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CANOPY ARCHITECTURE, LIGHT DISTRIBUTION, AND
PHOTOSYNTHESIS OF DIFFERENT DRY BEAN (*Phaseolus
vulgaris* L.) PLANT TYPES

presented by

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CANOPY ARCHITECTURE, LIGHT DISTRIBUTION, AND PHOTOSYNTHESIS OF DIFFERENT DRY BEAN (*Phaseolus vulgaris* L.) PLANT TYPES

By

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ABSTRACT

CANOPY ARCHITECTURE, LIGHT DISTRIBUTION, AND PHOTOSYNTHESIS OF DIFFERENT DRY BEAN (*Phaseolus vulgaris* L.) PLANT TYPES

By

Carlos Antonio Burga Mendoza

Crop architecture characteristics related to light penetration in the canopy, crop photosynthesis, and dry weight partitioning were studied in four dry bean (*Phaseolus vulgaris* L.) plant types: a) MSU experimental line 31908, a narrow bush type (CIAT type I), b) cultivar Seafarer, a normal bush type (CIAT type I), c) cultivar NEP-2, a narrow erect, short vine type (CIAT type II), and d) MSU experimental line 0686, a determinate but very vigorous vegetative type (resembling CIAT type III). Plant spacing (47, 20, and 9 plants/m^2) and light environments (full and 50% sunlight) were used to modify canopy architecture.

The vertical distribution of the area of green leaves in the crop profile varied during the course of the growing season. Seafarer attained its maximum LAI at approximately the same plant height, 10 to 30 cm from the bottom, during the period of 30 to 72 days after planting (dap). NEP-2, lines 31908 and 0686 had distribution curves nearly symmetrical with respect to maximum LAI at the middle of the plant height at 30 to 72 dap, thereafter the maximum shifted to higher plant layers.

Light distribution in the plant canopy changed with plant height in an exponential manner and fit Bouguer-Lambert's law. Relative light interception was closely associated with LAI and both had similar trends during plant development. Light penetration was greatest in Seafarer and lowest in the line 31908. NEP-2 and line 0686 showed intermediate values. LAI, leaf angle, percent of ground cover, and extinction coefficient accounted for 99.22% of the variance in light penetration.

Seafarer and NEP-2 could be classified as erectophile and planophile foliar structure, respectively, using de Wit's system. Neither Seafarer nor NEP-2 had leaves oriented with more frequency in or toward any azimuth. Light environments did not affect spatial bean leaf orientation.

Photosynthesis rates increased from bottom to top leaves of Seafarer and NEP-2. Maximum CO_2 uptake rates for each plant stratum occurred at the time of initial pod filling. The shade environment decreased CO_2 uptake rates but similar trends were observed under both light environments.

The ontogenetic patterns of dry weight distribution among plant organs suggested a movement of materials from leaves to stems to pods. Similar trends were observed for stem dry weight and starch accumulation in the stems during the growing season. Storage material translocation from stems to pods was affected by plant spacing.

To Cesar and Carol, my lovely children

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INTRODUCTION

Two principal physiological processes can be considered for improvement of crop yields: photosynthate production and photosynthate partitioning to the economically important organs. Photosynthate production is affected by: 1) the properties of the leaves comprising the stands, such as their stomatal number and behavior, response of the mesophyll cells to irradiance, reflectance and transmittance properties, effects of temperature on dark respiration and photorespiration, and their physical resistances and carboxylation characteristics, 2) by the architecture of the stands, including the total leaf area covering a unit area of ground, leaf distribution along the stem, and the angle of leaf inclination from the horizontal, and 3) by ambient climatic factors, such as air temperature, wind speed, CO_2 concentration, relative humidity, soil moisture, and nutrient availability.

The potential for increasing crop productivity by optimizing canopy structure has been documented by experimental research, modeling, and computer simulation. Pendleton *et al*. (1968) working with isogenic corn hybrids differing in leaf angle and mechanically changed the leaf orientation observed increases in grain yield on corn hybrids with more vertically oriented leaves. Tanaka *et al*. (1969) working with rice, demonstrated by mechanical manipulation that a horizontally-oriented leaf canopy showed low photosynthetic rates and a plateau-type response of photosynthesis to LAI while an erect-leaved canopy showed a high photosynthetic rate and

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increased its photosynthesis with increasing LAI. The higher photosynthetic activity of an erect-leaved canopy produced a higher grain yield.

Assimilate partitioning is a very dynamic process and varies with the stage of plant development. In the vegetative stage of dry bean (Phaseolus vulgaris L.) plants the distribution of assimilates is dominated by proximity between the "source" and "sink", although a phyllotactic pattern is superimposed. After flowering, when the developing pods become major sinks, there is a more complex pattern, although the relationship between leaves and pods in their own axils still predominates. Both the use of $^{14}CO_2$ as a tracer, and changes in dry weight of specific organs have been important tools in helping to understand assimilate distribution, but many important aspects of this process, i.e., mechanism(s) of regulation, redistribution of storage assimilates, etc., still remain to be studied in order to provide guidelines for the increase of yields by manipulation of photosynthate partitioning.

The objectives of this investigation were to define comprehensively those canopy architecture characteristics relevant to light penetration in the canopy, to measure light penetration, canopy photosynthesis and ontogenetic carbohydrate partitioning. For these purposes four dry bean genotypes differing in growth habit were selected and grown under conditions of differential plant spacing and light environments in order to modify the above mentioned characteristics.

CHAPTER 1

LITERATURE REVIEW

Canopy structure

Measurements of canopy structure. The canopy structure of a plant stand can be characterized by the vertical and horizontal distribution of leaf area and by its spatial inclination and orientation. Several methods and kinds of equipment have been devised and used for determining canopy structure.

The stratified foliage clipping method of Monse and Saeiki (1953) was devised to determine the vertical profiles of each plant element within the canopy. For stratified sampling, a number of horizontal layers are cut from a rectangular or circular sampling area and the foliage area in each layer is determined separately.

Foliage inclination and orientation can be measured directly by holding a compass and a protractor against the foliage (Nichiporovich, 1961; de Witt, 1965; Ross and Nilson, 1967). The leaves are then classified in intervals of 10 or 15° degrees with respect to inclination and 20 or 45° degrees with respect to azimuth. It is often desirable to use a frame to delimit the sampling area and to harvest each piece of foliage as it is measured.

Loomis et al. (1968) measured leaf area index (LAI), the inclination of leaves, and leaf arrangements in corn canopies by using the so-called silhouette method. The plants are placed vertically against a chart with horizontal lines drawn at 10 cm intervals. Then, each leaf is marked at t

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the points where its midrib intersects the horizontal grid lines. The length and width of each leaf segment is measured; its inclination and stratum position are also noted.

The inclination point quadrat method was developed by Warren Wilson (1959) for non-destructive sampling of foliage area index and foliage area index and foliage inclination. The method uses a quadrat which has a probe with a sharpened steel knitting needle at its top. The probe is passed slowly through the vegetation, and each time the point touches foliage, this is recorded, together with the position, azimuth and inclination of the probe. Ten probes are generally moved in each direction (North, South, East, and West) and inclination; and the mean number of contacts $f_1.\beta$ for a given probe inclination is calculated. The mean inclination angle of leaves, β_1, and the leaf area density f_1, can be estimated by using the following relations:

$$\tan \beta_1 = \frac{\pi}{2} (0.1\ f_{1.0}/\ f_{1.90}) \qquad (1)$$

$$f_1 = f_{1.90} \times \sec \beta_1 \qquad (2)$$

where $f_{1.0}$ and $f_{1.90}$ are the mean number of contacts with leaves in the horizontal and vertical direction, respectively.

Wide-angle lens photography has been suggested by Anderson (1964) as a quick technique for recording crop structure. However, it has more often been used for measuring light penetration through tall trees than for plant architecture.

Vertical profiles of leaf area density. Monsi et al. (1973) indicated that in spite of wide differences in plant species, it is possible to recognize two main types of vertical profiles, namely grass and forb types. The grass type characterized by a leaf area density profile with its maximum in the middle height of the canopy. This plant type has been observed in rice (Oryza sativa L.), corn (Zea mays L.), and wheat (Triticum aestivum L. em. Thell.) (Ito, 1969; Ross and Nilson, 1967). The forb type has the maximum leaf area density in the upper 8th and 9th tenths of the canopy. This plant type was observed in soybean (Glycine max (L.) Merr.) and broad bean (Vicia faba L.) (Ito and Udawa, 1971; Ross and Nilson, 1967). Other types of vertical profiles of leaf area have also been observed; the sorghum (Sorghum bicolor (L.) Moench.) canopy has two peaks of leaf area density, one at the upper (7th and 8th tenths) and one at the lower (2nd and 3rd tenths) level of the canopy (Ross, 1975); and the ryegrass (Lolium multiflorum L.) canopy has most of its leaf area density in the lower 3rd level of the canopy (Warren Wilson, 1959). The difference between the leaf area density profile types is closely associated with the difference in canopy structure, particularly in leaf angle distribution. Ross and Nilson (1967) observed no changes in leaf density profile function of a corn stand during the growing season, but there was a shift of the maximum leaf density from the middle of the plant canopy, at the initial stage of growth, to a lower canopy height, as the season progressed.

Leaf distribution with respect to azimuth angle. Although crop plants seem to display leaf area equally with respect to azimuth angle, plant arrangement and planting rates may change this.

Nichiporovich (1961) presented data showing no preferred azimuth directions for wheat and corn. Similar results have been reported for soybean (Blad and Baker, 1972; Ito and Udagawa, 1971; Lemeour, 1973), Jerusalem artichoke (Helianthus tuberosus L.) (Lemeour, 1973), and broad l

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bean (Ross and Nilson, 1967). However, Ross and Nilson (1967) and Loomis and Williams (1969) reported a marked preference of corn canopies for azimuthal directions perpendicular to the direction of the planting rows. Probably this preferential orientation was related to the adaptation of the corn plant to the distribution of radiation in the canopy. Lemeour (1973) also showed that sunflower (*Helianthus annuus* L.) leaves have three preferential azimuthal directions due to the spiral phyllotaxis of sunflower and to a superimposed effect of heliotropism.

Leaf distribution with respect to inclination angle. de Wit (1965) distinguished four types of canopies based on the corresponding leaf inclination function. These functions are represented by plotting the cumulative frequency of occurence of the inclinations against the inclination, ranging from 0° for a horizontal leaf to 90° for a vertical one. Planophile canopies are characterized by a predominance of horizontal leaves, erectophile canopies by vertical leaves, plagiophile canopies by obliquely inclined leaves, and extremophile canopies by high frequencies by both horizontal and vertical leaves.

Nichiporovich (1961) suggested that the relative frequency of leaf inclinations of corn leaves was the same as the relative frequency of the inclinations of the surface elements of a sphere. This leaf angle distribution function is a special erectophile type in terms of de Wit's classification scheme, since vertical leaves still occur with more frequency.

Loomis and Williams (1969) cited several studies showing that the canopy morphology of different cultivars of corn varies widely from strongly erectophile to strongly planophile. Soybeans also have y

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canopy structures that are dependent on cultivar: Chippewa 64 and Hark cultivars are moderately planophile (Blad and Baker, 1972) while Amsoy is erectophile (Lemeur, 1973).

Leaf inclination functions may show marked changes during plant growth and with position in the plant. de Wit's data (1965) showed that for perennial ryegrass, there was an increased proportion of horizontal leaves as the season progressed. Loomis _et_ _al_. (1968) observed that the upper leaves of corn shifted to a more horizontal position after tasseling. Warren Wilson (1959) reported that clover (_Trifolium_ _repens_ L.) leaves adopted a more vertical position from the top to the bottom of the plant. Lemeur (1973) found that sunflower has a uniform horizontal foliage, older leaves have a plagiophile structure while the upper part of the plant is extremely planophile. Thus, younger leaves are more horizontal.

Heliotropic response of leaf orientation. It is known that many plants grow or move their leaves in response to the direction of illumination.

Shiman (1967) noted that sycamore maple (_Acer_ _pseudoplatanus_ L.) and lettuce (_Letuca_ _sativa_ L.) leaves had leaf inclination values which changed during the day. The maximum number of sycamore leaves with horizontal position occurred at noon, while for lettuce it was in the morning and evening. Lang (1973) found that cotton (_Gossypium_ _hirsutum_ L.) plants had leaves with orientation, azimuth angle and inclination values which were different in the morning compared to those in the afternoon. As such, 67% of the leaf area was illuminated in the morning and 71% in the afternoon.

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Shell et al. (1974) observed and measured the leaf inclination of sunflower and beans (Phaseolus vulgaris L.) in the morning, noon, and afternoon. Sunflower leaves faced east to northeast in the morning, tended to disperse during the day and then turned with the sun in the afternoon to take up a new westerly azimuth. This response decreased with age of plants; however, the younger third of the leaves of old plants exhibited similar behaviour to the leaves of young plants. Leaf inclination apparently did not change with time of day. Bean leaves had a net northeasterly azimuth in the early morning and middle of the day; this changed to a northerly azimuth in the afternoon. Again with increasing age, the tendency for a net preferred azimuth diminished. For sunflower the average phase angle (angle between the sun'vector and the vector which is the projection of the leaf, normal to the solar plane) varied from a lead angle of 16° in the morning to a lag of 15° at midday and 38° in the afternoon. For beans the average phase angle varied from a lead angle of 38° in the morning to a lag of 13° at midday and 44° in the afternoon. Wien and Wallace (1973) demonstrated that the pulvinules are the light receptor organs controlling leaflet movements in dry beans and that there are cultivar differences in this response.

Grancher and Bohomme (1972), comparing measurements on young leaves which orient in relation to the sun and using a single model in which the leaves were considered fixed, showed that the heliotropism of the leaves of cowpea (Vigna unguiculata L.) favored the interception of light in the early hours of the day, with a decrease in energy absorbed during the hot part of the day.

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Light environment within plant canopies

The radiation environment within plant canopies is composed of four kinds of radiant fluxes, i.e., direct and diffuse solar radiation fluxes penetrating the canopy and the upward and downward fluxes of complementary diffuse radiation due mainly to transmission and reflection by plant elements.

Light penetration: theoretical approach. The study of radiative transfer in a plant canopy is complicated and no satisfactory general solution has yet been found. The radiation regime in a plant canopy is determined by the following factors: a) conditions of incident radiation: direct and diffuse solar radiation and complementary radiation, b) optical properties of leaves, stems, flowers, and fruits: reflection, transmission, and absorption coefficients, and c) canopy structure.

One of the main problems in the study of radiation climatology of vegetation is how the penetration function of direct and diffuse solar radiation should be determined. Nilson (1971) classified leaf dispersion of the plant canopies into:

1. Random leaf dispersion. The random dispersion is the most popular distribution function and as such is most frequently used in radiation models. With this dispersion it is assumed that each leaf section can be found with the same probability at each position in the canopy. This leaf arrangement has a Poisson distribution. P_o, the zero term of the distribution, represents the probability that a light ray is not intercepted within a layer of the canopy. It is equal to:

$$P_o = \frac{I(f)}{I_o} = \exp(-kL) \qquad (3)$$

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where $I(f)$ = the intensity of solar radiation penetrating to a depth f in the canopy

I_o = the intensity of direct radiation above the canopy

K = extinction coefficient

L = downward accumulation of leaf area index (LAI)

2. Regular leaf dispersion. With regular leaf dispersion the leaves are assumed to be arranged in a systematic way which tends to form a closed mosaic. Mutual shading of leaves is small. The probability of light interception in the canopy is defined by a positive binomial distribution.

3. Clumped leaf dispersion. With clumped leaf arrangement there is a strong tendency for mutual shading and frequent gaps of large size are possible. The probability of light interception in the plant canopy is defined by the negative binomial distribution.

Calculation of the penetration and interception of diffuse radiation with both clear and overcast conditions is difficult and this may explain why few publications present detailed explanations of the calculations (Cowan, 1968, Anderson and Denmead, 1969). For more details the reader is encouraged to see the excellent reviews by Anderson (1966, 1971), Lemeur and Blad (1974), Ross (1975), and Saeki (1975).

