally) of the terminal inflorescence at the sixth mainstem node.

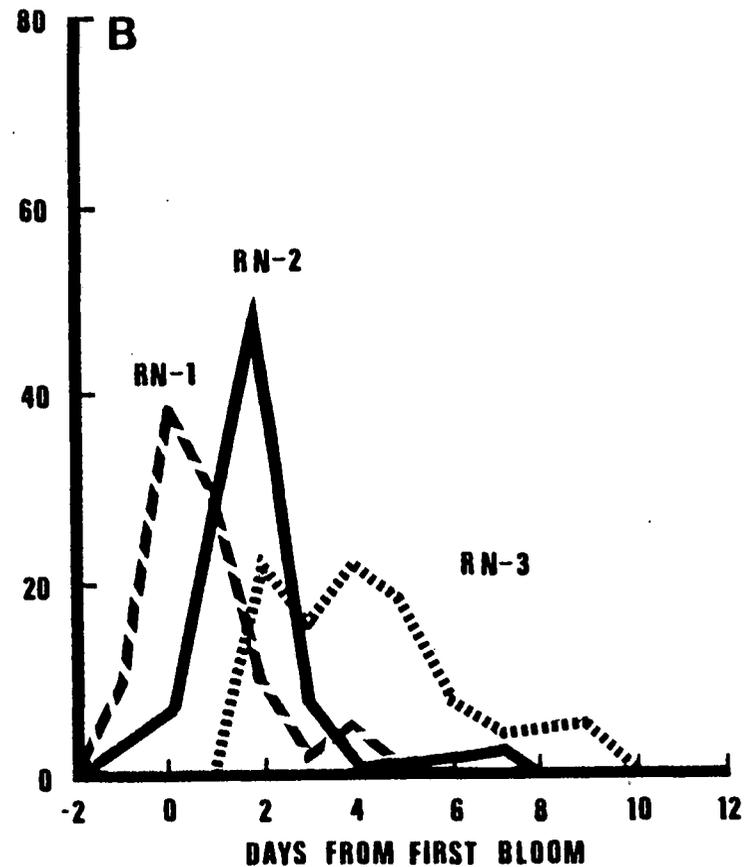
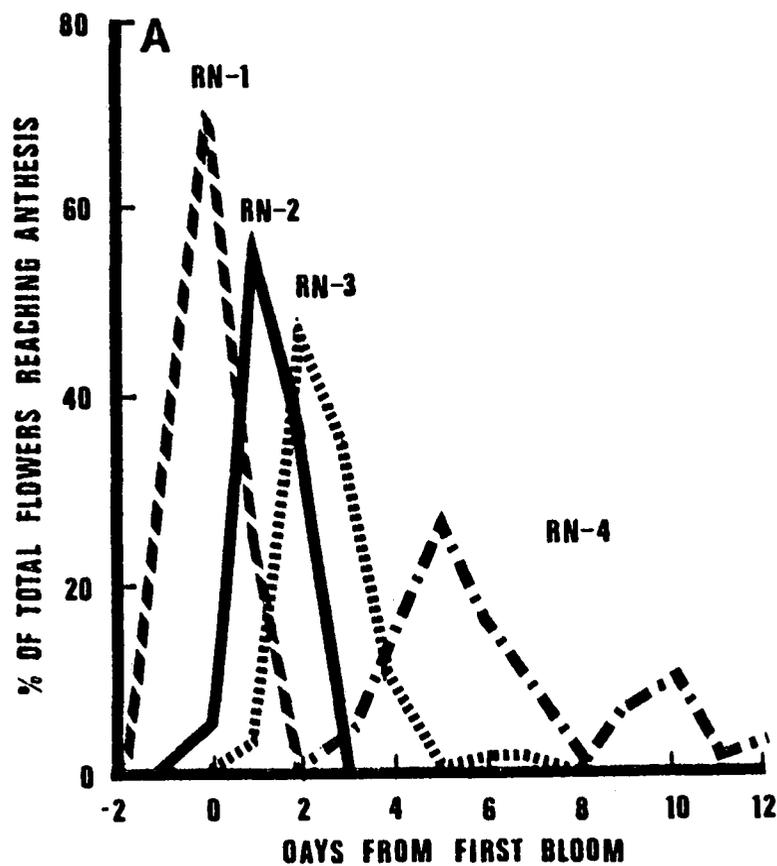


Fig. 2. Percent of total flowers that reached anthesis at each raceme node position (numbered acropetally) in inflorescences arising from the sixth mainstem node, 6-T (A) and the main inflorescence, 2-A, at the second node (B) for the 1978 season.

compared to only 4-5 for RN's 1-3. The same general flowering patterns were observed among raceme nodes of the 2-A inflorescence, however, the flowering period for each raceme nodes was an average of 1-3 days longer than corresponding raceme nodes of the 6-T inflorescence (Fig. 2B).

Flowering at RN-1 and RN-2 of the 6-T inflorescence in 1979 was similar to patterns observed in 1978, except that the peak at RN-3 was reached 3 days after that of RN-2 (Fig. 3A). Flowering at raceme nodes of the 2-A inflorescence preceded that of corresponding 6-T raceme nodes by 1 day, but the flowering period was again longer. The last raceme node formed in each inflorescence in 1979 exhibited a more condensed flowering period than those in 1978.

In general, all snap bean yield parameters decreased acropetally from the first to last raceme node within each inflorescence. For example, the relative flower production at each raceme node of the 6-T inflorescence in 1978 was: RN-1, 1.00; RN-2, 0.82; RN-3, 0.73; and RN-4, 0.58. The number of pods formed by the lower 2 raceme nodes in this inflorescence was 63% higher than that of the upper half (Table 1). Percent set was also increased 22 percentage units and number of pods harvested at RN-1 plus RN-2 were more than 3 times greater than that on the upper raceme nodes. Number of flowers formed at RN-1 of the 6-T inflorescence was slightly greater under low irrigation due to emergence of a third flower late in the 1978 season. High irrigation significantly increased the number of pods formed at RN-3, in addition to percent set and final number of harvested pods at both RN-2 and RN-3. There were no effects of density, however, on yield parameters

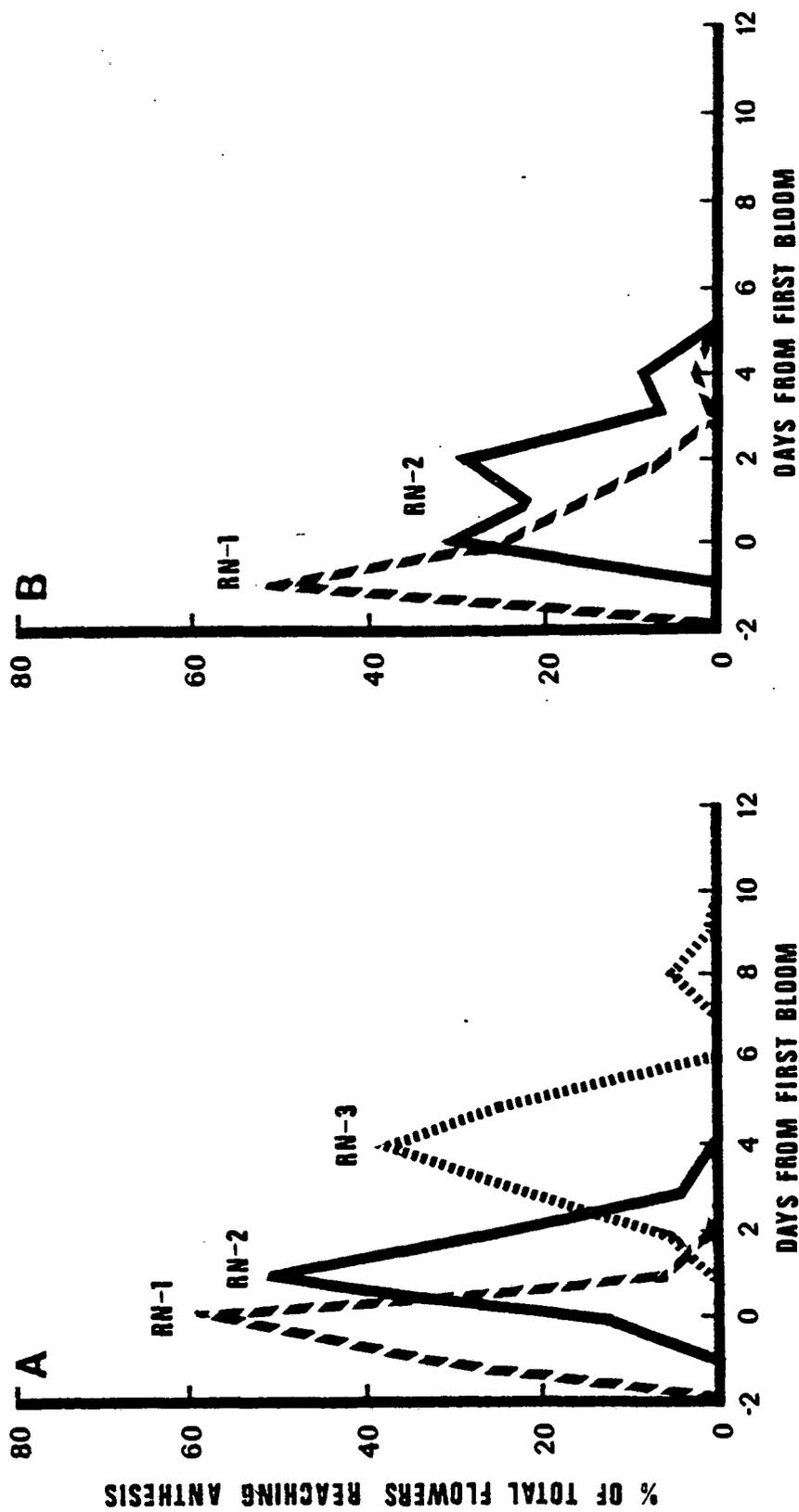


Fig. 3. Percent of total flowers that reached anthesis at each raceme node position (numbered acropetally) in inflorescences arising from the sixth mainstem node, 6-T (A) and the main inflorescence, 2-A, at the second node (B) for the 1979 season.

Table 1. Influence of irrigation and plant population density on snap bean yield parameters of 'Oregon 1604' at individual raceme nodes (numbered acropetally) in inflorescences arising from the sixth mainstem node, (6-T), and the main inflorescence (2-A) at the second node for the 1978 season.

Yield parameter	Inflorescence	Raceme node	Treatment <sup>Y</sup>				Population mean
			Irrigation		Density		
			High	Low	Low	High	
Number of flowers	6-T	1	2.53 <sup>z</sup>	2.81	2.59	2.75	2.67
		2	2.19	2.19	2.19	2.19	2.19
		3	1.88	2.00	1.94	1.94	1.94
		4	1.81	1.31	1.47	1.66	1.56
	2-A	1	2.28	2.43	2.47	2.25	2.36
		2	2.09	2.34	2.34 <sup>*</sup>	2.09	2.22
		3	1.81	1.97	1.97	1.81	1.89
	Number of pods formed	6-T	1	1.81	1.81	1.88	1.75
2			1.06	0.84	0.97	0.94	0.95
3			1.31 <sup>***</sup>	0.25	0.72	0.84	0.78
4			1.03	0.78	1.00	0.81	0.91
2-A		1	1.63	1.38	1.69	1.31	1.50
		2	1.78 <sup>**</sup>	1.06	1.59	1.25	1.42
		3	1.44	1.06	1.41	1.09	1.25
Percent set		6-T	1	58.5	48.2	57.2	49.5
	2		35.1 <sup>*</sup>	14.5	23.2	26.3	24.8
	3		22.9 <sup>**</sup>	4.7	17.7	9.9	13.8
	4		22.9	19.4	26.7	15.5	21.2
	2-A	1	60.1 <sup>*</sup>	38.7	54.7	44.1	49.4
		2	59.7 <sup>*</sup>	23.3	50.6	32.4	41.5
		3	43.3 <sup>*</sup>	23.9	37.3	29.9	33.6
	Number of harvested pods	6-T	1	1.47	1.34	1.47	1.34
2			0.75 <sup>*</sup>	0.31	0.50	0.56	0.53
3			0.44 <sup>*</sup>	0.09	0.34	0.19	0.27
4			0.28	0.41	0.28	0.41	0.34
2-A		1	1.38	0.94	1.34 <sup>*</sup>	0.97	1.16
		2	1.25 <sup>*</sup>	0.53	1.13	0.66	0.89
		3	0.78	0.47	0.72	0.53	0.63

<sup>z</sup>\*, \*\*, \*\*\* Indicate levels of significance at 5%, 1%, and 0.1% respectively, as determined by F-test for means within irrigation or density treatments. Each value is the mean of 32 observations.

at the 6-T inflorescence in 1978.

Yield parameter increases in the 6-T inflorescence in 1979 were similar to those observed the previous season for the means of RN-1 plus RN-2 versus RN-3 (Table 2). Most pronounced was the 3-fold increase in number of pods harvested at RN-1 plus RN-2. Although number of pods formed was significantly greater under high irrigation at RN-2, irrigation effects were much less marked compared to 1978. There was, however, an effect of plant population in that the number of flowers (RN-2) and number of pods formed (RN-1 and RN-2) were significantly increased by low density.

In the 2-A inflorescence in 1978, number of flowers and pods formed at RN-1 and RN-2 were 53% and 17% greater, respectively than at RN-3 (Table 1). Percent set declined from 49% to 34% and number of harvested pods fell by 46% from RN-1 to RN-3. Percent set was significantly increased by high irrigation at all raceme nodes, in addition to number of pods formed and harvested at RN-2. Density had little effect except that number of pods formed at RN-1 was also significantly greater under low density, as was number of flowers produced at RN-2.

In 1979, only 2 raceme nodes were formed in the 2-A inflorescence and differences in yield parameters between them were slight except that the number of harvested pods was 37% greater at RN-1 than RN-2 (Table 2). Percent set was significantly greater under high irrigation at both nodes, and the number of harvested pods was increased more than 117%. Number of flowers and pods produced were significantly increased by low density at RN-2, as were percent set and number of harvested pods at RN-1.

Table 2. Influence of irrigation and plant population density on snap bean yield parameters of 'Oregon 1604' at individual raceme nodes (numbered acropetally) in inflorescences arising from the sixth main-stem node, (6-T), and main inflorescences (2-A) at the second node for the 1979 season.

