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Title: RESPONSES OF THE BUSH SNAP BEAN (PHASEOLUS VULGARIS L.) TO POPULATION DENSITY AND PLANTING ARRANGEMENT

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Responses of the bush snap bean (Phaseolus vulgaris L.) to population density and planting arrangement were studied in the field and in the greenhouse. Investigations centered in three areas: plant morphology, chemical composition of leaves and stems, and assimilatory rates. Attempts were made to correlate results with those of flowering and fruiting studies performed concurrently.

Pod yield per acre increased with increasing population density through the range 2.62 to 9.60 plants/ft^2 while yield per plant declined. Increased yields at high densities were a direct result of larger numbers of pods and were highly positively correlated with the leaf area index. Yields per plant at higher populations were lower due to reduced numbers of pods and a reduction in average pod size. Range of pod maturity and duration of bloom appeared to be more

condensed at high densities and may have been due to earlier termination of overall development at closer plantings.

Plant size and numbers of most plant parts including leaves and reproductive organs declined with increasing plant population. Vegetative growth and development began to terminate at anthesis at closer plantings while plants grown under less crowded conditions gained weight and produced foliage at a relatively constant rate throughout the season.

Leaf and stem sugar levels in field grown plants increased with increasing planting density. Several factors including earlier cessation of vegetative development at closer plantings and population effects on starch-sugar interconversions may be involved. Leaf nitrogen levels declined with increasing density and sugar and nitrogen levels were therefore inversely related. Starch levels in leaves were generally higher at lower populations but differences were not statistically significant.

Leaf sugar levels declined markedly at anthesis in one experiment suggesting that newly-formed flowers and pods were acting as metabolic sinks. Gradual post-bloom increases in sugar content may have been due in part to declining vegetative growth demands.

Net assimilation rates in the field and net photosynthesis studies in the laboratory using infrared analysis showed decreasing rates of CO_2 fixation per unit leaf area at higher populations. However,

fixation per soil area was higher at higher planting rates in the field. Total net photosynthesis rates at bloom increased with increasing plant populations in the chamber while rates at pod maturity declined under crowded conditions.

Responses of the Bush Snap Bean (*Phaseolus vulgaris* L.) to Population Density and Planting Arrangement

by

Alvin Ray Mosley

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INTRODUCTION

Oregon leads the nation in the production of snap beans for processing. In 1970 Oregon growers produced 132,150 tons of snap beans on 28,100 acres for an average yield of approximately 4.7 tons per acre. Value of the processed crop to growers was $13.7 million. New York ranked second in production with a crop value of $9.2 million.

Investigations at Oregon State University and elsewhere have shown bush snap beans to respond to relatively high seeding rates by producing higher yields. In Oregon, five varieties produced largest yields at 5 or 6 inch square spacings as compared to 4, 7, 8, or 9 inch square arrangements. Furthermore, equidistant spacings resulted in yields 15, 31, and 27 percent higher than did similar populations in 12, 24, and 36 inch rows. In view of these and other reports, most investigators have concluded that combinations of relatively high plant population density and square planting arrangements are necessary for achieving maximum pod yields.

Physiological and development responses of the individual snap bean plant to population density and planting arrangement are not well documented. Studies with other crops, including leguminous species, have demonstrated responses to plant population in most phases of growth and development. For purposes of optimization of cropping conditions and the development of new, efficient varieties adapted to dense stands, evaluation of population density and spacing effects on individual plants is essential.

The purpose of work discussed herein is to assess responses of the snap bean, cv. Gallatin-50, to population density and row spacing in the general areas of growth and development, chemical composition of leaves and stems, and assimilatory rates. Attempts will be made to correlate findings with pod yield per individual plant and per acre.

REVIEW OF LITERATURE

Carbon represents less than one percent of the earth's crust and yet is the essence of all life. Approximately 100 million tons are photosynthetically oxidized each day (89). One hundred fifty billion tons of carbon dioxide is fixed each year and in the process 120 billion tons of oxygen are released. Thus, the earth's entire complement of carbon dioxide is photosynthetically recycled through green plants each 250 years (88).

Photosynthetic efficiency is usually the overall limiting factor in the production of crop yields (20, 89, 109). In a cropping situation, efficiency is frequently dependent on light absorption (106, 129, 160). Since leaves are the major light-intercepting organs in most horticultural crops, photosynthetic rate is highly dependent on the amount of leaf surface area and its manner of display (14, 62, 78).

Tillage for purposes of controlling weeds is becoming less important due to the advent of herbicides (14, 17, 33, 43). Restrictions on row width and seeding rates formerly imposed by tillage requirements are no longer in effect for some crops; consequently, growers are free to choose plant populations and planting arrangements conducive to optimum leaf display and maximum yields.

Plant Population

Effect on the Leaf Area Index (LAI)

High plant populations have been shown to result in earlier canopy closure and attainment of a given leaf area per soil area or LAI (2, 64, 129). Canopy closure leads to the formation of basipetal light gradients which are intensified with each increase in planting density (65). In a fully developed canopy, the majority of available radiant energy is intercepted in the top portion (124, 131). Thus Vicia faba at relatively high population densities of 55-65 plants/m^2 permits only 0.3 of full sunlight to reach the soil surface while up to 38 percent of the plant receives less than 0.1 of full daylight (65). Fifty-one percent of net radiation is exchanged in the top quarter of a soybean canopy and only 40 to 50 percent of the leaves intercept 90 percent of available sunlight at full bloom (127, 131). Since leaves normally use full sunlight less efficiencly than lower light intensities, much of the solar energy is wasted under these conditions (118). Studies indicate only minor spectral shifts as light passes through the canopy (46, 167).

Light interception increases with increasing leaf area if other factors are constant (15, 21, 62, 78, 128). An LAI sufficient to absorb 95 percent of noon sunlight has been described as the "critical LAI" or L95 (23). Maximum growth and photosynthetic rates are not attained for many species until this value is reached (23, 58, 109, 129). Ninety-five percent interception may require LAI's of 3 to 10 depending on a number of factors among which leaf angle and stand geometry are important (93). For ryegrass and orchardgrass 95 percent interception occurs at an LAI of about 5.0 while soybeans require an LAI of 3.5 to 4.5 (118, 129).

Dry matter production is a function of interception of visible light and the efficiency with which the absorbed light is utilized (128, 160). High plant population and LAI are therefore generally associated with a high production of plant dry matter per soil area (2, 21, 28, 46, 129, 143, 160). Dry weight per individual plant and population density are generally inversely related (2, 28).

Evidence has been presented in support of the concept of an "optimal LAI" response in which dry matter production would be highest at intermediate or optimal LAI values and progressively less toward either extreme (12, 36, 37, 150). Presumably, the decline in dry matter production at higher LAI's would be due in part to respiratory requirements of the lower non-photosynthesizing leaves. Conversely, other reports suggest a "critical LAI" type of response in which dry matter production increases with increasing LAI, reaches a maximum and remains essentially constant over further increases in leaf area (21, 29, 82, 94, 128, 136, 160). Communities which describe an optimum LAI ultimately produce less dry matter per unit soil area (128).

Effects on Flowering and Fruiting

Yields tend to increase with increasing population density for most species (2, 15, 18, 50, 51, 52, 75, 96, 110, 116). However, populations favoring maximum seasonal light interception and dry matter production may not favor maximum reproductive yield (129). Seed yield of soybeans apparently shows no correlation with either total dry matter production, dry matter produced during seed formation or solar radiation intercepted over the season even though maximum interception during pod formation seems to be necessary for highest production (129). Radiotracer studies show that less than three percent of the final yield of snap beans is contributed by photosynthesis occurring prior to flower opening (78). Nevertheless, LAI established prior to flowering may influence pod yield indirectly through effects on numbers of flowers and photosynthetic capacity at bloom (145).

Yield of soybeans appears to be largely a function of diversion of photosynthate to pods (129). The term harvest index (HI) expresses the percentage of total plant dry weight represented by the marketable parts (40, 145). Mathematically, HI is calculated by dividing the dry weight of the organ(s) in question by total plant dry weight and multiplying by 100. High population density in any one single direction, or non-uniform plant arrangement tends to result in low HI for soybeans and possibly other crops (129). The major contribution of plant breeders to increased crop production may be in partitioning assimilates for economic yield (39). Three methods for increasing yield of soybeans have been suggested: (1) increase the length of the economic production period, (2) increase the efficiency of utilization of intercepted solar energy, and (3) select for a diversion of photosynthate to seed production.

Crop species frequently produce more leaf area than is necessary for maximum yields (1, 21, 22, 36, 128, 129, 134, 143, 161). Some varieties of soybeans produce LAI's approaching twice that necessary for 95 percent absorption of available solar radiation. This may account for the occasional poor correlation between LAI and seed yield (129).

Yield-plant population relationships tend to describe a parabolic curve with yield being highest at intermediate densities (18, 41, 67, 156). Exceptions have been noted. Several reports indicate an assymptotic rise in yield with increases in plant population (29, 51, 155). The nature of individual experimental curves depends on the population levels chosen. Population ranges must be sufficiently large to introduce competition from a low to a very high value in order to accurately assess overall effects.

It has been suggested that economic yield of several crop and pasture plants including corn and wheat occurs at the minimum population density producing maximum biological yields (41). However, soybeans have been reported to produce maximum seed yield at a population of 104, 544 plants per acre whereas dry matter production is highest at 209, 088 plants per acre (129). Yield per plant generally decreases with increasing density for most species despite increased yields per acre (2).

Other aspects of yield such as size of organs (5, 15, 97, 111, 123) and range of maturity (15, 51) are influenced by plant population. For many vegetable crops size of the marketable organs can be reduced without a corresponding loss of yield (15, 97). This appears to be the case for tomatoes (111), snap beans (5, 97) and several of the root crops (15). Small or intermediate-sized fruit often command a higher price. Thus return to the grower can be substantially elevated by production of smaller organs.

Dark-skinned Perfection peas grown in square arrangements at several populations showed a high density of 8.2 plants/ft^2, in comparison to 0.6 plants/ft^2, to result in a crop with a relatively small range in pod maturity due to a reduction in numbers of stems and pod-bearing nodes (15). Tomatoes respond to higher populations by producing fewer fruit and fewer clusters with fruit per plant (20, 81). Similarly, spacing trials with snap beans indicate a narrower range of maturity at high densities (96). Lettuce produces smaller heads in response to high populations but quality may be adversely affected (123).

A small range in maturity is necessary for efficient mechanical harvest of most vegetable crops (1, 120).

Numbers of flowers and fruit per plant decline with increasing plant population for most species including snap beans, broadbeans, and soybeans (29, 64, 78). Fruit set appears to decline slightly at close spacings for soybeans, corn, and broadbeans (29, 64, 162). Yield of corn may be limited at high densities by poor fruit set while reduced numbers of flowers may be limiting at wider spacings (162).

Effects on Growth and Development

Elevated plant populations have been reported to result in taller individuals in most cases (28, 63, 75, 110, 129, 153). However, time of sampling is critical in determining response pattern. For example, broadbeans respond to close spacings by increased height at bloom due to greater internode elongation; height differences tend to become smaller with increasing maturity due to increased numbers of nodes per plant at wider spacings (64). Height of corn increases with increasing population to an optimum value and decreases with further increases in population; furthermore, plants at relatively dense populations may be more uniform in yield and height than those grown at either lower or higher planting rates. Competitive interaction at very high densities results in less hardy corn plants being shorter, barren and weak (45).

Maintenance of maximum canopy height is considered to be of major importance in pea breeding programs while snap bean breeders seem to prefer a more compact plant (46, 120). Shorter plants at a given leaf area lead to increased canopy density which may adversely affect photosynthetic rate and predispose plants to attack by fungal and bacterial diseases due to poor air circulation (104).

Close spacing results in smaller plants as indexed by either weight or leaf area (2, 18, 28, 46, 113, 129, 153). The proportion of plant weight represented by dry matter appears to be higher at uniform spacings for a given population (15).

Numbers of most plant parts including leaves, branches, flowers and fruit are often reduced by high plant densities (2, 28, 65, 78, 153). Soybeans branch less and exhibit smaller leaflets and a less dense canopy at close spacings (129); however, taller plants at closer planting show more lodging and fewer pods and seeds per plant (28, 153). Shading of the lower nodes of broadbeans reduces the number of pods at those nodes and may result in fewer inflorescence-bearing nodes although inflorescence size appears to be little affected (65). Kidney beans, snap beans, and peas produce fewer flowers and pods per plant at high populations (2, 58, 78).

Size of plant parts including fruit, stem height and diameter, petiole length and flower trusses have been reported to decrease with closer spacing for selected species (29, 58, 75, 96, 111, 154).

However, spacing trials with soybeans and broadbeans show no difference in seed weight or number of seeds per pod due to population or planting arrangement (64, 87). The proportion of total plant weight represented by various plant organs can be substantially influenced by population density (45, 112). Shading by grasses in pastures leads to an increased shoot per root ratio for plantains (112). Soybeans also produce higher shoot per root ratios under shaded conditions (45). Since population density effects on the shoot per root balance are similar to those of shading, an interrelationship between plant population and light intensity is indicated and is supported by the fact that, in contrast to low light, decreased nutrient and water levels result in lowered shoot per root ratios (18, 24, 30, 65, 149).

Leaf orientation and thickness may be altered by population density. Leaf thickness has been described as a sensitive indicator of competition for light with shaded leaves being thinner (158, 165). Thus leaves are thinner at higher planting rates for corn and peas (46, 161). Lower leaves in dense stands are not only thinner, but both the photosynthetic saturation and compensation points may be lower (19, 94). Reduced respiratory rates of shaded leaves may account in part for the lower compensation point (44, 78, 94, 157).

Several reports concern the influence of population density on leaf angle (15, 91). In denser stands the upper leaves may assume a more vertical angle which permits greater light penetration to the lower leaves thus lessening light gradients and favoring increased photosynthetic efficiency (127, 151, 159, 162). Air circulation, canopy roughness and the efficiency of eddy turbulence are positively influenced by more vertical leaf angles (92). The angle of leaf display assumes greater importance at higher populations. In general, at LAI's below 3.0, photosynthesis proceeds faster with prostrate leaves while at LAI's above 3.5 to 5.0, photosynthetic rate increases with increasing leaf angle (44, 46, 89).

Effects on Chemical Composition

Oil content of soybean seeds is positively correlated with light penetration into the canopy and is highest at low plant populations while protein content seems to increase with increasing density (42, 63, 77, 126). Sugar content of corn stalks declines with increasing plant density (162). Nitrogen content of soybean plants decreases with increasing density while phosphorus content remains unaffected (30). Since protein content of plant tissues is sometimes calculated as 6.00 to 6.25 times organic nitrogen levels, it would appear that protein levels in soybean plant tissue are lower at higher populations as contrasted to findings for seeds (4, 30, 84).

Effects on Assimilatory Rates

Distribution of solar radiation over the plant canopy is a prime factor in determining efficiency of light utilization (129, 145). At normal atmospheric CO_2 levels, a single soybean leaflet is light-saturated at approximately one-third of full sunlight and therefore wastes much of the available energy (19, 25, 83, 125). A soybean canopy, on the other hand, may not be saturated at full sunlight because of extensive self-shading (25, 124).

Carbon fixation per unit leaf area is substantially reduced by high population density. For example, net assimilation rate, or NAR, for kale decreases with increasing LAI throughout the range 1 to 5 while NAR for sugarbeets decreases at LAI's above 3 (150). Alfalfa and ladino clover show a curvilinear decline in NAR with increasing LAI with the initial optimum LAI coinciding with that required for 95 percent interception (157). A similar situation exists for corn and other crops (30, 150, 161). Studies of net CO_2 uptake using single intact leaves and infrared analysis likewise show a decline per unit leaf area at higher populations or under shaded conditions (9).

Net photosynthesis per soil area apparently increases with increasing plant population and LAI to intermediate densities affording approximately 95 percent interception; beyond this point little change occurs with further increases in population (94, 114, 157). The failure of photosynthetic rates to decline at densities higher than required for 95 percent interception may be explained by the fact that dark respiration per unit leaf area frequently decreases as the LAI and associated mutual shading increase (45, 46, 76, 78, 94). Higher temperatures may lead to increasing respiratory rates and lower net photosynthetic efficiency (94). Furthermore, the possibility exists that the photosynthetic compensation point decreases with increasing depth in the canopy and with closer spacing (88, 94, 157).

Dry matter production in soybeans increases assymptotically with increasing LAI (128). The fact that rate of production does not decline at higher LAI has been interpreted as an indication that lower leaves are not parasitic and do not detract from net photosynthesis of the upper leaves (7, 128, 165). Radiotracer studies show that $^{14}CO_2$ assimilated by the upper leaves of alfalfa and soybeans is usually not detectable in the lower leaves (25, 165). Photosynthetic rate may be accelerated by the presence of metabolic sinks such as flowers and expanding fruit (7, 46, 132, 136, 137, 143).

Planting Pattern

Square or equidistant plant arrangements complement effects of high population density on yield and total dry matter production (5, 15, 26, 35, 86, 87). Equidistant arrangement appears to minimize plant competition due to optimum leaf and root display afforded by reduced physical overlapping of leaves and roots. Furthermore, equidistant spacing leads to earlier canopy closure and shortens the time to maximum interception. With the optimum plant density, the more nearly equidistant spacing is used, the higher is the yield for most crop species. For example, peas apparently yield best at a population of about six plants per square foot and in 7-inch rows as compared to 14 and 21-inch row widths (15). Seed yield of soybeans is favored by high plant density and narrow rows (87); for lima beans, plant spacings with equal dimensions are likewise usually superior to spacings with equal area but unequal dimensions (86). Arrangements resulting in less crowding at a given population result in higher yields of dry beans (26). Snap bean population and spacing trials in Oregon have shown that 5 or 6 inch square plantings consistently produce heavier yields than 4, 7, 8, or 9 inch arrangements. In addition, yields at any given population are higher in square spacings than in 12, 24, or 36 inch rows (96). Elsewhere, highest snap bean yields have been obtained in 2 x 7 inch arrangements as compared to 2, 4, or 6 inch spacings in 7, 14, 28, or 35 inch rows (33). High population density appears to favor small pod size for snap beans in some cases but not in others (5, 35, 96).