Light penetration: measurements. For the measurements of radiant flux density at different heights in a crop, the Epply solarimeter (Baker and Meyer, 1966) or tube solarimeter (Szeicz, 1965) have been widely used. Photochemical methods of integrating light energy, i.e., ozalid paper, also have been used (Friend, 1961). The photosynthetically active radiation (PAR), spectrum of 400 - 700 nm wavelength,

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is adequately measured by instruments with selenium or silicon photovoltaic cells, or photo-emmission cells (Kubin, 1971).

Niilisk et al. (1970) and Ross (1975) found that the spectral distribution of penetrating direct and diffuse radiation does not change with canopy depth and is the same as for incident radiation. However, the spectral composition of complementary radiation (radiation scattered by the leaves and the ground) depends strongly on the optical properties of the foliage, and therefore its pattern is wavelength dependent.

The spectral distribution of the mean total radiation changes with depth in the canopy. The fraction of PAR decreases, especially in the blue and the red regions, whereas the fraction of near infrared radiation (NIR) increases considerably. Federer and Tanner (1966) observed that the spectral composition of total radiation differs in sunflecks and shaded areas; in sunflecks the spectral distribution is similar to that of incident total radiation, but in the shaded areas NIR predominates.

The review of the values of extinction coefficients (k) for various crops and grasses by Monteith (1969) indicates that k ranges from 1.05 for crops with horizontal leaves (cotton and clover) to 0.24 for grasses with vertical leaves (ryegrass), and exhibits diurnal variation depending on the angle of incident radiation.

Photosynthesis in relation to canopy structure

Measurements of canopy photosynthesis. Tanaka et al. (1966) observed a relationship between the photosynthetic rates of a rice stand and light intensity at different growth stages. The photosynthetic rate and saturation point of the plant population increased with age until panicle initiation, at which time there was no saturation point, and then declined. At high light intensity the upper leaves received

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light in excess of their saturation point, while the lower shaded leaves were below the saturation point and would still respond to increased light.

Tanaka (1972) demonstrated by mechanically manipulating leaf inclination that a horizontal-leaved rice canopy shows a plateau type response of photosynthetic rate to radiation, whith low photosynthesis, while an erect-leaved rice canopy shows a higher photosynthetic rate. The rice yield of the horizontal-leaved rice canopy was 70% that of the vertical-leaved rice canopy.

Pearce _et al_. (1967) reported that seedlings of Wong barley (_Hordeum vulgare_ L.) with more vertically oriented leaves had higher canopy photosynthetic rates than seedlings with more horizontal leaves, due to better light penetration. Angus and Wilson (1972) investigated the vertical profile of net photosynthesis in two wheat cultivars, one an erect leaf type and the other a lax leaf type, using a $^{14}CO_2$-technique. The patterns of net photosynthesis indicated that the localization of carbon dioxide uptake was near the top of the horizontal-leaved canopy and at the middle of the vertical-leaved canopy. Pendleton _et al_. (1968), working with isogenic corn hybrids differing in leaf angle and mechanically changing the leaf orientation of another corn hybrid, observed increases in grain yield of the corn hybrids with more vertically oriented leaves. They suggested that upright leaves permit better light penetration into the plant canopy and allow lower leaves to receive higher light intensity.

Beuerlein and Pendleton (1971) found that leaves at the top of field-grown soybean plants have higher net photosynthesis (NP) than leaves at the bottom of the plants due not to leaf age, but to acclimation to a low light regime after having been shaded by young leaves. Older leaves of debranched plants kept in full sunlight retained high NP. Johnston _et al_. (1969) found apparent photosynthetic rates of naturally shaded bottom and middle leaves to be 13 and 60% less than those of top leaves. Rates of the same bottom and middle leaves exposed to full sunlight increased by 258 and 50% respectively, but the rates were only 26 to 90% those of top leaves in full sunlight.

Turner and Incoll (1971), working with sorghum and tobacco (_Nicotiana tabacum_ L.), reported that photosynthesis declined with depth in the canopy during day light hours and was correlated with the attenuation of light by the crop and by stomatal resistance. Peet _et al_. (1977) measured the photosynthetic rates of nine bean cultivars at first flowering, early pod development, and late pod development. They found that photosynthetic rates in all cultivars differed at different developmental stages with the highest rates occurring at early pod development.

Theoretical approaches to canopy photosynthesis. Canopy photosynthesis has been theoretically studied by two methods. The first method is based upon the light interception theory and the second is based on carbon dioxide transfer theory.

Canopy photosynthesis models based on light interception theory. One of the first models for canopy photosynthesis was that of Monsi and Saeki (1953). This model was constructed on the basis of the light attenuation law within plant canopies and on the basis of light photosynthesis curves of leaves. They expressed net photosynthesis ($q = p - r$) per unit of leaf area by the following equation:

$$q = \frac{bI}{I + aI} - r \qquad (4)$$

where r indicates respiration per unit leaf area, and a and b are coefficients related to the photosynthetic capacity of a single leaf. By substituting light intensity in equation (4) by equation (3) and integrating from 0 to F for LAI, the equation for total net photosynthesis of a plant canopy (P) becomes:

$$P = \frac{b}{aK} \ln \frac{1 + akIo}{1 + akIo.\ \exp\,(-kF)} - rF \quad (5)$$

As the use of high speed digital electronic computers has stimulated the development of procedures for calculating and simulating canopy photosynthesis in relation to canopy structure, and as more mathematical theories have been developed for describing light penetration within plant canopies (Warren Wilson, 1968; Ross, 1971) numerous models for crop photosynthesis have been proposed. Advanced models have included leaf transmissibility (Saeki, 1960), type of radiation flux in the canopy (de Wit, 1965; Duncan et al., 1967), sunlit leaves on which direct and diffuse radiation flux acts (Ross, 1975), and age of the leaf (Holt et al., 1975).

Models and computer simulation of canopy photosynthesis have permitted broad generalizations as follows:

- Leaf inclination is an important factor in total crop photosynthesis. Maximum photosynthesis is found when leaf inclination changes gradually from 90° at the top layer to 0° at the lowest layer of the canopy. It has been stated that the "ideal foliage" consists of layers with continuously changing inclination so that available light is evenly spread over all available leaf area.

- Light saturation points for photosynthesis in a plant population becomes higher with increasing leaf area. The light-photosynthesis curve is markedly affected by the extinction coefficient as well as by leaf area.

- Net photosynthesis of a plant population with vertical foliage is greater than that with horizontal foliage, at a high LAI. However, at low LAI the plant population with horizontal oriented leaves shows greater photosynthesis per unit land area.

Canopy photosynthesis models based on carbon dioxide transfer theory. An alternative approach for studying canopy photosynthesis is the carbon dioxide transfer model based on the following differential equation which describes carbon dioxide exchange between the plant canopy and the surrounding atmosphere.

$$-\frac{d}{dz}\left(K\frac{dC}{dz}\right) = -f_1(z)p(z) + f_1(z)r(z) \qquad (5)$$

where:

K = turbulent transfer coefficient

C = CO_2 concentration in the air among leaves

$f_1(z)$ = the height-leaf area distribution function

$p(z)$ = height function of photosynthesis

$r(z)$ = height function of respiration

The CO_2 transfer model is suitable; and it has been used for assessing the influence of micrometereological factors, wind velocity, soil CO_2 flux, and artificial CO_2 enrichment on canopy photosynthesis (Partridge, 1970; Allen *et al.*, 1971; Lemon, 1973; Allen *et al.* 1974).

Light limitation of photosynthesis

It is well documented that the photosynthetic characteristics of many species of plants, i.e., light-dependent CO_2 uptake curves, s

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are influenced by the spectral composition and intensity of radiation under which the plant is grown.

Light intensity during growing affects leaf morphology, chloroplast structure, and a number of component processes of photosynthesis. High intensity radiation: induces additional development of the palisade and spongy mesophyll regions, resulting in thicker leaves (Pearce and Lee, 1969; Ludlow and Wilson, 1971; Bjorkman et al., 1972; Mobel et al., 1975); increases stomatal frequency (Holmgren, 1968; Crookston et al., 1971; Bjorkman et al., 1972); changes mesophyll resistance (r_m), r_m is higher in plants grown at low light (Holmgren, 1968; Ludlow and Wilson, 1971; Crookston et al., 1975); and changes the content of solube protein per unit leaf area and amount and activity of RdDP carboxylase (Blenkinsop and Dake, 1974; Crookston et al., 1975). Several factors are modified when plants are grown at different light intensities, and there is no consensus concerning any factor as the prime cause of the altered photosynthetic capacity.

Dale (1965), working with bean plants, found that leaf number was greater with high light intensity treatments and also that this effect was due to development of leaves on lateral branches. There was also an effect of radiation on leaf expansion and on the unfolding rate of leaves on the main stem. Maximum rate of leaf growth was similar for different light intensities, but the maximum rate was maintained for a longer period under high light regimes. Rajan et al. (1971), working with bean and corn plants, observed that the spectral composition of light, red/infra red ratio (ri), greatly affected plant growth. Plant height and leaf area increased as ri increased from 2.4 to 7.6, while specific leaf dry weight decreased.

REFERENCES

Anderson, M. C. 1966. Stand structure and light penetration, II. A.theoretical analysis. J. Appl. Ecol. 3: 41-54.

Anderson, M. C. and O. T. Denmead. 1969. Short wave radiation on inclined surfaces in model plant communities. Agron. J. 61: 867-872.

Anderson, M. C. 1971. Radiation and crop structure. In Sestak, Z., J. Catsky, and P. G. Jarvs (ed.) Plant Photosynthesis Production. Manual of Methods. pp. 412-466. Dr. W. Junk N.V. Publishers, The Hague.

Angus, R. and J. H. Wilson. 1972. A comparison of barley cultivars with different leaf inclination. Aust. J. Agr. Res. 23: 945-947.

Allen, L. H., Jr., S. E. Jensen and E. R. Lemon. 1971. Plant response to carbon dioxide enrichment under field conditions: Assimilation. Science 173: 256-258.

Allen, L. H., Jr., D. W. Steart and E. R. Lemon. 1974. Photosynthesis in plant canopies: Effect of light response curves and radiation source geometry. Photosynthetica. 8: 184-207.

Baker, D. N. and R. E. Meyer. 1966. Influence of stand geometry on light interception and net photosynthesis in cotton. Crop Sci. 6: 15-19.

Beuerlein, J. E. and J. W. Pendleton. 1971. Photosynthetic rates and light saturation curves of individuals soybean leaves under field conditions. Crop Sci. 11: 217-219.

Bjorkman, O., N. K. Boardman, J. M. Anderson, S. W. Thorne, D. J. Goodchild and N. A. Pyliotis. 1972. Effect of light intensity during growth of Atriplex patula on the capacity of photosynthetic reactions, chloroplast components and structure. Carnegie Inst. Washington Yearb. 71: 115-135.

Blad, B. and D.G. Baker. 1972. Orientation and distribution of leaves within soybean canopies. Agron. J. 61: 26-29.

Blenkinshop. P.G. and J.E. Dale. 1974. The effect of shade treatment and light intensity on ribulose-1,5-diphosphate carboxylase activity and fraction I protein level in the first leaf of barley. J. Exp. Bot. 25: 899-912.

Cowan, I. R. 1968. The interception and absorption of radiation in plant stands. J. Appl. Ecol. 5: 367-379.

Crookston, R. K., K. J. Treharne, P. Ludford and J. L. Ozbun. 1975. Response of beans to shading. Crop Sci. 15: 412-416.

Dale, J. E. 1965. Leaf growth in Phaseolus vulgaris L. I. Temperature effects and the light factor. Ann. Bot. 29: 293-308.

Duncan, W. G., R. S. Loomis, W. A. Williams and R. Hanau. 1967. A model for simulating photosynthesis in plant communtieis. Hilgardia 38: 181-205.

Friend, D. G. C. 1961. A simple method for measuring integrated light values in the field. Ecology 42: 577-580.

Grancher, C. V. and R. Bonhomme. 1972. Utilisation de l'energie solaire par une culture de Vigna Sinensis L. I. Etude theorique de l'influence de l'heliotropisme des feuilles sur l'intercion des rayonnements. Ann. Agron. 23: 407-417.

Holgren, P. 1968. Leaf factors affecting light-saturated photosynthesis in ecotypes of Solidago virgaurea from exposed and shaded habitats. Physiol. Plant. 21: 676-698.

Holt, D. A., R. J. Bula, G. E. Miles, M. M. Schreiber and R. M. Peart. 1975. Environmental physiology, modeling and simulation of alfalfa growth: I. Conceptual development of SIMED. Agr. Exp. St., Purdue University. Research Bull. 907. pp. 1-26.

Ito, A. 1969. Geometrical structure of rice canopy and penetration of direct solar radiation. Proc. Crop Sci. Sco. Jap. 38: 355-363.

Ito, A. and T. Udagawa. 1971. Phytometrical studies of crop canopies. I. Geometrical structure of soybean canopy and sunlight penetration. J. Agr. Meteorol. 26: 187-195.

Johnston, T. J., J. W. Pendleton, D. B. Peters and D. R. Hicks. 1969. Influence of supplemental light on apparent photosynthesis, yield, and yield components of soybeans (Glycine max. L.). Crop Sci. 9: 577-480.

Kubin, S. 1971. Measurement of radiant energy. In Sestak, Z., J. Catsky, and P. G. Jarvis (ed.) Plant Photosynthetic Production. Manual of Methods. pp. 703-765. Dr. W. Junk N. V. Publishers. The Hague.

Lang, A. R. G. 1973. Leaf orientation of a cotton plant. Agric. Meteorol. 11: 37-51.

Lemeur, R. 1973. A method for simulating the direct solar radiation regime in sunflower, jerusalem artichoke, corn, and soybean canopies using actual stand structure data. Agr. Meteorol. 12: 229-247.

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Lemon, E. 1973. Predicting crop climate and net dioxide exchange. Photosynthetica 7: 408-413.

Loomis, R. S., W. A. Williams, W. G. Duncan, A. Dovrat, and F. Nunez. 1968. Quantitative descriptions of foliage display and light absorption in field communities of corn plants. Crop Sci. 8: 352-356.

Loomis, R. W. and W. A. Williams. 1969. Producitivity and the morphology of crop stands: Pattern with leaves. In Eastin, J. D., F. A. Haskins, C. Y. Sullivan and C. H. M. Van Bavel. (ed.) Physiological Aspects of Crop Yield. pp. 27-47. Am. Soc. Agron. Madison, Wisconsin.

Ludlow, M. M. and G. L. Willson. 1971. Photosynthesis and illuminance history. Aust. J. Biol. Sci. 24: 1065-1075.

Monsi, M. and T. Saeiki. 1953. Uber den lichtfaktor in den pflanzengesellschften und seine bedeutung fur die stoffproduktion. Jap. J. Bot. 14: 22-52.

Monsi, M., Z. Uchijima and T. Oikawa. 1973. Structure of foliage canopies and photosynthesis. Ann. Rev. Ecol. Syst. 4: 301-327.

Monteith, J. L. 1969. Light interception and radiative exchange in crop stands. In Eastin, J. D., F. A. Haskins, C. Y. Sullivan and C. H. M. Van Bavel (ed.) Physiological Aspects of Crop Yield. pp. 89-111. Am. Soc. Agron. Madison, Wisconsin.

Nichiporovich. A. A. 1961. Properties of plant crops as an optical system. Sov. Pl. Physiol. 8: 428-435.

Niilisk, H., T. Nilson and J. Ross. 1970. Radiation in plant canopies and its measurements, In Prediction and Measurement of Photosynthetic Productivity. pp. 165-177. Proc. of the IBP/PP Technical Meeting, Trebon, 14-21 Sept. 1969.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. Agric. Meterol. 8: 25-38.

Nobel, P. S., L. J. Zaragoza and W. K. Smith. 1975. Relation between mesohyll surface area, photosynthetic rate and illumination level during developmentof leaves of Plectranthus parviflorus Henckel. Plant Physiol. 55: 1067-1070.