Yield parameter	Inflorescence	Raceme node	Treatment				Population mean
			Irrigation		Density		
			High	Low	Low	High	
Number of flowers	6-T	1	2.88	2.97	2.97	2.88	2.92
		2	2.69	2.59	2.88 <sup>***z</sup>	2.40	2.64
		3	1.81	1.38	1.56	1.63	1.59
	2-A	1	2.09	2.34	2.22	2.22	2.22
		2	2.00	1.88	2.13 <sup>*</sup>	1.75	1.94
	Number of pods formed	6-T	1	2.25	2.16	2.31 <sup>*</sup>	2.10
2			2.19 <sup>***</sup>	1.81	2.13 <sup>*</sup>	1.88	2.00
3			1.18	1.06	1.09	1.16	1.13
2-A		1	1.84	1.78	2.00	1.63	1.81
		2	1.69	1.38	1.78 <sup>*</sup>	1.28	1.53
Percent set		6-T	1	63.4	64.2	63.2	64.5
	2		59.0	52.0	54.3	56.9	55.6
	3		31.7	33.3	38.8	27.2	32.5
	2-A	1	77.6 <sup>*</sup>	66.9	82.6 <sup>*</sup>	61.9	72.2
		2	76.3 <sup>*</sup>	39.3	60.8	54.9	57.8
	Number of harvested pods	6-T	1	1.91	1.81	1.88	1.84
2			1.59	1.47	1.56	1.38	1.47
3			0.44	0.56	0.53	0.47	0.50
2-A		1	1.59	1.53	1.78 <sup>**</sup>	1.34	1.56
		2	1.56 <sup>*</sup>	0.72	1.31	0.97	1.14

z\*, \*\*, \*\*\* Indicate levels of significance at 5%, 1%, and 0.1%, respectively, for means within irrigation or density treatments. Each value is the mean of 32 observations.

The first raceme node accounted for 80% of the total pod yield within the 6-T inflorescence in 1978 (Table 3). In fact, nearly all the total pod yield was contributed by the 2 proximal raceme nodes with less than 5% from RN-3 and RN-4. Average pod fresh weight at RN-1 was approximately 2, 10, and 17 times greater than at RN-2, RN-3, and RN-4. Yield was more evenly distributed between RN-1 and RN-2 of the 6-T inflorescence in 1979, however, RN-1 still contributed 66% of the yield, yet the highest raceme node, RN-3, was only responsible for 3%.

At the 2-A inflorescence, RN-1 accounted for the major percentage of pod yield, 65-67%, during both years, whereas, RN-2 produced 27-30% of the yield (Table 3). Average pod fresh weight at RN-1 was approximately 1.5 and 5 times greater than at RN-2 and RN-3, respectively, whereas the difference between raceme nodes was slight in 1979 (Table 3). Pooling all raceme nodes, average fresh weight per harvested pod on either the 6-T or 2-A inflorescence was relatively constant between years, however, pods harvested were 81% heavier on the 2-A inflorescence.

#### Discussion

Pre-bloom temperature stress is extremely detrimental to flower bud differentiation and growth in beans (94a, 94b, 95a, 230a). High temperatures exceeding 32°C the week prior to first bloom in 1979 (Fig. 1) were probably a major contributing factor to the decreased raceme node number per inflorescence compared to 1978. Since the existence of a raceme node in the present study was based on visual recognition of floral bud emergence (4-5 days pre-anthesis), the

Table 3. Snap bean pod yield of 'Oregon 1604' expressed as percent total inflorescence pod weight and average weight per pod at individual raceme nodes (numbered acropetally) in inflorescences arising from the sixth main stem node, (6-T), and main inflorescence (2-A) at the second node for the 1978 and 1979 seasons.

Yield parameter	Mainstem node inflorescence	Raceme node	Populations means <sup>Z</sup>	
			1978	1979
Distribution of pod yield within an inflorescence	6-T	1 <sup>Y</sup>	80.1	65.9
		2	15.3	30.6
		3	2.2	3.4
		4	2.4	----
	2-A	1	64.7	66.6
		2	27.1	32.7
		3	6.6	----
	Average fresh weight (g/pod)	6-T	1	6.62
2			3.12	3.82
3			0.38	1.08
4			0.66	----
			(2.70) <sup>Y</sup>	(2.75)
2-A		1	8.05	5.54
		2	5.28	4.16
		3	1.61	----
		(4.98)	(4.90)	

<sup>Z</sup>Means are averages pooled over all irrigation-density treatments for each year.

<sup>Y</sup>Values in ( ) denote the mean of all raceme nodes for an inflorescence.

reduced number of raceme nodes was due to either a decrease in floral bud differentiation and/or abscission of floral buds which went undetected.

Position of a raceme node within an inflorescence was the major factor determining the duration and peak of the flowering period (Fig. 2, 3). The most distal raceme node exhibited an erratic flowering pattern in both the 6-T and 2-A inflorescences for each year which may be related to a reduced growth rate compared to more proximal raceme nodes. Others (56, 116) noted that discrepancy in flowering patterns among raceme nodes in bean inflorescences and reported that removal of proximal flowers of anthesis promoted flowering and shortened the flowering period at more distal raceme nodes. With the exception of low density treatment in 1979 (Appendix II, Table A), irrigation and plant population had little influence on the number and pattern of flowering of raceme nodes, which are characteristic of the genotype (156, 241). It was observed in the present study that 'Oregon 1604' formed no more than 5 raceme nodes per inflorescence.

The consistent acropetal decline in yield parameters was reduced by high irrigation at both inflorescences and low density at the 2-A inflorescence (Tables 1, 2). Low irrigation and high density, on the other hand, magnified the effect of raceme node location and enhanced the rate of acropetal decline in yield parameters within an inflorescence. The effect of high irrigation on percent pod set was quite pronounced at higher raceme nodes of the 6-T inflorescence and first 2 raceme nodes of the 2-A inflorescence, especially in the more stressful year of 1978 (Table 1). The resultant increase in pods harvested

under high irrigation in 1978 was largely attributable to a concomitant reduction in flower and pod abscission (Chapter III). Increased irrigation can also lessen the deleterious effect of high temperatures via reduced water stress, whereas low density could indirectly influence photosynthate supply through a larger leaf area (Chapter I). The discrepancy in yield parameters among raceme nodes, however, is still quite marked regardless of irrigation and/or density treatment (Tables 1, 2). This noticeable acropetal decline within an inflorescence was observed in other legumes (100, 194, 199, 220), suggesting that later-to-form flowers and pods may be inherently weaker than those developing earlier. Ojechomon (155), for instance, found that persisting cowpea flowers at the basal raceme node had heavier ovaries than those of more frequent-to-abscise flowers at the third raceme node at the same developmental stage. Ovaries from proximal soybean flowers enlarged significantly when grown in vitro, whereas those from more distal positions failed to exhibit any growth (93). In addition to being smaller, ovaries from lupin flowers at more distal raceme nodes exhibit a reduced rate of development which may contribute to their inability to compete with rapidly growing proximal pods (220).

The distribution of yield within each inflorescence was greatly influenced by raceme node position in which pods at the first raceme node accounted for the largest portion of yield (Table 3). RN-1 is the first to develop and is not in competition with any other raceme node until after it has set pods. As pods develop at other raceme nodes, a greater degree of competition for assimilate may emerge which could limit growth and development at later formed flowers and pods, particu-

larly under stress conditions which reduce the supply of photosynthate. This would account for the greater contribution of lower compared to higher raceme nodes in the more stressful year of 1978 (Table 3), where more developed proximal pods could have monopolized a reduced assimilate supply. This could in turn result in decreased pod growth of inherently weaker organs higher in the inflorescence. The first raceme node in broad beans (Vicia faba L.) inflorescences also accounted for most of the yield and its contribution increased greatly in a season characterized by high temperatures (100).

The asynchrony in pod growth between the first and last raceme node in bean is quite marked with the lowermost pods exhibiting their maximum rate of growth when the uppermost ones are just being formed (19a, 223a). As a result, pods at more distal raceme nodes are at an inherent disadvantage due to the intrinsic pattern of development within an inflorescence. If these earlier-to-form bean flowers and pods are removed, however, the growth and retention of those emerging later at more distal raceme nodes are substantially improved (58, 116). Although this can be interpreted as an effect due to removal of competitive sinks that monopolize available photosynthate or other nutrients, it might also be attributed to the absence of a detrimental hormonal influence exerted by older pods upon younger more distal ones (93, 155, 220). Tamas et al (211), for example, discovered that removal of older bean pods at lower raceme nodes diminished the abscisic acid content of younger pods which exhibited enhanced retention and growth.

Possibly the most beneficial approach to increasing snap bean

yields would be to select for genotypes that possess a larger number of inflorescences per mainstem node rather than attempting to induce greater pod production at higher raceme nodes. It may also be desirable that such genotypes exhibit a more concentrated flowering pattern to equalize the competition among raceme nodes and avoid the situation where large pods exist at the base of an inflorescence before those at the apex even emerge. In regards to cultural practices, more research is needed to further evaluate the potential of high irrigation and/or low density as a means to more evenly distribute yield within an inflorescence.

## Chapter III

FLOWER AND POD ABSCISSION IN SNAP BEAN AS  
INFLUENCED BY INFLORESCENCE POSITION, RACEME NODE,  
AND IRRIGATION-DENSITY TREATMENT<sup>1</sup>

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Abstract. Abscission and/or retention of flowers and pods formed on inflorescences at the sixth (terminal) and second mainstem nodes of 'Oregon 1604' snap bean were studied during the 1978 and 1979 seasons. The influence of high (-0.6 bars) and low (-2.5 bars) irrigation and plant population were also assessed. High and low plant densities were 45 vs. 18 and 54 vs. 33 plants/m<sup>2</sup> for 1978 and 1979, respectively. Percent abscission was significantly reduced by high (62%) compared to low (74%) irrigation at node 6 in 1978, and at node 2 in both years. Although plant population density had no effect at node 6, percent abscission at node 2 was significantly less under low than high density, 56% vs. 64% and 44% vs. 52% for 1978 and 1979, respectively. An acropetal decline in abscission occurred within the terminal inflorescence

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at node 6 ranging from 36% to 44% at the proximal to 68% to 86% at the most distal raceme node. The acropetal pattern of abscission was less marked at node 2. More stressful conditions (low irrigation and/or high density) caused a relatively greater amount of abscission at the more distal compared to proximal raceme nodes. A sharp rise in abscission during flowering and pod set in 1978 immediately followed a 3 day period of temperatures exceeding 34°C. This early peak in abscission was lessened by high irrigation (nodes 6 and 2) and low density (node 2), but did not occur in the cooler 1979 season. The major portion of organs shed at either node abscised 1 day after reaching full bloom. High irrigation significantly delayed abscission at both nodes resulting in a higher percentage of abscission at later developmental stages. Low density also delayed abscission to a later stage at node 2, but had little effect at node 6.

## Introduction

The snap bean (Phaseolus vulgaris L.) flowers profusely, however, yield is often severely restricted by a high rate of flower and pod abscission. Abscission rates under field conditions for several bean cultivars ranged from 44-76% (11). Substantial losses of potential harvestable fruit due to premature shedding occurs in other legumes as well, often exceeding 65% in lupin (220) and over 80% in soybean (68, 169, 219). Abscission rates of snap beans are markedly dependent on the cultivar (207), and environmental factors such as temperature (95a, 205a), water availability (54, 55), and plant population density (127, 213).

Only in soybean (68, 237) has the canopy distribution of abscission been evaluated to determine the response of inflorescence position. These studies, however, were not related to crop management practices. Although greater yields per area are obtained under improved irrigation and higher density (129), more detailed knowledge of the integrated effects of irrigation and plant population on flower/pod abscission at the inflorescence level would be beneficial towards continuing to improve snap bean yields.

This investigation was initiated to catalog flower/pod abscission at individual raceme nodes and determine susceptibility of various reproductive growth stages under different irrigation regimes and plant population densities. The 2 main pod-bearing nodes, which exist in the uppermost and lowermost regions of the canopy, were selected for study.

## Materials and Methods

Techniques and methodology employed in this study were described previously in more detail (Chapters I, II). A field study was conducted during 1978 and 1979 using a split plot design, replicated 4 times, with 2 levels of irrigation as the main plots and 2 plant densities as the subplots. High and low plant population densities of 'Oregon 1604' were obtained, respectively by seeding at a 15 x 15 cm spacing or in 91 cm rows with 5 cm within-row spacing. This resulted in plant stands of 45 vs. 18 plants/m<sup>2</sup> in 1978 and 54 vs. 33 plants/m<sup>2</sup> in 1979. Plots were irrigated when soil water potential, based on gypsum block readings at the 30 cm soil depth fell to -0.6 bars (high) and -2.5 bars (low irrigation). Four uniform plants selected from each irrigation-density subplot totalling 64 plants for observation. Maximum and minimum daily air temperatures were recorded from planting (June 7, 1978, 11, 1979), until harvest (August 8 and 11, respectively). First bloom was defined as the day in which the majority of flowers produced in the axil of the terminal trifoliolate reached anthesis.

Numbering acropetally from the primary leaves at node 1, inflorescences arising from the second and sixth (terminal) mainstem nodes were identified. Node 6 forms only 1 inflorescence (designated 6-T), whereas, anywhere from 1 to 4 lateral branches, which originate at node 2, possess inflorescences (see Chapter I, Fig. 1). The first 2 branches to emerge each produce an inflorescence (denoted as 2-A and 2-B, respectively) which together account for essentially all of the yield at the second node because the other 2 inflorescences (2-C and 2-D) are small and form much later in the season.

Flower and pod development were monitored at individual raceme nodes (RN) of the 6-T and 2-(A-D) inflorescences every other day from first bloom until harvest. Although data was collected from all inflorescences formed at node 2, only the 2-A inflorescence was utilized for individual raceme node statistical analysis since it was the only one that possessed a sufficient number of organs at higher order raceme nodes RN-2 and RN-3. Observations on stage of development for each reproductive organ were separated into 4 categories: a) white flower buds 1-2 days prior to its anthesis, b) day of anthesis (full bloom) with corolla fully expanded, c) 1 day after full bloom, and d) greater than 1 day after full bloom characterized by further degradation of floral parts and noticeable ovary enlargement. Days prior to or after full bloom were used to identify stage of development to avoid confusion over differentiating between a declining flower and an immature pod, which was approximately 6-8 mm in length at 1 day after full bloom.

Number of days from the day of full bloom until the last day a reproductive structure (which subsequently abscised) was observed attached to the plant, was designated minimum mean days retention (MDR). This number was expressed as a minimum value since the assumed time of abscission reverted back to the last day flower or pod attachment was noted, and therefore allotted for abscission immediately after observation. MDR was calculated for all reproductive organs which subsequently abscised at the 6-T and 2-(A-D) inflorescences. On the basis of observed developmental patterns from -2 to +2 days from full bloom, the specific date of full bloom was determined for any

flower which failed to open on an observation day. The seasonal log and fate for each reproductive organ which at least reached the white flower bud stage were determined. Percent abscission was calculated from the ratio of the number of abscised flowers plus pods to the total number of flower buds which matured at least to the white bud stage. Analysis of variance was performed to statistically evaluate the effects of irrigation level and plant population density on percent abscission and stage of reproductive development at the time of shedding.