Minor deviations from squareness may have only small effects on yield (30, 41, 64, 68, 97). Probably no detectable yield differences exist between 9 x 3 and 5 x 5 inch spacings for snap beans (97).

Differences in row width have little influence on development of broadbeans at any given density in the range 11 to 67 plants per square meter (64). It has been suggested that an east-to-west row orientation results in higher yields of peas than do north-to-south rows (15). Equidistant plant spacing may lead to decreased weed growth and a lower incidence of root rot (27, 152).

Photosynthetic Efficiency

Crop species differ in photosynthetic capacity and efficiency (25, 71, 72, 109). Soybean leaves, for example, are only two-thirds as efficient as corn leaves in fixing CO_2 at full sunlight. A large number of weed and crop species have been divided into "efficient" and "non-efficient" types on the basis of biochemical characteristics affecting photosynthetic potential. Almost all weed species tested are members of the efficient group as are most tropical grasses including corn. The snap bean is described as non-efficient (11).

The maximum efficiency of corn has been calculated as 5.3 percent or 15 ug net dry matter production per calorie of solar radiation (158); however, actual efficiencies observed in the field for corn are in the neighborhood of 2.9 percent (160). In general, photosynthetic efficiency in most agricultural situations appears to be about 2.5 percent or less (47, 88, 160); in terms of dry matter production, values fall between 8 and 80 mg CO_2 per hour per 100 cm^2 of leaf area or about 45 grams of dry matter per square meter of soil per day (121).

Photosynthetic efficiency may be limited in a cropping situation by carbon dioxide levels and the efficiency of light utilization between 400 and 700 mu (78, 129, 160). Carbon dioxide levels are almost always suboptimal in the field (88); light intensity may be suboptimal depending on weather conditions, planting schemes, and other factors. A correlation of 0.95 between light intensity and assimilation has been reported for a stand of corn (106).

A green leaf absorbs about 80 percent of the light radiated to it regardless of intensity and the capacity for photosynthesis. Only about 15 percent of the absorbed light is used for photosynthesis depending on environmental conditions; the rest is lost as heat of transpiration, convection, and dry thermal radiation.

At normal atmospheric concentrations of CO_2, light saturation of individual leaves occurs at a relatively low intensity and the compensation point is elevated. The saturation point rises with increasing CO_2 levels whereas the compensation point may decline (25, 31, 69). Leaf senescence or a depletion of CO_2 levels around the leaf may lead to a higher compensation point (88).

At intensities above 5,380 lux, photosynthetic rates of single soybean leaves may be limited by CO_2 concentration of the atmosphere between 270 and 1670 parts per million (ppm) while below this intensity, photosynthesis is CO_2-saturated at 300 ppm. An increase in CO_2

concentration from 300 to 600 ppm has been shown to result in an average increase of 72 percent in the mean daily apparent photosynthesis rate (117). An accompanying decrease in transpiration for most varieties suggests a partial stomatal closure due to elevated CO_2 levels (117). Apparent photosynthesis for one soybean variety dropped 87 percent as CO_2 level decreased from 300 to 100 ppm.

At 300 ppm soybean communities do not reach light saturation at intensities encountered in the field; it has been suggested that both CO_2 supply to the reaction site in the leaf and light are limiting apparent photosynthesis in this situation (47). Small increases in CO_2 cause large decreases in stomatal aperture and in transpiration of corn with no evident accompanying decrease in assimilation (106).

Field levels of carbon dioxide range from 270 ppm during the daytime in a tightly meshed canopy to 300 ppm at night (109). Twenty percent of the net carbon uptake for many crops in summer may come from the soil. Usually atmospheric mixing is sufficiently vigorous that the concentration of CO_2 in the canopy and in the free atmosphere are similar and photosynthesis is independent of soil flux (104). Carbon dioxide concentration in the air near the soil may drop as much as 25 percent by midday (70). Although CO_2 enrichment of the greenhouse atmosphere has proven highly successful in most cases (57, 163), enrichment in the field is not feasible at present (25).

MATERIALS AND METHODS

General

Bush snap beans, cv. Gallatin-50, were grown in the greenhouse and in the field during 1969, 1970, and 1971 for purposes of evaluating population density and plant arrangement effects on growth and development, flowering and pod yield, chemical composition of leaves and stems and CO_2 fixation rates.

Field Studies (Experiments 1-4)

Snap beans were seeded in a split-plot design with three row widths of 5, 10, and 15 inches as main plots and five populations of 2.62, 3.20, 4.11, 5.76, and 9.60 plants/ft^2 as subplots. Planting, sampling, and harvest dates were as indicated:

	Experiment number			
	1	2	3	4
Year	1969	1970	1970	1971
Planting date	6-10	5-28	7-8	4-29
Seedling emergence	6-20	6-5	7-16	5-15
Samples taken (days from	45	25	25	--
emergence)	52	40	33	--
		48	40	--
			48	
Pods harvested	8-14	8-5	9-14	7-23

Henceforth, plantings will be identified by experiment number. For example, the 1969 planting will be referred to as Experiment No. 1.

The following spacing treatments were established in 20 x 3.5 ft. east-west oriented plots by hand-thinning:

Population plants/ft^2)	Row spacing, inches		
	5	10	15
2.62	5 x 11	10 x 5.5	15 x 3.70
3.20	5 x 9	10 x 4.5	15 x 3.00
4.11	5 x 7	10 x 3.5	15 x 2.33
5.76	5 x 5	10 x 2.5	15 x 1.70
9.60	5 x 3	10 x 1.5	15 x 1.00

In 1969, arrangements closer than 2.5 inches within rows were not attained due to poor germination. Ten and 15 inch rows were omitted from statistical analyses in this instance. Numbers of replications varied from 6 for Experiments No. 1 and 2 to 4 for Experiments No. 3 and 4.

Fertilizer rates ranged from 800 to 1000 lbs of 8-24-8 per acre with 500-600 lbs being broadcast prior to planting and the remainder banded about two inches to the side and one to two inches below the seed. Irrigation was supplied by overhead sprinklers at the rate of one inch or more per week as needed. Excellent weed control was obtained by use of a combination of 3/4 lb trifluralin per acre disked in before planting and 4 lb of DNBP amine before emergence.

Greenhouse Studies (Experiments 5 and 6)

Experiment No. 5 consisted of four replications of six square arrangements ranging from 1 to 16 plants/ft^2 and was conducted primarily to extend morphological and yield studies over a wider range in population density. Experiment No. 6 consisted of four replications of four square treatments ranging in population from 0.5 to 8.0 plants/ft^2 and was conducted chiefly for CO_2 fixation studies.

Greenhouse studies followed a simple randomized block design. In Experiment No. 5, February to May, 1971, plants were grown in the greenhouse at temperatures of 80°F during the day and 70°F at night. Lighting consisted of natural daylight supplemented by 300 to 400 foot candles from a mixed fluorescent source from 5 a.m. until 9 p.m. Plants for Experiment No. 6, June to August, 1971, were grown in the greenhouse under natural daylight and illumination. When the second trifoliate leaf began to expand on June 21, 1971, spacing treatments were initiated outside the house.

Planting procedures were identical for the two greenhouse studies. Snap beans were planted in 4-inch metal cans of 6-inch depth; media consisted of well-mixed soil amended by 5g of 8-24-8 commercial fertilizer and 3g of anhydrous ground lime per gallon of soil; a 1:1 mixture of sand and sawdust was used as a surface mulch to prevent excessive evaporation.

Flowering and Fruiting

Yield studies are based primarily on the four field plantings, Experiments No. 1 through 4. Yield and pod counts are based on all pods exceeding one inch in length. Pods were harvested by hand on a once-over basis at commercial pod maturity as indicated by sieve size distribution. Sieve size data were obtained by use of a commercial grader.

Flower counts were made on July 29, 1969; August 8, 1969; and on July 20, 1970. Counts in 1969 were taken specifically to quantify numbers of flowers per plant and included all flowers showing any trace of white, i.e., "popcorn stage". Counts in July 1970 coincided with initial or incipient bloom and were made in an attempt to determine population and spacing effects on time of bloom; therefore, only fully open flowers were included on that date.

Morphological and Developmental Responses

Studies are based primarily on Experiments No. 1 through 3.

Leaf area was measured by use of a modified air-flow planimeter as suggested by Jones (74). The machine consists basically of a grid on which leaves are placed, a blower to provide uniform suction through the grid and a flow-meter to monitor relative amounts of air-flow obstructed by leaves placed on the grid; meter readings are proportional to leaf area (see Appendix Figure 1). Leaf area measurements are based on either two or four plants per sample, depending on harvest date and plant size.

Fresh and dry weights are based on the above-ground portions of five plants in most instances. Dry weights were obtained by placing plant samples in a forced-air tunnel dryer maintained at 70°C; after a minimum drying time of 48 hours, plants were removed and weighed to the nearest 0.01 g.

Plant height was measured from the axil of the first true monofoliate leaf to the uppermost growing point. Height measurements may not reflect exact canopy height in all cases since leaves frequently extended slightly beyond the terminal meristem. Lengths of the two longest leaves per plant were taken coincidently with plant height measurements. Numbers of trifoliate leaves per plant are based on all leaves exceeding one inch in length.

Chemical Composition

Sample Collection and Preservation

Studies are based on Experiments No. 1 through 3. Samples were collected at several intervals for each planting in the following manner: representative leaves were removed from five plants, placed in a cheesecloth bag with a suitable label and immediately placed into a chest containing 15-20 lbs of dry ice. Care was taken that all portions of the canopy were equally represented with the exception of obviously yellow or senescent leaves. After sample collection was complete, the frozen tissue was freeze-dried to about two percent moisture; samples were then ground in a Wiley mill to pass a 40-mesh screen and stored until analysis.

Analytical Methods

Sugar determinations. Levels of reducing and total sugars were determined by use of the ferricyanide method (66) as modified for the Technicon Autoanalyzer (Technicon Corp., Tarrytown, N. Y.). The procedure involves measurement of yellow color loss when ferricyanide is reduced to ferrocyanide and is widely used for sugar analyses although it is non-specific and measures other reducing agents as well. Reduction is plotted as glucose.

Procedure. -- A 200-mg sample of dried, ground leaf tissue was placed in a 50-ml erlenmeyer flask containing 20 ml of 0.2-percent benzoic acid. The flasks were then capped and placed on a shaker for 30 minutes, at which time the contents were filtered through Whatman No. 1 paper. An aliquot of the filtrate was then analyzed for sugar content.

The recorder was adjusted to 100 percent transmittance with water only flowing through the lines (see Figure 16, Appendix). If when ferricyanide was added to the flow, transmittance was above 16 percent, small amounts of five percent ferricyanide were added to the colorimetric solution until the value fell within the acceptable range (13-16 percent). If the percent transmittance was too low, two percent sodium carbonate was added as needed.

Reagents. -- (1) Alkaline ferricyanide

sodium chloride	162.0 g
potassium ferricyanide	4.5 g
sodium carbonate	360.0 g
water to	18,000.0 ml

Each of the chemicals was dissolved in about one liter of water and then combined in a five gallon bottle and diluted to volume. Brij, a detergent, was added just prior to use at the rate of 0.5 ml/1000 ml.

(2) Stock glucose standard, 10 mg/ml

dextrose	20.0 g
benzoic acid	4.0 g
water to	2,000.0 ml

The dextrose and benzoic acid were dissolved in about 1 liter of water and transferred to a 2-liter volumetric flask and diluted to volume.

(3) Dilute glucose standards

Volume of stock	dilute to	ug/100 ml	percent
25 ml	1000 ml	25	2.5
50	"	50	5.0
75	"	75	7.5
100	"	100	10.0
125	"	125	12.5
150	"	150	15.0
200	"	200	20.0

Each of the stock solutions was diluted to 1000 ml with 0.2 percent benzoic acid.

(4) Stock sulfuric acid, solution, 0.25N

sulfuric acid, conc.	125 ml
water to	18,000 ml

(5) Working sulfuric acid solution, 0.05N

stock solution	400 ml
water to	2,000 ml

(6) Benzoic acid solution, 0.2 percent

benzoic acid	36.0 g
water to	18,000.0 ml

Starch determinations. Determinations of starch concentrations in bean leaf tissue were achieved by application of the anthrone colorimetric method (105) to the Technicon Autoanalyzer as suggested by Syamananda, *et al.* (138). The anthrone reagent reacts with starch to produce a characteristic blue-green color whose degree of formation is proportional to carbohydrate levels. The method is, therefore, colorimetric in nature and involves a quantification of color produced at 620-mu. Color formation has been attributed to the reaction product of hydroxymethylfurfural or furfural and anthrone.

Procedure. -- A 250-mg sample of ground leaf tissue was placed in a 50-ml centrifuge tube and extracted three times with 20 ml of 80 percent ethanol in a hot water bath with shaking. The suspension was then centrifuged and the supernatant containing sugars and other alcohol-soluble products was discarded. The extraction was repeated at least twice. Starch was then extracted from the sugar-free residue according to the method of Hassid and Neufeld (60) which involves solubilization of the starch present by a combination of 52 percent perchloric acid and boiling water baths, precipitation of the liberated starch with iodine-potassium iodine and removal of the iodine with 0.25N sodium hydroxide. Concentrations were determined by application of the anthrone method (105) to the Technicon Autoanalyzer (138).

Reagents. -- See Hassid and Neufeld (60).

Nitrogen determinations. Determination of total nitrogen content (excluding nitrate nitrogen) of leaf and petiole tissue was achieved by use of an automated micro-Kjeldahl procedure (49). All Kjeldahl procedures involve essentially two steps; these are: (1) digestion to convert nitrogen to ammonium sulfate and (2) measurement of the ammonia formed. With the automated system (49), the liquid sample--a thick slurry--is digested, diluted and aspirated into a colorimetric system. The solution is then made alkalide with sodium hydroxide. Alkaline phenol (color reagent) and sodium hypochlorite (clorox) are then added. The stream then passes through a time delay coil to allow for color development and the blue-green color formed is measured at 630-mu and recorded. Three to five standards (nitrogen content previously determined) ranging in concentration from 2.0 to 4.5 percent were placed between groups of 10 to 15 samples.

Procedure. -- 0.5 g of ground leaf tissue was placed in a 150-ml beaker containing 15 ml of distilled water. After setting three to four hours and preferably overnight to allow for thorough wetting, 15 ml of concentrated sulfuric acid was added for purposes of pre-digestion. After 30 minutes of pre-digestion, 30 ml of distilled water was added to the suspension; 30 minutes later the beaker contents were stirred and an aliquot was decanted into a large analyzer cup and analyzed.

Reagents. -- See Ferrari (49).

Assimilatory Rates

Net Assimilation Rate (NAR)

Experiment No. 3 was used for NAR studies. Samples were taken at 25, 33, 40, and 48 days from emergence and consisted of the above-ground portion of five plants for weight measurements. Due to time limitations and excessive numbers of samples, only two plants were used for leaf area measurement. Leaf area was measured by use of an air-flow planimeter as suggested by Jenkins (74) and described earlier. After leaf area measurements were completed, plants were placed in a forced-air tunnel dryer at 70°C for a minimum of 48 hours; plants were then removed, dry weights were obtained, and NAR values were calculated according to the following equation:

$$NAR = \frac{(W_2 - W_1)(\text{Log}_e\, L_2 - \text{Log}_e\, L_1)}{(L_2 - L_1)(t_2 - t_1)}$$

Where W_2 and W_1 represent total dry weight at times t_2 and t_1, respectively; L_2 and L_1 represent leaf area at times 2 and 1 in dm^2 and Log_e refers to the natural logarithm of leaf area. The quantity t_2-t_1 represents the time lapse between sampling dates 1 and 2 in days. NAR values are an estimate of dry weight accumulated per unit leaf area over a given span of time.

Net Photosynthesis (P_n)

Plants from Experiment No. 6 were used for net photosynthesis studies. Carbon-dioxide exchange rates were measured at approximately full bloom and pod maturity by infrared analysis. Plants were allowed to equilibrate to laboratory conditions at least 24 hours prior to actual measurements.

Infrared analysis. -- A plexiglass chamber (2 x 2 x 2 feet) was constructed to serve as an assimilation chamber. A small squirrel-cage fan was mounted on the removable chamber bottom to insure air movement and minimize temperature stratification. Holes were drilled in opposing walls to facilitate air intake (from outside the building) and exhaust to a Beckman 215-A infrared CO_2 analyzer.

Air was drawn from outside the building and passed through the analyzer and/or assimilation chamber at the rate of 12L per hour. Flow rate was maintained at a uniform level by use of a water column pressure buffer. Light intensity at plant level was approximately 3,000 ft-c depending on canopy height and was supplied by a combination of two 500-watt quartz-iodine lamps and two 250-watt Sylvania blue photoflood lamps. Temperature was held at less than 85°F by use of a 10-cm water filter which removed wavelengths beyond 1000 mu. Relative humidity normally ranged from 90 to 95 percent at steady-state conditions.

Readings. -- Levels of CO_2 were measured by use of a Beckman 215-A infrared analyzer in the following manner: plants were placed in the chamber, a thin layer of vaseline was spread on the rubber gasket and the top was replaced and sealed into position by use of attached clamps; the water filter was then positioned, lights were placed in position at one foot above the water surface and turned on; the air-flow was then diverted through the chamber and after a time lapse sufficient to allow for attainment of steady-state fixation rates (one to two hours) CO_2 readings for net photosynthesis were made.

Effects of soil respiration were minimized by fastening plastic bags over the containers and around the base of the plants. When photosynthesis readings were complete, the lights were turned off and after sufficient time lapse for equilibration, respiration readings were taken. Plants were then removed and leaf area and dry and fresh weights were measured. Photosynthetic and respiratory readings were based on deviations from CO_2 content of outside air which was approximately 300 ppm.

The sample detector in the analyzer failed after one replication had been completed at bloom. Therefore, it became necessary to replace the assembly before further measurements could be made. During the interim, several plants were lost so that data presented are based on only one run for each population for each sampling date. Although the instrument was recalibrated to read correctly at 0 (pure nitrogen), 300 (ambient atmosphere), and 3050 ppm (standard gas) of CO_2, the possibility remains that differences in response between the two dates may be influenced by instrumental variability.