Norman, J. M., E. E. Miller and C. B. Tanner. 1971. Light intensity and sunfleck-size distribution in plant canopies. Agron. J. 63: 743-748.

Paltridge, G. W. 1970. A model of a growing pasture. Agr. Meteorol. 7: 93-130.

Pearce, R. B., R. H. Brown and R. E. Blaser. 1967. Photosynthesis in plant communities as influenced by leaf angle. Crop Sci. 7: 321-324.

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Pearce, R. B. and D. R. Lee. 1969. Photosynthetic and morphological adaptation of alfalfa leaves to light intensity at different stages of maturity. Crop Sci. 9: 791-794.

Peet, M. M., A. Bravo, D. H. Wallace and J. C. Ozbun. 1977. Photosynthesis, stomatal resistance and enzyme activities in relation to yield and field-grown dry bean varieties. Crop Sci. 17: 287-293.

Pendleton, J. W., G. E. Smith, S. R. Winter and T. J. Johnston. 1968. Field investigation of the relationships of leaf angle in corn (Zea Mays L.) to grain yield and apparent photosynthesis. Agron. J. 60: 422-424.

Rajan, A. K., B. Betteridge and G. E. Blackman. 1971. Interaction between the nature of the light source, ambient air temperature, and the vegetative growth of different species within growth cabinets. Ann. Bot. 35: 323-343.

Ross, Y. K. and T. Nilson. 1967a. The vertical distribution of biomass in crop stands. In Nichiporovich, A. A. (ed.) Photosynthesis of Productive Systems. pp. 75-85. Translated edition. Israel Prog. Sci. Trans., Jerusalem.

Ross, Y. K. and T. Nilson. 1967b. The spatial orientation of leaves in crop stands and its determination. In Nichiporovich, A. A. (ed.) Photosynthesis of Productive Systems. pp. 86-95. Translated edition. Israel Prog. Sci. Trans., Jerusalem.

Ross, J. 1975. Radiative transfer in plant communities. In Monteith, J. L. (ed.) Vegetation and the Atmosphere, Vol. II. pp. 1-55. Academic Press, New York.

Saeki, T. 1960. Interrelationships between leaf amount, light distribution and total photosynthesis. Bot. Mag. 73: 55-63.

Saeki, T. 1975. Distribution of radiant energy and CO_2 in terrestral communities. In Cooper, J. P. (ed.) Photosynthesis and Productivity in Different Environments. pp. 297-322. Cambridge University Press. New York.

Shell, G. S., A. R. G. Lang and P. J. M. Sale. 1974. Quantitative measurement of leaf orientation and heliotropic response in sunflower, bean, pepper and cucumber. Agric. Meteorol 13: 25-37.

Shiman, L. M. 1967. Determination of the orientation of plant leaves in space. Sov. Plant Physiol. 14: 326-328.

Szeicz, G. 1965. A miniature tube solarimeter. J. Appl. Ecol. 2: 145-147.

Tanaka, A., K. Kawano and J. Vamaguchi. 1966. Photosynthesis, respiration and plant type of the tropical rice plant. Int. Rice Research Inst. Tech. Bull. 7.

Tanaka, T. 1972. Studies on the light-curves of carbon assimilation of rice plants. The interrelation among the light-curves, the plant type and the maximizing yield of rice. Bull. Nat. Inst. Agr. Sci. A. 19: 1-100.

Turner, N. C. and L. D. Incoll. 1971. The vertical distribution of photosynthesis in crops of tobacco and sorghum. J. Appl. Ecol. 8: 581-591.

Warren Wilson, J. 1959. Analysis of the spatial distribution of foliage by two-dimensional point quadrats. New Phytol. 58: 92-101.

Wien, H. C. and D. H. Wallace. 1973. Light-induced leaflet orientation in Phaseolus vulgaris L. Crop Sci. 13: 721-724.

Wit, C. T. de. 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. No. 663. Center Agri. Publ. Doc. Wageningen. 57 p.

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CHAPTER 2

CANOPY ARCHITECTURE, LIGHT PENETRATION AND GROWTH CHARACTERISTICS OF FOUR DRY BEAN (*Phaseolus vulgaris* L.) PLANT TYPES

ABSTRACT

Four dry bean genotypes were selected on the basis of their different growth habits. The genotypes and growth habits were: a) MSU experimental line 31908, a narrow bush type (CIAT type I), b) cultivar Seafarer, a normal bush type (CIAT type I), c) cultivar NEP-2, a narrow erect, short vine type (CIAT type II), and d) MSU experiemental line 0686, a determinate but very vigorous vegetative type (resembling CIAT type III). Light measurements within the canopies were estimated using the ozalid paper technique of Friend (1961). Formulae used in making the calculations of growth parameters are those listed by Radford (1967). Different plant densities (47, 20, and 9 plants/m^2) were used to modify the canopy architecture.

In general, similar results were obtained for light penetration in the plant canopy and for final seed yield for the three plant spacings, independent of plant type. Vertical leaf distribution varied during the growing season. The maximum Leaf Area Index (LAI) was approximately at the middle of the plant height, which later shifted to higher plant layers for NEP-2, lines 31808 and 0686, but not for Seafarer. Light distribution in the plant canopy fit Bouger-Lambert's

law, with relative illumination as an exponential function of LAI. Light penetration in the canopy was found to be greater in Seafarer and lower in line 31908: while NEP-2 and line 0686 showed intermediate values. Relative Growth Rate (RGR) was higher for Seafarer and lower in line 31908. NEP-2 and line 0686 had intermediate RGR values. Differences in RGR were due to differences in Net Assimilation Rate (NAR) rather than in Leaf Area Ratio (LAR). RGR for any plant type was affected by plant spacing. Plant spacing did not affect the patterns of the ontogenetic partitioning of dry weight among, leaves, stems, petioles, flowers and pods for any plant type.

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INTRODUCTION

The weight of dry matter produced by a crop is essentially the integral of the crop's rate of photosynthesis throughout the growing season, and economic yield might be expected to depend to some extent on crop photosynthesis and partitioning of material to the economic plant organs. Crop architecture parameters related to light penetration in the plant canopy and leading to increased crop production, e.g., leaf inclination, have been identified; and optimizing the structure of the canopy in order to effect an improvement in crop productivity has been proposed. Most of the experimental evidence concerning the effects of leaf inclination on the processes leading to yield comes from work with graminaceous crops; very few attempts have been made with economically important dicotyledoneous crops.

The present work aims to determine crop architecture parameters relevant to light penetration and light penetration measurements, as well as ontogenetic patterns of dry weight partitioning among the plant organs of four dry bean plant types. Different plant densities were used to modify crop architecture.

MATERIALS AND METHODS

This experiment was conducted at the Saginaw Valley Bean-Beet Research farm, on a fine texture soil classified as Charity Clay Loam.

Four dry bean genotypes were selected on the basis of their differential growth habits. These genotypes and growth habits were: a) MSU experimental line 31908, a narrow bush type (CIAT type I),

b) cultivar Seafarer, a normal bush type (CIAT type I), c) cultivar NEP-2, a narrow erect, short vine type (CIAT type II), and d) MSU experimental line 0686, a determinate but very vigorous vegetative type (resembling CIAT type III). Effective planting densities of 47, 20, and 9 plants/m^2 were established by use of three spacings, 5, 10, and 15 cm within the row and a constant space of 70 cm between rows. The experimental units were arranged in a randomized block design with three replications. Each plot consisted of six rows 5.8 m long. Planting date was the second week of June, 1976. During planting, a band application of 500 kg/ha of 18 - 46 - 0 plus 4% Mn and 2% Zn fertilizer was applied. All plots received 2 cm of sprinkler irrigation during the last week of July to compensate for the deficiency in natural rainfall during that period.

The four central rows of each plot were used for periodic collection of data. Five uniformly spaced plants were harvested at weekly intervals for 10 consecutive weeks starting 30 days after planting (dap). The samples for the final harvest (normal maturity for each genotype) were taken from 2 m of row. On each date, the plants to be harvested were cut and harvested in 10 cm segments, beginning from the ground. The plant material within each section was separated into stems and petioles, flowers, pods and leaves. This material was then dried in a forced-air dryer at 45 to 50° C to a constant dry weight. For specific leaf dry weight (SLDW) determination, a sample of five central leaflets was randomly chosen from the harvested leaves of each plant height segment of each plot and their area was measured with a portable leaf area meter (Lambda Instruments Model LI-300). The leaflets were then dried as were the other plant

parts. Leaf area was determined by multiplying SLDW by the total leaf dry weight of each plant height segment of each plot in each harvest.

Light measurements were estimated using the ozalid paper technique of Friend (1961). Twelve sheets of ozalid paper (402 ZT sepia paper, Gaf Corporation, New York, NY 10020) were stapled together and then cut into packets of 2 by 2 cm. These were placed with the light sensitive side up in black-painted petri dishes of 4.0 cm diameter and 1.7 cm height. The booklets were pressed close to the cover by a foam pad in the container. Light reached the booklet through a .5 cm (diameter) unpainted "window" on the cover. The containers were sealed with plastic vinyl tape to protect the booklets from rainfall. The containers with the ozalid papers were placed at 10 cm intervals from the ground up into the canopy and between two plants in the same row. They were held by a fixed metal rod in the ground in each plot. The same location was used in sampling for amount of light penetration during the growing season. The containers were placed in position between 9:00 - 10:00 a.m. on each sampling date and collected after 24 hours. To develop the exposed booklets, they were placed in a wire basket and suspended in a coffee can which contained concentrated ammonium hydroxide. The booklets were left in the air-tight container for 1 to 3 hours. A count of the number of bleached papers gave an estimate of the amount of light for that particular plant position and date. To convert the number of papers bleached to light energy values, a calibration curve was made by exposing the ozalid papers for varying lengths of time to a light source and/or direct sunlight and directly measuring light intensity with a light meter (Lambda Instruments Model LI-170 with a quantum sensor).

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RESULTS AND DISCUSSION

In general, similar results were obtained for light penetration and final seed yield for the three plant spacings, independent of plant type. Most of the data presented will be for the 5 cm plant spacing, but remarks relating to other plant spacings will be given when appropriate.

Plant canopy and light interception

Light attenuation, percent of full sunlight and Leaf Area Index (LAI) profiles, during the growing season, of four dry bean plant types are presented in Figures 1 to 5. Some features are readily apparent. The values of LAI increased with time during the season. Maximum LAI for the four genotypes were attained at different times.

The vertical distribution of the area of green leaves varied during the course of the growing season. The maximum LAI increased (from 0.3 to 1.3) and its position shifted to higher profile layers at maximum total LAI. At the 30 to 70 days after planting (dap) stage of plant development the distribution curves were nearly symmetrical with respect to the maximum, which occurs approximately at the height of h/2, where h is the canopy height. As the plant grew the maximum shifted to higher layers (above h/2). Observations of the variation in the leaf area of individual layers revealed an increase, a maximum and then a decrease in every layer, as time progressed.

NEP-2, lines 31808 and 0686 showed the same leaf vertical profile trends as soybeans and broad beans (Ross and Nilson, 1967; Ito and Udawa, 1971). Seafarer had its maximum LAI at approximately the same plant height, 10 to 30 cm from the bottom, during the period of 30 to 72 dap. These vertical profiles are good for characterizing and

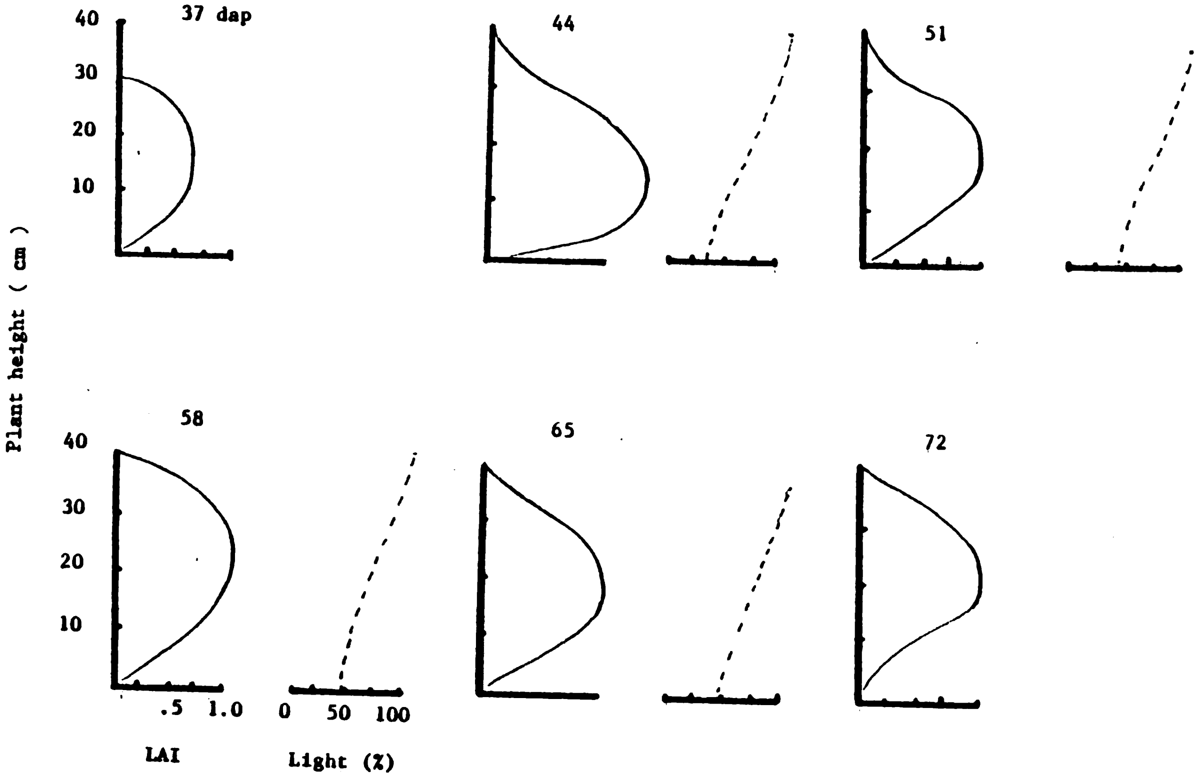

Figure 1. Light attenuation and LAI of Seafarer at 5 cm plant spacing during the growing season.

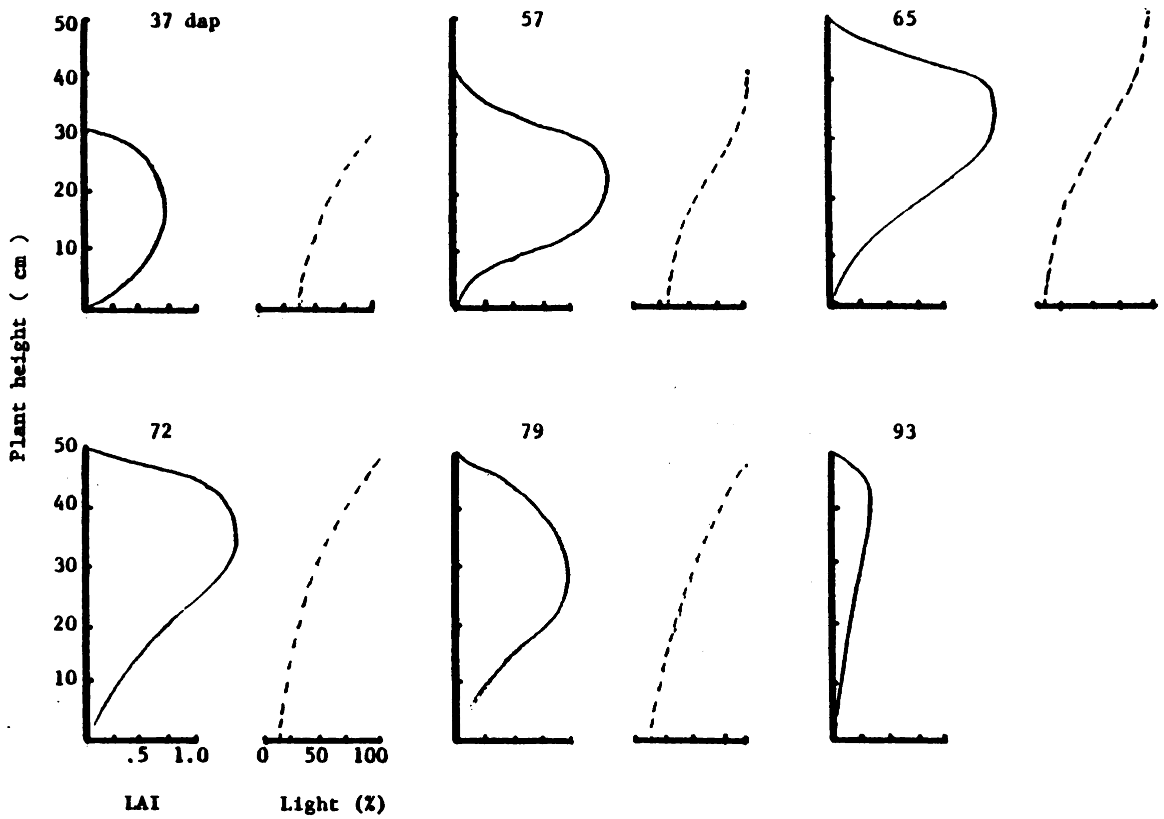

Figure 2. Light attenuation and LAI profiles of NEP-2 at 5 cm plant spacing during the growing season.