### Results

Abscission at each inflorescence mainstem node. Abscission of reproductive organs at both inflorescence positions was enhanced by reduced irrigation (Table 1). At the 6-T inflorescence, percent abscission at low irrigation was significantly greater than high irrigation in 1978, but not 1979. For lateral inflorescences 2-(A-B), percent abscission in each year was about 1.5-fold greater at the low irrigation treatment.

With all treatments pooled and inflorescences combined, the percent abscission in 1978 was 64% compared to only 48% in 1979. There were no significant density effects at the 6-T inflorescence for either year, however, high population density significantly increased abscission by 15-19% at the 2-(A-B) inflorescences both years (Table 1).

Seasonal abscission patterns at node 6 for 1978 (Fig. 1) displayed a dramatic rise in percent abscised organs at 4 days after first bloom in low irrigation, (LI) at both low (LD) and high (HD) density, in relation to high irrigation, HI (HI/LD and HI/HD). On this date, the

Table 1. Effect of irrigation and plant population density on percent abscission of snap bean flowers/pods of 'Oregon 1604' at the terminal, (6-T) inflorescence of the sixth mainstem node and lateral inflorescences 2-A and 2-B of the second mainstem node in 1978 and 1979.

Treatment	Abscission (%)			
	<u>6/T inflorescence</u>		<u>2/A, 2/B inflorescences</u>	
	1978	1979	1978	1979
<u>Irrigation</u>				
High	61.6	45.9	48.0	36.6
Low	73.8 <sup>**x</sup>	50.8	71.3 <sup>*</sup>	59.6 <sup>*</sup>
<u>Density</u>				
Low	65.5	47.1	55.5	44.0
High	70.0	49.5	63.7 <sup>*</sup>	52.3 <sup>*</sup>
Population means	67.7	48.3	59.6	48.1

x<sup>\*</sup>, \*\* Indicates significant F values at 5% and 1% levels, respectively between means in columns for different levels of irrigation or density.

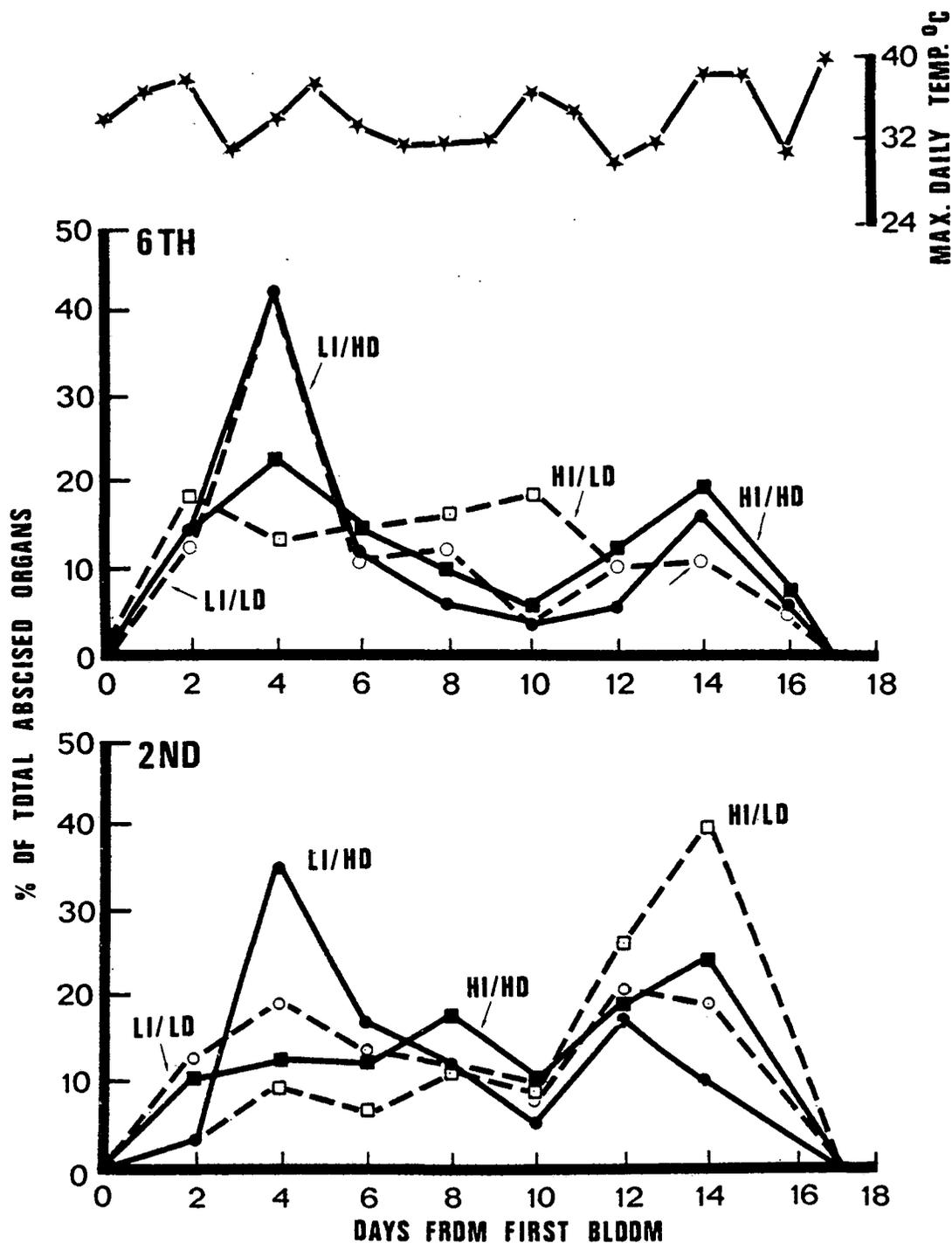


Fig. 1. Seasonal abscission patterns at the sixth (upper) and second (lower) node in 1978 as influenced by irrigation-density treatment. First bloom refers to the day in which flowers at the first raceme node of the terminal inflorescence at node 6 reached full bloom. Treatments are denoted: HI/LD, HI/HD (high irrigation, low and high density, respectively), and LI/LD, LI/HD (low irrigation, low and high density).

abscission for low irrigation was almost 3-fold greater than high irrigation. This peak in abscission was preceded by a 3 day period in which daily maximum temperatures ranged from 34-38°C. There was an additional, lesser peak in abscission on day 14 which followed another temperature rise of 34-36°C from 10-11 days after first bloom.

At node 2, a peak in abscission on day 4 occurred only in the LI/HD treatment. Percent abscission on this day was significantly greater, 145%, in the lower irrigation treatment and in the higher population density, (63%). Another rise in abscission started after day 10 in all irrigation-density treatments, but this increase prevailed through day 14 under high irrigation, most noticeably in HI/LD. This increase was largely attributable to losses of flowers and pods from later formed, poor yielding inflorescences (2-C, D) which were more likely to form under HI/LD treatment.

Abscission patterns in the generally cooler 1979 season were not appreciably affected by irrigation-density treatment at either node (Appendix III, Fig. A). Within the 6-T inflorescence, a sharp increase in percent abscission was noted in all treatments at 11 days after first bloom which was preceded by a 2 day period where temperatures varied from 33-36°C. Abscission at node 2, however, was not as responsive to this rise in temperature.

Developmental stage at the time of abscission. The greatest proportion of the abscission of reproductive organs occurred just after full bloom. For example, in the 6-T inflorescence in 1979 with all treatments pooled, the proportion of abscised organs shed at the 4 developmental stages was as follows: 2.5% before full bloom (FB); 15% at FB; 40%

1 day past FB (FB + 1), and the remainder, 43%, at times greater than FB + 1. Pods which abscised at the >FB + 1 stage could be dropped anytime before harvest. High irrigation tended to delay the stage at which abscission occurred in 6-T, (Fig. 2). Under low irrigation, a mean of 17% of reproductive organs abscised at FB compared to only 13% with high irrigation, and the respective values at FB + 1 were 48% vs. 31%. However, under high irrigation, 53% of the abscission took place in the last developmental stage (>FB + 1) compared to only 33% under low irrigation. Similar differences were noted at the 6-T inflorescence in 1978 where the FB + 1 stage accounted for 57% and 43% of the abscission under low and high irrigation, respectively (Appendix III, Fig. B). Density effects upon percent abscission by reproductive stage at the 6-T inflorescence were negligible in both years.

In 1978, the percent distribution of abscised organs at the 2-A inflorescence for combined treatments was similar to that of 6-T inflorescence in 1979, with the largest proportion of abscission at stages FB + 1 (37%), and >FB + 1 (39%). High irrigation caused a substantial reduction in percent abscission at FB + 1 (28% vs. 47%) and a concomitant increase in percent pod abscission at >FB + 1 (47% vs. 31%), (Fig. 3). Under low compared to high density, a larger proportion of organs were shed at FB (24% LD vs. 14% HD), but markedly less at FB + 1 (32% LD vs. 43% HD), (Fig. 3). In terms of irrigation-density interaction, a steady increase in percent abscission at the FB + 1 stage occurred from HI/LD (25%) to LI/HD (55%).

With treatments pooled, the major proportion of abscission at the second node in 1979 also took place at stages FB + 1 (37%) and >FB + 1

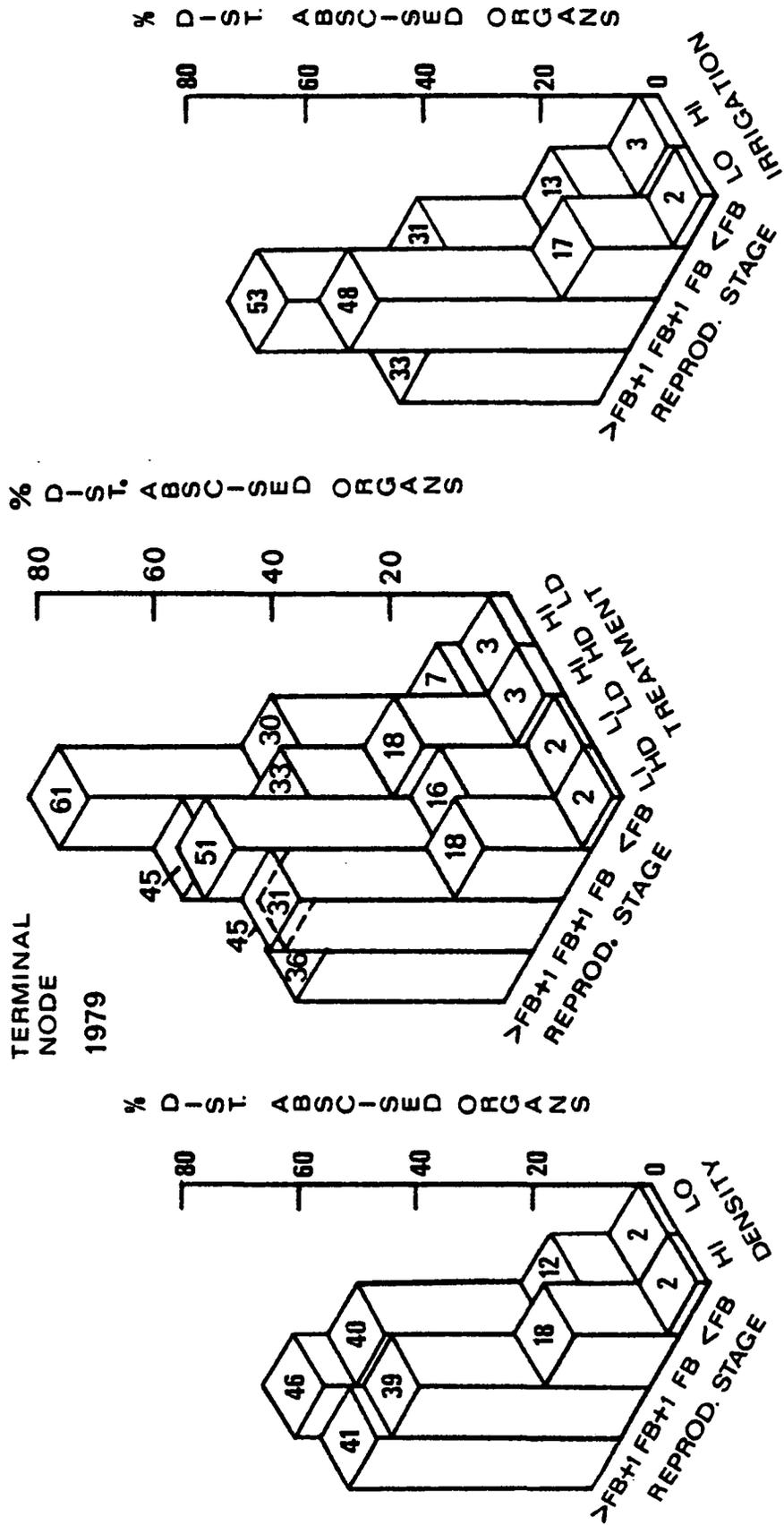


Fig. 2. Percent distribution of abscised organs of 'Oregon 1604' snap bean at the terminal node in 1979 within 4 reproductive stages as influenced by irrigation-density treatment (center) and main effects of irrigation (right) and density (left). Reproductive stages are denoted as days from full bloom: <FB (prior to), FB (day of), FB+1 (one day after), and >FB+1 (greater than one day after).