FLOWERING AND FRUITING

Results and Discussion

Population Effects

Yield studies show a decline in yield per plant with increasing population density in all cases. As shown by Table 1, differences were statistically highly significant in most instances. Reductions in yield were a function of both reduced numbers of pods per plant (Table 5) and a reduction in average size as indicated by a greater proportion of pods of sieve size No. 4 and smaller (Table 1) and decreased average pod length (Table 6).

Pod yield in tons per acre increased with increasing population despite lower average yields per plant. Yield from the highest population of 9.60 plants/ft^2 ranged from less than 10 percent, Experiment No. 1, to almost 100 percent, Experiment No. 3, higher than yields from the lowest population of 2.62 plants/ft^2. Results of plant population-yield studies are therefore consistent with the literature in most respects.

Increased fruit yields at higher populations appear to be connected with high leaf area index or LAI for most crop species. The relationship has not been tested for snap beans. Leaf area measurements were made about seven days prior to harvest for Experiment No. 3

Table 1. Yield and size distribution of pods of snap beans as influenced by population density and row spacing.

Population	Experiment Number											
	1			2			3			4		
(Plants/ft^2	T/A	g/p	%=4	T/A	g/p	%=4	T/A	g/p	%=4	T/A	g/p	%=4
2.62	10.15	80.8	79	9.56	75.6	68	5.32	42.3	--	7.00	55.8	--
3.20	10.05	65.6	82	9.57	62.5	76	6.31	41.2	--	8.03	52.4	--
4.11	10.67	54.0	86	11.11	56.4	76	7.19	36.5	--	9.84	50.0	--
5.76	10.79	39.1	87	9.76	35.6	80	7.71	28.0	--	9.41	34.1	--
9.60	10.82	23.6	89	12.19	26.5	79	10.19	22.1	--	9.91	21.5	--
LSD$_{.05}$	N.S.	8.00	3.60	1.41	7.32	3.40	2.35	7.22	--	1.51	8.04	
$_{.01}$		10.90	4.92	1.87	9.74	4.60	3.13	9.62	--	2.01	10.91	
Row spacing (inches)												
5	--	--	--	11.02	54.0	72	6.98	31.5	--	9.47	45.1	--
10	--	--	--	9.42	46.7	79	6.81	31.7	--	9.19	45.1	--
15	--	--	--	10.89	53.2	76	8.25	40.5	--	7.85	38.0	--
LSD$_{.05}$	--	--	--	N.S.	N.S.	N.S.	N.S.	N.S.	--	1.13	N.S.	--
$_{.01}$										1.70		

+ - 5-inch rows only.
LSD - least significant difference between means.
NS - values not significantly different.
T/A - tons of pods per acre.
g/p - grams of pod per plant.
%=4 - percent of pods sieve size 4 or smaller.

and slightly earlier for Experiment No. 2. LAI's were calculated and were compared with yield in tons per acre by means of linear-regression-correlation techniques. Results (Table 2) show a significant positive relationship in both instances (R = 0.44 and 0.54 for Experiments No. 2 and 3, respectively). The relationship may be partly academic, however, since differences in LAI accounted for less than 30 percent of the variation in yield in Experiment No. 3 and less than 20 percent for Experiment No. 2.

As shown in Table 2, LAI ranged from 4 to almost 8 for Experiment No. 3 at one week prior to pod harvest. Excess foliage may account in part for the relatively poor correlation between LAI and yield. Total reproductive yield and dry matter production are frequently maximum at LAI's sufficient to absorb 95 percent of available sunlight for several species. Ninety-five percent interception occurs at LAI's of approximately 5.0 for ryegrass and orchard grass and 3.5 to 4.5 for soybeans. Since the growth habits of soybeans and snap beans are similar, foliar complements required for 95 percent interception should be approximately equivalent. In consideration of this line of reasoning, it seems that LAI's in excess of 4.5 or 5.0 may have been superfluous and hence largely non-functional under conditions employed in these studies.

Both numbers of pods and flowers per unit soil area increased with increasing population density despite lowered production per plant (Table 5, Figure 1). Increased yields per acre were directly related to increased numbers of pods at the higher populations. Numbers of ears have been equated with photosynthetic "sink" size for corn and may limit yields at low populations (162). The possibility exists that numbers of pods were yield-limiting at lower populations in these studies, likewise. Further investigation is required before definite relationships can be established, however. Specific recommendations are made at the end of this section.

Table 2. Yield of pods, leaf area index (LAI) and average leaf size for 'Gallatin-50' snap beans as influenced by population density and row spacing.

Population	Experiment Number				
	2		3		
(Plants/ft^2)	T/A(Y)	LAI(X)	LS(X)	T/A(Y)	LAI(X)
2.62	9.56	4.05	82.7	5.32	4.06
3.20	9.57	4.10	87.0	6.31	4.95
4.11	11.11	4.24	85.4	7.19	5.57
5.76	9.79	4.64	67.2	7.71	5.28
9.60	12.19	5.64	70.1	10.19	7.44
Rx, y	0.54**		-0.37**		0.44**

LSD - least significant difference between means.
R - correlation coefficient for LAI and T/A.
T/A - tons of pods per acre.
LAI - leaf area index (upper leaf surface area per unit soil area).
LS - average leaf size in square centimeters.
** - statistically significant at the 1% level.

Snap bean breeders have suggested that small-leaved varieties may be desirable commercially due to disease resistance afforded by a more open canopy and enhanced air movement and higher yields due to greater light penetration to the lower leaves. Average leaf size and pod yield were compared by correlation-regression techniques for Experiments No. 2 and 3. A significant negative relationship was noted for Experiment No. 3 (R = -0.37) (Table 2) suggesting that small leaf size may have stimulated yield in this instance. However, the relationship did not hold for Experiment No. 2. A direct promotive influence of leaf size on yield under conditions encountered in these studies is questionable, therefore. Reduced leaf size may be a symptom of population effects on plant development and unrelated to yield. More work is needed in order to clarify the situation.

Results of pod size studies (Tables 1 and 6) show a reduction in size with increasing population density as indexed by a greater proportion of pods of sieve size No. 4 and below and reduced average pod length. Thus the higher populations of 5.76 and 9.60 plants/ft^2 lead to a smaller range in pod size than did lower populations. Visual observations suggested a prolonged period of bloom at lower populations which may have been responsible for these trends. A small range in pod size is desirable for purposes of mechanical harvest. Mack noted a similar reduction in pod size of snap beans at higher populations while Atkin and Cutcliffe concluded that population density had little effect on pod size. These studies support the work of Mack. Since results were statistically highly significant in all cases tested in these studies, the conclusion must be drawn that high population density does indeed result in a reduction in size of pods.

Differences in pod size at harvest do not appear to be due to differences in maturation rates. Studies discussed in a later section show a reduction in size of snap bean leaves (Table 7) and of entire plants (Figures 2 and 5) as indicated by reduced weight and leaf area. In view of this information, it would appear that reduced pod size may be involved as part of a general reduction in size of plant parts at high densities. Reductions in the final mature size of tomatoes, lettuce, and several root crops at high populations support this viewpoint.

Small or intermediate-sized pods command a higher price per unit weight and are desirable from a commercial viewpoint. However, other quality factors such as fiber content, taste, and pod conformation may not be favorably influenced by higher populations and need to be evaluated in assessing overall effects on commercial snap bean production.

Neither the proportion of total weight represented by pods nor pod production per unit leaf area was significantly altered by population treatments in these studies (Table 3). Results were highly variable. Time of harvest could have influenced these ratios if indeed population density influences rates of pod maturation.

Table 3. Average pod weight per total plant weight and per unit leaf area as influenced by population density and row spacing.

	Experiment Numbers					
	1		2		3	
Population (Plants/ft^2)	PW/TW %	PW/LA gm/dm^2	PW/TW %	PW/LA gm/dm^2	PW/TW %	PW/LA gm/dm^2
2.62	47.8	--	36.4	5.32	35.1	2.95
3.20	45.8	--	38.5	5.25	33.9	2.87
4.11	48.8	--	40.5	5.88	38.0	2.90
5.76	43.5	--	36.7	4.75	33.2	3.29
9.60	42.7	--	39.7	4.85	31.3	3.07
LSD$_{.05}$	N.S.	--	N.S.	N.S.	N.S.	N.S.
Row Spacing (inches)						
5	--	--	38.8	5.35	34.0	2.78
10	--	--	36.6	5.20	35.1	3.19
15	--	--	39.7	5.20	33.9	3.13
LSD$_{.05}$			N.S.	N.S.	N.S.	N.S.

N.S. - values are statistically non-significant.
LSD - least significant difference between means.
PW - weight of pods per plant.
TW - average total (green) plant weight.
LA - leaf area per plant.

In an attempt to determine possible treatment effects on days to anthesis and rates of pod maturation, numbers of open flowers per plant were counted at a very early stage of bloom in Experiment No. 3. At that time plants averaged 0 to 0.85 open flowers per plant. Results (Table 4) show a statistically significant decline in numbers of open flowers with increasing population. However, overall patterns were similar to those obtained at full bloom in Experiment No. 1 (Figure 1) suggesting that differences were not due to effects on earliness, but instead to effects of population density on the ultimate number of flowers per plant. However, numbers of open flowers ranged from 0 to 4.33 from the highest to the lowest population in 15-inch rows while the range in number of pods per plant (Table 5) was only about two-fold. This indicates that flowering may be slightly delayed under combinations of high population density and wide row spacing. Effects of planting pattern on time of flowering and pod maturation should be further investigated.

Numbers of pods (Table 5) and flowers (Figure 1) per plant declined in a similar manner with increasing population. The similarity of response suggests that planting density had only minor effects on fruit set despite reports of increasingly poor set for soybeans, corn, and broadbeans at high populations. Calculations indicate a percent set of about 52, 60, 65, 49, and 52, respectively, for increasing population levels in the field. It must be noted that percent set is only

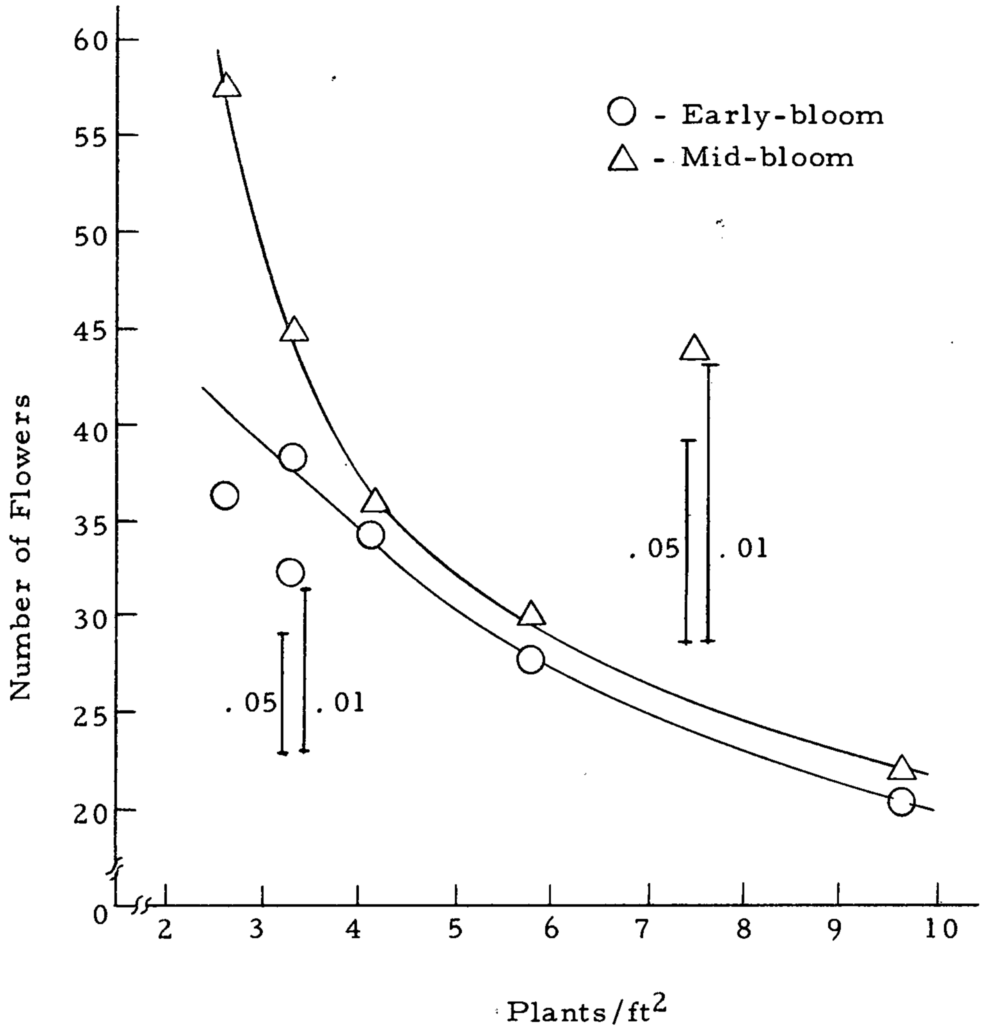

Figure 1. Average number of flowers per plant at two stages of bloom as influenced by population density. Vertical bars represent LSD's. Experiment No. 1.

approximated, however, since flower counts were based on Experiment No. 1 while pod counts were based on Experiment No. 2.

Table 4. Average number of open flowers per plant at 'incipient bloom' as influenced by population density and row spacing. Experiment No. 2.

Population	Number of Flowers			
(Plants/ft^2)	5"	10"	15"	X
2.62	2.33	1.17	4.33	2.61
3.20	2.33	0.67	2.67	1.89
4.11	2.67	0.33	2.00	1.67
5.76	2.00	1.17	0.50	1.22
9.60	1.17	0.83	0.00	0.67
Mean	2.10	0.83	1.87	--
LSD .05		N.S.		1.09
.01				1.45

LSD - least significant difference between means.
NS - means not significantly different.

Table 5. Average number of pods per plant at commercial maturity as influenced by population density and row spacing.

Population (Plants/ft^2)	Experiment Number							
	2				3			
	5"	10"	15"	Mean	5"	10"	15"	Mean
2.62	29.8	27.9	31.8	29.8	19.5	23.2	24.2	22.3
3.20	27.4	27.2	26.4	27.0	22.8	23.0	26.3	24.0
4.11	27.7	20.3	22.8	23.6	15.2	17.1	25.4	19.2
5.76	13.9	15.3	13.2	14.1	14.3	13.9	18.6	15.6
9.60	10.6	8.7	13.5	10.9	13.8	13.4	13.0	13.4
Mean	21.9	19.9	21.5		17.1	18.1	21.5	
LSD .05		N.S.		3.80		N.S.		3.59
.01				5.05				4.78

N.S. - values not significantly different.
LSD - least significant difference.

Row Spacing Effects

Effects of row spacing on yield were highly variable and statistically non-significant with the exception of Experiment No. 4. In this instance, yield increased progressively with decreasing row width, i.e., with increasing uniformity or squareness of planting arrangement (Table 1). However, the lack of similar response for Experiments 2 and 3 indicates that row widths of 5, 10, and 15 inches may differ little with regard to yield. Most investigators have concluded that the more nearly planting arrangements approach squareness, the higher will be the yield. Results of these studies suggest that costs of seeding and harvest of snap beans may be more important in determining row spacing to be used than prospective yields at row widths of 5 to 15 inches.

Effects of row width on aspects of flowering and fruiting other than pod yield were statistically non-significant.

Table 6. Average pod length at commercial maturity as influenced by row spacing and population. Experiment No. 3.

Population (Plants/ft^2)	Pod Length, cm			
	5"	10"	15"	Mean
2.62	19.5	23.2	24.2	22.3
3.20	22.8	23.0	26.3	24.0
4.11	15.2	17.1	25.4	19.2
5.76	14.3	13.9	18.6	15.6
9.60	13.8	13.4	13.0	13.4
Mean	17.1	18.1	21.5	--
LSD $_{.05}$		N.S.		4.88
.01				6.50

N.S. - values not statistically significantly different.
LSD - least significant difference.

Summary and Recommendations

The lack of consistency of row spacing effects on pod yield and other aspects of flowering may be due in part to the experimental design employed. The split-plot design emphasized subplot or population density effects at the expense of main plot or row spacing influence in these studies. A different field layout should be employed in studies emphasizing row width effects.

Further work needs to be done in determining causes for increased yields at higher populations. Population effects on LAI and photosynthetic sink size, as represented by numbers of flowers and pods per plant, have been suggested as possibilities. A combination of defoliation studies for evaluating the role of LAI in pod production at higher populations and radiotracer and pod removal studies for determining effects of pods and flowers on photosynthetic rates and translocation of assimilates appear to be in order.

Although pod size was reduced at higher populations, reasons are not entirely clear. The suggestion is made that differential rates of pod maturation are not involved. To clarify this situation, further work involving a series of harvests for each of several plantings needs to be done. At each harvest, factors of sieve size distribution, fiber content and perhaps seed size should be calculated in order to evaluate relative maturity for each population. Leaving pods on the plants until dry maturity should help in determining whether pod size reduction at high densities is due to delayed maturation or to a general reduction in the ultimate size of pods. Possibly sieve size grading should be re-evaluated in terms of varietal types, i.e., small-seeded vs. large-seeded cultivars, and cultural conditions and populations at which the plants were grown.

MORPHOLOGICAL AND DEVELOPMENTAL RESPONSES

Results and Discussion

Effects of row width were statistically non-significant except as specifically indicated. Therefore, row spacing effects are not emphasized in data presentation and discussion and treatments are considered to consist solely of populations.

Experiments 1, 2, and 3 were used for morphological measurements. Seasonal sampling patterns were more complete for Experiment No. 3. Therefore, data from Experiment No. 3 are used almost exclusively for illustration of seasonal response patterns.