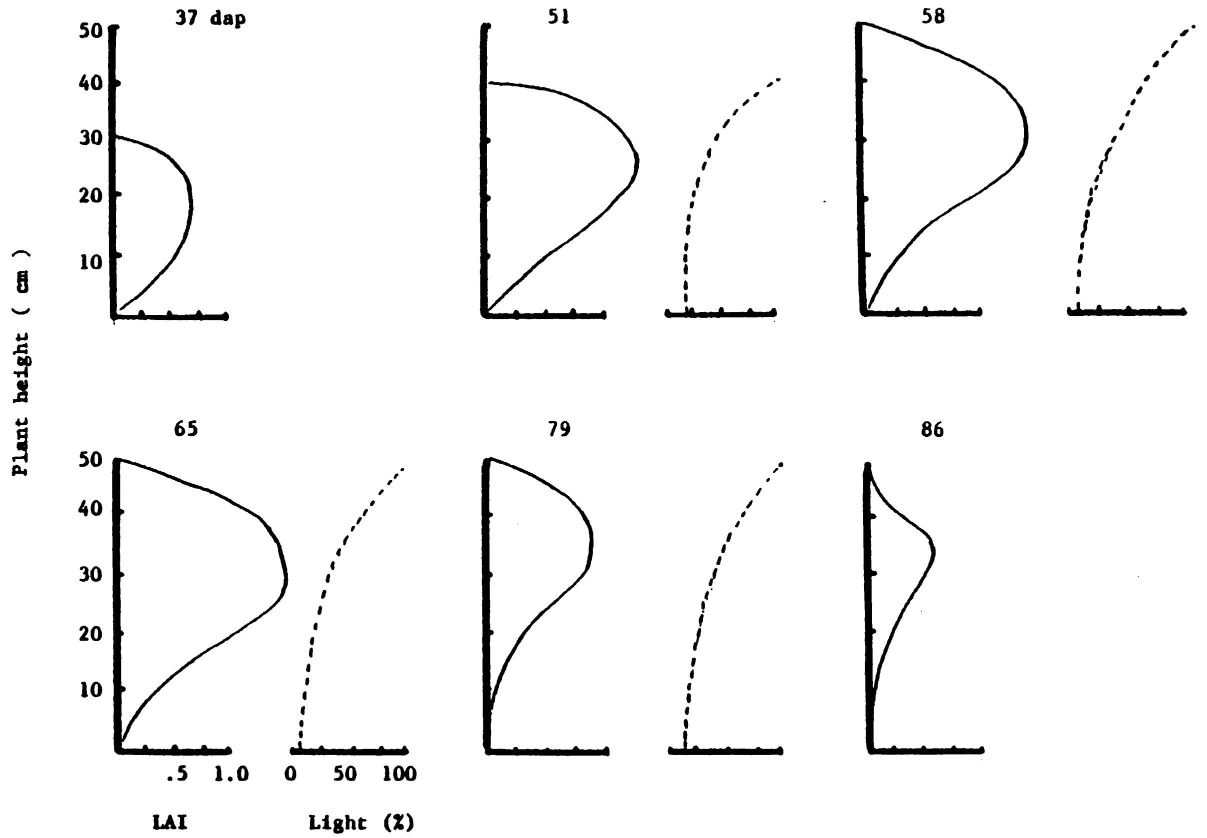

Figure 3. Light attenuation and LAI profiles of Line 31908 at 5 cm plant spacing during the growing season.

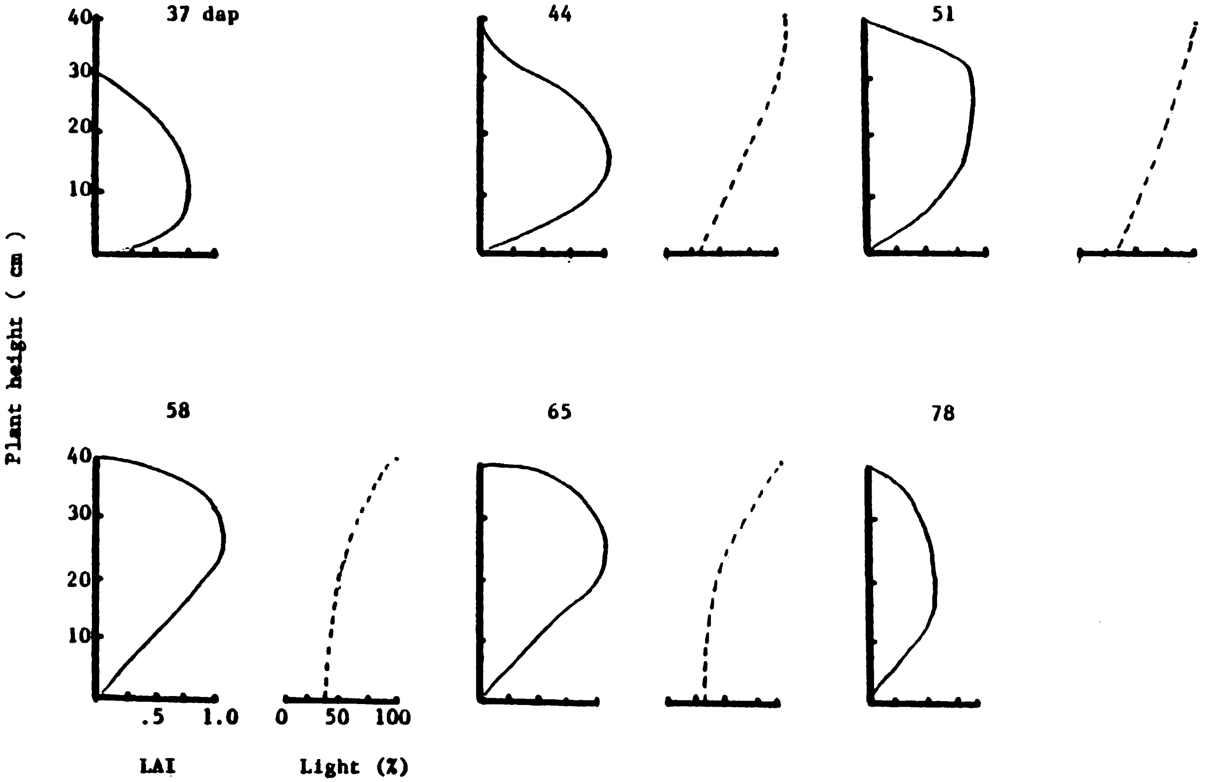

Figure 4. Light attenuation and LAI profiles of Line 0686 at 5 cm plant spacing during the growing season.

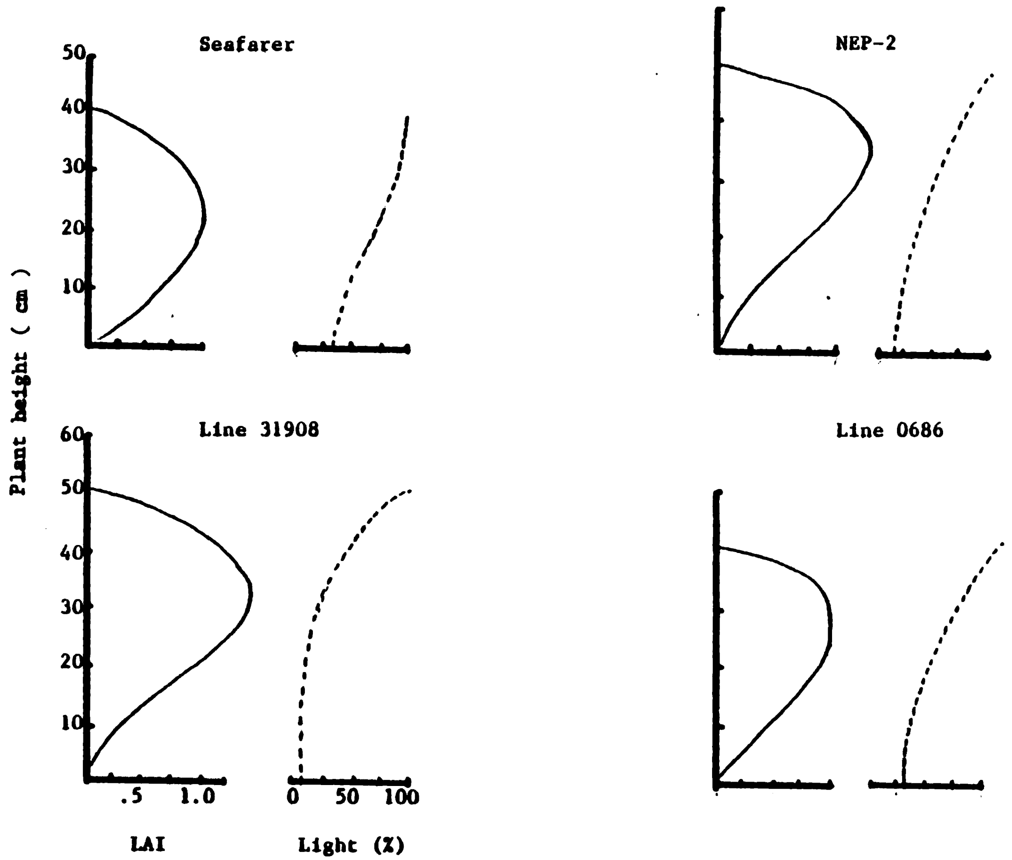

Figure 5. Light attenuation and LAI profiles at maximum LAI and 5 cm plant spacing of four dry bean genotypes.

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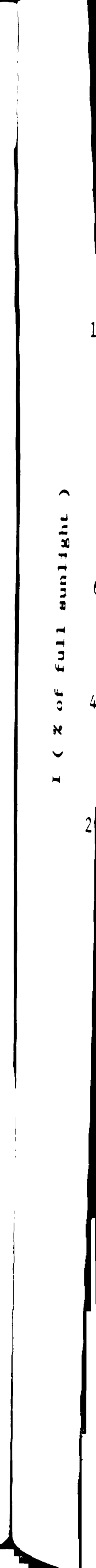
describing plant type and light penetration through the plant canopy; however, they do not provide information about the leaf disposition and dispersion with plant width or row width, i.e., if the leaves are close to the stem or more dispersed across the row.

Light attenuation profiles showed that light interception is closely related to LAI profiles. The greatest amount of intercepted light occurred at the layer(s) of maximum LAI. Light distribution in the plant canopy changed with plant height in an exponential manner and fit Bouguer-Lambert's law (equation 3), with relative illumination as an exponential function of LAI. Since the first introduction of Bouguer-Lambert's law into plant studies by Monsi and Saeki in 1953, many attempts have been made to describe light environment in crop communities. Results with broad beans (Ross and Nilson, 1967), corn (Loomis *et al.*, 1968), and soybeans (Hicks *et al.*, 1968; Lee, 1976), indicate that light distribution can be adequately characterized by an exponential function of LAI. Probably it is not the best function to be used, because its assumptions are not always met by the plants; however, its simplicity makes it the most popular equation in use.

Attenuation of sunlight by the plant canopy as a function of LAI is presented in Figures 6 to 8. Some features are apparent. Figure 6 shows that with similar LAI, these plant types intercepted different amounts of light, i.e., at LAI of 3, Seafarer intercepted 42% of sunlight, while line 31908 with the same LAI intercepted 66%. These differences are assumed to be due to differences in morphological characteristics between the plant types, such as leaf size, leaf shape, leaf angle, number of branches, etc. Figures 7 and 8 show that in each plant type, light interception, during the growing season, was greatly associated with LAI. The light interception data are grouped


I (% of full sunlight)

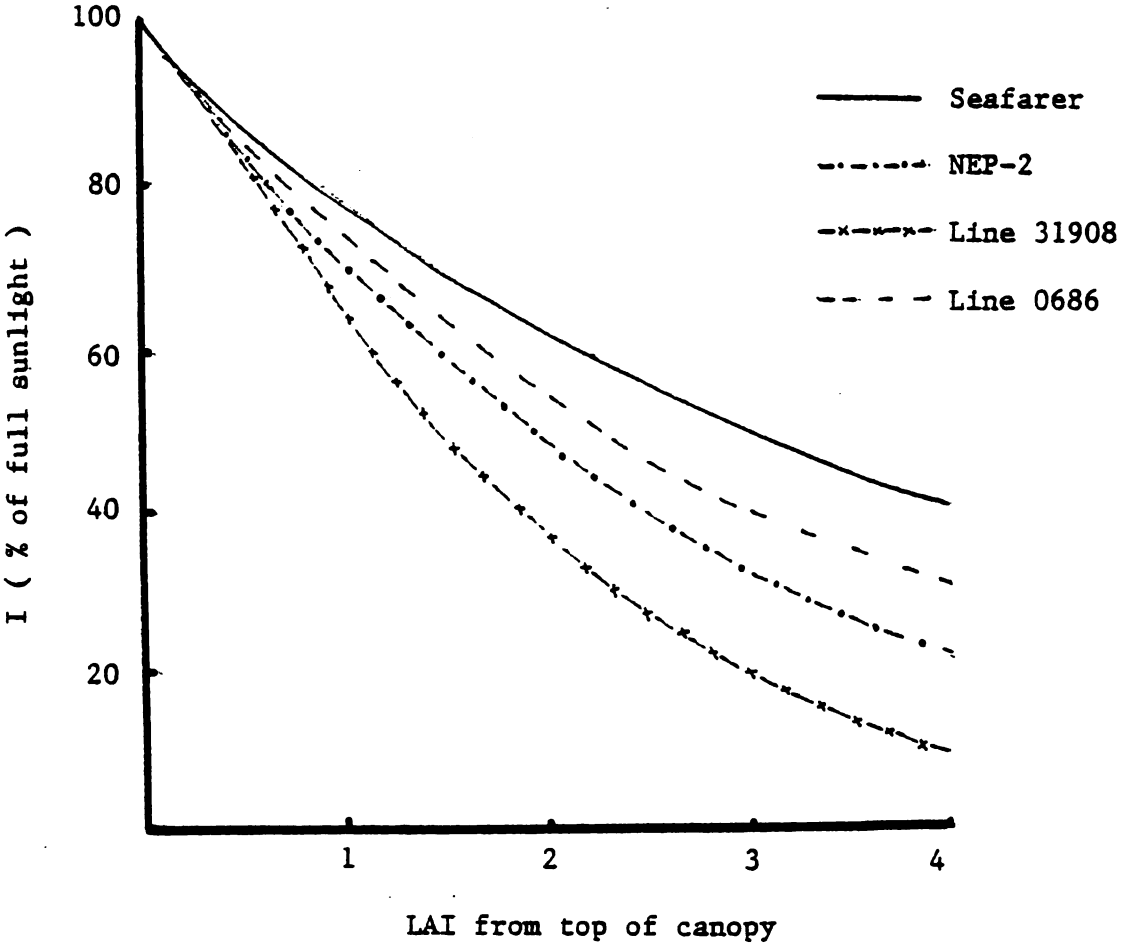


Figure 6. Attenuation of sunlight by the canopy of four dry bean genotypes at the time of maximum LAI and at 5 cm plant spacing.