2ND NODE  
1978

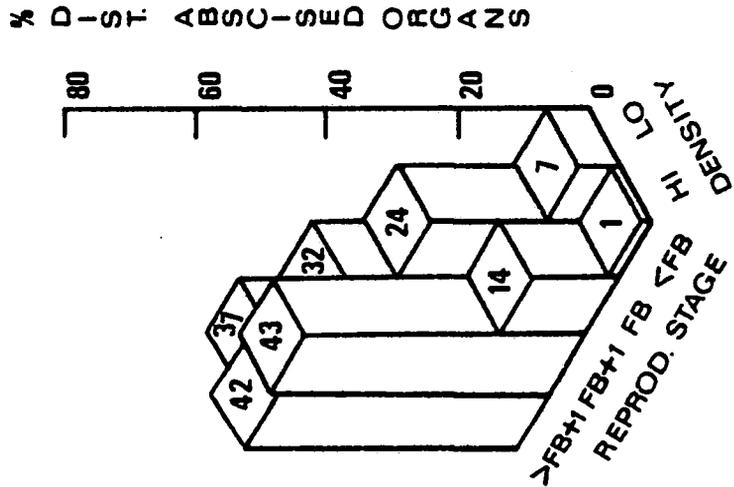
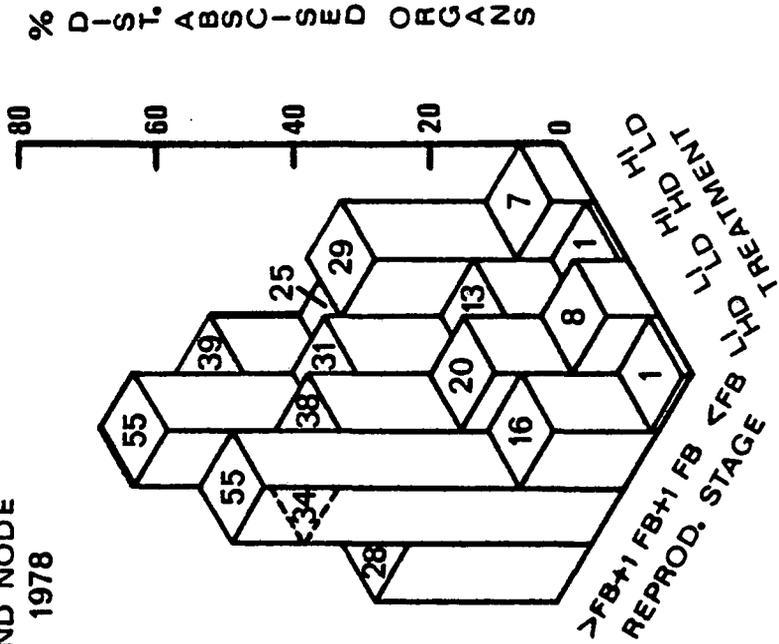
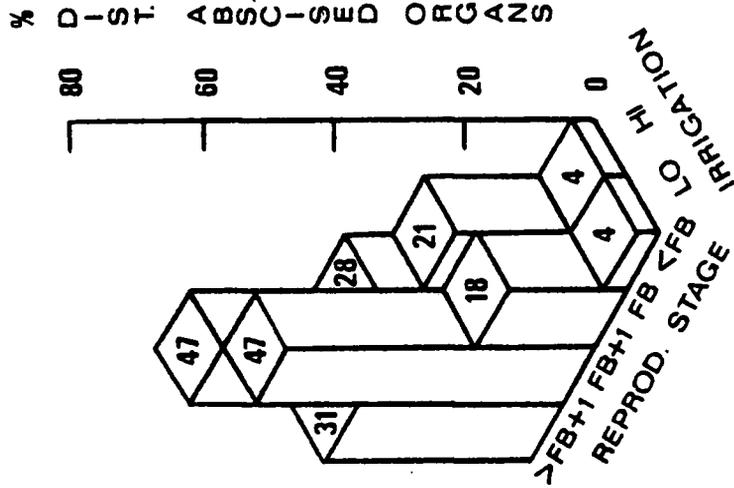


Fig. 3. Percent distribution of abscised organs of 'Oregon 1604' snap bean at the second node in 1978 within 4 reproductive stages as influenced by irrigation-density treatment (center) and main effects of irrigation (right) and density (left). Reproductive stages are denoted as days from full bloom: <FB (prior to), FB (day of), FB+1 (one day after), and >FB+1 (greater than one day after).

(37%). There was little influence of irrigation and density treatment, however, in comparison to the pronounced effects the previous year at node 2 (Appendix III, Fig. C).

Abscission at individual raceme node. There was an acropetal increase in percent abscission at each successive raceme node in an inflorescence. Pooled treatment means reflected this in abscission within the 6-T inflorescence in both years (Table 2). Abscission of analogous raceme nodes, however, were much greater in 1978 than 1979, especially at RN-2 and RN-3. Percent abscission at each raceme node of the terminal, 6-T inflorescence was accentuated by low irrigation, however, the effect was not significant at RN-1. The highest recorded rate of abscission was 95% at RN-3 under low irrigation in 1978. Irrigation effects were slight in 1979. Density failed to significantly influence the percentage of abscission at any 6-T raceme node in either year (data not shown).

Percent abscission also increased acropetally within the 2-A inflorescence and was most pronounced in 1978 (Table 3). Abscission at each raceme node of the 2-A inflorescence was increased, although not always significantly, by lower irrigation, as well as higher population density in both years.

Mean days retention. The range of mean MDR's was very narrow (1.9 to 2.7 days) for different irrigation and/or density treatments (Table 4). Flowers and pods at the 6-T inflorescence that subsequently abscised were retained significantly longer, and therefore exhibited greater MDR, under high irrigation in both years. The same irrigation effects were noted for the MDR of abscised organs at the 2-A inflorescence,

Table 2. Abscission response at each raceme node of 'Oregon 1604' snap bean in the terminal (6-T) inflorescence as influenced by irrigation level for the 1978 and 1979 seasons.

Irrigation treatment	Abscission (%)					
	1978			1979		
	Raceme node			Raceme node		
	1	2	3	1	2	3
High	38.2 (25.0) <sup>z</sup>	60.9	77.1	35.4 (14.1)	38.0	68.4
Low	50.6 (41.2)	83.3 <sup>y</sup>	95.3 <sup>**</sup>	35.4 (10.9)	47.4	66.5
Population mean	44.4 (33.1)	72.1	86.2	35.7 (12.5)	42.7	67.5

<sup>z</sup>Values in ( ) denote abscission rates for the first raceme node omitting data from abscission of a third flower that formed late in the season.

<sup>y</sup>, <sup>\*\*</sup> Indicate significant F values at 5% and 1% levels, respectively between irrigation treatments at the same raceme node.

Table 3. Abscission response of 'Oregon 1604' snap bean flowers and pods at each raceme node of the lateral, 2-A inflorescence at the second mainstem node as influenced by irrigation and plant population density in 1978 and 1979.

Treatment	Abscission (%)				
	1978			1979	
	Raceme node			Raceme node	
	1	2	3	1	2
<u>Irrigation</u>					
High	33.5	37.5	56.8	20.6	19.8
Low	58.9 <sup>z</sup>	77.6 <sup>**</sup>	72.9	39.1 <sup>*</sup>	57.5 <sup>*</sup>
<u>Density</u>					
Low	41.7	49.5	62.5	21.9	33.8
High	50.7	65.6	67.2	37.8 <sup>*</sup>	43.4
Population Mean	46.2	57.6	64.9	29.8	38.6

<sup>z</sup>, <sup>\*\*</sup> Indicates significant F values at 5% and 1% levels, respectively between irrigation or density treatments at the same raceme node.

Table 4. Minimum mean days retention prior to abscission of flowers and pods of 'Oregon 1604' snap bean at the terminal 6-T and lateral 2-(A-D) inflorescences as affected by irrigation and plant population density in 1978 and 1979.

Inflorescence(s)	Year	Minimum mean days retention			
		Irrigation		Density	
		High	Low	Low	High
Terminal (6-T)	1978	2.67 <sup>**z</sup>	2.13	2.26	2.53
	1979	2.69 <sup>*</sup>	1.92	2.54	2.06
Lateral (2-(A-D))	1978	2.65	2.12	2.09	2.68 <sup>*y</sup>
	1979	2.29	2.10	2.46 <sup>***</sup>	1.93

<sup>z</sup>\*, \*\*, \*\*\* Indicates significant F values at 5%, 1%, and 0.1% levels, respectively between different irrigation or density treatments for the same year and inflorescence.

<sup>y</sup>There was a significant irrigation-density interaction in which high irrigation - high density was significantly greater than any other treatment combination.

yet they were not statistically significant. There were no significant density effects on MDR at the 6-T inflorescence, however, low was substantially greater than high density in 1979 (2.54 vs. 2.00). MDR was significantly increased in the 2-A inflorescence under high density in 1978 primarily due to a significant interaction where the largest MDR value 3.25 occurred under HI/HD treatment. In contrast, MDR was significantly greater under low density in 1979. Effects of irrigation and density on MDR at individual raceme nodes of 6-T and 2-A inflorescence (Appendix III-Table A) were not nearly as pronounced as those expressed on an inflorescence basis.

#### Discussion

Flower and pod abscission from inflorescences at both node 6 and 2 were significantly reduced by high irrigation, whereas low density only decreased abscission at node 2 (Table 1). Gabelman and Williams (54, 55) also reported that greater snap bean yield under high irrigation was the result of a reduction in flower/pod abscission. The decrease in abscission under low density in the present study could have been the result of less interplant competition, especially for light. The density effect was only pronounced at node 2 lower in the canopy where irradiance under high density would be expected to be low. Wiebold et al (237) found that abscission in determinate soybean genotypes increased with greater canopy depth possibly due to a decrease in available carbohydrate.

Seasonal abscission patterns at nodes 6 and 2 were markedly

affected by irrigation-density treatment and high temperatures, particularly during the more stressful year of 1978 (Fig. 1). A rise in abscission during the initial week of flowering and pod set in that year followed a prominent peak in maximum daily temperature, however, this increase was twice as great for low than high irrigation. Iwami (95a) discovered a high negative correlation between temperatures above 32°C and pod set in beans. Several researchers (38, 100, 219) found that excessive rates of flower/pod abscission in other legumes occurred shortly after periods of extreme temperature stress. Temperatures were much lower during flowering and pod set in 1979 when no early rise in abscission was evident (Appendix III, Fig. A). High irrigation lessened plant water stress through increased soil moisture availability (Chapter I), and possibly reduced canopy air temperature as previously shown for irrigated vs. nonirrigated beans (4, 30) and soybeans (177a).

The early rise in abscission at node 2 in 1978 (Fig. 1) only occurred in the most stressful irrigation-density treatment, LI/HD, which illustrates the interaction of plant density and irrigation on abscission. By imposing stress through both reduced irrigation and increased plant population, abscission on day 4 was twice as much compared to any other treatment combination. The rise in abscission for node 2 at 10 to 14 days after first bloom under HI/LD followed a period of high temperature stress and was mainly at the expense of flowers and pods formed late in the season on inflorescences 2-C and 2-D (see Chapter I, Fig. 1). Occurrences of high temperatures late in season are not as important to yield as those during the critical periods of bloom and pod set, since the majority of pods retained at harvest are

set within a few days after first bloom in 'Oregon 1604' (Chapters I, II) and other determinate snap bean genotypes (207).

The largest proportion of abscission occurred at the FB + 1 stage, and this percentage was markedly decreased by high irrigation at node 6 in both years, and node 2 in 1978 (Figs. 2, 3). By the time a reproductive organ reaches the FB + 1 stage, fertilization has occurred and embryogenesis has begun (223a). The FB + 1 stage represents the transitional period between full bloom and pod set which is reported to be the most critical period for further retention of snap bean (2, 54, 55) and soybean (68, 169, 195) reproductive organs. With the onset of stress in snap beans, small pods most recently set (1-2 days after full bloom), are usually the first to abscise followed by freshly opened flowers (2). In determinate soybean cultivars, the majority of reproductive organs abscise as pods less than 2 cm, 1-2 days after full bloom (237).

Plant population exhibited much less of an effect on the developmental stage of abscised organs than irrigation, however, low density substantially reduced abscission at the sensitive FB + 1 stage at node 2 in the more stressful year of 1978 (Fig. 3). Under low compared to high density, flowers/pods are retained longer on the plant and are more likely to abscise at the > FB + 1 stage. This is also reflected in the significantly greater MDR's for abscised organs under low density treatment (Table 4).

Abscission within each inflorescence studied increased acropetally, however, this trend was reduced by high irrigation at the 6-T inflorescence in 1978, and the 2-A inflorescence in both years (Tables 2,3).

High irrigation sharply reduced abscission, particularly at more distal raceme nodes, which may be associated with a decrease in ovular abortion as previously reported for snap beans (54, 55) and soybeans (102) under increased irrigation. Low density also lessened the acropetal rise in abscission at node 2 (Table 3) suggesting that competition between raceme nodes was less under decreased plant population. The larger leaf area per plant (Chapter I), reduced plant competition, and potential for greater irradiance at lower canopy depths under low density could result in a greater supply of photosynthate to support flowers and pods at more distal raceme nodes and avert their abscission.

Results of this study demonstrate that crop management practices of irrigation and plant density can be utilized to manipulate flower and pod abscission. Although increased irrigation and lower plant population significantly reduce abscission, the physiological processes involved are uncertain, but possibly distinct for the 2 cultural conditions. The increase in pod set and number of pods harvested per node under CO<sub>2</sub> enrichment in beans (116) and soybeans (69) strongly suggests that photosynthate supply is a major factor in flower/pod abscission. Evidence also exists that older bean pods hormonally inhibit the development of younger ones through a direct regulatory influence on their endogenous ABA levels (208, 211). The influence of irrigation and plant population on photosynthate supply and endogenous hormone levels merits further investigation.

## Chapter IV

<sup>14</sup>C-PHOTOSYNTHATE PARTITIONING DURING FLOWERING AND POD  
FORMATION IN PHASEOLUS VULGARIS L. AS INFLUENCED BY IRRIGATION  
AND PLANT POPULATION<sup>1</sup>

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Additional index words. snap bean, inflorescence, raceme node, anthesis, <sup>14</sup>C-translocation

Abstract. <sup>14</sup>C-photosynthate partitioning was assayed during reproductive development in field-grown snap bean plants of 'Oregon 1604' under high and low soil moisture (irrigation at -0.6 bars or -2.5 bars soil water potential) and high and low density (54 and 33 plants/m<sup>2</sup>, respectively). A single trifoliolate leaf, either at lower (node 2 or 3) or higher (node 5) canopy position was briefly dosed with <sup>14</sup>CO<sub>2</sub> on July 25, 27, and 31 which corresponded to when flowers at each of 3 successive raceme nodes (RN) in the terminal inflorescence (6-T) at the sixth mainstem node were at 1-2 days post-anthesis. Plants were harvested 27 hours later. Irrigation-density effects were slight at 6-T, but frequently significant at the main lateral inflorescence (2-A) arising

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from node 2. Flowers/pods at the first (RN-1) and second (RN-2) raceme nodes of the 6-T inflorescence received only 2-3% of the  $^{14}\text{C}$ -photosynthate translocated from the node 5 leaf on July 25. Five days later, pods at these raceme nodes were increasing rapidly in dry weight and the values rose to 19% and 12%, respectively. Organs at RN-3 were less developed and did not increase in dry weight, they only acquired 2-4% of the  $^{14}\text{C}$ -photosynthate on any date and abscised more readily than more proximal organs. Similarly, the most distal organs in the 2-A inflorescence at RN-2 were more prone to abscission and acquired only 3-4% of the  $^{14}\text{C}$ -photosynthate translocated from the node 2 leaf on July 25 or 27, whereas flowers/pods at RN-1 gained 6% and 14%, respectively. On July 31 the node 3 leaf was dosed and percentage of  $^{14}\text{C}$ -activity at both RN-1 and RN-2 was about 5-fold greater under lower density. Abscission in this inflorescence was 40% under high but only 28% under low density. Import capacity (percent translocated  $^{14}\text{C}$ -photosynthate per unit dry weight) of organs at RN-1 and RN-2 in both the 6-T and 2-A inflorescences reached a peak at 2 to 4 days after anthesis then declined. In 6-T, values for organs at RN-3 was always less than those at RN-1 and RN-2, which were similar. In 2-A, RN-2 had a much lower import capacity than RN-1 on the first 2 dates. The subsequent fate of flowers/pods at individual raceme nodes may be associated with their ability to accumulate photosynthate during flowering and pod set.