Leaf Area

Leaf surface area per plant decreased with increasing population density (Figure 2). In general differences were readily evident as early as 25 days after seedling emergence and became more pronounced during the season. Reduced leaf area was due to a reduction in both numbers of leaves per plant (Figure 3) and their average size in square centimeters (Table 7) at the higher populations. Numbers of leaves and leaf area per plant tended to reach a maximum at about 40 days from emergence, or approximately mid-bloom, at higher densities but continued to increase throughout the season at the two lower plant populations. LAI calculations showed an increase with

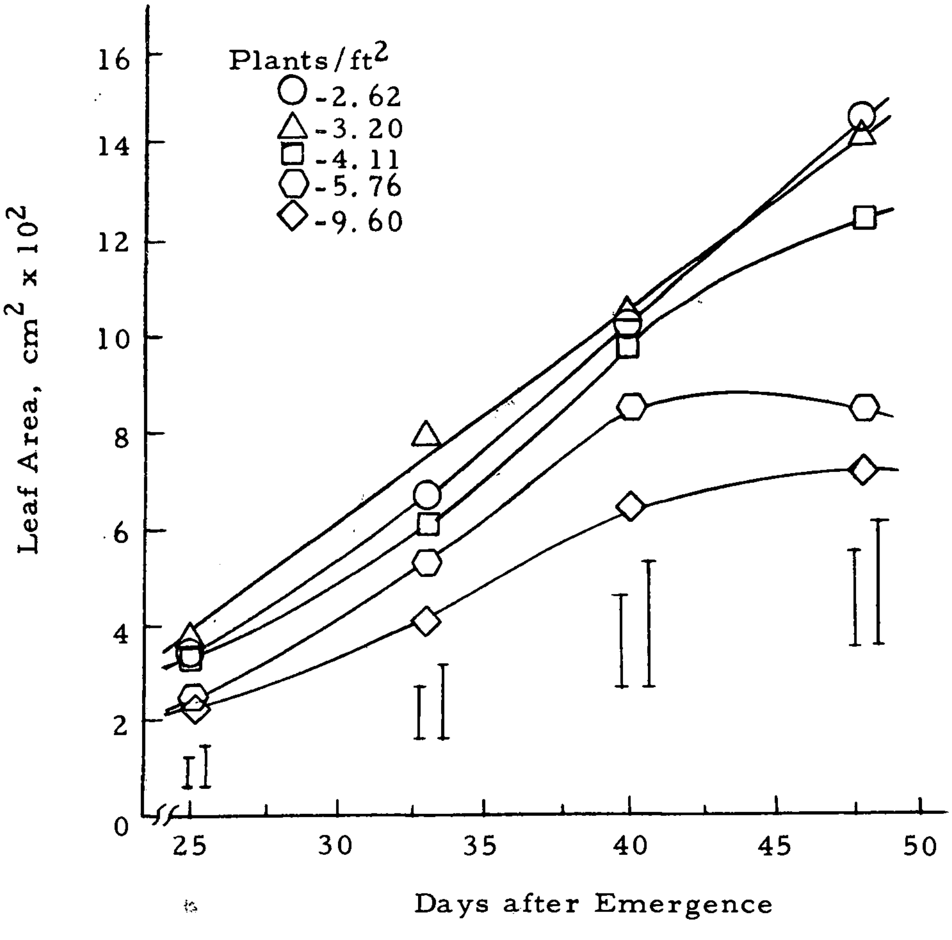

Figure 2. Average leaf area per plant at four stages of development as influenced by population density. (Points are averages for 5, 10, and 15 in. rows). Vertical bars represent LSD's. Experiment No. 3.

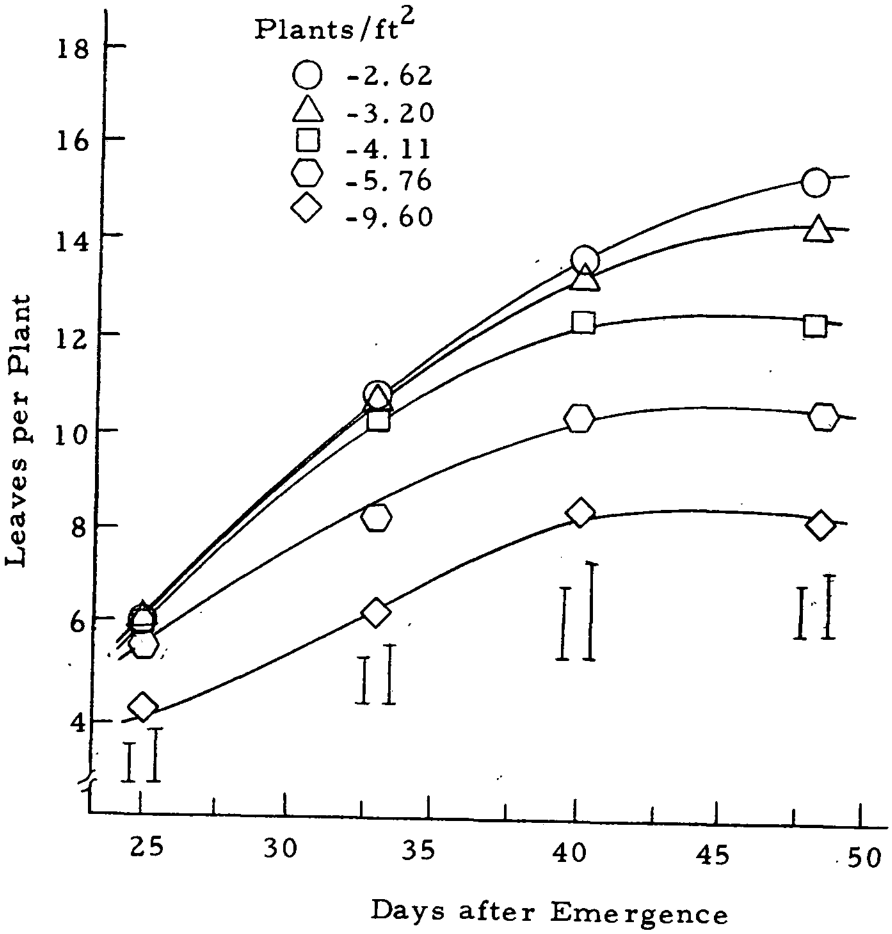

Figure 3. Numbers of trifoliate leaves per plant at four stages of development as influenced by population density (points are averages for 5, 10, and 15 in. rows). Vertical bars represent LSD's. Experiment No. 3.

Table 7. Average area (cm^2) and area per weight (cm^2/g) of snap bean leaves at different stages of development as influenced by population density and row spacing.

Plant	Days from Emergence											
	Expt. No. 2		Expt. No. 3									
Population	-25-	-48-	-25-		-33-		-40-		-48-		Mean	
(Plants/ft^2)	A	A	A	A/W	A	A/W	A	A/W	A	A/W	A	A/W
2.62	28.9	82.7	41.8	33.6	53.8	34.5	63.6	35.0	82.7	39.2	79.3	35.6
3.20	28.2	75.9	46.0	31.0	62.0	36.6	66.8	34.6	87.0	39.5	70.4	35.4
4.11	26.4	65.3	46.1	35.8	54.2	38.9	66.0	37.3	85.4	39.2	56.9	37.8
5.76	25.1	61.1	33.8	37.0	50.7	36.9	66.5	40.1	67.2	39.4	49.4	38.3
9.60	20.8	51.2	37.5	37.6	48.5	39.4	60.7	40.7	70.1	40.2	41.6	39.5
LSD .05	5.42	10.1	8.21	3.46	9.04	3.34	N.S.	3.42	12.55	N.S.	17.39	3.14
.01	7.21	13.5	10.94	6.04	12.04	4.45		4.56	16.72		23.17	N.S.
Row spacing (inches)												
5	27.9	65.7	39.3	34.2	53.1	36.2	61.3	35.6	76.8	38.1	--	--
10	22.7	66.6	40.4	35.2	51.3	38.0	57.7	37.8	71.8	39.3	--	--
15	27.0	69.3	43.4	35.7	57.1	37.5	75.2	39.2	86.8	41.1	--	--
LSD .05	N.S.	N.S.	N.S.	N.S.	N.S.	1.27	N.S.	N.S.	N.S.	N.S.	--	--
.01						N.S.						

A - average area per leaf in cm^2.

W - average fresh weight per leaf in g.

N.S. - values not statistically significantly different.

LSD - least significant difference between means.

increasing population despite reduced area per plant.

Rates of increase in LAI were also influenced to some extent by population treatments. In general, lower populations showed an essentially linear increase in LAI throughout the season (Figure 4). At higher populations, the relationship became more curvilinear; thus, LAI for the two highest populations of 5.76 and 9.60 plants/ft^2 increased at a faster rate than lower populations early in the season but at a noticeably slower rate after full bloom which occurred between 33 to 40 days after emergence.

High LAI's typically lead to increased light interception under most conditions. Since LAI values ranged from about 4.0 to almost 8.0 prior to pod harvest for Experiment No. 3, substantial differences in interception should exist. Limited data based on both the Ozalid booklet technique (54, 55) and foot-candle measurements with a Weston illumination meter (Appendix Table 1) support this viewpoint since light intensity at soil level was considerably lower at closer plantings. Furthermore, leaves of plants were thinner at closer spacings and later in the season as indicated by greater surface area per unit leaf weight (Table 7). Leaf thickness declines under crowded or shaded conditions and has been described as a sensitive indicator of competition for light (162). Therefore, thinner leaves in combination with light intensity measurements suggest that competition for light may account in part for observed responses of snap beans to population

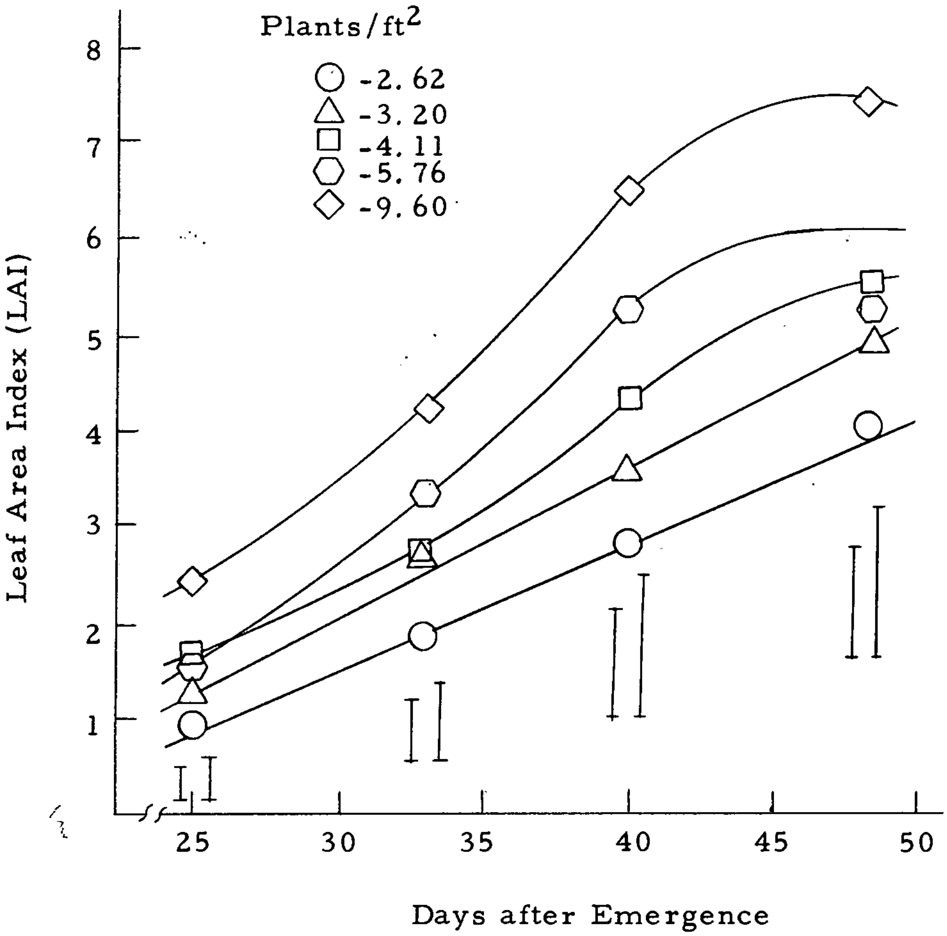

Figure 4. Leaf area index of snap beans at four stages of development as influenced by population density. (Points are averages for 5, 10, and 15 inch rows). Vertical bars represent LSD's. Experiment No. 3.

density in these studies.

High LAI and subsequent increased light interception are frequently associated with increased yields of fruit and total dry matter. As shown in the preceding section, pod yields in tons per acre and LAI's for Experiments No. 2 and 3 were significantly positively related (Table 2).

Plant Weight

Both green weight (Figure 5) and dry weight (Figure 6) of individual plants decreased with increasing density while total dry matter production per unit soil area was highest at higher plant populations (Figure 7). Since the size of individual plants was reduced at closer plantings, increased production of dry matter is accounted for solely by a greater number of plants at high densities. In general, dry [illegible] weight per fresh weight ratios did not fluctuate significantly with population (Table 8) indicating that observed weight differences were not due to succulence or water content.

Seasonal rates of weight gain per plant (Figures 5 and 6) and per unit soil area (Figure 7) show an earlier decline at higher populations in a manner consistent with results of leaf area studies (Figures 2, 3, and 4). Plants grown at the two lowest populations show an accelerated weight gain from 40 to 50 days after emergence while plants cultured at the two higher populations exhibited declining rates

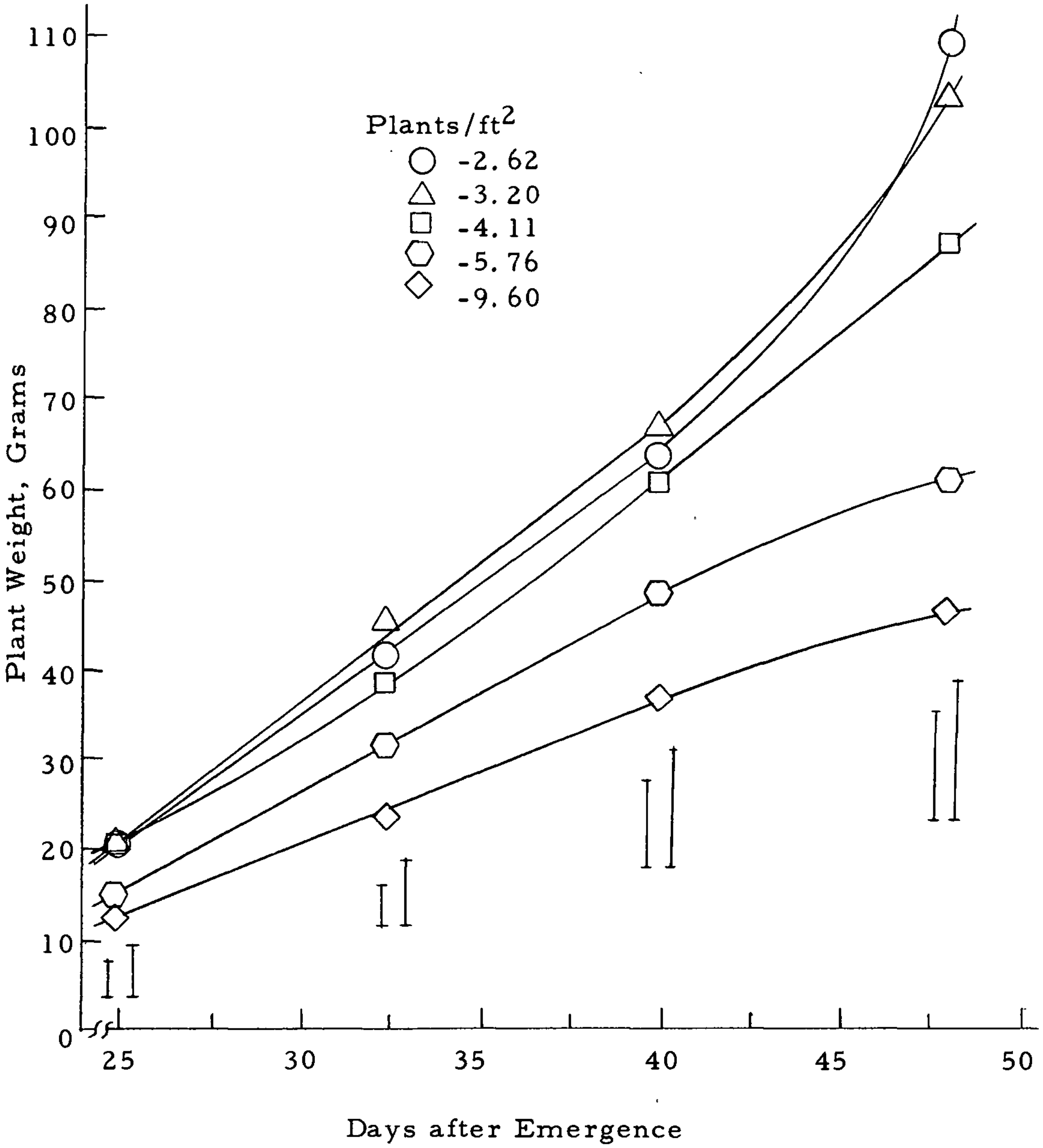

Figure 5. Average green weight per plant at four stages of development as influenced by population density. (Points are averages for 5, 10, and 15 inch rows). Vertical bars represent LSD's. Experiment No. 3.