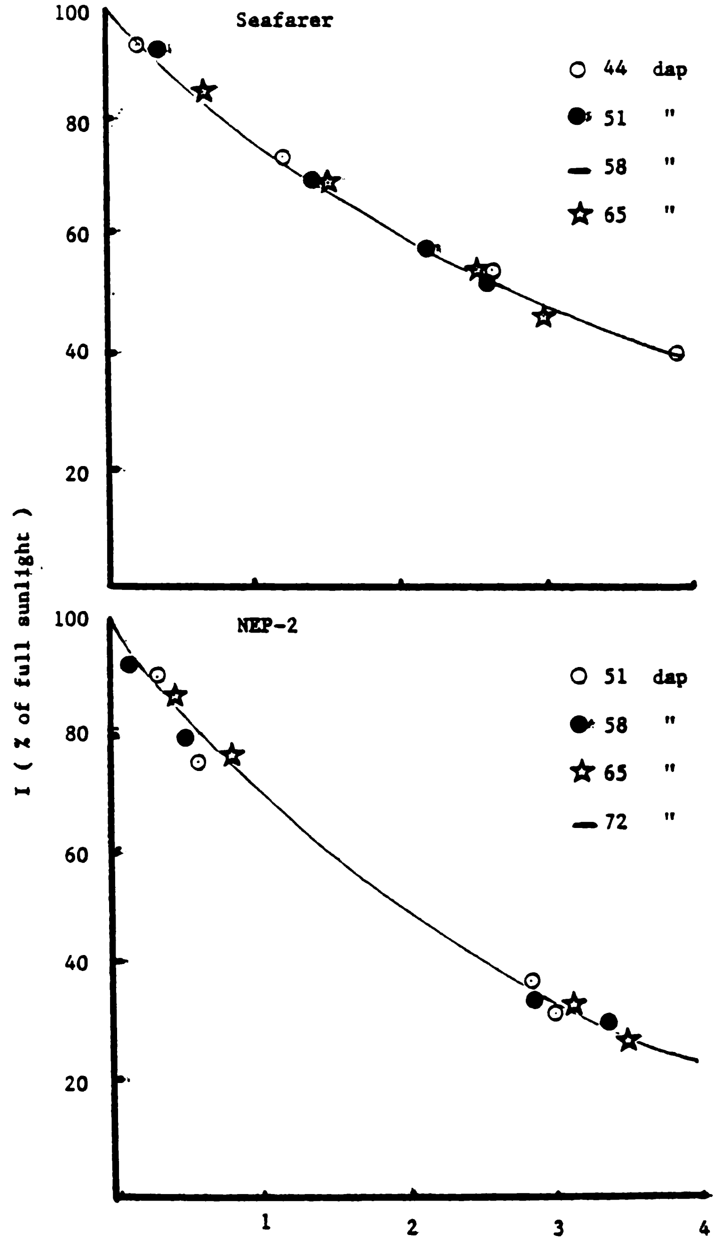


Figure 7. Attenuation of sunlight at 5 cm plant spacing during the growing season. The line is at the time of maximum LAI.

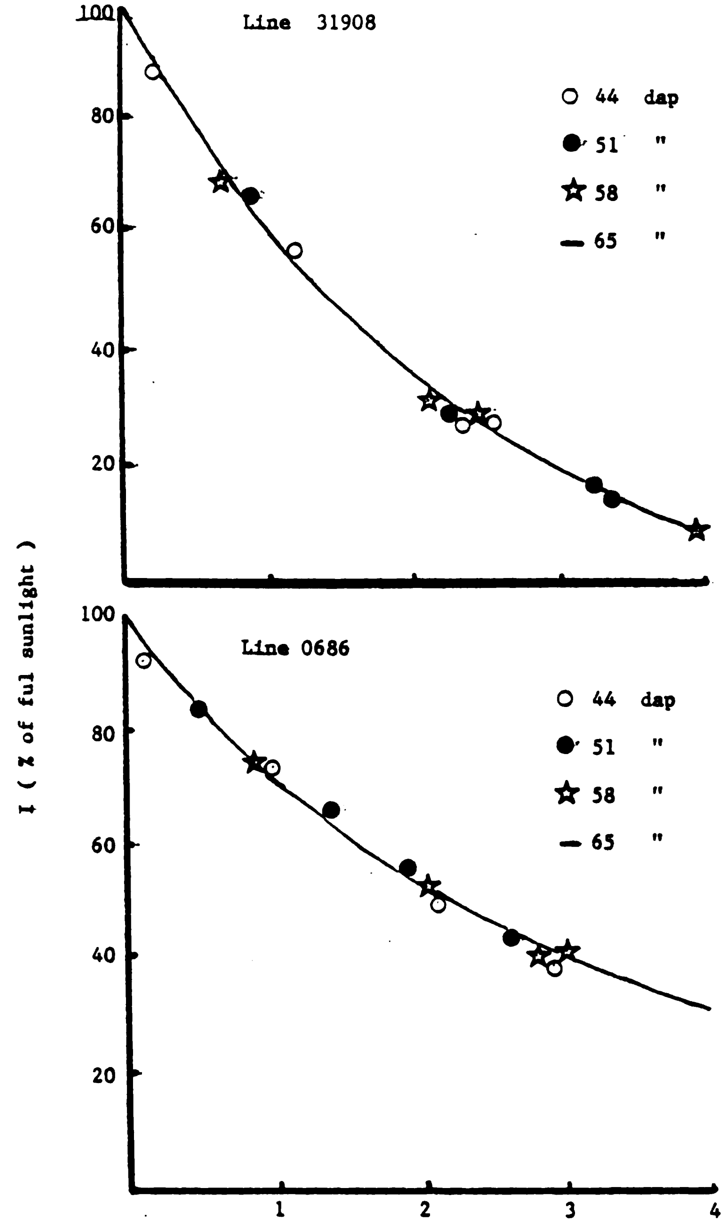


Figure 8. Attenuation of sunlight at 5 cm plant spacing during the growing season. The line is at the time of maximum LAI.

around the line for maximum LAI which indicates that in each plant type, LAI was a major factor in light interception. Leaf size changed during ontogenesis of the four plant types. Dry bean plants orient their leaves with the position of the sun in the sky. This response is affected by leaf age, and genotype (Wien and Wallace, 1973). Apparently, the method used for light measurements was not precise enough to detect these physiological and morphological changes.

Extinction coefficient (k) in equation 3, is a dimensionless parameter describing the light absorption properties of a particular type of foliage. It depends on many factors such as chlorophyll concentration in the leaf, leaf shape, leaf size, leaf angle, heliotropism, etc. Values of k were estimated at maximum LAI and are presented in Table 1. The results show a particular pattern for each plant type; k values were very similar with slightly higher values for wider plant spacing. As was expected, Seafarer had the lowest k values, since it was the cultivar with the lowest light interception.

A common standard procedure is to measure light distribution and leaf angle at noontime in order to avoid heliotropic effects. Even when dry bean leaf angles change during the day, representative determination of leaf angle at midday can be used for estimating differences during the ontogenesis of the plants or between genotypes. During the time of maximum LAI for each plant type, angle of divergence from the horizontal was measured between 10:00 and 12:00 a.m. EDT on a sunny day, by placing a protractor on the adazial surface of the central leaflet. The number of leaflets was recorded and grouped in one of 9 angle classes of 10-degree intervals (0-10,...,80-90). The results are presented in Figure 9. The average leaf angle were: 73.04, 63.80, and 50.20 for Seafarer, NEP-2, and line 31908, respectively.

Table 1. Extinction coefficient (k) at three plant spacing and maximum LAI of four dry beans genotypes.

Genotype	Plant spacing (cm)		
	5	10	15
Line 31908	.4629	.4789	.4773
Seafarer	.2615	.2746	.2775
Nep-2	.3396	.3426	.3424
Line 0686	.2993	.3051	.3079

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Leaf angles were not determined for Line 0686, because the measurement of its many leaves presented a physical time limitation. However, it had leaves of similar shape and size as Seafarer, and it is expected that the leaf angle should be similar to Seafarer. Figure 9 shows that these plant types did differ in the frequency of leaf angle inclination as well as in the average leaf angles. These plant canopies, according to their leaf angle distribution, could be classified as different degree of erectophile foliar structure by using de Wit's system (1965). However, de Wit's system uses leaf area accumulation, while I used leaf number accumulation, which might lead to different results. Soybean plants have erectophile structure and differences between genotypes have been observed (Blad and Baker, 1972; Lemeur, 1973).

Relative light interception for the whole plant canopy was calculated by substracting light penetrating to the bottom of the canopy from total incident light. The time courses of relative light interception and LAI are presented in Figures 10 and 11. These results show that relative light interception was closely associated with LAI and both have similar trends during ontogenesis of the four plant types. Seafarer with a LAI of 3.7 had 56% of light interception 44 dap. A LAI of 7.5 to 8.0 is needed by this cultivar for interception of 95% of the sunlight. At 51 dap, LAI's of the four plant types were similar, but intercepted different amounts of sunlight on the same day. This may be caused by other morphological characteristics such as leaf angle.

Several of the proposed plant "Ideotypes" (Donald, 1967; Mock and Pearce, 1975; Adams, 1973) consider the following as valuable characteristics of a crop community: its ability to have a better light distribution in the canopy, maximum light interception, rapid accumula-

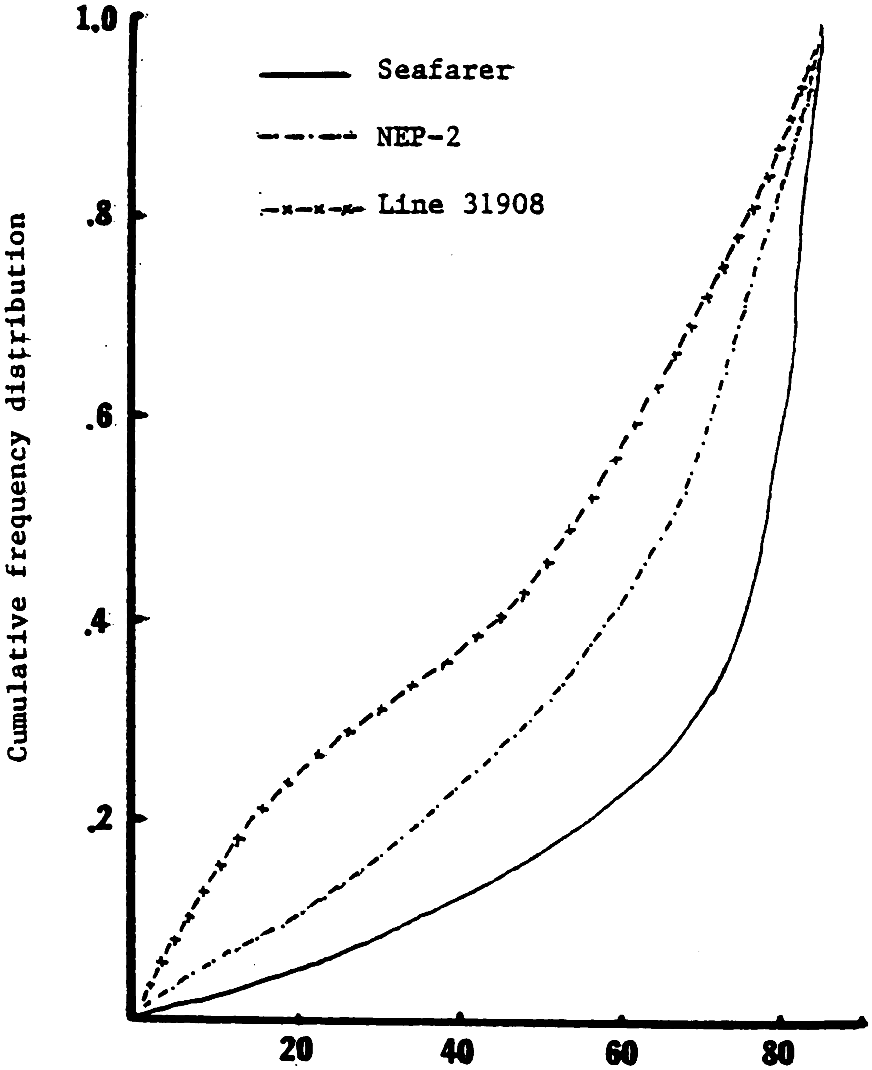


Figure 9. Leaf number distribution of three dry bean genotypes, at 5 cm plant spacing and maximum LAI, as a function of leaf inclination.

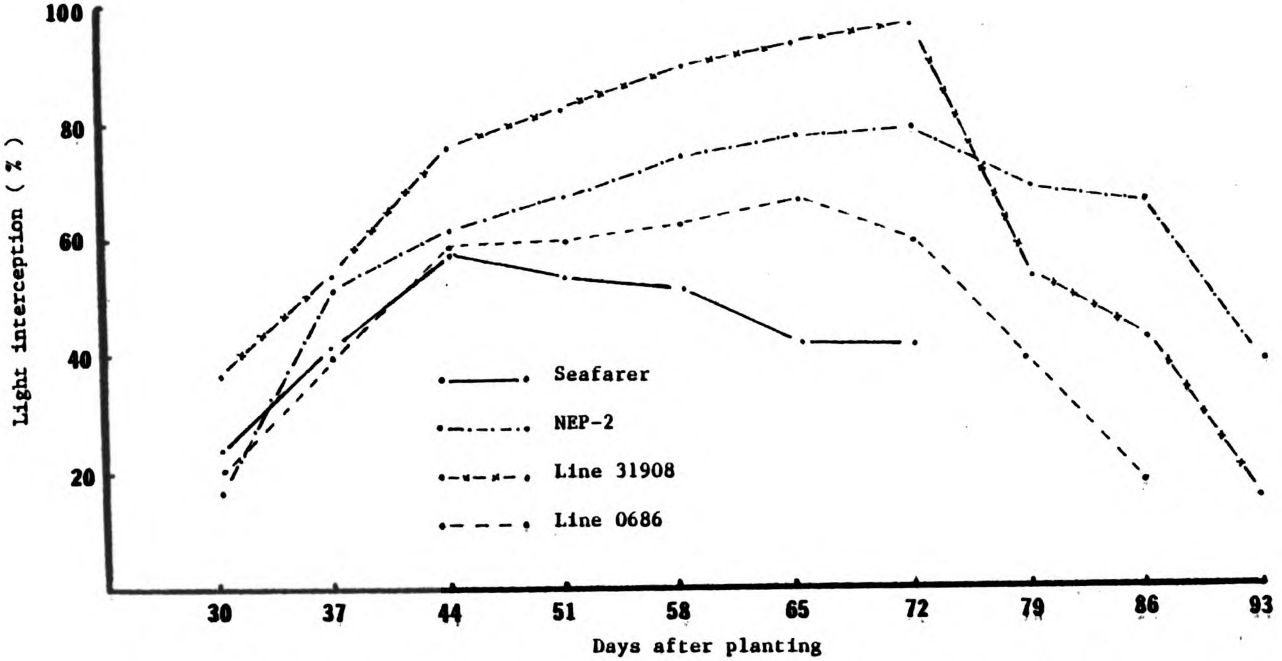


Figure 10. Time course of relative light interception (% full sunlight) by four dry bean genotypes at 5 cm plant spacing.

tion of maximum leaf area, and leaf area duration as long as possible, among others. All of the previously mentioned characteristics are related with better light interception and utilization through photosynthesis. The results in Figures 9 and 10 indicate that it would be desirable to have, under some condition such as long growing season, early planting, or higher plant density, a commercial dry bean cultivar with the leaf area duration of NEP-2 and the leaf orientation and seed characteristics of Seafarer.