## Introduction

The period of flowering and initiation of pod growth in snap beans is the most critical time for retention of reproductive structures (Chapter III). Water stress (24, 32, 54) and increased plant competition (2, 6) during this stage of development greatly increases the number of flowers which subsequently abscise. The internal plant processes responsible for these effects are not well understood. A more thorough comprehension of the mechanism by which environmental conditions affect flower/pod abscission would be applicable towards increasing the number of harvestable pods.

Abscission in snap beans may result from competition for a limited supply of photosynthate among flowers and pods with the same and/or different inflorescences (12, 213). Water stress and high plant populations might be expected to intensify this competition. Photosynthate partitioning during reproductive development has been investigated in bean (213, 231, 238), but generally not in conjunction with these factors. Plant population, however, was found by Waters et al (231) not to influence the distribution of  $^{14}\text{C}$ -photosynthate in a greenhouse grown dry bean cultivar. Most studies on photosynthate partitioning have been done with container grown plants and lack detail in terms of the response of flowers/pods at individual inflorescences and/or raceme nodes. Assuming a close relationship exists between the procurement of photosynthate by a developing flower or pod and its subsequent fate, it should be most evident during the critical period just after anthesis.

This study examines the influence of irrigation-plant density treatments on  $^{14}\text{C}$ -photosynthate distribution in the shoot and within an individual inflorescence during flowering and pod set.

#### Materials and Methods

The determinate, bush snap bean 'Oregon 1604' was field grown at 2 population densities and 2 irrigation levels on a Chehalis loam-type soil. The experiment was designed as a split-plot, with 4 replications, and irrigation as the main plot and plant density as the subplot treatment. Seeding was (June 11, 1979) in either 91 cm rows, with 5 cm within-row spacing or in a 15 x 15 cm arrangement, which resulted in plant stands of 33 and 54 plants/m<sup>2</sup> for low and high density, respectively.

Irrigation was applied by an overhead sprinkler system at planting, at primary leaf expansion, and thereafter when soil water potential readings reached -0.6 bars (high) and -2.5 bars (low irrigation). Differential irrigation treatment was initially based on gypsum block readings at the 15 cm soil depth and thereafter at 30 cm. The low and high regimes involved 4 and 8 irrigations, respectively, over the period from primary leaf expansion until harvest on August 11.

First bloom was recorded on July 23 when flowers at the first raceme nodes (RN-1) of both the terminal mainstem (node 6) inflorescence designated 6-T and the earliest formed lateral inflorescence at mainstem node 2 (designated 2-A) reached anthesis (see Fig. 1). The primary leaf node was designated node 1.

On July 25, 27, and 31, 2 uniform plants were selected from each of the 16 subplots. One was dosed with  $^{14}\text{CO}_2$  at an upper canopy leaf (node 5), whereas a lower leaf (node 2) on the other plant was used. On July 31, the node 2 leaf was starting to turn yellow and some had abscised so the node 3 leaf was substituted. The 3 dates corresponded to the days when flowers at each of the 3 successive raceme nodes (RN) within the terminal mainstem (node 6) inflorescence (denote 6-T) were sequentially at 1-2 days past anthesis (Table 1). Usually both flowers at a raceme node reach anthesis on the same or within one day.

Two hours prior to exposure to  $^{14}\text{CO}_2$ , 25 uCi  $\text{Na}_2\text{CO}_3$  (specific activity 20 uCi/umole, Amersham) was pipetted onto dry filter paper discs previously treated with 0.1 N NaOH. The discs were immediately placed in gelatin capsules for transport to the field. In mid-morning, the leaf to be treated was situated in a 18 x 20 cm polyethylene 'Ziplock' bag along with a gelatin capsule in a plastic boat and the bag sealed around the petiole with 'Permagum' sealing compound.  $^{14}\text{CO}_2$  was generated by injecting excess 50%  $\text{HClO}_3$  into the gelatin capsule and immediately sealing the puncture hole in the bag, which was removed 30 min later. Weather for all treatment days was clear and sunny. Twenty-seven hr after release of  $^{14}\text{CO}_2$ , the plants were removed from the soil and the fibrous roots discarded. Plants were cooled on ice, transported to the laboratory, immediately sectioned into parts (see Fig. 1), dried at  $55^\circ\text{C}$  for 48 hr, weighed, and ground to 40 mesh.

An in-vial combustion method, similar to that developed by Gupta (62a) was used in the assay of radioactivity. A 3 mg aliquot of ground tissue and a small cotton plug were wrapped in blackened lens tissue

Table 1. Days from anthesis of flowers/pods of 'Oregon 1604' snap bean at each raceme node (RN) of the terminal 6-T inflorescence of the sixth mainstem node and the main lateral inflorescence 2-A at the second mainstem node on 3  $^{14}\text{CO}_2$  exposure dates.

Date of $^{14}\text{CO}_2$ exposure	Days from anthesis <sup>2</sup>				
	6-T inflorescence			2-A inflorescence	
	RN-1	RN-2	RN-3	RN-1	RN-2
July 25	+1 to +2	0 to +1	-4 to -5	+1 to +2	-2 to 0
July 27	+3 to +4	+2 to +3	-2 to -3	+3 to +4	0 to +2
July 31	+7 to +8	+6 to +7	+1 to +2	+7 to +8	+4 to +6

<sup>2</sup>Pre-anthesis, negative values; post-anthesis, positive values.

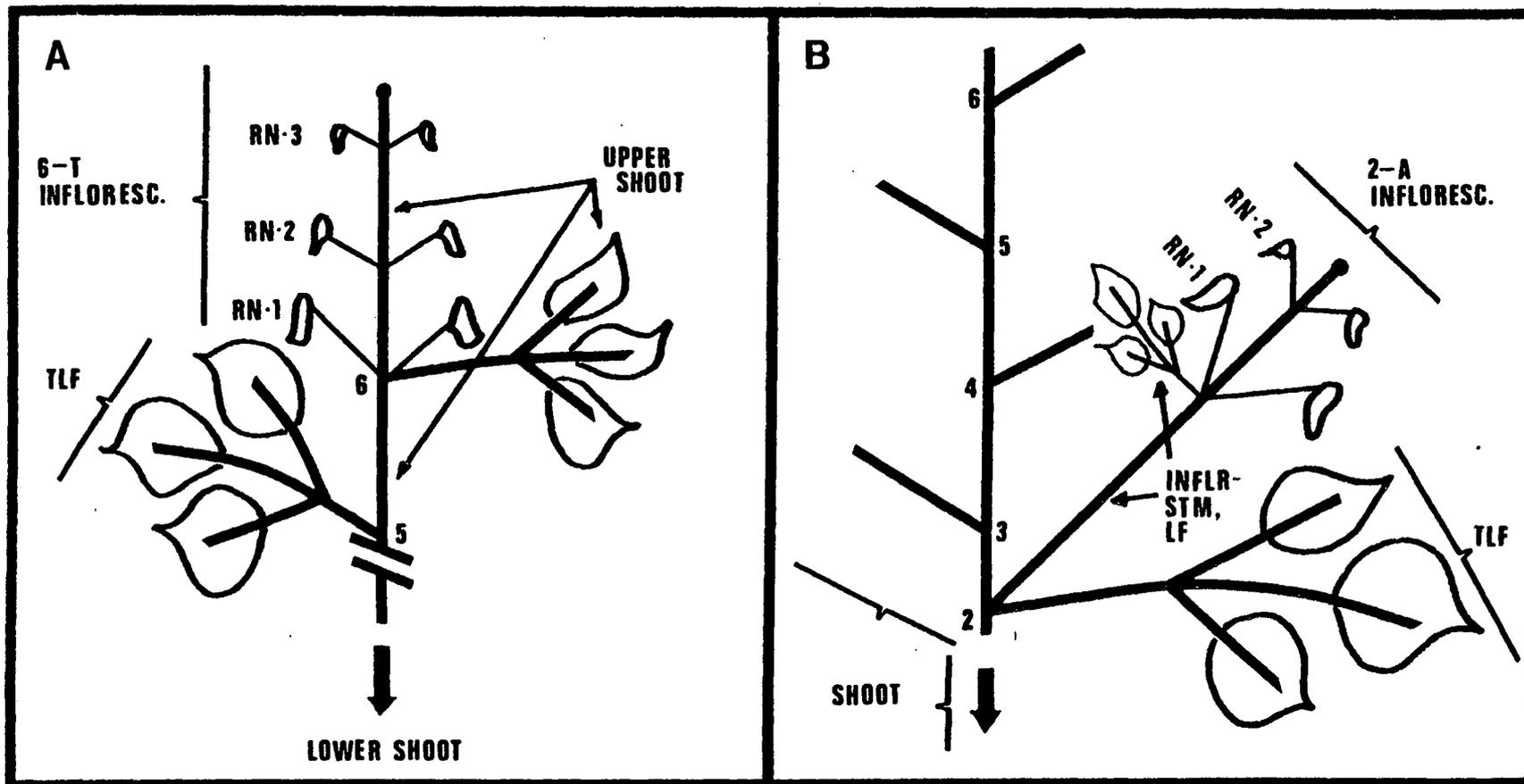


Fig. 1. Separation of plant organs upon harvest of plants in which a trifoliate leaf at either node 5 (A) or node 2 (B) was exposed to  $^{14}\text{CO}_2$ . Part designations (A): TLF -  $^{14}\text{CO}_2$  treated leaf; LOWER SHOOT - tissue below the treated leaf at node 5; UPPER SHOOT - mainstem internode tissue between nodes 5 and 6, extended peduncle of the 6-T inflorescence, node 6 leaf; RN-1, RN-2, RN-3 - pods and flowers at each raceme node, respectively. Analogous abbreviations pertain for (B), except for SHOOT - tissue above and below the treated leaf. The node 3 leaf was substituted for the one at node 2 at the third date.

and burned in a 20 ml scintillation vial previously flushed with  $O_2$ , and ignited by exposure to an infrared lamp. After 10 min, 0.2 ml phenethylamine was injected through a septum in the vial cap onto a glass fiber disc previously placed in the vial. The next day 15 ml of scintillation cocktail (5g PPO, 300 mg dimethyl-POPOP, and 50 ml MeOH per liter toluene) was added, and the vial shaken vigorously to dissolve carbamate residues formed during combustion and absorption of  $CO_2$ . After 4 hr in darkness,  $^{14}C$ -activity in each vial was determined with a scintillation counter. A quench correction was not used in calculating  $^{14}C$ -activity since the amount of quench, as determined with an external standard, varied little among samples.

The  $CO_2$  dosed leaf was discarded, and radioactivity per plant part (counts adjusted to total organ dry weight), was expressed as a percent of total recovered translocated activity. Values for an individual plant organ such as a flower or pod ranged from  $3 \times 10^4$  to  $1.8 \times 10^6$  cpm depending on the stage of development and irrigation-density treatment. Relative import capacity of flowers/pods was calculated as percent translocated  $^{14}C$  recovered in the tissue per unit dry weight. Analysis of variance was performed to evaluate the effects of irrigation-density treatment on the distribution of  $^{14}C$ -photosynthate among flowers and pods at individual raceme nodes within the 6-T and 2-A inflorescences.

## Results

Dry weights of plant parts. Although irrigation and/or plant popula-

tion had little significant effect on the dry weight of individual plant parts, they were consistently greater under high irrigation and/or low density (Appendix IV, Table A). Due to the noticeable lack of an irrigation-density effect, however, treatments were pooled for flowers/pods formed at each raceme node of the 6-T and 2-A inflorescences. Data is represented as days from anthesis, referring to the anthesis day for each particular raceme node so that organ size at the same developmental stage can be easily compared. At 7-8 days after their day of anthesis, pods at RN-1 of both the 6-T and 2-A inflorescences were more than twice the weight of those at RN-2 (Figs. 2A, B). However, at 0-4 days after anthesis organ dry weights at all raceme nodes were nearly identical. Dry weights of pods at RN-1 and RN-2 of the 6-T inflorescence were 41% and 51% greater, respectively, than those at the 2-A inflorescence. Although the 6-T inflorescence formed one more raceme node (RN-3) than the 2-A inflorescence, plants were harvested before they had the opportunity to exhibit the weight increase demonstrated by other organs after 4 days from anthesis.

Percent  $^{14}\text{C}$ -distribution. There were also few significant effects of irrigation and/or density on percent  $^{14}\text{C}$ -photosynthate recovered in any component of the 6-T inflorescence when the upper canopy leaf was fed  $^{14}\text{CO}_2$ ; therefore the data is combined for all treatments. The fraction of  $^{14}\text{C}$ -photosynthate translocated from the treated leaf at node 5 and recovered in the flowers/pods within the 6-T inflorescence increased from 9% on July 25 to 33% 6 days later (Fig. 3). On the last 2 exposure dates, pods at the most proximal raceme node (RN-1) received a larger percentage of  $^{14}\text{C}$ -photosynthate than the combined flowers/pods

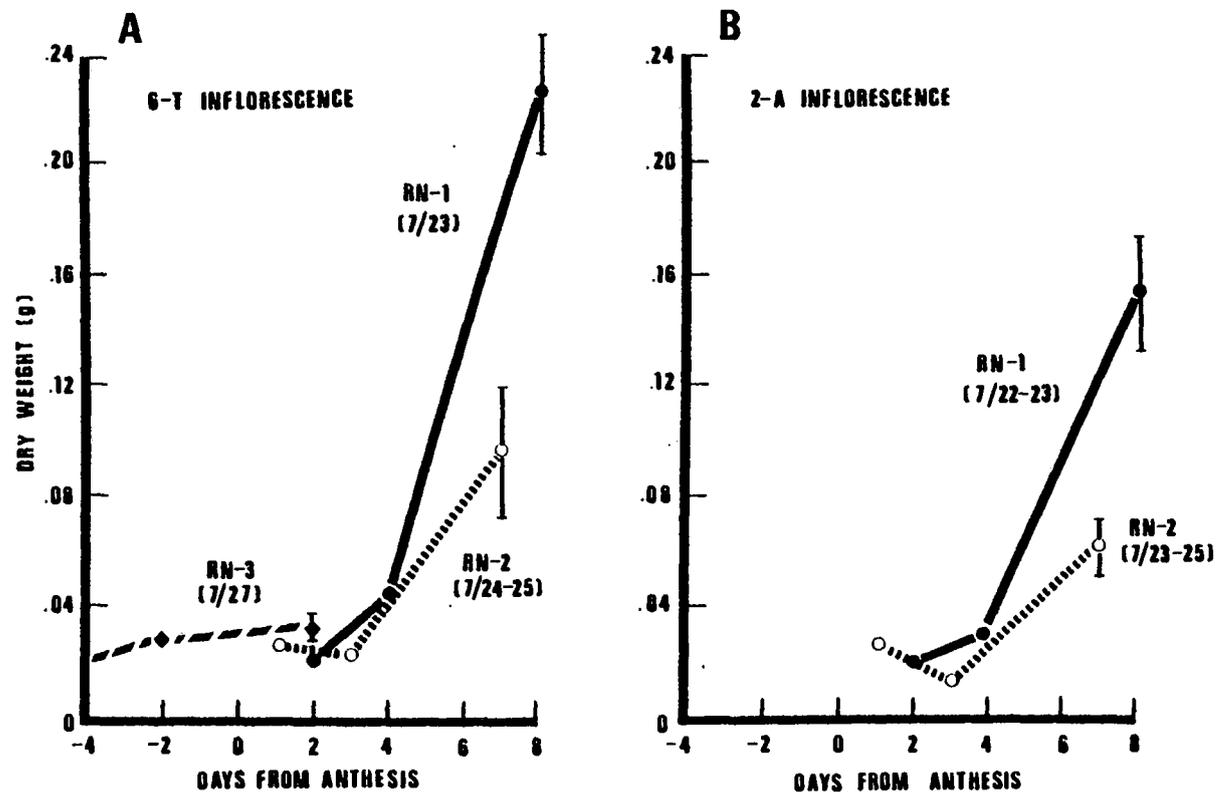


Fig. 2. Dry weights of reproductive organs at the 6-T (A) and 2-A (B) inflorescences vs. days from the date of anthesis of flowers at each particular raceme node. RN-1, RN-2, and RN-3 denote raceme node positions (numbered acropetally) within each inflorescence for developing flowers and pods. Numbers in ( ) refer to dates of peak flowering for each raceme node.