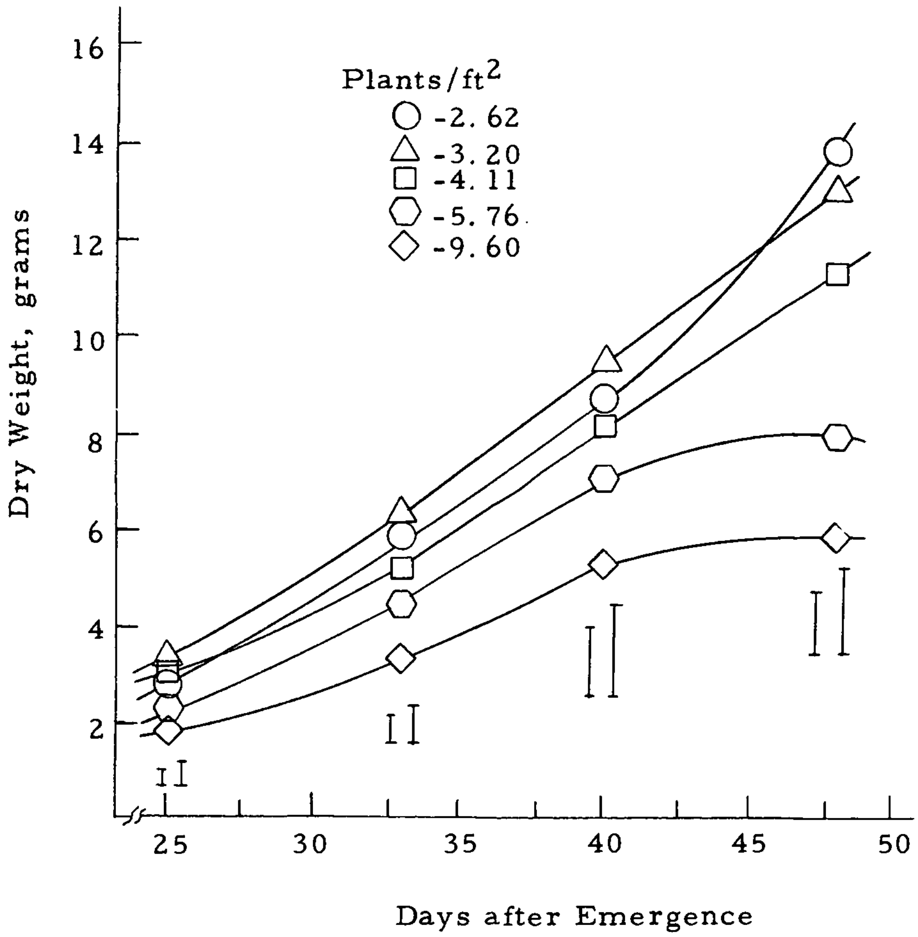

Figure 6. Average dry weight per plant of snap beans at four stages of development as influenced by population density. (Points are averages for 5, 10 and 15 inch rows). Vertical bars represent LSD's. Experiment No. 3.

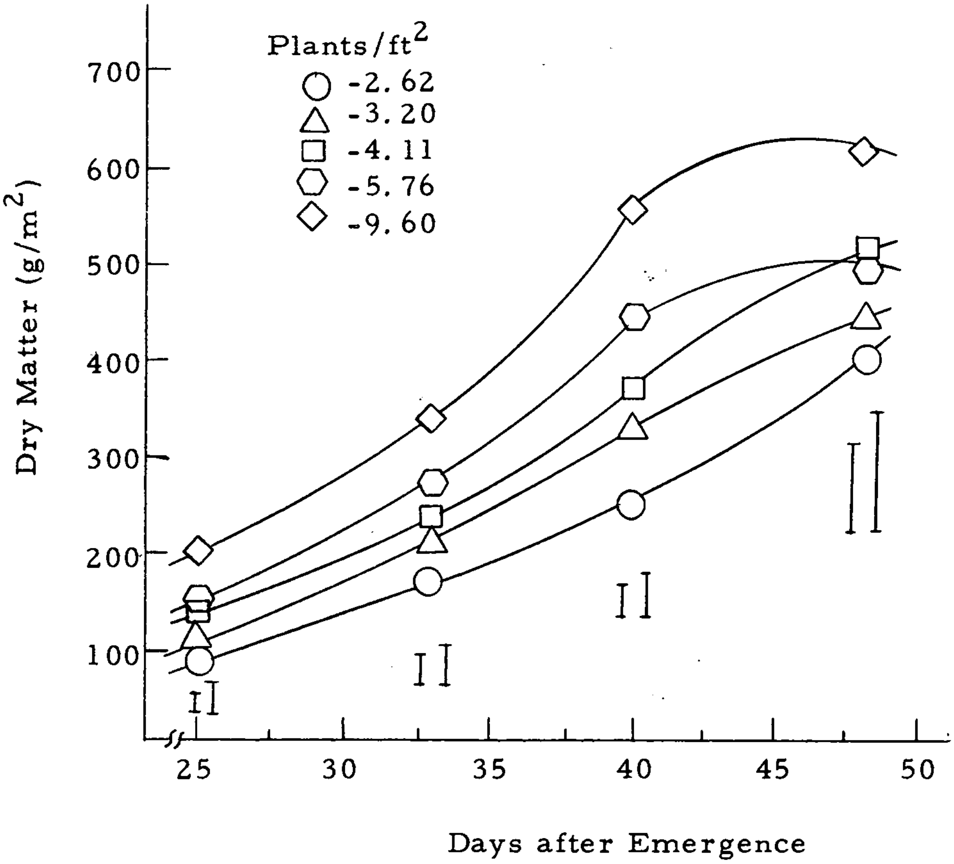

Figure 7. Total dry matter production of snap beans per square meter of soil at four stages of development as influenced by population density. (Points are averages for 5, 10, and 15 inch rows). Vertical bars represent LSD's. Experiment No. 3.

of gain during the same period. The intermediate density of 4.11 plants/ft^2 was generally intermediate in response.

Table 8. Percent dry weight of plants at four stages of development as influenced by population density and row spacing.* Experiment No. 3.

Population (Plants/ft^2)	Days from Emergence 25	33	40	48
2.62	14.7	14.0	13.9	12.7
3.20	14.2	13.9	14.3	12.8
4.11	15.3	13.7	14.1	13.2
5.76	15.9	14.2	15.0	13.1
9.60	15.2	14.1	14.5	13.1
LSD$_{.05}$	N.S.	N.S.	N.S.	N.S.

N.S. - Differences between means are statistically non-significant by the F-test.
LSD - Least significant difference between means.
* - Row-width effects were not significantly different at the 5% level.

Plant Height and Leaf Length

Plant height, as measured from the axil of the first monofoliate leaf to the upper-most growing point, appeared to increase slightly with increasing population for Experiment No. 3 (Table 9). Differences due to population were more pronounced at anthesis in this instance; Experiment No. 2 did not show significant differences in height at bloom but differences were significant at 25 days from emergence. Interestingly, in this instance plant height seemed to decrease with increasing population. It is possible that prior to the onset of competition for light, larger biomass at closer plantings may have lead to competition for water or nutrients (see next section for Nitrogen studies; Appendix Table 2 for soil moisture determinations).

Timing of height measurements appears to be important. A single sampling at mid-bloom for Experiment No. 3 would have suggested an erroneous general increase in height with increasing density while samples at other dates generally would have indicated no effect of plant population. Increased height at anthesis in Experiment No. 3 was apparently due to greater internode elongation at closer spacings since high density plants exhibited fewer leaves and nodes at that time (Figure 3).

Maintenance of adequate pod height above the soil is critical in preventing pod rot and in facilitating mechanical harvest. Although pod height was not measured specifically, visual observations indicated that a considerably larger portion of the pods were borne in the upper regions of the canopy at closer plantings.

Leaf length responded in a manner similar to that observed for plant height (Table 9) since differences were most pronounced at bloom (Table 10). At bloom, leaves were considerably longer for plants grown at closer spacings. Increased length was due largely to petiole elongation. Leaf blade length did not respond significantly to plant population and may have declined slightly at higher populations

Table 9. Stem length (height) of snap beans in cm. at several stages of development as influenced by population density and row spacing.

Population (Plants/ft^2)	Days after Emergence								
	Expt. No. 2				Expt. No. 3				
	25	40	48	Mean	25	33	40	48	Mean
2.62	7.56	31.5	44.0	27.7	10.4	26.2	37.9	47.9	30.6
3.20	7.77	32.3	43.2	27.8	12.0	29.5	42.6	50.3	33.6
4.11	7.45	31.9	44.6	28.0	13.0	28.6	42.0	50.6	33.5
5.76	6.74	31.4	43.6	27.3	11.3	27.2	43.0	49.9	32.9
9.60	6.53	30.2	44.6	27.1	11.6	27.3	46.2	49.8	33.7
LSD$_{.05}$	0.87	N.S.	N.S.	N.S.	N.S.	N.S.	3.26	N.S.	*
$_{.01}$	1.16						4.35		
Row spacing (inches)									
5	7.4	33.5	46.5	--	11.2	26.3	40.6	46.8	--
10	6.4	29.8	41.5	--	11.5	27.8	40.7	49.1	--
15	7.8	31.1	44.1	--	12.3	29.2	45.7	53.2	
LSD$_{.05}$	0.88	N.S.	2.43	--	N.S.	N.S.	N.S.	N.S.	--
$_{.01}$	N.S.		3.46						

N.S. - differences not statistically significantly different.
LSD - least significant difference between means.

* - differences significant at the 5% level; LSD$_{.05}$ not significant.

Table 10. Length (cm) of leaves, petioles and laminae of snap beans at several stages of development as influenced by population density.* Experiment No. 3.

Plant Population (Plants/ft^2)	Days after Emergence											
	25			33			40			48		
	L	P	LB	L	P	LB	L	P	LB	L	P	LB
2.62	22.9	10.3	12.6	27.8	13.3	14.5	29.5	14.1	15.4	32.7	17.0	15.7
3.20	23.6	10.8	12.8	28.2	13.5	14.7	31.4	15.7	15.7	33.6	16.7	16.9
4.11	24.4	11.2	13.2	28.6	14.2	14.4	31.4	16.0	15.4	32.2	16.6	15.6
5.76	23.4	11.2	12.2	28.2	14.3	13.9	30.8	15.4	15.4	31.7	16.5	15.2
9.60	23.8	12.0	11.8	27.7	14.6	13.1	31.6	16.5	15.1	32.3	17.2	15.1
LSD $_{.05}$	N.S.	0.68	N.S.	N.S.	0.96	N.S.	0.88	0.78	N.S.	N.S.	N.S.	N.S.
$_{.01}$		0.91			1.27		1.31	1.04				

L - leaf length
P - petiole length
LB - leaf blade length
N.S. - differences not statistically significantly different by the F-test
* - row spacing effects were not statistically significant at the 5% level.

in accordance with the general reduction in average area of individual leaves.

Summary and Recommendations

The bush snap bean is normally considered to be determinate. It is popularly felt that demands of fruiting on carbohydrate reserves account in part for cessation of vegetative development. As shown by these studies, snap bean plants grown at relatively high populations of 5.76 and 9.60 plants/ft^2, as compared to populations of 2.63, 3.20, and 4.11 plants/ft^2, begin to terminate vegetative growth at bloom as indicated by reduced rates of leaf area production and weight increase. The determinate nature of bush beans is therefore complemented by high population density.

As indicated in the preceding section, yield per acre was highest at the above-mentioned higher populations. The fact that high density treatments lead to both earlier cessation of vegetative growth and development and higher yields could be vital. With other factors constant, cessation of vegetative demands at bloom should allow for diversion of relatively more photosynthate to pod production and hence favor higher yields as was noted in these studies. Varieties which terminate vegetative growth at anthesis would appear to be desirable for these reasons.

Denser plantings seemed to shorten certain phases of reproductive development as well as vegetative processes. Although specific measurements were not made, visual observation in the field indicated that duration of bloom might have been shorter at closer plantings. This is consistent with observations of a shorter range in pod maturity at populations higher than 4.11 plants/ft^2 as indicated by pod size studies in the preceding section.

More than 90 percent of all bush beans are now mechanically harvested. Since mechanical harvest is a once-over, plant-destructing process, a short range in pod maturity is indispensable. Flowers formed after some critical period, yet to be determined, may be largely wasted effort since development would be curtailed by harvesting operations. A thorough study of duration of bloom as a function of population density would be worthwhile.

Plant height responded less dramatically than available information for other species indicated. The major importance of height in snap beans may be in an indirect effect on elevation of pods above the soil. Contact with the soil frequently results in fungal and bacterial pod rots under humid conditions; in addition, greater pod height may favor cleaner harvests. Investigations of pod height and placement in relation to the major plant stem may prove fruitful. Cursory examination indicates that pods may be clustered near the main stem axis at higher populations.

As mentioned earlier, LAI and yield per acre were positively related for Experiments No. 2 and 3; although the relationship was significant, variation in LAI accounted for less than 30 percent of the variation in yield. The relatively poor correlation may be due in part to the fact that high populations may have lead to excess foliage. Critical studies need to be performed in determining minimal LAI's capable of producing maximal yields. Simple defoliation studies should be informative.

Although LAI and yield were positively correlated, the possibility should be considered that photosynthetic sink capacity in the form of pods is yield-limiting.

High density snap bean plantings may be subject to bacterial and fungal diseases under humid conditions due to larger masses of foliage and associated reductions in air circulation and higher humidity within the canopy. Furthermore, excess foliage and vegetative material may hamper mechanical harvest operations. For these reasons elimination of non-essential leaf area should be a major objective of snap bean breeding programs.

Since high density snap bean plantings are becoming more common, all new varieties should be tested for performance across a relatively wide range in populations as well as geographic areas. Breeder's objectives should include the development of varieties exhibiting a minimum of vegetative development, particularly with regard to foliage, and maximum reproductive capacity for use in high density plantings.

CHEMICAL COMPOSITION

Row spacing effects were generally statistically non-significant and are not discussed in order to facilitate clarity in presentation of data.

Results and Discussion

Sugar Determinations

Population averages across all sampling dates show an increase in levels of reducing and total sugars with increasing population density for Experiments No. 2 and 3 (Tables 11 and 12). Results for individual sampling dates indicate similar increases for Experiment No. 1. Stem tissues were analyzed for sugar content at 25 days from emergence for Experiment No. 2. In general, results were similar to those obtained for leaves. Stem sugars were slightly higher at that time (Figure 8).

A concurrent increase in leaf and stem sugar and population density was not expected and appears to be atypical. Higher population density and LAI's ordinarily lead to reduced leaf efficiency due to mutual shading. Respiratory demands in combination with declining efficiency would be expected to lead to a depletion of carbohydrate and other storage products under these conditions. For example, Williams reported a general decline in stalk sugar content of corn at several

Table 11. Reducing sugar (glucose) content (mg/g) of snap bean leaves as influenced by population density at different stages of development$^+$.

	Days from Emergence										
Population	Expt. No. 1		Expt. No. 2				Expt. No. 3				
(Plants/ft^2)	39	46	25	40	48	Mean	25	33	40	48	Mean
2.62	56.5	44.3	38.0	41.6	45.0	41.3	49.3	39.9	43.9	51.5	46.1
3.20	60.3	50.0	38.5	40.2	45.5	41.2	50.1	39.3	46.8	52.4	47.1
4.11	58.7	45.8	38.2	40.8	44.9	41.4	50.8	51.6	49.8	55.5	49.4
5.76	59.0	54.7	38.3	41.1	46.4	41.9	55.1	42.4	50.8	57.0	51.3
9.60	58.2	52.7	39.0	41.4	48.7	43.4	55.4	44.3	52.9	58.3	52.7
LSD$_{.05}$	N.S.	7.47	N.S.	N.S.	N.S.	N.S.	4.07	3.56	3.19	4.12	5.04
$_{.01}$		10.14					5.43	4.74	4.25	5.49	6.71
Mean	58.5	49.5	38.4	41.2	45.9	--	52.1	41.5	48.9	54.9	--
				**				**			

N.S. - differences are statistically non-significant.

LSD - least significant difference between means.

** - means are significantly different at the 1% level.

+ - population effects are averaged across three row spacings of 5, 10, and 15 in.

Table 12. Total (reducing and non-reducing) sugar content (mg/g of dry weight) of snap bean leaves as influenced by population density at different stages of development+.

Population (Plants/ft^2)	Days from Emergence										
	Expt. No. 1		Expt. No. 2				Expt. No. 3				
	49	56	25	40	48	Mean	25	33	40	48	Mean
2.62	73.5	63.5	52.5	62.8	60.6	58.4	70.4	57.1	62.1	71.7	65.3
3.20	78.5	66.3	54.5	61.3	61.4	59.2	70.7	56.3	61.8	72.3	65.3
4.11	76.2	64.5	54.5	64.0	60.8	60.4	74.6	60.3	63.6	74.6	68.3
5.76	75.5	72.2	52.9	64.0	64.4	60.7	74.7	59.8	64.6	73.2	68.1
9.60	76.2	75.0	53.8	61.1	65.4	60.5	75.3	60.2	68.3	78.8	70.6
LSD .05	N.S.	N.S.	N.S.	N.S.	3.49	N.S.	3.80	N.S.	4.22	4.97	4.72
.01					4.64		5.06		5.62	6.61	6.28
Mean	--	--	53.6	63.4	62.5	--	73.1	58.7	64.1	74.1	--
				**					**		

N.S. - values are statistically non-significant by the F-test.

LSD - least significant differences between means.

** - means are significantly different at the 1% level.

+ - population effects are averaged across three row spacings of 5, 10, and 15 in.