To establish a relationship between light interception, % of ground cover by the plant canopy (plant canopy width/row width), leaf size (average of central leaflet area at maximum LAI, in cm^2), leaf angle, extinction coefficient (k), number of branches, canopy height (cm), and canopy width (cm), simple correlation coefficients were calculated and are presented in Table 2. Extinction coefficient was positively and significantly correlated to leaf size and negatively correlated to leaf angle. As the leaf angle is increased, more light should penetrate the plant canopy (lower k value). Apparently, big leaves require more energy and/or present more physical resistance to be moved and tend to orient themselves less than small leaves. This could explain the negative relationship between leaf size and leaf angle. However, leaf size and leaf angle depend upon the position in the plant canopy, which confound the primary cause for the negative relationship.

To determine the simultaneous relative importance of the above characteristics to light interception, the statistical procedures used were Step-Wise Multiple Regression and Backward Elimination. The results were equal with both procedures, which indicates the prevalent relative importance of the characteristics which were significant;

Table 2. Simple correlations of nine characteristics of four dry bean genotypes

Table 2. Simple correlations of nine characteristics of four dry bean genotypes.

	% Ground cover	LAI	Leaf size	Leaf angle	Ext. co. (k)	No. branch	Canopy height	Canopy width
LAI	-.2898							
Leaf size	-.6175**	.2244						
Leaf angle	.5356	-.4324	-.9231**					
Ext. coef. (k)	-.3578	.3639	.9174**	-.9916**				
Number branches	.7659**	-.6833**	-.6874**	.8082**	-.7413**			
Canopy height	-.5440	.5636	.7717**	-.8616**	.8088**	-.7984**		
Canopy width	.9718**	-.3476	-.6571*	-.6103	-.5288	.8133**	-.6501	
Light intercep.	-.4157	.8265**	.6682*	-.8450**	.8009**	-.8550**	.8606**	-.5099

Table 3. Analysis of Variance (ANOVA) of overall regression of light interception by four dry bean genotypes.

Source of Variance	df	SS	MS	F
Regression	4	2812.9977	703.2494	255.69**
Error	7	19.2522	2.7503	

Table 4. A model of light interceiption relationship with some characteristics of four dry bean genotypes.

Characteristic	Regression coef.	Partial cor. coef.	R^2 delete
Constant	367.0385	.8577	.9742
Ground cover (%)	.3646	.8486	.9757
LAI	9.3445	.9650	.9010
Extinction coef. (k)	-298.3075	-.7805	.9826
Leaf angle	-3.8837	-.8680	.9724
Total R^2 = .9922			

results are presented in Tables 3 and 4. LAI, leaf angle, % of ground cover, and the extinction coefficient were the most important characteristics, accounting for 99.22% of the variance in light penetration.

Growth Characteristics

Yield and yield components

Analysis of Variance (ANOVA) did not show statistically significant differences either among plant densities or for the plant density X plant type interaction. A summary of the results is presented in Table 5. The observed yields (Kg/ha) are in the normal range obtained with these plant types at Saginaw, Michigan. However, the seed dry weights (gr/100 seeds) were lower than those usually observed in these plant types, i.e., Seafarer normally has a seed dry weight of 18 to 19 gr/100 seeds, at a seed moisture content of 15%, while I obtained 15.55. This could be due to the oven drying of the seeds for the determination of this characteristic.

Growth analysis.

Techniques used to quantify the components of crop growth are collectively known as "growth analysis". Watson (1952) has reviewed the traditional techniques of growth analysis. Radford (1967) presented a review of the growth analysis formulae, their derivation, and necessary conditions for their use. More recently, there are reports with excellent reviews of growth analysis techniques (Richards, 1969; Kuet *et al*., 1971; Ondok and Kvet, 1971; Hunt and Parsons, 1974).

In the present work, the data were used to select functions which described the total dry weight and leaf area vs. time relationships. Presented in Table 6 are polynomials of best fit, determined using a least squares procedure, which described the time course of total dry weight and LAI for each plant type. They were then used to calculate,

Table 5. Final yield and yield components of four dry bean genotypes at three plant spacings: 5, 10 and 15 cm.

Genotype	5	10	15 cm	Mean	5	10	15 cm	Mean	5	10	15 cm	Mean	5	10	15 cm	Mean
	---------- gr/m^2 ----------				---------- No pods/m^2 ----------				----- No seeds/pod ----				------- gr/100 seeds -----			
Seafarer	142.86	158.10	137.14	146.03a	226.67	233.81	216.19	225.56b	4.09	4.11	4.32	4.17b	15.39	15.20	16.06	15.55a
NEP-2	249.99	237.62	246.17	244.59b	396.67	378.10	349.05	374.06d	4.47	4.51	5.52	4.83b	13.50	12.90	14.80	13.73a
31908	150.95	149.52	158.60	153.02a	153.33	144.76	141.90	146.66a	2.68	2.35	3.25	2.76a	36.16	38.04	40.24	38.15b
0686	207.61	207.19	197.41	205.07c	260.76	270.95	262.14	264.62c	4.34	4.60	4.44	4.46b	19.06	17.73	17.87	18.23a

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

Table 6. Polynomial equations of total dry weight and LAI, of four dry bean genotypes at 5 cm plant spacing, as function of days after planting (t).

Genotype	Characteristic	Equation	R^2
Seafarer	Total dry weight	$571.427390 - 46.889263t + 1.276642t^2 - .009220t^3$	.9759
	LAI	$- 22.273003 + 1.357674t - .023161t^2 - .001219t^3$	.9268
NEP-2	Total dry weight	$929.348229 - 59.208717t + 1.240338t^2 - .007016t^3$	.9726
	LAI	$- 1.883046 + .029877t + .002803t^2 - .000029t^3$	.9600
31908	Total dry weight	$96.893975 - 7.994876t + .243894t^2 - .001371t^3$	.9763
	LAI	$- 6.386659 + .278669t - .001016t^2 - .000013t^3$	.8180
0686	Total dry weight	$231.336374 - 18.494877t + .526417t^2 - .003262t^3$	.9418
	LAI	$- 2.414438 + .075994t + .002144t^2 - .000030t^3$	.9522

for selected days during the growing season, instanteous values of Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LGR), Leaf Dry Weight/Total Dry Weight Ratio (LW/TW) and Leaf Area/Leaf Dry Weight Ratio (LA/LW). Formulae used in making the calculations are those listed by Radford (1967) and Ondok and Kvet (1971).

Tables 7 to 10 present the results of the use of growth analysis techniques. To visualize the data on RGR, they are also graphically presented in Figure 12. For purposes of the following discussion, note the relationships, RGR = NAR X LAR, and LAR = (LW/TW) X (LA/LW).

Very similar trends in RGR, NAR, and LAR were observed between plant type and plant spacing. In general, RGR for any plant type was affected by plant spacing with the lower values for the closest plant spacing. Similar results have been reported for broad beans (Ishag, 1972). The argument used to explain these results has been that NAR is related to or measures the photosynthetic capacity of the plants. At a low plant density, enough light passes through the plant canopy, such that the lower leaves have higher photosynthetic rates and maintain these rates for a longer time (delayed senescence). In the present work, the percent ground cover by Seafarer at maximum LAI was 64, 57, and 60% for 5, 10, and 15 cm plant spacings, respectively. These data and light penetration measurements indicated that light was not limiting at the bottom of the plant canopies. Differences in the time required for the lower leaves to become yellow, and percent of yellowing were not observed between plant spacings. These results suggested that light penetration in the plant canopy was not the only cause for differences in NAR between plants at different plant spacings.

Table 7. Growth analysis characteristics of Seafarer at three plant spacings: 5, 10, and 15 cm.

Date	RGR			NAR			LAR		
dap	5	10	15 cm	5	10	15 cm	5	10	15 cm
		$g\ g^{-1}\ day^{-1}$			$g.m^{-2}\ day^{-1}$			$m^2\ g^{-1}$	
30	.0721	.0928	.0821	4.5899	5.6597	6.1730	.0157	.0164	.0133
37	.0856	.0917	.0995	4.1981	5.5257	5.4711	.0204	.0166	.0182
44	.0508	.0885	.0830	3.1164	5.4610	5.2502	.0163	.0162	.0152
51	.0451	.0699	.0633	3.4978	5.9821	6.3340	.0129	.0177	.0100
58	.0174	.0289	.0366	2.2540	3.6089	3.8108	.0077	.0080	.0096
56	.0013	.0136	.0208	0.2095	2.0034	3.5811	.0061	.0068	.0058
72	- .0197	.0021	.0093	- 3.2763	0.3829	2.5723	.0060	.0054	.0036

Table 8. Growth analysis characteristics of NEP-2 at three plant spacings: 5, 10, and 15 cm.

Date	RGR			NAR			LAR		
dap	5	10	15 cm	5	10	15 cm	5	10	15 cm
	$g\ g^{-1}\ day^{-1}$			$g\ m^{-2}\ day^{-1}$			$m^{2}\ g^{-1}$		
30	.0467	.0397	.0517	5.0771	4.2231	4.0644	.0092	.0094	.0112
37	.0464	.0804	.0794	2.4148	4.0665	4.7918	.0192	.0262	.0195
44	.0717	.0846	.1393	3.9423	5.9570	7.6971	.0182	.0142	.0181
51	.0611	.0669	.1400	4.1880	5.0330	6.2721	.0146	.0133	.0154
58	.0405	.0503	.0508	3.9711	3.8086	3.8179	.0100	.0132	.0133
65	.0332	.0374	.0426	3.4905	4.0175	3.7328	.0095	.0092	.0114
72	.0278	.0267	.0293	3.5656	3.0041	3.0937	.0078	.0089	.0095
79	.0102	.0195	.0240	1.6149	2.7444	3.2451	.0063	.0071	.0074
86	.0028	.0081	.0130	0.6084	1.7659	2.7715	.0046	.0046	.0047
93	- .0015	.0021	.0258	- 8.2933	1.1455	2.3488	.0025	.0017	.0011

Table 9. Growth analysis characteristics of Line 31908 at three plant spacings: 5, 10, and 15 cm.

Date	RGR			NAR			LAR		
dap	5	10	15 cm	5	10	15 cm	5	10	15 cm
	----- $g\ g^{-1}\ day^{-1}$ -----			------- $g\ m^{-2}\ day^{-1}$ ------			-------- $m^{2}\ g^{-1}$ ---------		
30	.0544	.0894	.0573	5.9408	5.9580	6.4401	.0108	.0150	.0089
37	.0706	.0787	.1019	4.7680	5.0824	4.4476	.0151	.0155	.0187
44	.0455	.0764	.0937	3.3418	4.3177	3.1601	.0148	.0177	.0189
51	.0318	.0508	.0938	2.6247	3.7618	2.5049	.0136	.0135	.0164
58	.0241	.0412	.0564	2.1163	3.3761	2.1747	.0121	.0122	.0142
65	.0142	.0332	.0362	1.6518	3.1885	3.0011	.0104	.0106	.0101
72	.0073	.0264	.0217	1.1073	3.0315	3.0444	.0086	.0087	.0071
79	.0009	.0208	.0201	0.2430	3.1525	2.4625	.0066	.0066	.0065
86	- .0001	.0156	.0125	- 2.0305	3.9065	3.7778	.0039	.0040	.0033

Table 10. Growth analysis characteristics of Line 0686 at three plant spacings: 5, 10, and 15 cm.

Date	RGR			NAR			LAR		
dap	5	10	15 cm	5	10	15 cm	5	10	15 cm
	----- $g\ g^{-1}\ day^{-1}$ -----			------ $g\ m^{-2}\ day^{-1}$ -------			--------- $m^{2}\ g^{-1}$ --------		
30	.0689	.7400	.0417	4.4420	4.5965	4.0059	.0155	.0160	.0104
37	.0690	.1136	.0803	3.9863	6.3200	3.4326	.0173	.0263	.0234
44	.0561	.0757	.0696	3.6182	3.6555	4.5102	.0155	.0203	.0188
51	.0433	.0546	.0645	3.3033	3.5454	4.7790	.0131	.0154	.0135
58	.0312	.0379	.0467	3.0215	3.2951	4.6208	.0101	.0115	.0101
65	.0240	.0215	.0320	3.2016	2.8078	4.1026	.0087	.0087	.0078
72	.0160	.0109	.0190	2.4636	3.5336	3.1127	.0065	.0061	.0061
79	.0066	.0039	.0062	1.6514	1.0415	1.2870	.0040	.0037	.0048

RGR was affected by plant spacing in each genotype. This was the result of differences in NAR rather than in LAR. LAR was apparently not affected by plant spacing. RGR trends among plant types were similar with peak values at 37 dap for Seafarer, Lines 31908 and 0686, and at 44 dap for NEP-2. These values were observed at early flowering for each cultivar, thereafter, RGR values decreased. Figure 12 shows that Seafarer had the highest RGR values before and at 37 dap, with a second peak at 51 dap during pod filling. Figure 13 presents results for Seafarer at the 5 cm plant spacing; similar trends have been observed for the other plant spacings and with the other plant types. The initial peak (Figure 12) is primarily the result of a similar peak in LAR (Figure 13b). Thereafter, the similarity between the RGR and NAR curves indicated that RGR was being affected by NAR. Trends in LAR and LW/TW indicated that LW/TW was the primary factor affecting LAR. The increase in NAR at 51 dap is interpreted as a response of the leaves to an increased demand for assimilates during pod filling. Similar increases in NAR during pod filling have been reported previously for broad beans (Ishag, 1972), soybeans (Koller _et_ _al_., 1970), and peas (_Pisum_ _sativum_ L.) (Easting and Gritton, 1969). The net photosynthetic rate has been observed to increase in soybeans (Dornhoff and Shibles, 1970) and dry beans (Peet _et_ _al_., 1977), during pod filling.

Partitioning of dry matter: Harvest Index

Harvest Index (HI) is probably the most popularly and commonly used index of dry matter partitioning. This index has been proposed as a selection criterion to increase the economic yield of crops (Nichiporovich, 1975; Donald and Hambling, 1975; Wallace _et_ _al_., 1975).