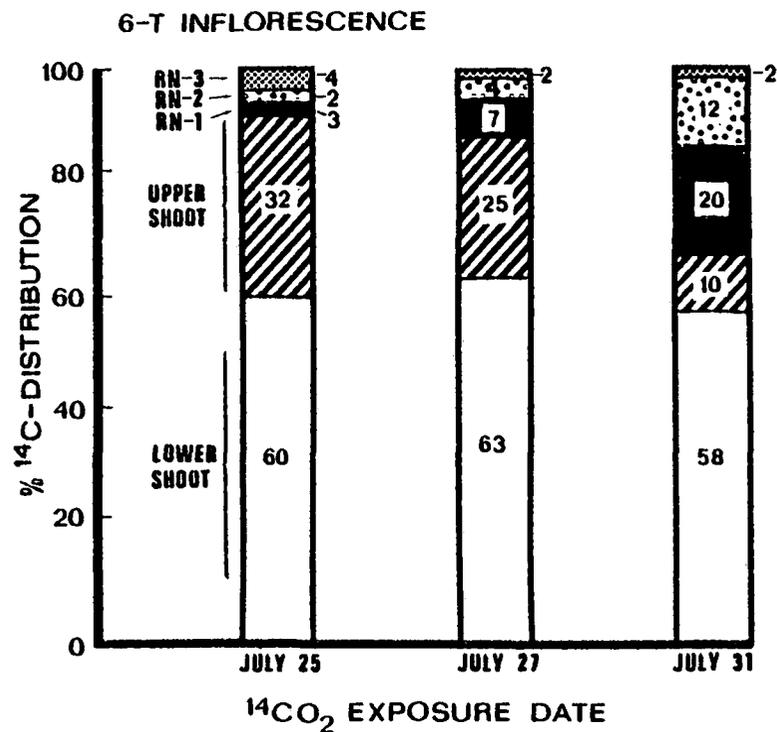


Fig. 3. Percent distribution of  $^{14}\text{C}$ -photosynthate after  $^{14}\text{CO}_2$  exposure of the node 5 trifoliolate leaf on 3 dates. RN-1, RN-2, and RN-3 represent flowers/pods at those raceme nodes (numbered acropetally), whereas, UPPER SHOOT denotes mainstem internode tissue between nodes 5 and 6, extended peduncle of the terminal inflorescence 6-T, and node 6 leaf. LOWER SHOOT refers to tissue below the node 5 trifoliolate leaf.

of RN-2 and RN-3. The percent  $^{14}\text{C}$ -photosynthate recovered in flowers/pods at RN-1 and RN-2 increased from 3% to 20% and 2% to 12%, respectively, over the 6 day period, whereas, RN-3 organs exhibited a slight decrease.

On the first 2 dates of  $^{14}\text{CO}_2$  exposure, the percent translocated  $^{14}\text{C}$ -photosynthate in leaf and structural tissue above node 5 (upper shoot) greatly exceeded that recovered in flowers/pods at RN-1 through RN-3 combined. This situation was reversed on the last date where percent  $^{14}\text{C}$  in the combined flowers/pods was more than 3 times greater than that in the upper shoot. Tissue below the treated leaf (lower shoot) accumulated about 60% of the translocated  $^{14}\text{C}$  on each date of exposure to  $^{14}\text{CO}_2$ . This plant part also contained the inflorescence formed at node 5, which was only found to accumulate 1-3% of the  $^{14}\text{C}$ -photosynthate (data not shown).

Within the 2-A inflorescence, the percentage of  $^{14}\text{C}$ -assimilate translocated from the treated leaf low in the canopy was 2-3 times greater in flowers/pods at RN-1 than those at RN-2 (Fig. 4). Comparing the distribution on July 25 and 27, percent  $^{14}\text{C}$ -photosynthate in RN-1 flowers/pods increased from 6 to 14%, whereas, that in RN-2 was essentially unchanged. Over the same period, the shoot decreased as a sink for photosynthate as indicated by the decrease in  $^{14}\text{C}$ -assimilate from 60% to 42%.

Although there were no significant irrigation and/or density effects on the first 2 dates, on the last date there was a marked influence of density on  $^{14}\text{C}$  distribution from the node 3 leaf. Here the percentage of  $^{14}\text{C}$ -photosynthate recovered in RN-1 and RN-2 flowers/

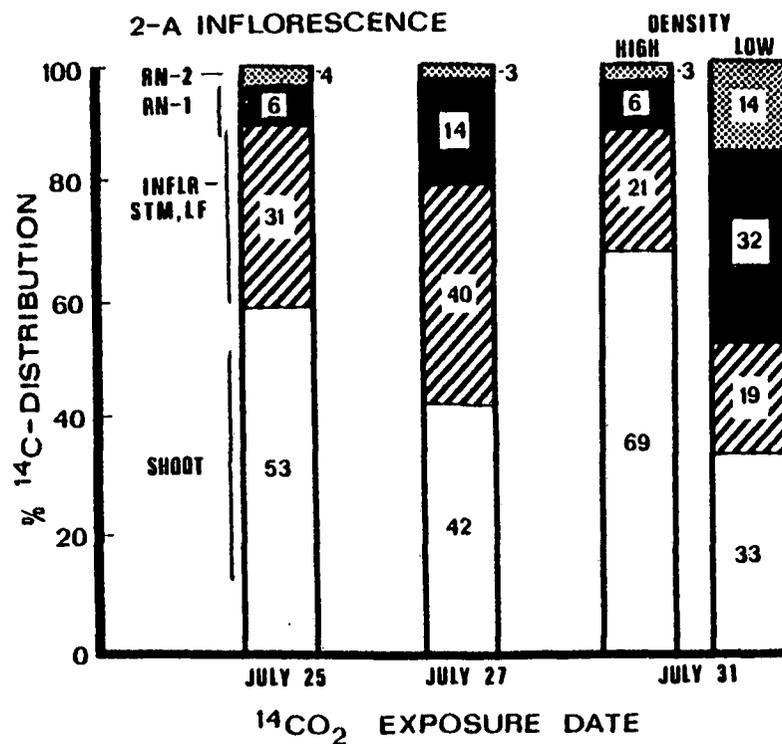


Fig. 4. Percent distribution of <sup>14</sup>C-photosynthate after <sup>14</sup>CO<sub>2</sub> exposure of the node 2 leaf on 3 dates. RN-1 and RN-2 refer to flowers and pods at those raceme nodes (numbered acropetally), whereas, INFLR-STM, LF denotes inflorescence structural tissue above and below the treated leaf. Treatment date 7/31 is partitioned into high and low density treatment.

Pods was about 5 times greater under low density, whereas that in shoot tissue decreased by more than half. Although interaction data is not presented, over 40% of the translocated  $^{14}\text{C}$ -photosynthate was recovered in RN-1 under low irrigation-low density treatment.

Import capacity of reproductive organs. In the 6-T inflorescence, patterns of relative import capacity (calculated as the percent  $^{14}\text{C}$ -photosynthate per unit organ dry weight) were similar in organs at RN-1 and RN-2, rising to a maximum at 3 to 4 days after anthesis and gradually declining thereafter (Fig. 5). In contrast, reproductive structures at RN-3 exhibited maximum import capacity at 4 days before anthesis and steadily declined afterwards. In an associated study using the same plots (Chapter III), the abscission rates for flowers and pods at RN-3 were over 65% compared to 36% and 43% for those at RN-1 and RN-2, respectively.

Within the 2-A inflorescence, flowers/pods at RN-1 exhibited twice the  $^{14}\text{C}$ -photosynthate import capacity of those at RN-2 from 1 to 4 days after anthesis (Fig. 5). The decline in import capacity for RN-1 and RN-2 structures after 3 to 4 days post-anthesis was partially due to exposing the leaf at node 3 to  $^{14}\text{CO}_2$  on the last date rather than that at node 2. Flower/pod abscission was determined in another study from plants in the same plots (Chapter III) and were 30% and 39% for RN-1 and RN-2, respectively.

Irrigation and/or density had little effect on relative import capacity of reproductive organs within the 6-T inflorescence. Although the influence of irrigation was minimal, relative import capacity of RN-1 and RN-2 organs within the 2-A inflorescence was 3 and 8-fold,

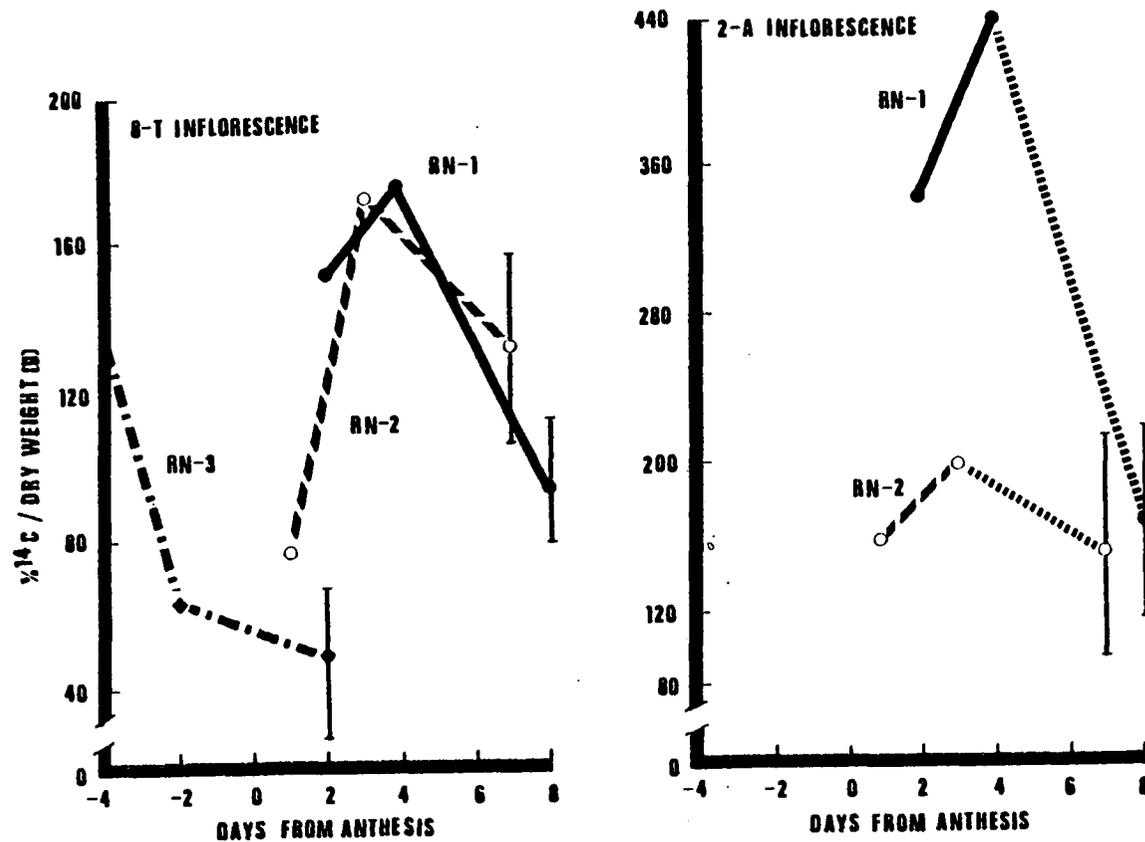


Fig. 5. Relative import capacity (percent <sup>14</sup>C-photosynthate recovered per organ dry weight) for reproductive organs at the 6-T and 2-A inflorescences vs. days from the date of anthesis of flowers of each particular raceme node. RN-1, RN-2, and RN-3 denote flowers and pods at those raceme nodes (numbered acropetally) within each inflorescence.

respectively under low density at 7 and 8 after anthesis (Appendix IV, Table B). Abscission was reduced at RN-1 and RN-2 under low (22%, 34%) vs. high (38%, 43%) density, respectively.

### Discussion

Results show that flowers/pods vary in their growth and ability to accumulate photosynthate depending on their relative position within an inflorescence, inflorescence canopy location, and stage of development. The acropetal succession of development within an inflorescence results in asynchronous growth, particularly between the most proximal and distal raceme nodes. Basal flowers at RN-1, for example, set pods 1-5 days before those at the most distal raceme node reach anthesis (Chapter II). This asynchrony in reproductive development is reflected in much greater pod dry weights at RN-1 vs. RN-2 after 4 days from their respective days of anthesis (Fig. 2). Although the experiment was terminated before later-to-form RN-3 organs had an opportunity to exhibit a marked increase in weight after 4 days from anthesis, they were declining in dry weight and usually exhibit a high percentage of abscission (Chapter III, 211, 213). This rise in pod dry weight starting 4 days after anthesis corresponds to the time of rapid increase in pod length in snap bean (19a) followed by a substantial gain in embryo growth 3-4 days later (223a).