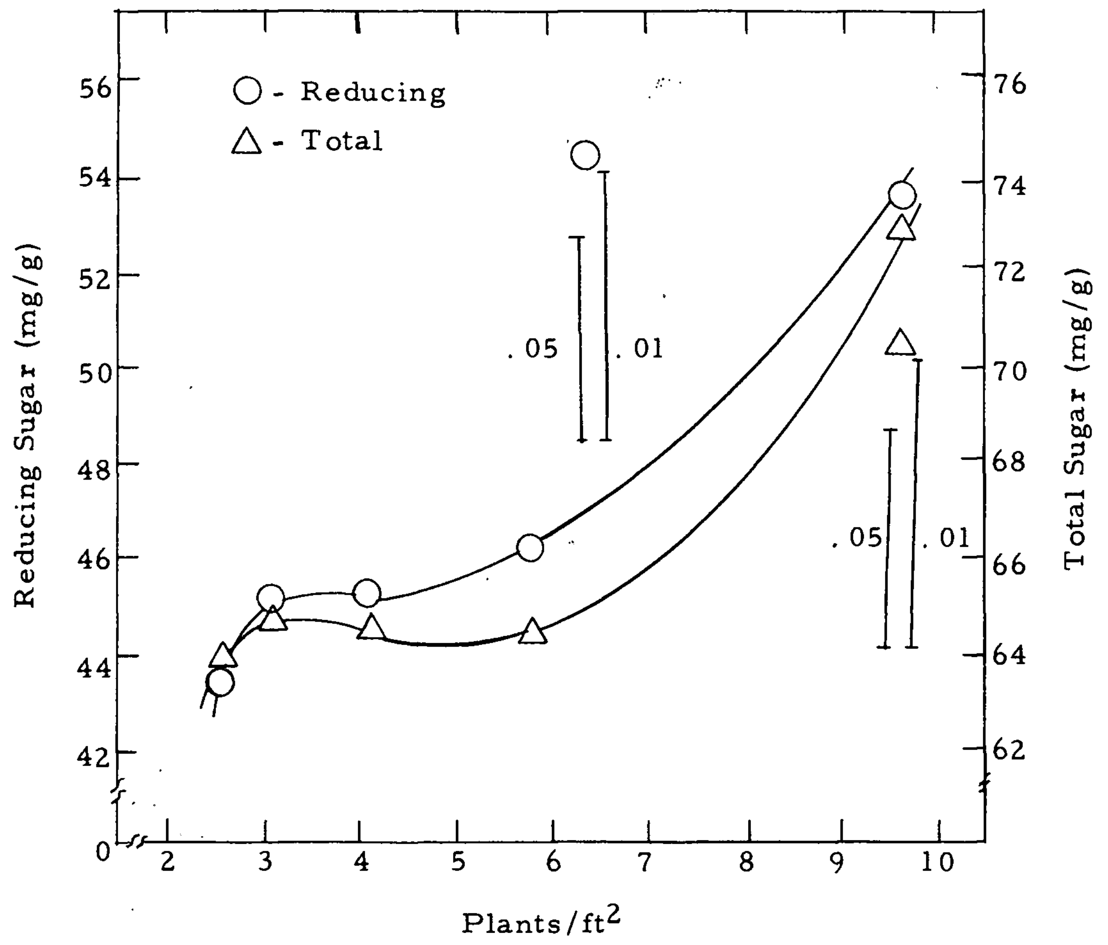

Figure 8. Sugar content of snap bean stems as influenced by population density. (Points are averages for 5, 10, and 15 inch rows). Vertical bars represent LSD's. Experiment No. 2.

stages of development with increasing density of planting. Similarly, oil content of soybean seeds is reduced at higher populations. The fact that snap bean leaves and stems apparently respond in an opposite manner could be significant.

Causes for sugar accumulation in stems and leaves of snap beans at closer plantings are not obvious. Tentatively, the following factors might be involved in causing sugar buildup at high densities: (1) reduced respiratory rates per unit leaf mass at higher populations, (2) reduced photosynthetic sink size due to lower numbers of flowers and pods per plant, (3) earlier cessation of vegetative growth and development, (4) enhanced starch-to-sugar conversion, and (5) favorable carbohydrate-nitrogen relationships at closer plantings. These points will be discussed in succession. The latter two will be incorporated in starch and nitrogen subsections.

The literature indicates a possible decrease in the photo-compensation point for leaves at high densities or LAI's which appears to be due in part to reduced dark respiration rates per leaf mass. With other factors constant, lower respiratory rates should demand less carbohydrate and thus result in a buildup of sugars in the tissues. However, as noted above, the photosynthetic rate per unit leaf area also declines with increasing density; thus it appears unlikely that reduced respiratory rates could account for observed sugar buildup.

Williams suggested that low photosynthate sink capacity in corn due to low numbers of ears may have allowed sugars to accumulate in the stalks at the dent stage. However, plant size and numbers of flowers and pods per plant decreased concurrently in these studies with the result that the proportion of total plant weight represented by reproductive tissue and the production of pods per unit leaf area were not significantly different (Table 3). Furthermore, differences in leaf sugar concentrations were evident as early as 25 days after emergence -- before flowering was well under way. Thus differences in sink size on a relative basis were perhaps not a factor in determining sugar levels in snap bean tissues.

Seasonal changes. Experiments No. 2 and 3 show overall seasonal increases in reducing and total sugar content of leaves (Tables 11 and 12). Experiment No. 1 included samples at only 45 and 52 days after emergence; in this instance, values were lower at 52 days possibly due to advanced leaf senescence. Analyses for Experiment No. 3 show a marked decline in sugar concentration at or about full bloom, 33 to 40 days after emergence, which was not evident for other plantings (Figure 9). Corresponding declines for other plantings may have been obscured since sampling dates did not correspond with bloom.

A general decline in sugar levels at anthesis indicates that new demands of fruiting in combination with pre-existing vegetative requirements lead to a greater requirement for substrate synthesis than

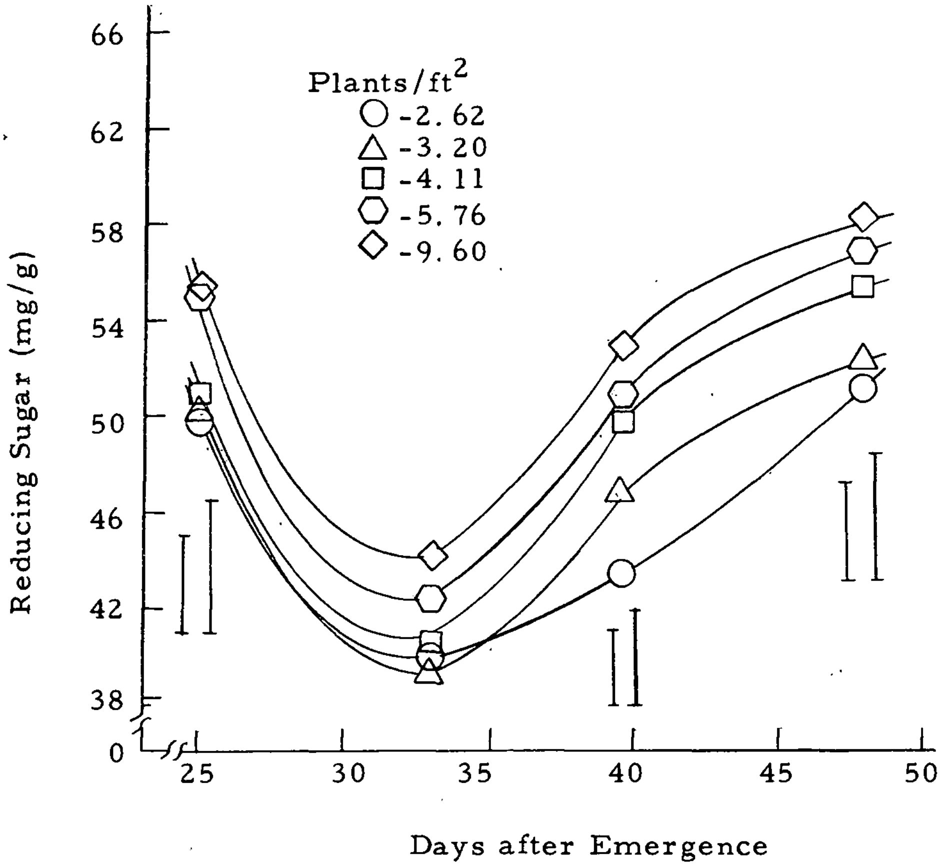

Figure 9. Reducing sugar content of snap bean leaves as influenced by population density. (Points are averages for 5, 10, and 15 inch rows). Vertical bars represent LSD's. Experiment No. 3.

the plants were able to supply causing a decline in tissue sugar levels. The recovery and continued rise in concentration after anthesis indicates a gradual adjustment of sugar levels which could be due to decreased vegetative demands on carbohydrate reserves.

Bush snap beans are determinate in growth habit and curtail vegetative development shortly after anthesis in most instances. Evidence presented in the preceding section shows that high density plantings lead to early declines in rates of weight gain (Figures 5 and 6) and leaf area formation (Figures 2 and 4) while plants grown at low populations continued to form leaves and gain weight at a relatively constant rate throughout the season. Therefore, these studies suggest that high population density complements the determinate nature of snap beans. Since vegetative growth leveled off earlier at closer spacings, proportionately less carbohydrate would be required for growth and development thus allowing for an accumulation in leaves and stems as was observed. Therefore, earlier termination of vegetative processes at closer plantings may account for higher sugar levels after anthesis but not before.

Yield relationships. Pod yield and sugar content of leaves and stems seemed to be positively related since both pod production per acre (Table 1) and sugar levels (Tables 11 and 12) increased with increasing planting density. However, a comparison of tons of pods per acre and leaf sugar levels for Experiment No. 3 by means of linear regression-correlation showed no significant relationships. On the other hand, pod yield per plant and average seasonal levels of both reducing and total sugars were significantly negatively correlated (R = -0.47 and -0.44, respectively, for reducing and total sugar). A comparison of yield per plant and sugar levels at bloom produced similar results (R = -0.33 and -0.27 n. s.). Sugar concentrations were generally statistically non-significant for Experiment No. 2 and correlations were not tested. Since the proportion of total weight represented by pods and pod production per unit leaf area were not significantly different, fluctuations in sugar concentration do not seem to influence fruit load or photosynthate sink size on a relative basis (Table 3).

Starch Determinations

Leaf tissue was analyzed for starch content at 33 and 48 days after emergence for Experiment No. 3. Results varied and differences were statistically non-significant at the 5% level (Table 13). However, differences for the earlier sampling approached significance at the 5% level and were significant at the 10% level.

Table 13. Starch concentration of snap bean leaves (mg/g of dry weight) as influenced by population density at two stages of development+. Experiment No. 3.

Population (Plants/ft^2)	Days from Emergence		
	33	48	Mean
2.62	98.7	97.0	97.8
3.20	100.0	98.3	99.1
4.11	92.0	95.5	93.7
5.76	89.8	103.9	96.8
9.60	96.5	85.8	91.1
LSD$_{.05}$	N.S.	N.S.	N.S.

N.S. - values are not significantly different by the F-test.
LSD - least significant difference between means.
+ - Population effects are averaged across three row spacings of 5, 10, and 15 in.

It appears that starch concentrations are generally higher at the lower populations perhaps indicating an inverse relationship between starch and sugar levels since sugar levels were lowest for these treatments. If indeed sugar and starch levels are inversely related, the possibility exists that higher sugar levels observed at higher populations may be due primarily to a conversion of starch to sugar; possibly total carbohydrate content of leaves is not significantly altered by population. However, lack of statistical significance indicates that more work is required before definite statements can be made in regard to starch concentrations.

Nitrogen Determinations

Samples for organic nitrogen analyses were collected on two dates in 1969 and on six dates in 1970. Results show a general decrease in nitrogen content with increasing population (Table 14). Differences were not statistically significant on all dates.

Declines in leaf nitrogen levels with increasing density could involve either differential uptake of the element as influenced by population, or soil nitrogen levels which were too low to adequately supply the larger biomass produced at closer spacing. Probably the latter has more merit. While studying effects of combinations of fertilizer and population density on development of soybeans, Buttery noted a decline in nitrogen content at closer spacings and concluded that plants were competing for a substance in limited supply. However, no deficiency symptoms were noted and no interaction between fertilizer rate and population density was evident. Valle and Harmon reported that increasing the seeding rate of turnip greens from 2.5 to 10 lb per acre decreased leaf blade weight and color but apparently had no significant effect on nitrogen content of tissues. Interactions between population density and fertilizer rate were again non-significant.

Protein content is sometimes calculated as 6.00 to 6.25 times tissue levels of organic nitrogen. Since nitrogen content of snap beans declined at higher densities in these studies, lower levels of protein

Table 14. Nitrogen content (percent of dry weight) of snap bean leaves as influenced by population density at different stages of development.

Population (Plants/ft^2)	Days from Emergence										
	Expt. No. 1+		Expt. No. 2				Expt. No. 3				
	49	56	25	40	48	Mean	25	33	40	48	Mean
2.62	3.07	3.13	4.54	4.31	3.02	3.98	4.20	3.88	3.67	3.55	3.82
3.20	3.02	3.00	4.47	4.36	3.07	3.95	4.18	3.87	3.60	3.55	3.80
4.11	3.00	2.98	4.52	4.37	2.90	3.95	4.14	3.91	3.63	3.58	3.82
5.76	2.94	2.78	4.46	4.26	3.95	3.87	4.07	3.70	3.56	3.61	3.73
9.60	2.92	2.74	4.43	4.16	2.91	3.83	3.94	3.88	3.56	3.46	3.71
LSD .01	N.S.	0.24	N.S.	1.25	1.28	1.30	1.48	N.S.	N.S.	N.S.	N.S.
.05		0.32		1.66	1.70	1.72	1.97				
Mean			4.49	4.28	2.99		4.11	3.85	3.60	3.55	
				**				**			

\+ - data for five inch rows only.

N.S. - values are not significantly different.

LSD - least significant differences between means.

** - means significantly different at the 1% level.

\+ - population effects are averaged across three row spacings of 5, 10, and 15 in.

are indicated. Buttery found nitrogen content of soybean tissue to be higher at low densities thus suggesting higher protein levels. Conversely, protein content of soybean seeds appears to be higher at higher populations. Snap bean seeds may show similar responses. However, nitrogen levels in mature seeds were not tested in these studies and may be academic since snap beans are harvested before seed maturity. Protein content of dry beans could be more critical. In view of results with soybeans, it seems that both yield and protein content of dry beans may be favored by high planting density. The relationship between protein levels and population in dry beans should be thoroughly tested.

<u>Seasonal changes</u>. Nitrogen levels decreased with days after emergence in all cases (Table 14). Since total dry matter increased during the season, declines in nitrogen appear to be consistent with the concept of depletion of finite soil nitrogen levels by larger biomass as outlined above (Figure 7).

Actual nitrogen levels observed in these studies ranged from 2.9 to 4.2 percent of dry weight. Mackay et al. recommended a snap bean leaf nitrogen level of 5.1 percent as being optimal at anthesis. Since levels observed at bloom in these studies averaged 3.8 to 3.9 percent and plants showed no deficiency symptoms except for small boundary effects, it is possible that these optima are high for conditions encountered in Oregon. No differential nitrogen rates were used in this study.

When tissue levels of nitrogen and sugars are compared, an interesting relationship becomes evident. Nitrogen concentrations decline with increasing population density and days after emergence (Table 14) whereas sugar levels increase under these conditions (Tables 11 and 12). It is popularly felt that high nitrogen levels hinder carbohydrate accumulation in plant tissues. For example, Ulrich *et al.* noted that the overuse of nitrogen fertilizer may be the major factor contributing to the decline in sucrose concentration in sugar beets in California. The possibility that nitrogen levels in leaves exert a regulatory influence on sugar levels in snap bean leaves and stems seems to be probable in view of these findings. However, differential nitrogen rates must be employed in studies of this nature before the relationship can be conclusively demonstrated.

Summary and Recommendations

Reasons for the accumulation of sugar in leaves at high populations are not clear. A number of factors may be involved. As shown in the preceding section, vegetative development terminates earlier at closer plantings. Lesser demands of growth and development on carbohydrate reserves could result in a buildup in leaves. However, sugar levels began to accumulate at 25 days after germination at closer spacing. At that time plants in high population treatments were growing at a faster rate than those at lower densities and bloom had not begun. It should seem that termination of vegetative development and growth could explain differences in post-bloom sugar levels but is inadequate for explaining pre-bloom accumulation at higher densities.

The possibility that starch-sugar interconversions are involved in determining tissue sugar levels should be investigated further. As shown in these studies, differences in starch content due to population density were not statistically significantly different although a trend toward higher starch levels at closer spacings may exist. Since lower population density and associated reductions in shading are popularly felt to result in a buildup of food reserves, the possibility that total carbohydrate in bean leaves is higher under these conditions should be investigated further. Larger numbers of samples may lead to more consistent results. In these studies only 120 leaf samples were analyzed for starch content.

Nitrogen levels may exert a regulatory effect on sugar levels. Data suggest an inverse relationship between sugar and nitrogen levels. Differential rates of nitrogen fertilizer should be employed in order to quantify the relationship more exactly.

The fact that leaf sugar levels declined dramatically at bloom could be of importance. A greater diversion of assimilates to reproductive development at bloom should enhance yields. Termination of vegetative development at bloom may be desirable in snap bean varieties in this context. Experiment No. 3 should be repeated and enlarged so that patterns of sugar accumulation can be pinpointed more exactly. Tissues of the same plants should be analyzed for starch and nitrogen content. Radiotracer studies may be desirable in determining source-to-sink relationships in terms of cessation of vegetative development and fruit formation.

ASSIMILATORY RATES

Results and Discussion

Net Assimilation Rate (NAR)

Data for NAR calculations were collected as part of Experiment No. 3. Seasonal population averages show a rapid initial decline in NAR followed by a more gradual decrease with increasing population (Figure 10). Average NAR's ranged from about 75 mg/dm^2/day at the lowest population to less than 55 mg/dm^2/day at the highest. Since NAR is considered to be an approximation of net photosynthetic rate per unit leaf area for a given period of time, it appears that the average leaf was less productive at higher populations. A maximum NAR of about 70 mg/dm^2/day has been reported for three dry bean types early in the season. However, effects of population density on the NAR were not evaluated since all data were based on three-plant hills spaced 2.5 ft apart in all directions (143).