HI is calculated as the ratio of economic (seeds) yield to the total yield of plant material (biological yield). True biological

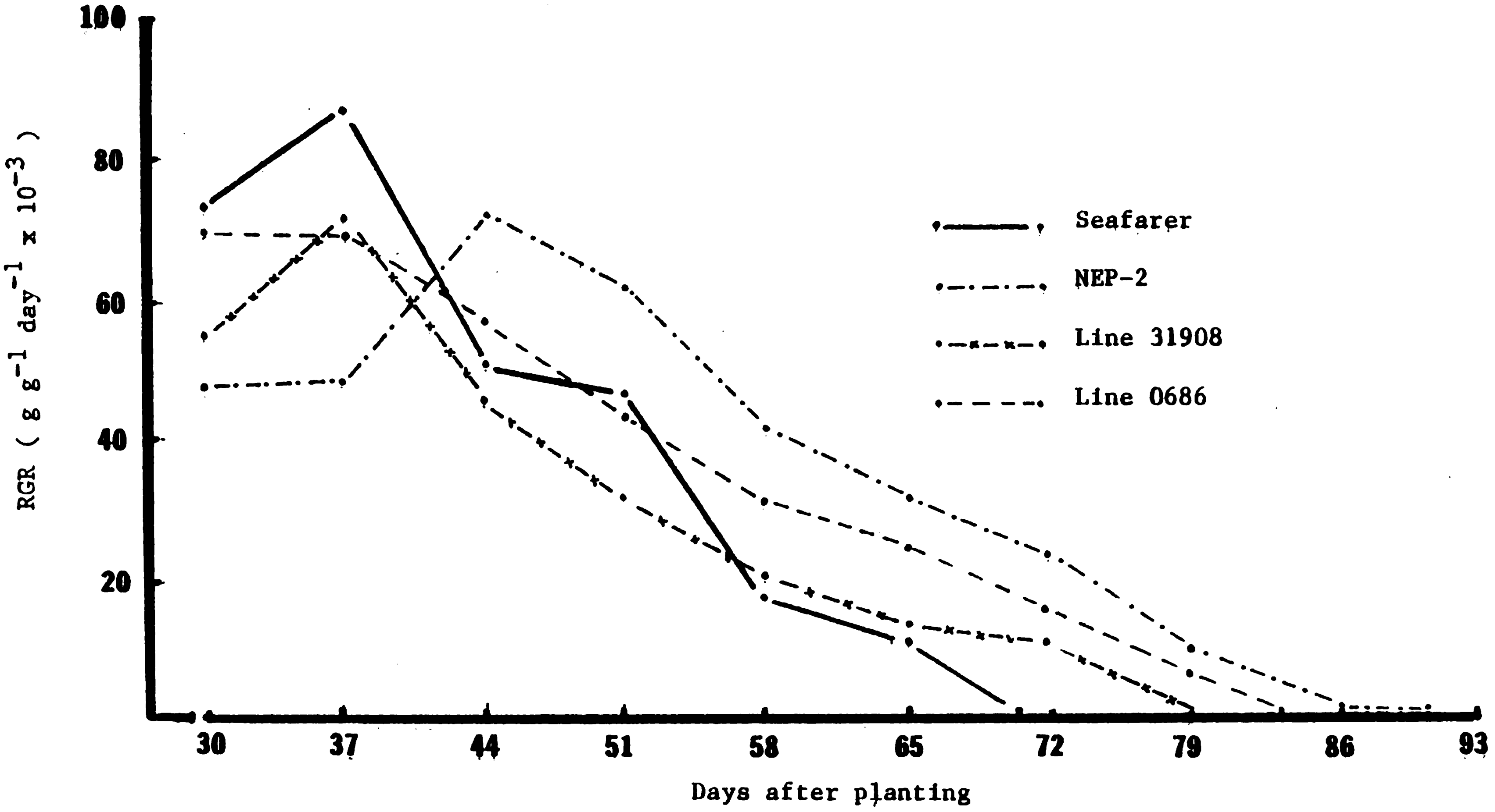
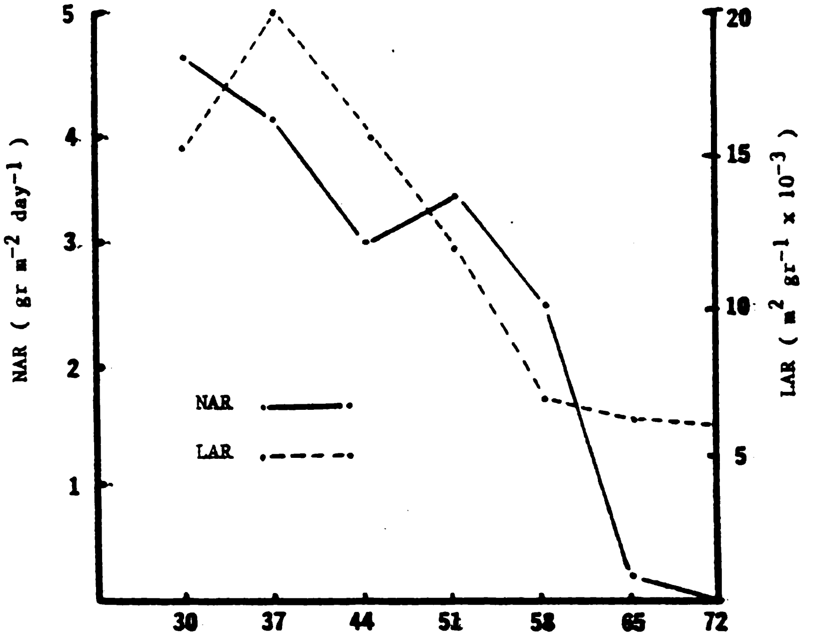


Figure 12. Time course of RGR of four dry bean genotypes at 5 cm plant spacing.



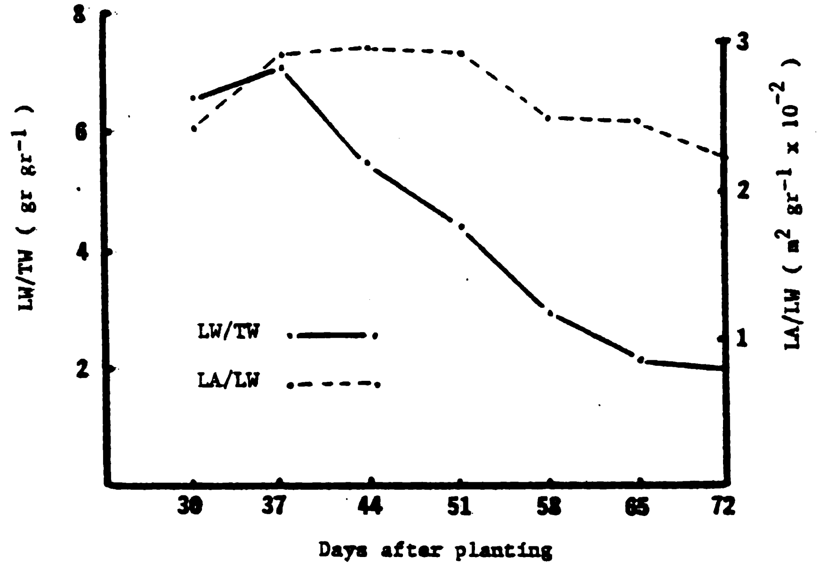


Figure 13. Ontogenetic trends in NAR, LAR, LW/TW, and LA/LW of Seafarer at 5 cm plant spacing.

yield includes the weight of roots, but since they are normally nonrecoverable, the term is usually applied to the total above ground weight. Sometimes the pulled roots are included.

HI values were calculated for the four plant types and are presented in Table 11. The results indicated that plant spacing affected HI, independent of plant types. The lowest HI value corresponds to the closest plant spacing (5 cm); however, no statistically significant differences were observed for 10 and 15 cm plant spacing. HI is a result of complex physiological processes and no single factor can be identified as the most important one in determining HI. In cereal crops, HI has been reported to be affected by plant population, water availability, nitrogen nutrition, genotype, and genotype X environment interaction (Donald and Hamblin, 1975).

Dry weight of plant components

The dry weight distribution of the four plant types at 5 cm plant spacing are presented in Figures 14 to 17. All plant parts, including leaves, stems, and pods, developed progressively later toward the top of the plant. However, the difference in growth stage among plant parts was much less in the case of pod walls and seed parts (hereafter termed pod) than for leaves and stems. Consequently, the time interval between vegetative and pod development was shorter toward the top of the plant. Due to the greater overlap of vegetative and pod growth toward the top of the plant, the distinction between vegetative and pod development stages becomes less apparent.

Dry weight of lower leaves started to decrease before flowering. Leaf dry weight was significantly related to leaf number, r = .98806, .98083, .98576, and .97549 for Seafarer, NEP-2 and Lines 31908 and 0686, respectively, which indicates that the decrease in leaf dry

Table 11. Harvest index values of four dry bean genotypes at three plant spacings.

Genotype	Plant spacing (cm)						
	5		10		15		
	HI	% *	HI	%	HI	%	Mean
Seafarer	.4976	87.48	.5321	93.55	.5688	100.00	.5328a**
NEP-2	.4722	80.86	.5651	96.74	.5840	100.00	.5404a
31808	.4884	84.06	.5563	95.75	.5810	100.00	.5419a
0686	.3239	63.30	.4449	85.57	.5199	100.00	.4296 b
Mean							
Mean	.4455a		.5239b		.5634 b		

* Harvest Index values (HI) as percent of 15 cm plant spacing.

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

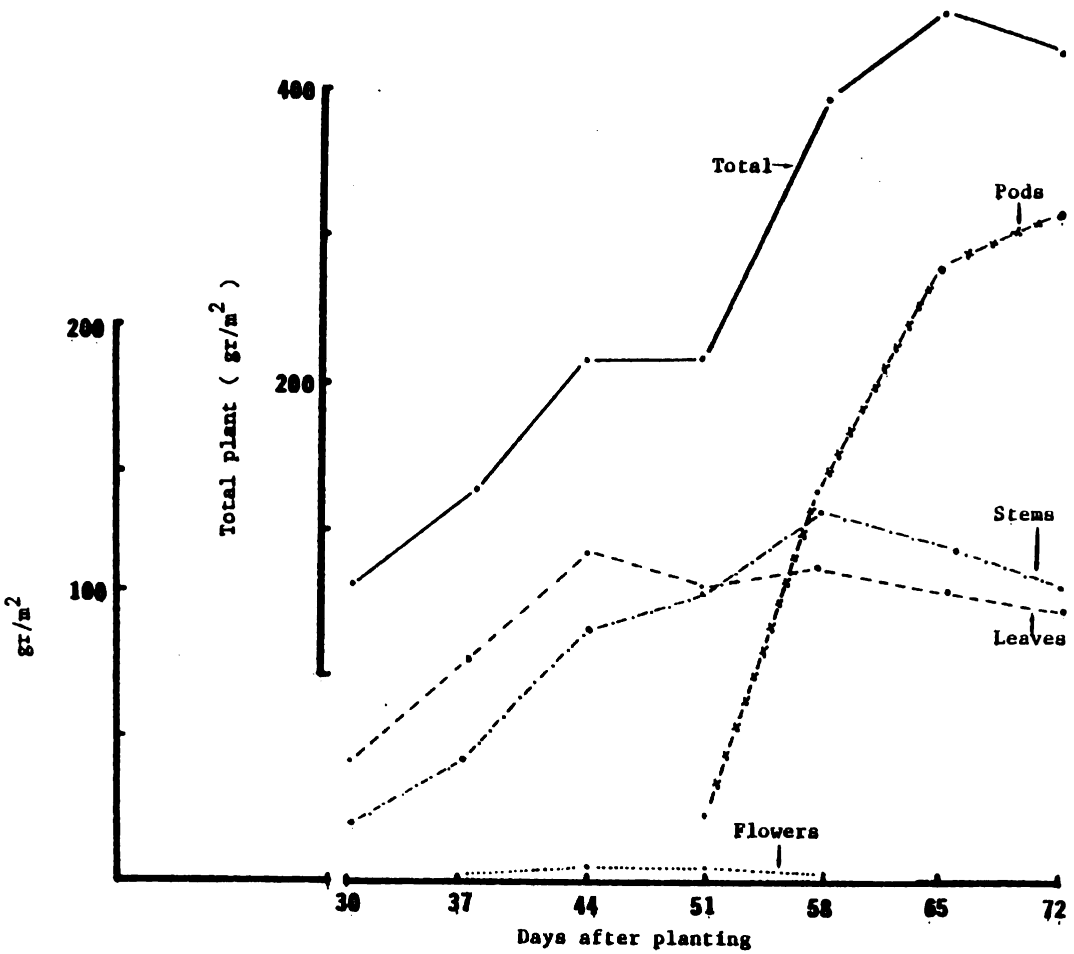


Figure 14. Ontogenetic distribution of dry weight of Seafarer.

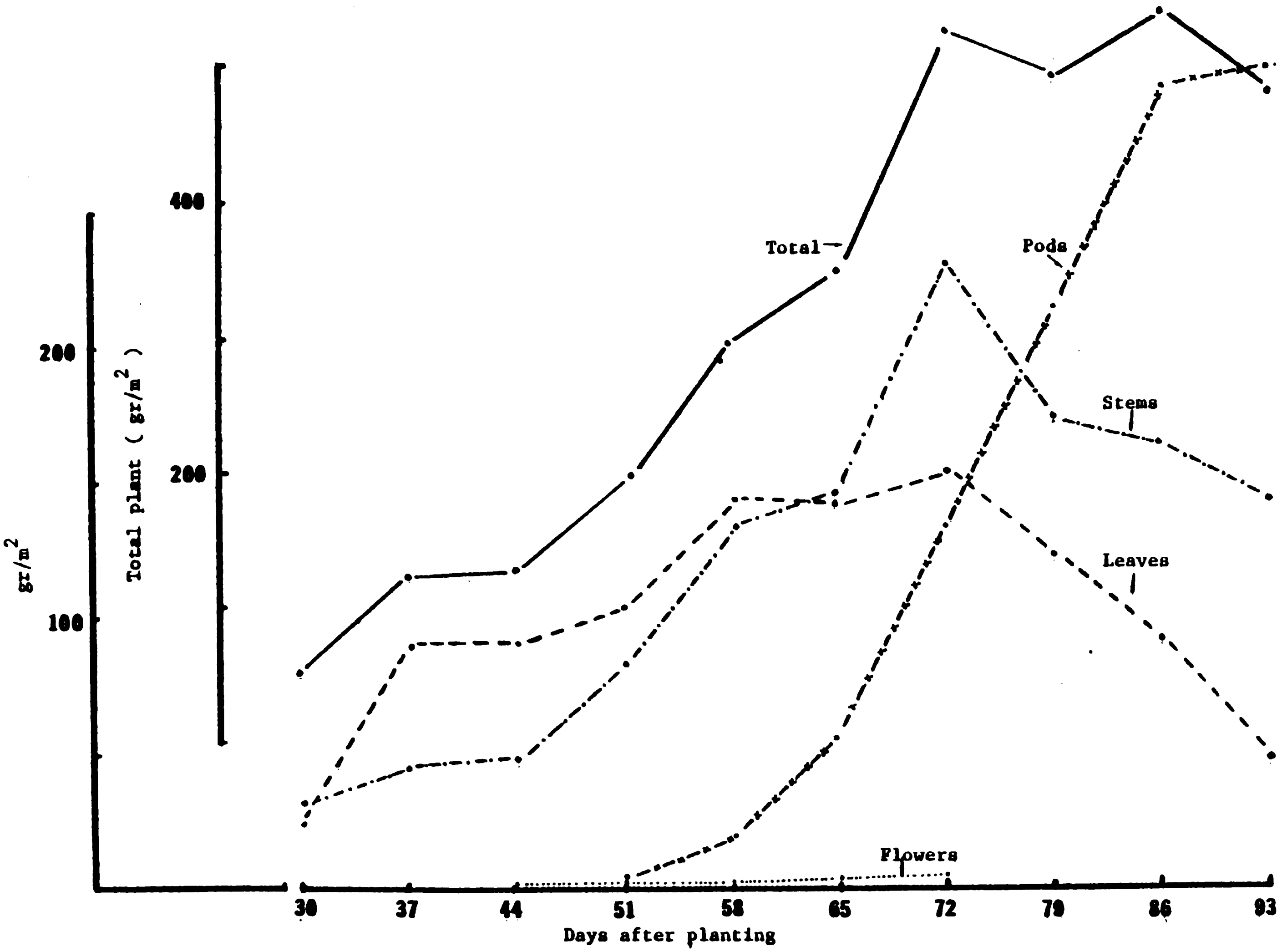


Figure 15. Ontogenetic distribution of dry weight of NEP-2.