The hierarchical pattern of reproductive growth in snap bean inflorescences exists in other legumes (194, 195, 220). Ojehomon (155) dissected ovaries from persisting, proximal flowers and found them to

be heavier than those within more frequent-to-abscise distal flowers. Although dry weights of entire flowers from anthesis to 4 days after did not vary in the present study (Fig. 2, Appendix IV, Table A), this doesn't preclude the possibility that ovary weights were actually different. The rapid gain in dry weight for organs at RN-1 compared to RN-2 after 4 days from anthesis could be due to the minimal degree of competition for photosynthate and other nutrients when RN-1 flowers and sets pods. However, when RN-2 and RN-3 develop, a greater degree of intra-raceme competition exists. Organs at RN-3 may also be inherently weaker as evidenced by the lack of growth in vitro of soybean ovaries from distal compared to proximal flowers (93). Herbert (77) noticed a similar situation in lupin inflorescences where flowers at more distal raceme nodes attained lower maximum dry weights at 5-10 days after anthesis and abscised at earlier developmental stages compared to organs at proximal positions. Irrigation and plant population had little effect on dry weights of flowers/pods, even though high irrigation and low density generally increased dry weights of other plant parts (Appendix IV, Table A). The lack of an effect could be due to the relatively small weight of flowers/pods (10-300 mg) in respective to larger plant organs (Appendix IV, Table A), and/or insufficient treatment difference to significantly influence flower/pod dry weights.

Distribution patterns of  $^{14}\text{C}$ -photosynthate illustrate a bias in favor of earlier-formed flowers/pods at RN-1 which consistently import a larger proportion of translocated  $^{14}\text{C}$ -activity at each successive  $^{14}\text{CO}_2$  exposure date (Fig. 3, 4). Although organs at RN-2 display a

similar, yet less dramatic increase in percent  $^{14}\text{C}$ -assimilate obtained, those at RN-3 never incorporated more than 2-5% at any date (Fig. 3). This suggests that organs at RN-1 and RN-2 may be monopolizing the supply of assimilate available to those forming later.  $\text{CO}_2$  enrichment (116) and removal of more proximal flowers/pods in beans (12, 239) promote development of those emerging later possibly due to an increased supply of photosynthate.

Although irrigation and/or density treatments had little significant effect on the  $^{14}\text{C}$ -distribution patterns within either inflorescence at the first and second dates of  $^{14}\text{CO}_2$  exposure, low density significantly increased percent  $^{14}\text{C}$ -photosynthate recovered in pods at RN-1 and RN-2 at the third date (Fig. 4, July 31). The cause of this is uncertain since the supply leaf was changed from node 2 to node 3 leaf at the third date. Possibly by the 3 date, low density treatment finally had an influence on  $^{14}\text{C}$ -distribution patterns. More than 40% of the translocated  $^{14}\text{C}$ -photosynthate was recovered in RN-1 pods under low irrigation-low density treatment (interaction data not presented). Water-stressed bean plants may be partitioning a larger percentage of assimilate to proximal organs which are more likely to develop and mature. Similar patterns of  $^{14}\text{C}$ -distribution were noted in soybeans (196) and wheat (99) under drought conditions.

Relative import capacity of flowers/pods within the 6-T inflorescence decrease acropetally at 1-2 days from anthesis (Fig. 5) illustrating the influence of raceme node position on an organ's potential to obtain photosynthate. This acropetal decline in import capacity is accompanied by an increase in abscission from RN-1 (36%) to RN-3 (68%).

Organs at RN-1 and RN-2 of the 6-T inflorescence exhibit similar patterns of development, relative import capacity, and abscission (36% vs. 43%) compared to those at the 2-A inflorescence. This discrepancy is probably attributable to the frequently longer period between the anthesis of RN-1 and RN-2 in the 2-A compared to 6-T inflorescence, 1-3 vs. 0-1 days, (Table 1). Although irrigation exhibited little effect, the relative import capacity of organs at RN-2 was significantly increased by low density at 8 days after anthesis (Appendix IV, Table B). Abscission of these organs was reduced by low (30%) in respect to high density (39%).

Although irrigation and plant population have marked effects on yield components (Chapters I, II) and abscission of flowers/pods (Chapter III), they exert less of an influence on short term  $^{14}\text{C}$ -photosynthate partitioning. The percentage of translocated assimilate imported by a developing flower/pod is more dependent on its location and stage of growth relative to other organs. Results suggest that a relationship exists between photosynthate obtained during flower-pod set and the subsequent fate of an organ. It is uncertain, however, whether or not reduced import is a consequence of a reduction in growth or due to an increase in competition and monopolization of photosynthate by other organs. Further research needs to be done to determine if reduced photosynthate triggers abscission, or is merely a consequence of inhibition of organ development by another factor.

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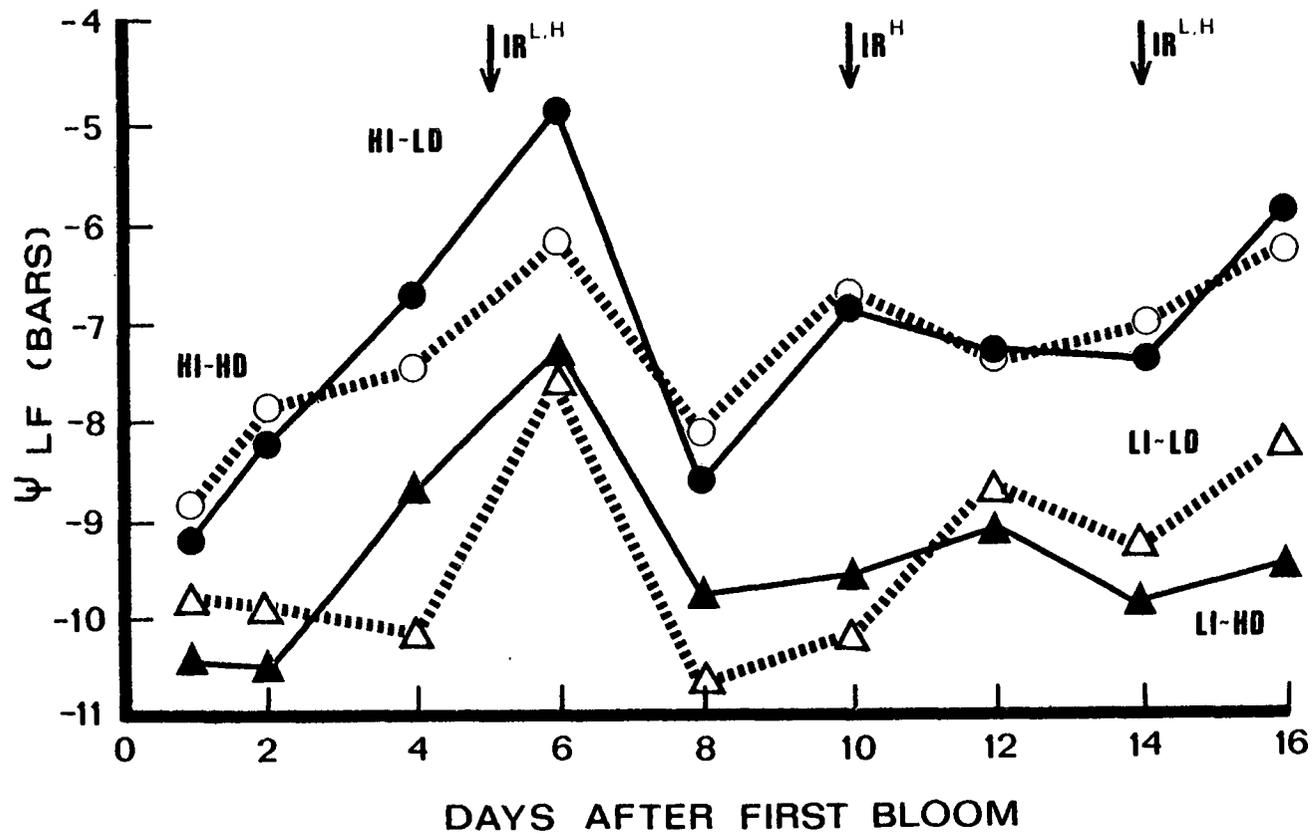
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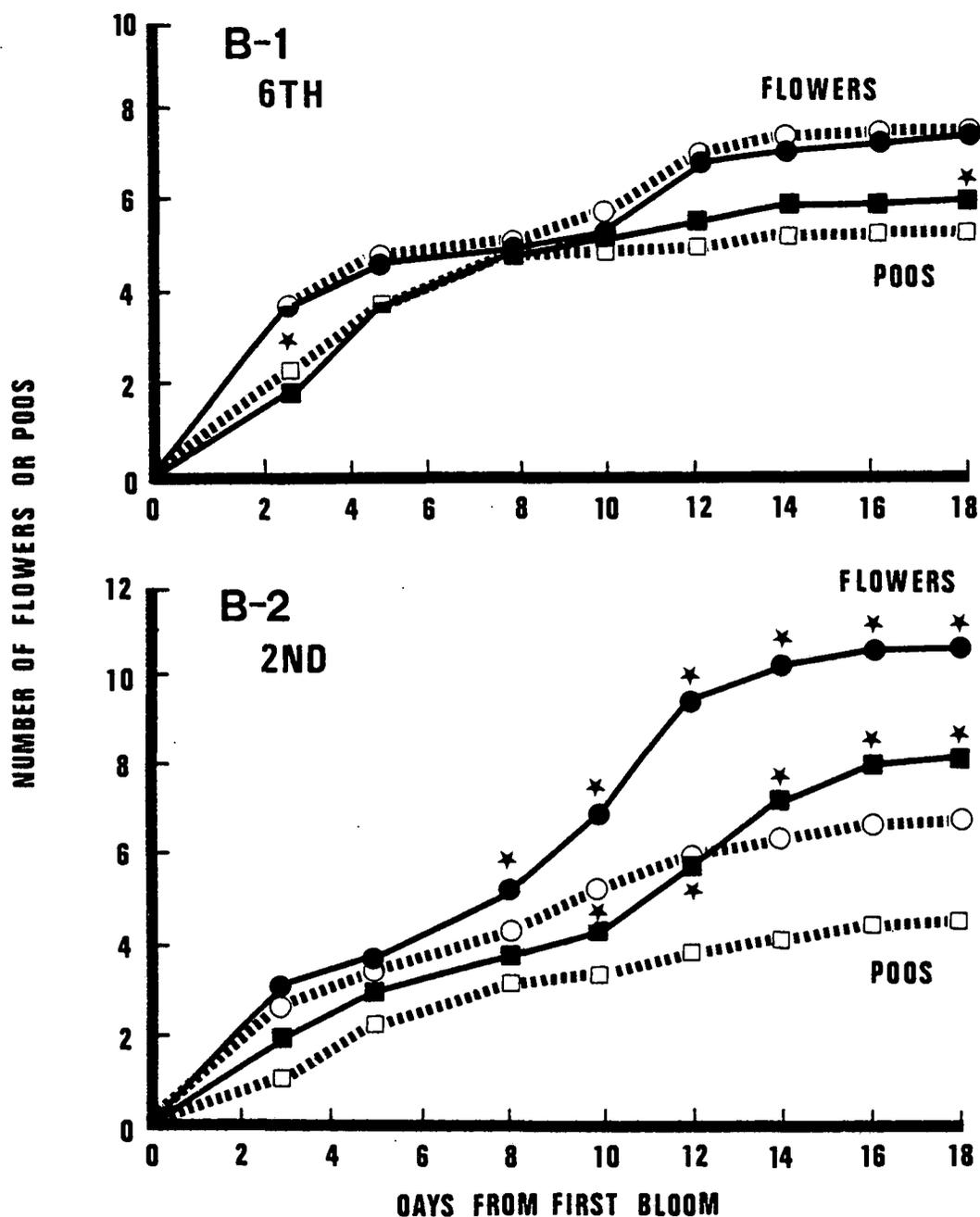
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APPENDICES



Appendix I, Fig. A. The influence of irrigation-density treatment on leaflet water potential ( $\Psi_{LF}$ ) from first bloom (anthesis of first-formed flowers at the base of the terminal inflorescence) until 16 days later. Treatments are abbreviated as follows: HI/LD, HI/HD; high irrigation, low and high density, respectively, and LI/LD, LI/HD low irrigation, low and high density, respectively. Designations atop the figure denote irrigation dates in 1979 when either high and low irrigation were both treated ( $IR^{L,H}$ ), or high alone ( $IR^H$ ).



Appendix I, Fig. B-1, B-2. Effects of irrigation at the sixth main-stem node (B-1) and population density at the second node (B-2) for 1979 on cumulative number of flowers or pods formed. Solid lines denote high irrigation (B-1) or low density (B-2), whereas, dotted lines represent low irrigation (B-1) or high density (B-2). \* Indicates level of significance at 5%.

Appendix II, Table A. Number of raceme nodes per terminal 6-T and lateral 2-A inflorescences at the sixth and second nodes, respectively, of 'Oregon 1604' as influenced by irrigation and plant population in 1978 and 1979.

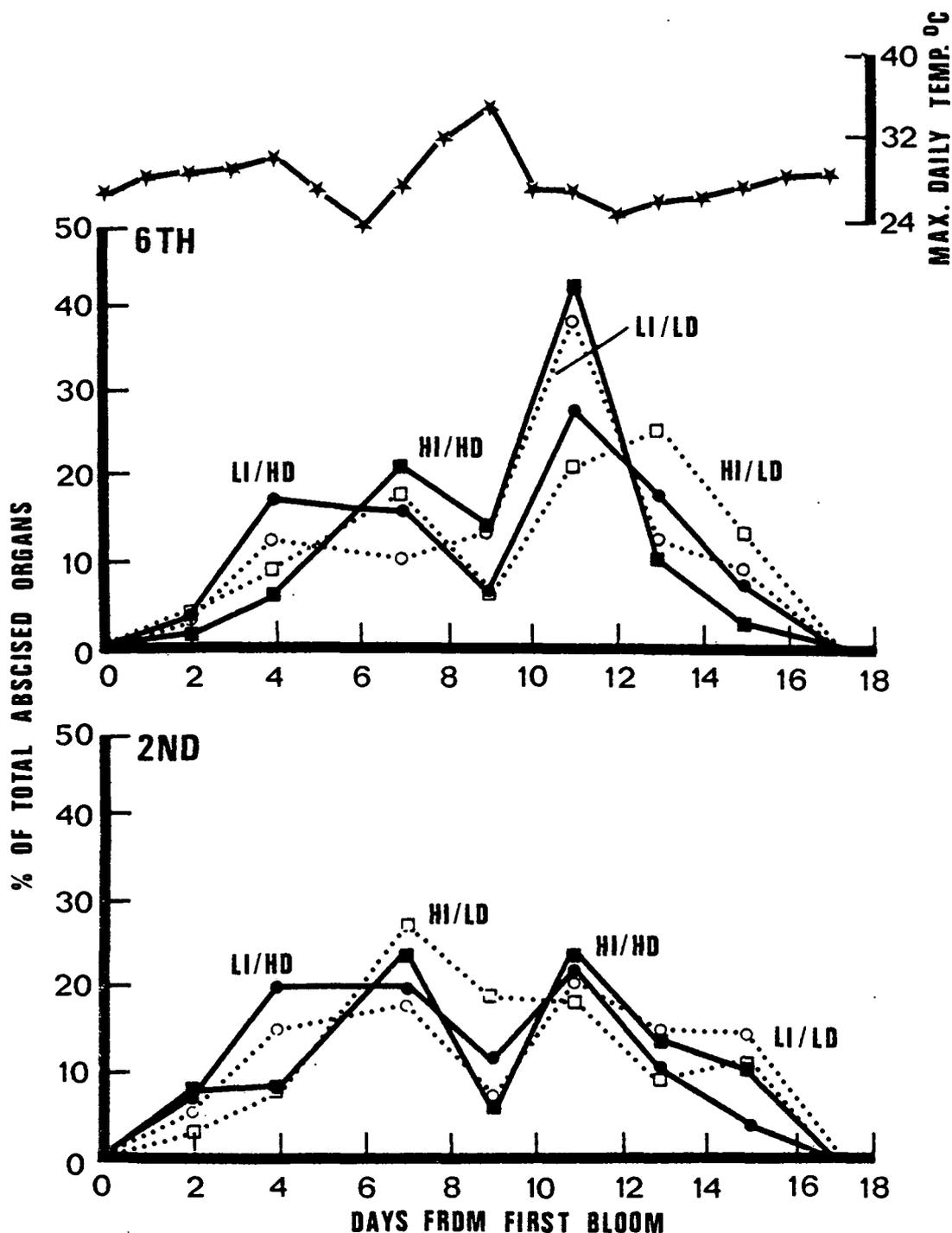
Inflorescence	Year	Number of raceme nodes per inflorescence			
		Irrigation		Density	
		High	Low	Low	High
6-T	1978	4.00	4.28	4.19	4.10
	1979	3.19	3.25	3.22	3.22
2-A	1978	3.22	3.31	3.35	3.19
	1979	2.56	2.41	2.81 <sup>***z</sup>	2.16

<sup>z\*\*\*</sup>, Indicates level of significance at 0.1% between low and high density.