Thinner leaves are associated with competition for light. In these studies, the typical leaf was thinner at closer spacings and later in the season indicating increased competition for light under these conditions (Table 7). Limited light intensity measurements support this viewpoint since light intensity at soil level was reduced at closer spacings (Appendix Table 1). Competition for light probably accounted

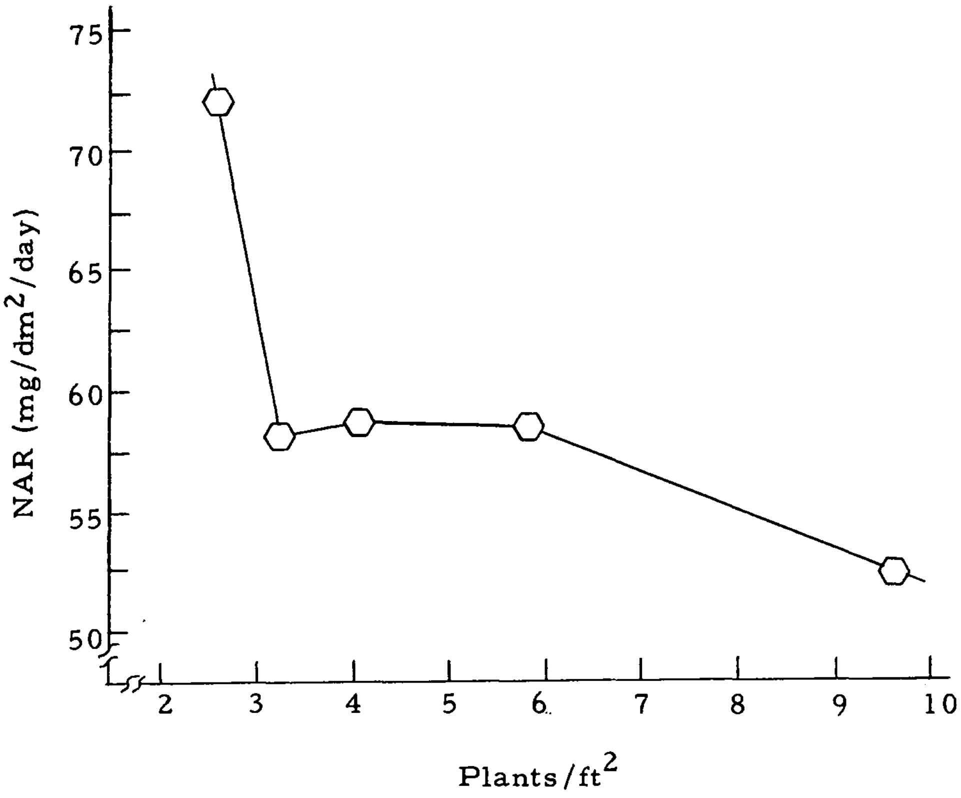

Figure 10. Net assimilation rate (seasonal averages) of snap beans as influenced by population density. (Points are averages for 5, 10, and 15 inch rows.) Experiment No. 3.

for reduced NAR at higher populations.

Additional leaf surface area at dense plantings more than compensated for reduced production rates of individual leaves. The LAI seasonal average more than doubled from the lowest to the highest population (2.62 vs. 9.60 plants/ft^2) while NAR decreased by less than one-third over the same range in population as shown:

Plants/ft^2	2.62	3.20	4.11	5.76	9.60
LAI	2.43	3.14	3.58	3.84	5.19
NAR (mg/dm^2/day	72.1	57.9	58.9	58.6	52.4

This indicates that net assimilation per unit soil area increased despite lowered NAR per unit leaf area; that is, fixation per unit leaf area and per soil area were inversely related. Furthermore, both total production of dry matter (Figure 7) and pod yield per acre (Table 1) were higher at higher populations. Closer plantings are more efficient in converting available sunlight to plant tissue on a soil area basis than are lower populations.

Net assimilation rate was highest at early to mid-season and declined considerably prior to pod maturity (Figure 11). Seasonal changes were most pronounced for close spacings with declines averaging approximately 20, 40, 40, 66, and 75 percent, respectively, for each successive increase in plant population from 2.62 to 9.60 plants/ft^2.

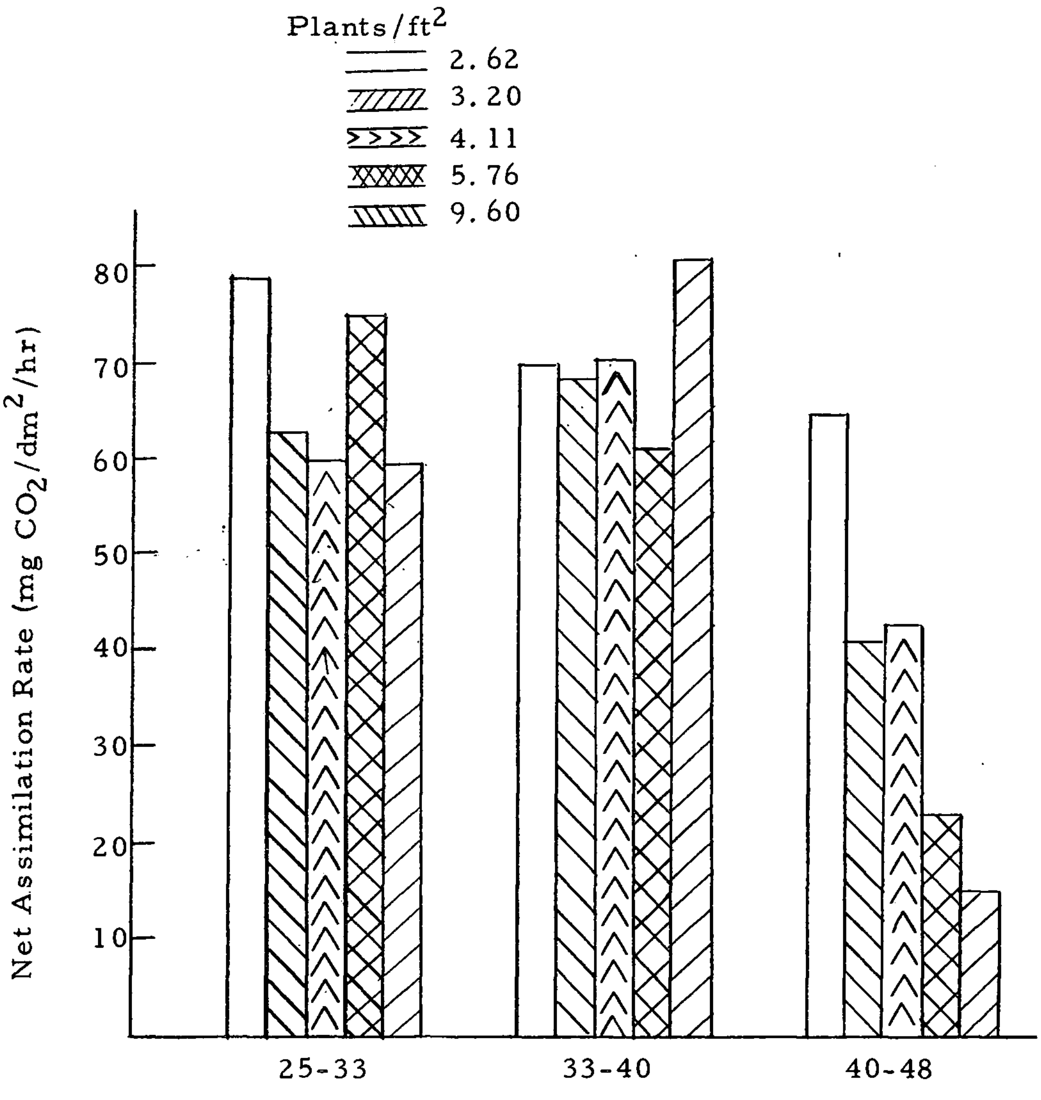

Figure 11. Seasonal changes in net assimilation rates of field grown snap beans as influenced by population density. Values represent population averages for 5, 10, and 15 inch rows. Experiment No. 3.

As shown in an earlier section, vegetative development terminated earlier at populations of 5.76 and 9.60 plants/ft^2 as compared to 2.62 and 3.20 plants/ft^2 (Section 2). The fact that NAR declined earlier and more dramatically at these arrangements suggests that the two may be related (Figure 11). Cessation of vegetative development may account for larger declines in NAR since leaves would have senesced earlier and become relatively inefficient at closer plantings. In addition, continued vegetative development at lower populations may have had a promotive influence on the photosynthetic apparatus.

Declines in NAR at close spacing did not appear to influence relative pod yield since pod weight per total weight and pod weight per unit leaf area were not significantly different at different populations (Table 3).

Net Photosynthesis (P_n)

Fixation per unit leaf area. Net CO_2 fixation rates per unit leaf surface declined with increasing population at both mid-bloom and maturity (Figure 12). Results are consistent with earlier findings for NAR (Figure 10) in that both techniques show declines in CO_2 fixation rates with increasing LAI and plant population.

Declines in leaf efficiency are often attributed to increased mutual shading and subsequent drops in average light intensity per unit area at closer plantings. Leaf area index values in the assimilation

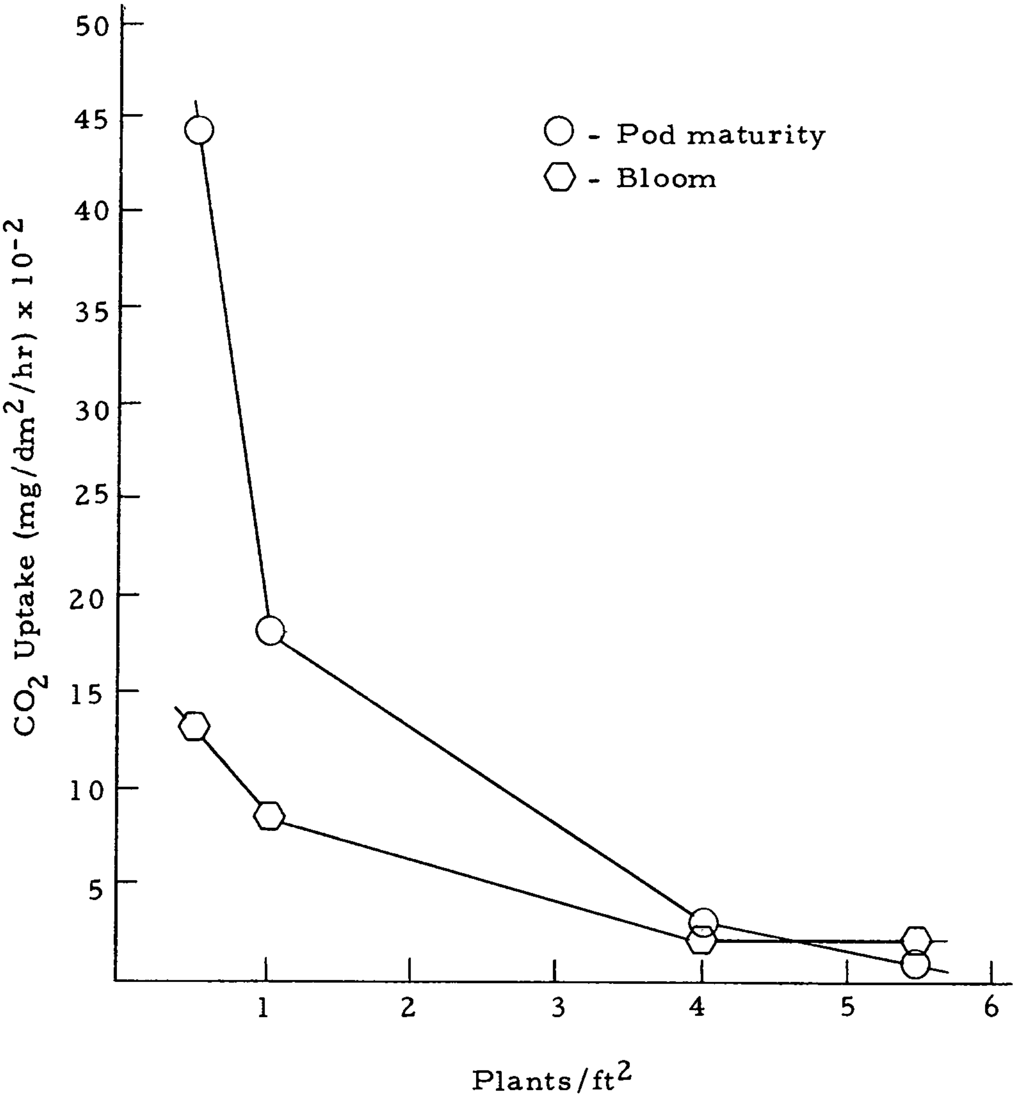

Figure 12. Net CO_2 uptake of snap beans per square decimeter of leaf at two stages of development as influenced by population density. Plants were cultured at populations of 0.5, 1.0, 4.0, and 8.0 plants/ft^2. Experiment No. 6.

chamber were calculated with the following results:

	Bloom				Maturity			
Plants/ft^2	0.50	1.00	4.00	5.50	0.50	1.00	4.00	5.50
LAI	0.30	0.66	3.30	5.30	0.30	0.62	3.95	4.55

At the two highest populations, mutual shading of leaves was pronounced so that lower leaves received only limited light intensity. Reduced light intensity per leaf could be responsible for lower Pn and NAR's.

Both Pn and NAR declined rapidly with increasing population at first and then more gradually. As shown by Figure 12, fixation rates at the lower populations were higher at pod maturity than at mid-bloom despite comparable LAI values. Reasons are not clear. On the average leaves were older at the latter date and should have been less efficient according to the literature. Furthermore, NAR measurements in the field indicated a decline toward the end of the season or with increasing age (Figure 11).

One could consider greater efficiency at maturity to be due in part to photosynthetic sink effects as represented by fruit load, or to circadian rhythms in photosynthetic rate. Neither possibility appears to be satisfactory.

Increases in photosynthetic rates due to sink effects have been suggested (7, 46, 132). However, sink effects appear to be most pronounced when growth of reproductive organs is maximal at bloom or early fruit expansion. Since pods were mature at the second sampling, a sink effect appears improbable. Similarly, the importance of circadian rhythms in regulating photosynthetic rates in these studies is questionable. Plants were placed in the laboratory under low light and moderate temperatures at least one full day before actual fixation rates were measured in order to minimize predisposing effects of high light intensity or water stress.

Overall population effects were similar for the two dates in that Pn per unit leaf area declined with increasing population. Therefore, it appears that general trends for either group of samples are consistent with available literature and with the other group. Discrepancies arise when the two dates are compared in terms of whole-chamber absolute fixation rates.

Net photosynthesis appeared to be higher at pod maturity for the two lower populations of 0.5 and 1.0 plants/ft^2 (Figures 12 and 13). Since leaf area and biomass did not differ greatly between the two sampling dates and in view of advanced leaf age at the latter date, it appears that increased LAI or leaf efficiency cannot account for observed responses. The remaining possibility is that the new detectors at maturity lead to consistently lower CO_2 readings at a given level which would have indicated erroneously high fixation rates.

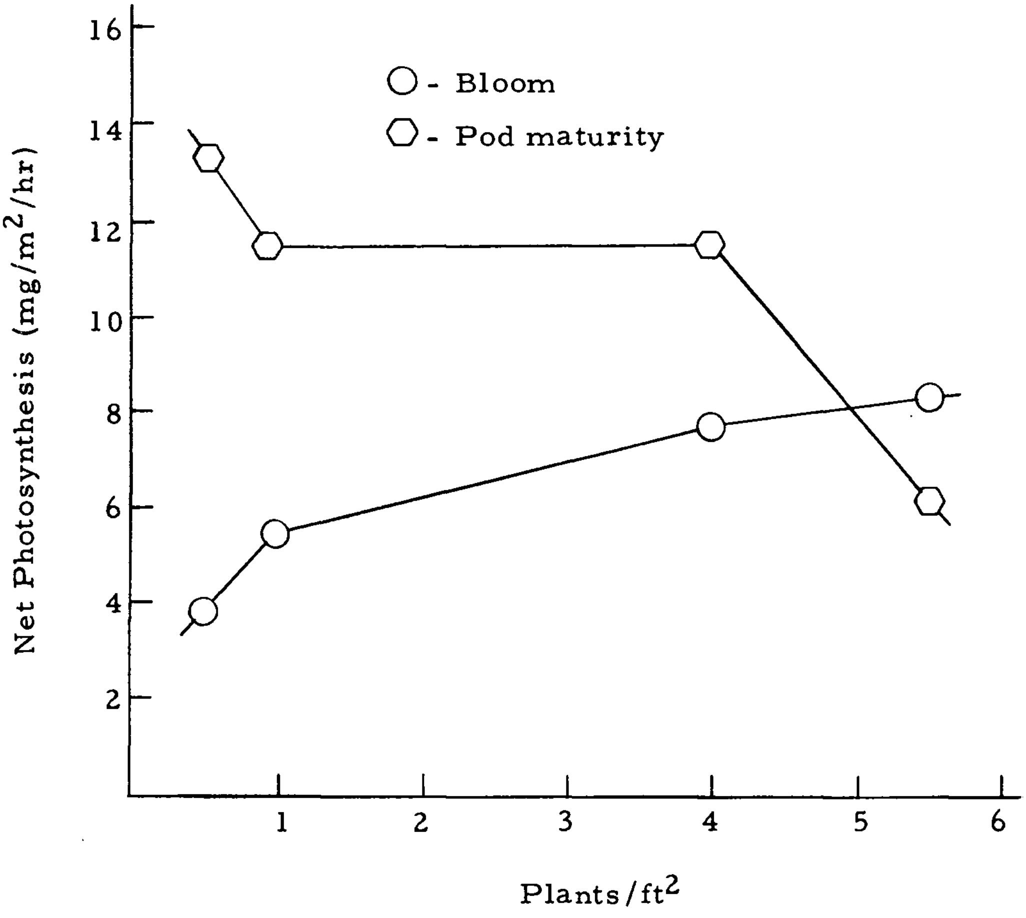

Figure 13. Net photosynthesis of snap beans as influenced by population density. Plants were cultured at 0.5, 1.0, 4.0, and 8.0 plants/ft^2. Experiment No. 6.

Ormrod studied net carbon exchange rates of snap beans grown in a controlled-environment chamber at 1500 ft-c from a mixed fluorescent source. He reported fixation rates of about 0.5 $mg/dm^2/$ hour at 3,000 ft-c which was the intensity employed in these studies. Similar values were obtained at pod maturity for the lowest plant population in these investigations (Figure 12). However, Ormrod's plants were grown at low light intensity and other conditions not normally encountered in the field. In addition, LAI's were somewhat artificial since plants were confined with wire hoops in the chamber.

General Considerations

Results of NAR studies were variable. Due to the nature of calculations involved, small deviations in leaf area or plant weight were considerably magnified. It would appear that extreme care must be taken in order to obtain consistent readings. Other workers have grown plants in three-plant hills at extremely wide spacings in order to eliminate competition and increase plant uniformity. This type of arrangement does not simulate actual field conditions, however.

Gaastra found several problems to be associated with infrared CO_2 analysis including (1) CO_2 stratification, (2) excessive leaf temperatures, (3) inadequate air circulation, (4) insufficient air-flow rates, (5) soil respiration effects, (6) pressure changes, (7) failure to reach steady-state conditions, and (8) plant height influences on light intensity at canopy level.