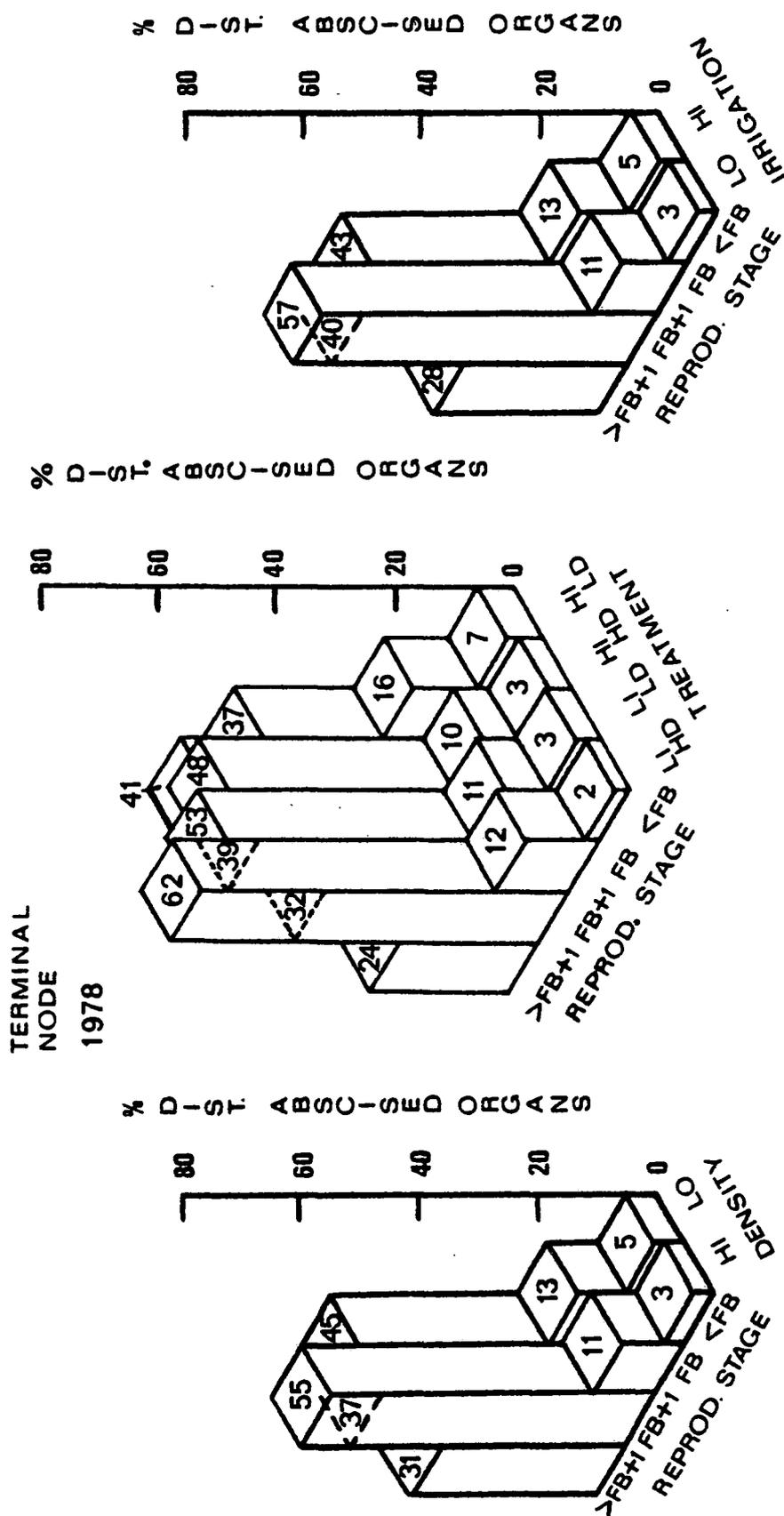
Appendix III, Table A. Minimum mean days retention of abscised flowers and pods of 'Oregon 1604' at each raceme node of the terminal 6-T and lateral 2-A inflorescence as influenced by irrigation and plant population in 1978 and 1979.

Inflorescence	Year	Raceme node	Minimum mean days retention			
			Irrigation		Density	
			High	Low	Low	High
6-T	1978	1	1.77	1.52	1.63	1.68
		2	2.23	2.47	2.37	2.34
		3	3.67 <sup>*z</sup>	1.89	2.29	3.27
		4	2.52	2.59	2.04	3.07
	1979	1	2.11	1.48	2.12	1.48
		2	2.65	2.75	2.51	2.88
3		3.56	1.73	2.97	2.31	
2-A	1978	1	1.53	1.97	1.43 <sup>***</sup>	2.08
		2	3.64 <sup>*</sup>	2.00	2.40	3.09
		3	2.87	2.60	2.58	2.89
	1979	1	2.59	2.02	2.94	1.83
		2	2.69	2.99	3.05	2.63

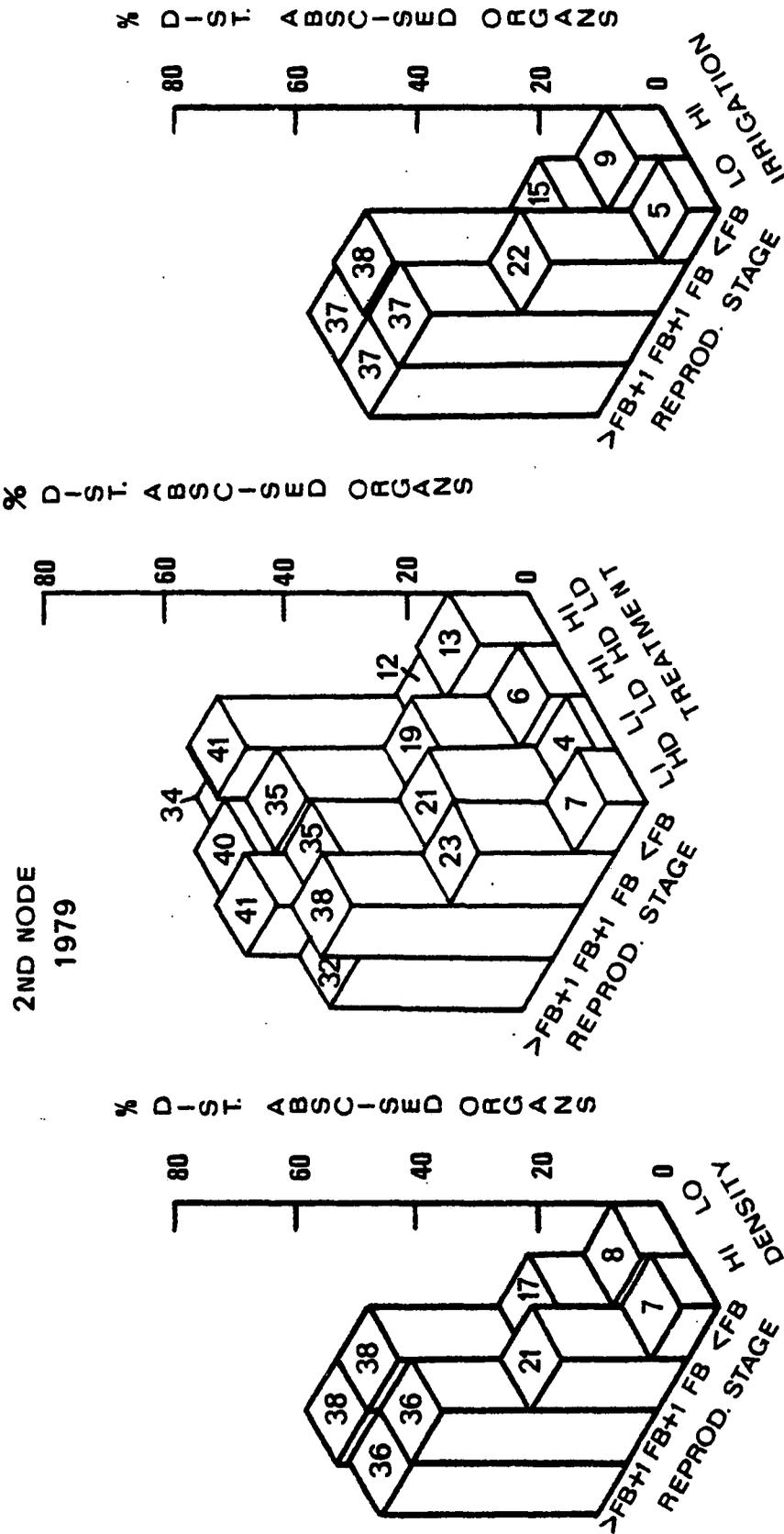
<sup>z\*</sup>, <sup>\*\*\*</sup> Indicate levels of significance at 5% and 0.1%, respectively, between irrigation or density treatments within the same inflorescence and raceme node.



Appendix III, Fig. A. Seasonal abscission patterns at the sixth (upper) and second (lower) mainstem nodes in 1979 as influenced by irrigation-density treatment. First bloom refers to the day in which flowers at the first raceme node of the terminal inflorescence at node 6 reached full bloom. Treatments are denoted: HI/LD, HI/HD (high irrigation, low and high density, respectively), and LI/LD, LI/HD (low irrigation low and high density).



Appendix III, Fig. B. Percent distribution of abscised organs of 'Oregon 1604' snap bean at the terminal node in 1978 within 4 reproductive stages as influenced by irrigation-density treatment (center) and main effects of irrigation (right) and density (left). Reproductive stages are denoted as days from full bloom: <FB (prior to), FB (day of), FB+1 (one day after), and >FB+1 (greater than one day after).



Appendix III, Fig. C. Percent distribution of abscised organs of 'Oregon 1604' snap bean at the second node in 1979 within 4 reproductive stages as influenced by irrigation-density treatment (center) and main effects of irrigation (right) and density (left). Reproductive stages are denoted as days from full bloom: <FB (prior to), FB (day of), FB+1 (one day after), and >FB+1 (greater than one day after).

Appendix IV, Table A. Dry weights of 'Oregon 1604' snap bean plant parts relative to the position of the  $^{14}\text{CO}_2$  exposed leaf at the second mainstem node as affected by irrigation and plant density at 3 exposure dates.

$^{14}\text{CO}_2$ date	Plant part <sup>2</sup>	Plant part dry weight (g)				Population mean $\pm$ SE
		Irrigation		Density		
		High	Low	Low	High	
7/25	SHOOT	5.26 <sup>*Y</sup>	4.01	5.53 <sup>**</sup>	3.75	4.64 $\pm$ 0.53
	INFLR-STM, LF	0.79	0.46	0.89 <sup>**</sup>	0.35	0.62 $\pm$ 0.12
	RN-1	0.020	0.018	0.023	0.015	0.019 $\pm$ 0.009
	RN-2	0.027	0.021	0.025	0.022	0.024 $\pm$ 0.01
7/27	SHOOT	5.51	4.99	5.93 <sup>*</sup>	4.65	5.30 $\pm$ 0.41
	INFLR-STM, LF	0.75	0.58	0.74	0.58	0.66 $\pm$ 0.08
	RN-1	0.026	0.035 <sup>*</sup>	0.03	0.031	0.03 $\pm$ 0.01
	RN-2	0.015	0.011	0.014	0.013	0.013 $\pm$ 0.003
7/31	SHOOT	8.22 <sup>*</sup>	5.23	6.53	6.91	6.73 $\pm$ 0.95
	INFLR-STM, LF	1.53 <sup>*</sup>	0.71	0.92	1.32	1.12 $\pm$ 0.23
	RN-1	0.19	0.13	0.16	0.16	0.16 $\pm$ 0.09
	RN-2	0.07	0.06	0.05	0.07	0.06 $\pm$ 0.004

<sup>2</sup>Plant parts are defined as SHOOT - tissue above and below the treated leaf; INFLR-STM.LF - extended peduncle of the 2-A inflorescence, and lateral leaf; and RN-1 and RN-2 - flowers and/or pods at the first and second raceme nodes, respectively.

Y\*,\*\* Indicate levels of significance at 5% and 1%, respectively, between irrigation or density levels for the same plant part and  $^{14}\text{CO}_2$  date.

Appendix IV, Table B. Effect of population density on relative import capacity (percent translocated  $^{14}\text{C}$ -photosynthate per unit dry weight) of 'Oregon 1604' snap bean flowers/pods in the main lateral inflorescence, 2-A, at the second mainstem node and abscission response per raceme node.

Raceme node	Days after anthesis	Relative import capacity		% Abscission <sup>z</sup>	
		Density		Density	
		Low	High	Low	High
1	2	284.5	402.8		
	4	313.0	559.4	21.9	37.8 <sup>*y</sup>
	8	255.7	80.3		
2	1	135.0	185.0		
	3	218.2	184.1	33.9	43.3
	7	261.4 <sup>*</sup>	34.2		

<sup>z</sup>Each value is the mean of 32 observations from plants in the same plots as those exposed to  $^{14}\text{CO}_2$ .

<sup>y</sup>Level of significance denoted by (\*) at 5% between density treatments at a particular raceme node and day from anthesis.