Attempts were made to eliminate several of the above problems in these studies by (1) installation of a fan to provide air movement, (2) use of a water filter to limit heat buildup, (3) attainment of steady-state conditions before readings were taken, and (4) sealing pots with plastic bags to minimize soil respiration effects. Despite these precautions, problems were encountered. Leaks around the chamber bottom were difficult to eliminate because of a slight pressure buildup, for example. Steady-state readings for respiration were unattainable for the second sampling at pod maturity since CO_2 content of the air-flow to the recorder continued to rise slowly, perhaps due to insufficient air-flow rates through the assimilation chamber.

Ormrod concluded that many readings should be taken with the infrared CO_2 analyzer before generalizations can be made and furthermore that interpretation of infrared work should be strictly confined to overall net CO_2 exchange. These studies are consistent with that viewpoint.

Summary and Recommendations

Results of NAR and Pn studies were variable. Measurements of net photosynthesis or Pn should be repeated with a few modifications. These investigations were plagued by detector malfunction and air-flow rates which were slightly too low. Flow rates were 12L per hour and should have been about 60L per hour for best results. A larger number of runs at a range of light intensities and plant populations should be conducted in order to fully determine response patterns.

In spite of considerable variability, results of assimilatory studies indicate a general decline in productivity per leaf area at higher populations and an increase in fixation per soil area in accordance with reports for other crops. Further NAR studies should be performed in order to determine fixation rates in terms of pod yield. The apparent relationship between cessation of vegetative growth and NAR should be further investigated.

Although results were variable, NAR studies should be performed in a fairly typical cropping situation where plant interaction may be substantial. Extrapolation of results obtained in the laboratory or in three-plant hills at wide spacing to the field may lead to considerable error. Pn studies using an assimilation chamber and infrared analysis should be on a scale large enough to allow for considerable plant interaction as would occur in the field.

Both NAR and Pn studies using an infrared analyzer hold considerable promise for photosynthetic studies and probably should be done in conjunction with each other. Both techniques entail considerable difficulty in application and use.

SUMMARY AND CONCLUSIONS

'Gallatin-50' snap beans responded to increasing plant population by producing higher yields per acre and reduced yields per plant. Effects of planting arrangement or row spacing were variable. In one of three plantings tested, pod yields decreased progressively with increasing row width, or with non-uniformity of arrangement. Due to the lack of consistency of row width effects, however, it appears that small departures from squareness may not affect yield significantly. Costs of harvest and seeding may be more important in determining row widths to be used than prospective yields at widths of 5 to 15 inches.

Higher yields per acre at the higher planting rates were a direct result of increased numbers of flowers and pods afforded by greater numbers of plants. Numbers of flowers and pods per plant decreased with increasing plant populations. Total yield and the leaf area index, or LAI, were significantly positively related for Experiments No. 2 and 3. However, variation in LAI accounted for less than 30 percent of the variation in yield. The relatively poor correlation may have been due to the fact that leaf area in excess of LAI 5.0 was probably wasted since 95 percent interception probably occurred at lesser leaf areas.

Despite the fact that yield and LAI were positively correlated, it seems possible that yield may have been limited by greater reproductive sink capacity at higher densities as represented by larger numbers of flowers and pods. Defoliation studies at various planting rates should be performed in order to clarify the situation. If defoliation at fairly high densities did not lead to reduced yields it could be assumed that LAI is not yield-determining for snap beans.

Morphological studies showed a reduction in weight and leaf area of plants grown at higher densities. Numbers, average surface area, and thickness of leaves declined with increasing density; leaf thickness decreased with days from emergence. Thinner leaves are considered to be indicative of competition for light and on this basis it should seem that competition increased with both increasing plant population and days from emergence. Similarly, light intensity measurements at soil level indicated increased interception at higher populations. Therefore, it is likely that competition for light accounted in large part for observed plant responses in these studies.

The leaf area index, or leaf surface area per soil area, increased with increasing population density. Rates of increase were also influenced by planting rate. In general, LAI increased faster at the higher populations early in the season, i. e. , prior to bloom, but at a slower rate later in the season. Rates of weight gain, increase in leaf number and, to a lesser extent, plant height increase showed similar patterns. Thus, morphological studies show an earlier cessation of vegetative growth at closer plantings. Plants grown at lower populations continued vegetative development at a relatively constant rate throughout the season.

Treatments resulting in highest LAI's also lead to increased yields and total production of dry matter probably as a consequence of increased light interception. Since yields were highest and vegetative growth ceased earliest at closer plantings, snap bean varieties which terminate vegetative development at or shortly after bloom may result in higher yields and increased economic return to growers.

Total and reducing sugars were generally higher at higher population densities. Several factors may be involved. Earlier cessation of vegetative growth and development at closer plantings may account in part for higher sugar levels for these treatments. It seems logical that reduced vegetative demands may allow for an accumulation in the tissues. Possibly population effects on starch-sugar interconversions are also involved. Starch levels tended to be lower at higher densities in a manner consistent with this line of reasoning. However, differences in concentration were statistically non-significant at the 5% level.

Nitrogen concentration in leaves declined with increasing population density in all cases. Thus foliar levels of sugar and nitrogen were inversely related. Furthermore, sugar levels increased with days after emergence while nitrogen levels declined. In view of this information and supporting reports in the literature, it seems probable that nitrogen levels exert a regulatory influence on sugar content of snap bean leaves. Differential rates of nitrogen fertilizer should be employed in further studies of this nature in order to quantify the relationship more exactly.

Leaf sugar concentrations for Experiment No. 3 showed a dramatic decline corresponding in time with early bloom. Similar concentration drops may have been obscured for other plantings since sampling did not coincide with anthesis. New substrate demands of fruiting in combination with pre-existing vegetative demands may account for the drop in concentration. Gradual post-bloom increases in sugar levels may be due to declining vegetative growth and associated demands for carbohydrate or, as noted above, to decreasing nitrogen levels.

Since population density did not influence ratios of pod weight per plant weight and pod production per unit leaf area, a relationship between sugar levels and sink size on a relative basis may be of little consequence. Yields of individual plants and sugar concentrations were significantly negatively correlated for Experiment No. 3, however. Higher sugar concentrations did not seem to enhance fruit set since percent set was fairly constant across populations.

Reduction in nitrogen levels at higher populations and later in the growing season appear to have involved a dilution of the available soil nitrogen complement by larger plant biomass under these conditions. Interestingly, yield per acre and leaf nitrogen levels were negatively related in these studies. This suggests the intriguing possibility that fairly low nitrogen levels may favor fruiting in snap beans at high populations due to a reduction in vegetativeness. Plants lowest in nitrogen ceased vegetative development earliest in accordance with this concept.

Plant morphology will probably be the ultimate limiting factor in high density plantings of snap beans. A relative reduction in leaf area is of the utmost importance. Not only does excessive leaf area result in increased respiratory demands on substrate levels and thus deprive reproductive processes, but excess foliage may also result in poor air circulation which leads to fungal and bacterial disease problems under humid conditions. Furthermore, light interception is approximately maximal at LAI's below ultimate leaf areas obtained in these studies. Reductions in leaf area and perhaps leaf size should be immediate goals of snap bean breeders.

Both net assimilation rate studies in the field and net photosynthesis measurements using infrared analysis in the laboratory show reduced fixation rates per unit leaf area at higher plant densities. Lower light intensity at closer plantings probably accounts for these trends. Infrared studies also indicated a rapid increase in whole-chamber CO_2 fixation rates up to intermediate densities and a more gradual increase thereafter at bloom. Results of studies at pod maturity show an essentially opposite response with fixation being highest at low populations. Trends at bloom appear to be more consistent with the literature.

Carbon-dioxide fixation rates per unit leaf area and on a whole-chamber basis were higher at pod maturity than at bloom for the lower populations of 0.5 and 1.0 plants/ft^2 despite comparable LAI's and biomass in the chamber. Possibly discrepancies between the two samplings may be due to (1) relatively lower CO_2 readings at a given concentration with the new detectors used at maturity and (2) relatively advanced leaf senescence and subsequent reduced photosynthetic efficiency at higher populations for the latter sampling.

Recalculation of net assimilation rate data from Experiment No. 3 in terms of CO_2 fixation per soil area indicated higher assimilatory rates at closer plantings despite lowered fixation per unit leaf area. Furthermore, both total production of dry matter and yield per acre were higher at closer plantings indicating that high density plantings are more efficient in fixing carbon on an acre basis.

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APPENDIX

Appendix Table 1. Light intensity at soil level in snap bean plantings in the field.

Population (Plants/ft^2)	Days from Emergence			
	1969+	1970++		
	44	27	34	39
2.62	1516.7	9.83	10.68	6.87
3.20	987.5	9.31	9.04	5.86
4.11	1295.8	9.39	9.21	6.58
5.76	320.8	8.61	8.50	5.39
9.60	457.2	7.03	7.09	4.71

\+ - values represent averages of readings in foot-candles by use of a Weston illumination meter for five-inch rows only.

++ - values represent numbers of pages of ozalid paper (super sepia - Keuffel & Esser, Seattle, Washington) exposed according to the method of Friend (52). Populations are averaged across three row widths of 5, 10, and 15 inches.

Appendix Table 2. Soil moisture tension in bars at 3 and 6-inch depths as influenced by population density in 5-inch rows. June, 1970.

Population (Plants/ft^2)	Days from Emergence											
	18		19		29		41		50		56	
	3"	6"	3"	6"	3"	6"	3"	6"	3"	6"	3"	6"
2.62	1.55	0.90	2.12	1.18	2.42	1.16	3.57	2.60	3.55	2.26	1.37	0.84
3.20	1.43	0.96	2.02	1.34	2.58	1.26	3.07	2.05	3.85	2.35	1.25	0.58
4.11	1.76	1.20	2.22	1.56	2.88	1.53	4.77	2.65	3.62	2.73	1.34	0.95
5.76	2.02	2.16	2.48	2.58	3.28	1.33	4.20	2.08	4.88	2.37	2.10	0.71
9.60	3.46	2.40	3.83	2.89	2.67	1.68	3.50	1.97	3.58	1.99	1.24	0.67
	**	**	**	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. - values are not statistically significantly different.
** - differences are statistically significant at the 1% level.

Note: Figures are based on moisture block readings at 4-6 days after irrigation. Each population value is an average across three row-widths.

Appendix Table 3. Effects of population density on CO_2 exchange at steady-state conditions. Experiment No. 6.

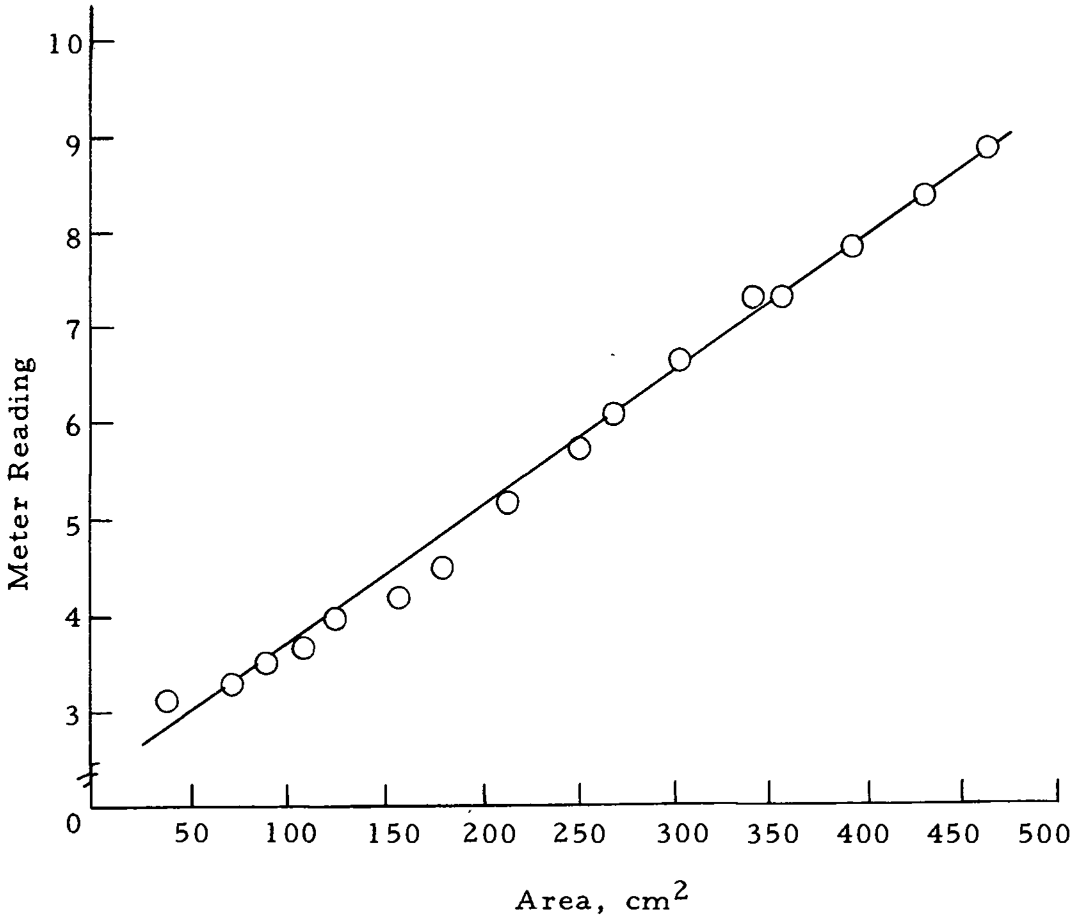
	Bloom			Pod Maturity		
($Plant/ft^2$)	ppm	mg/m2/hr	ml/12L/hr	ppm	mg/m2/hr	ml/12L/hr
0.5	315	3.95	0.75	112	13.5	2.55
1.0	235	5.56	1.05	140	11.5	2.13
5.0+	205	7.78	1.47	140	11.5	2.13
8.0+	185	8.41	1.59	225	6.3	1.20

ppm - CO_2 concentration in parts per million in the assimilation chamber at steady-state conditions.

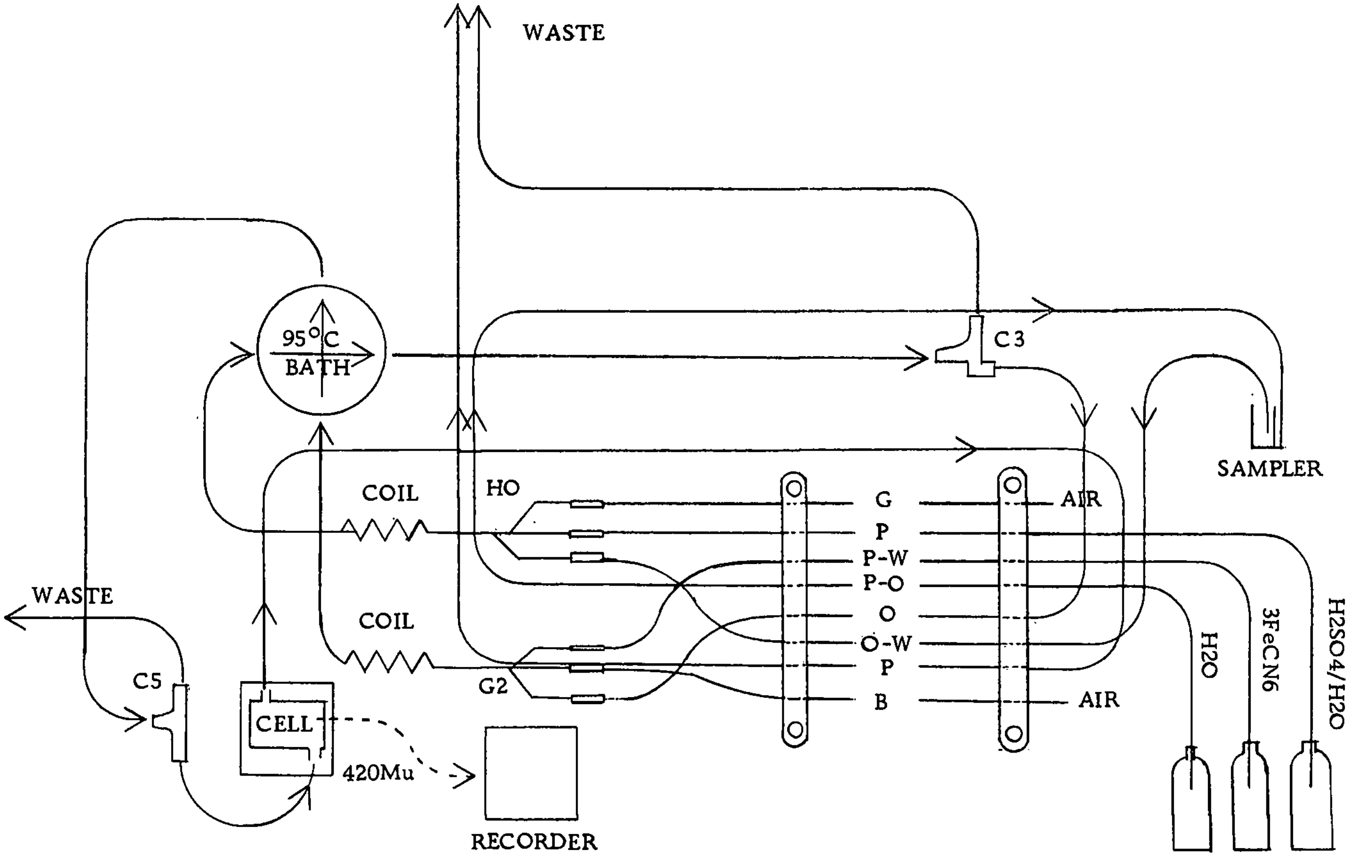
mg/m2/hr - mg of CO_2 fixed per square meter of cabinet bottom per hour.

ml/12L/hr - milliliters of CO_2 removed from the air-flow by photosynthesis.

+ - since chamber space was limited, the two higher populations were 4.0 and 5.5 plants/ft^2, respectively, in the chamber.



Appendix Figure 1. Calibration curve for the "air-flow planimeter". Area figures represent square centimeters of graph paper of various sizes and shapes.



Appendix Figure 2. Flow diagram for sugar determinations using the Technicon Autoanalyzer. Arrowed lines indicate tubing and direction of flow. Tube size is indicated by letter codes.