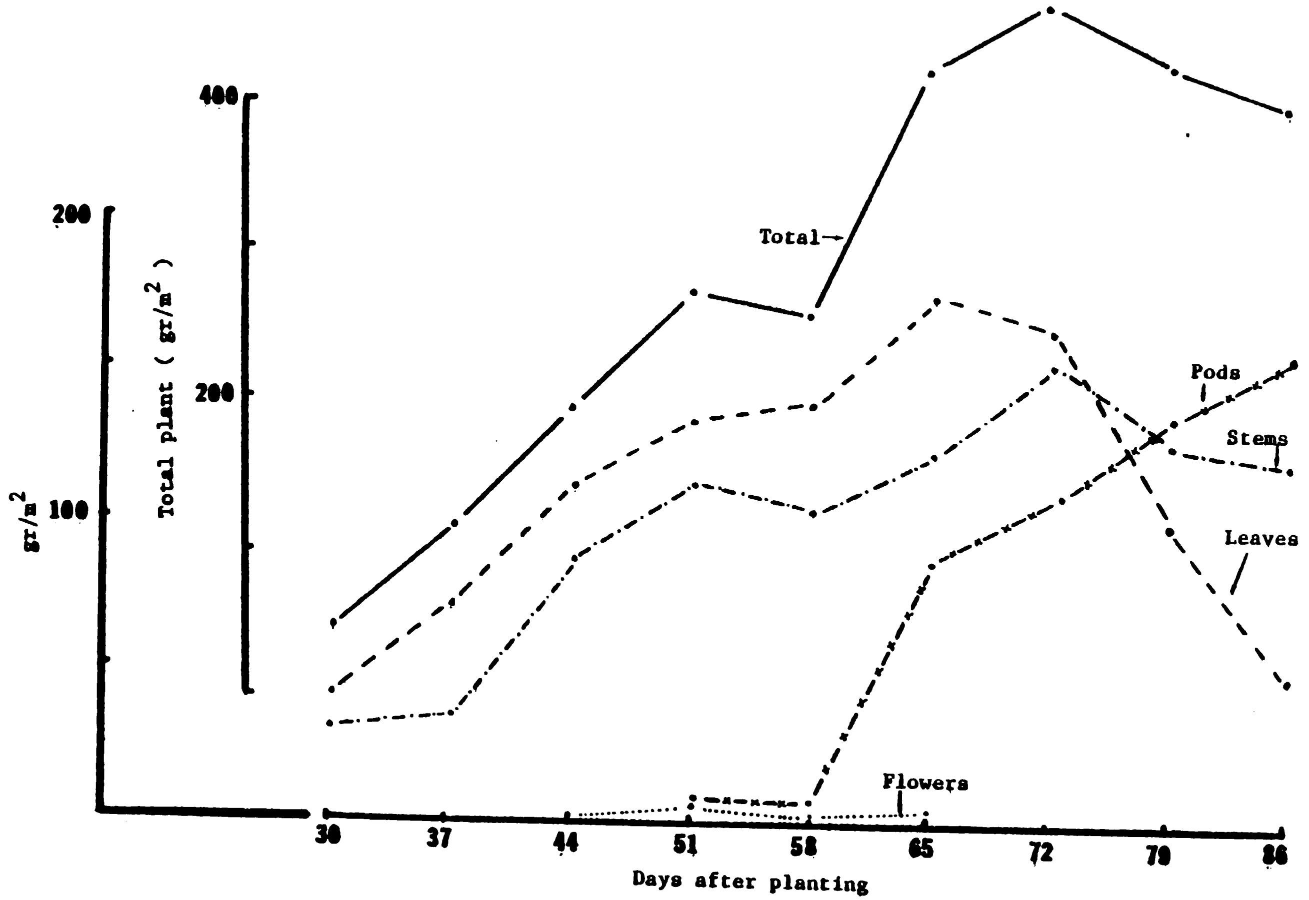


Figure 16. Ontogenetic distribution of dry weight of Line 31908.

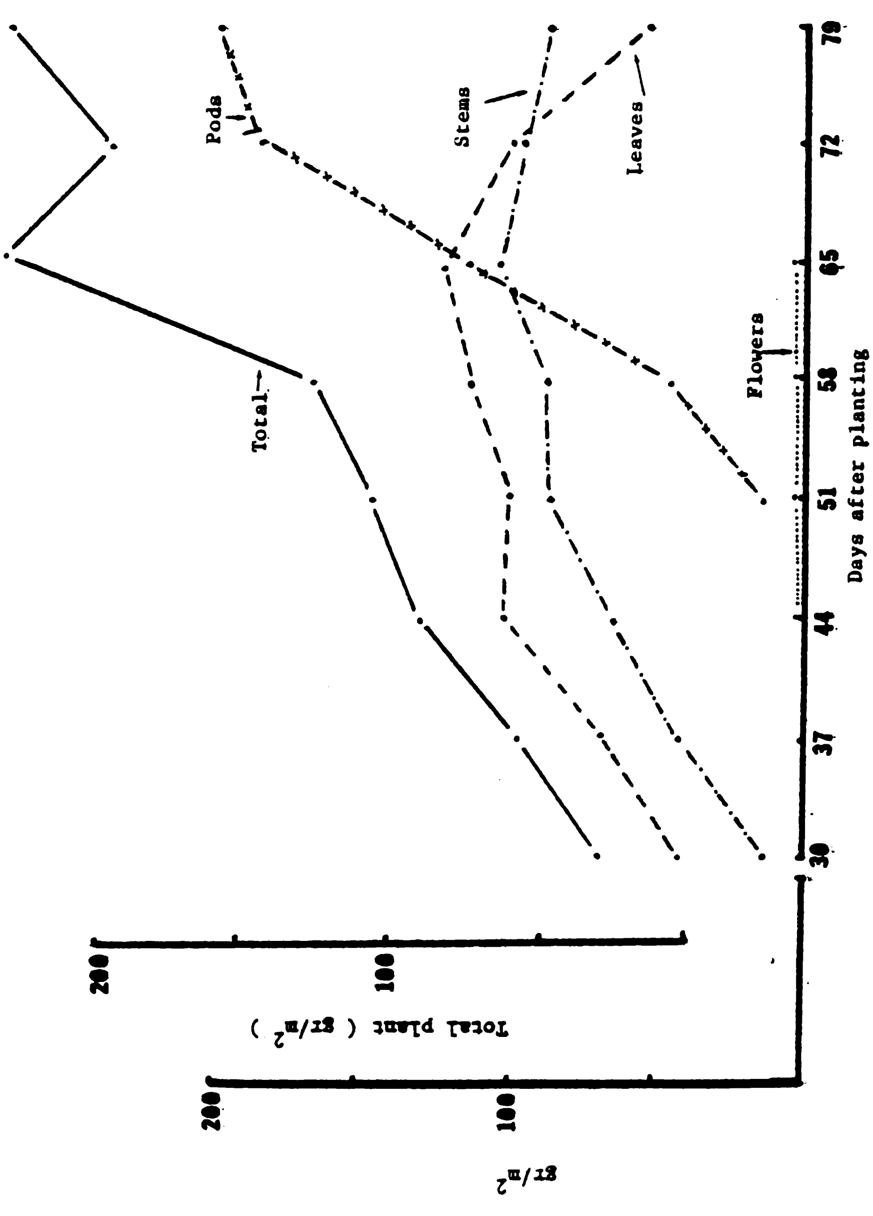


Figure 17. Ontogenetic distribution of dry weight of Line 0686.

weight was due to leaf drop. In the literature, the decrease in the leaf area of this stratum has been related to decreased N_2 - fixation.

Pod dry weight of the bottom and top of the plants, together constitute 16.32%, 11.30%, 0.51%, and 16.40% of the total pod dry weight of Seafarer, NEP-2, and Lines 31908 and 0686, respectively. Furthermore, these two strata also had the lowest leaf area of the whole plant canopy.

The trends of dry weight distribution among leaves, stems, and pod suggest movement of material from leaves to stems and pods. In the present report, changes in stem dry weight and pod dry weight will be used as an estimate of the possible contribution of storage material to the final seed and pod dry weight. This technique has been previously used by Gallagher et al. (1975, 1976) with small cereal grains. Changes in leaf dry weight were not considered because their changes were greatly affected by the loss of leaves. The dropped leaves were not collected. The stem and petioles were included in the stem dry weight. Dropped petioles were collected and also included in the stem dry weight.

Changes in stem dry weight and pod dry weight were calculated for the last three weeks for Seafarer and NEP-2, and for the last two weeks for the other cultivars. The results are presented in Table 12. This table shows that there are differences between plant types in the possible contribution of previously stored materials in the stem and petioles to the final pod dry weight. Differences were also observed between plant spacings in all plant types. For example, in Seafarer, previously stored materials in stems and petioles, if translocated to pods, may constitute 27.61% of the final pod dry weight.

Table 12. Changes in dry weights/m^2 of stems (ΔWS) and pods (ΔWP) during the last two weeks of the growing period of four bean genotypes at three plant spacings.

Genotype	Plant spac. (cm)	stems (ΔWS)	pods (ΔWP)	ΔWS/ΔWP
Seafarer	5	- 25.25	+ 91.09	.2761
	10	- 10.08	+ 82.40	.1223
	15	- 8.98	+ 110.31	.0814
NEP-2	5	- 89.33	+ 171.27	.5216
	10	- 54.80	+ 238.73	.2295
	15	- 41.02	+ 272.94	.1503
31908	5	- 43.82	+ 96.34	.4548
	10	- 20.27	+ 127.40	.1591
	15	- 16.14	+ 141.76	.1139
0686	5	- 17.62	+ 111.92	.1478
	10	- 17.30	+ 146.65	.1180
	15	- 14.85	+ 148.65	.0999

Table 13. Changes in dry weight/m^2 of stems (ΔWS) and pods (ΔWP) by plant strata during the last two weeks of the growing period of Seafarer at 5 cm.

Dates	Plant strata (cm from the bottom)				
	0 - 10	10 - 20	20 - 30	30 - 40	Σ
dap	ΔWS				
58 - 65	+ 4.38	- 1.15	- 7.15	- 6.23	- 10.15
65 - 72	- 18.46	- 1.15	- 1.62	+ 6.23	- 15.00
Σ	- 14.08	- 2.30	- 8.77	0.00	- 25.15
	ΔWP				
58 - 65	+ 18.91	+ 72.65	- 2.31	- 17.76	+ 71.49
65 - 72	- 4.85	- 5.30	+ 14.53	+ 15.22	+ 19.60
Σ	+ 14.06	+ 67.35	+ 12.22	- 2.54	+ 91.09

Table 14. Changes in dry weight/m^2 of stems (ΔWS) and pods (ΔWP) by plant strata during the last three weeks of the growing period of NEP-2 at 5 cm.

Date	Plant strata (cm from the bottom)					
	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	Σ
dap			ΔWS			
72 - 79	- 7.61	- 16.60	- 14.30	- 10.38	- 8.99	- 57.88
79 - 86	- 4.85	- 2.70	- 3.63	+ 2.84	- 1.38	- 9.72
86 - 93	- 4.84	- 9.84	- 5.60	- 2.37	- .92	- 21.73
Σ	- 17.30	- 29.14	- 23.53	- 9.91	- 9.45	- 89.33
			ΔWS			
72 - 79	+ 8.30	+ 34.60	+ 25.14	+ 9.46	+ 2.54	+ 80.04
79 - 86	- 1.16	+ 34.30	+ 38.41	+ 11.82	- 1.69	+ 81.68
86 - 93	+ 10.00	+ 10.58	- 20.50	+ 7.78	+ 1.69	+ 9.55
Σ	+ 17.14	+ 79.48	+ 43.05	+ 29.06	- 2.54	+171.27

Table 15. Changes in dry weight/m^2 of stems (ΔWS) and pods (ΔWP) by plant strata during the last two weeks of the growing period of Line 31908 at 5 cm.

Date	Plant strata (cm from the bottom)					
	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	Σ
dap			ΔWS			
72 - 79	- 5.45	+ 4.62	- 12.22	- 8.76	- 7.38	- 29.19
79 - 86	- 2.63	- .85	- 1.01	- 8.07	- 2.07	- 14.63
Σ	- 8.08	- 3.77	- 13.33	- 16.83	- 9.45	- 43.82
			ΔWS			
72 - 79	0.00	+ 21.43	+ 31.59	+ 23.14	- 3.54	+ 72.62
79 - 86	0.00	+ 9.02	+ 8.88	+ 11.00	- 5.22	+ 23.68
Σ	0.00	+ 40.45	+ 40.47	+ 34.14	- 8.76	+ 96.30

Table 16. Changes in dry weight/m^2 of stems (ΔWS) and pods (ΔWP) by plant strata during the last two weeks of the growing period of Line 0686 at 5 cm.

Date	Plant strata (cm from the bottom)				
	0 - 10	10 - 20	20 - 30	30 - 40	Σ
dap	ΔWS				
65 - 72	- 5.47	- 5.84	- 2.31	+ 5.54	- 8.08
72 - 79	+ 7.78	- 2.84	- 3.69	- 10.84	- 9.54
Σ	+ 2.31	- 8.68	- 5.90	- 5.30	- 17.62
	ΔWS				
65 - 72	+ 9.46	+ 63.10	- 12.68	+ 7.61	+ 67.49
72 - 79	- 7.61	+ 51.30	+ .51	- .23	+ 44.43
Σ	+ 1.85	+114.40	- 12.17	+ 7.38	+111.92

Changes in stem dry weight and pod dry weight were also calculated by plant strata and the results are presented in Tables 13 to 16. These tables show that there are differences in the change of stem dry weight and changes in pod dry weight among strata. Apparently the dry weight changes in the stem are equivalent to the changes in dry weight of pods at the bottom and top strata of all plant types with the exception of Line 31908 at the lowest strata where no pods were present. This may result in an important mechanism especially in the lowest strata where leaf fall starts before flowering. Changes in stem and root dry weight late in the growing season have been reported to be related to changes in reducing sugars and total nonstructural carbohydrates (Subhadrabandhu, 1976; Martinez, 1976; Bouslama, 1977). Salazar et al. (1977) reported the presence of differential amounts of starch in stems and roots of 24 dry bean cultivars at physiological maturity.

The decrease in dry weight of petioles, stems, and roots, late in the growing season, could be due to the use of stored materials in the respiration of these organs, translocation of stored materials to pod and seed, and/or leaching out of stored materials from the roots into the soil due to root leakage. The stored materials could also be used in late regrowth of the plant from the base of the stem. This subject warrants further study.

REFERENCES

Adams, M. W. 1973. Plan architecture and physiological efficiency in the field bean. Potential of field beans and other food legumes in Latin America. Series Seminars @E. Centro Internacional de Agricultura Tropical. Cali, Colombia. pp. 266-295.

Blad, B. L. and D. G. Baker. 1972. Orientation and distribution of leaves within soybean canopies. Agron. J. 61: 26-29.

Bouslama, M. 1977. Accumulation and partitioning of carbohydrates in two cultivars of navy beans (Phaseolus vulgaris L.) as influenced by grafting and source-sink manipulation. M.S. Thesis. Michigan State University. E. Lansing, Michigan.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

Donald, C. M. and J. Hamblin. 1975. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. in Agron. 27: 361-405.

Dornhoff, G. M. and R. M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves. Crop Sci. 10: 42-45.

Fried, D. G. C. 1961. A simple method of measuring integrated light values in the field. Ecology 42: 577-580.

Gallagher, J. N., P. V. Biacoe and R. K. Scott. 1975. Barley and its environment, V. Stability of grain weight. J. Appl. Ecol. 12: 319-336.

Hicks, D. R., J. W. Pendleton, R. L. Bernard and T. J. Johnston. 1969. Response of soybean plant types to planting patterns. Crop Sci. 297-307.

Kuet, J., J. Svoboda, J. P. Ondok, and P. G. Jarvis. 1971. Methods of growth analysis. In Sestak, Z., J. Castsky and P. G. Jarvis (ed.) Plant Photosynthetic Production. Manual of Mehtods. pp. 343-391. Dr. W. Junk N. V. Publishers, The Hague.

Ishag, H. M. 1973. Physiology of seed yield in field beans (Vicia faba L.) II. Dry matter production. J. Agr. Sci. Camb. 80: 191-199.

Koller, H. R., W. E. Nyquist and I. S. Chorush. 1970. Growth analysis of the soybean community. Crop Sci. 10: 407-412.

Lemeur, R. 1973. A method for simulating the direct solar radiation regime in sunflower, jerusalem artichoke, corn and soybean canopies using actual stand structure data. Agr. Meteorol. 12: 229-247.

Martinez, R. R. 1976. Nitorgen fixation and carbohydrate partitioning in Phaseolus vulgaris L. Ph.D. Thesis. Michigan State University. E. Lansing, Michigan.

Mock, J. J. and R. B. Pearce. 1975. An ideotype of maize. Euphytica 24: 613-623.

Monsi M. and T. Saeki. 1953. Uber den lichtfaktor in den pflanzengesellschaften und seine bedutung fur die stoffproduktion. Jap. J. Bot. 14: 22-52.

Nichiporovich, A. A. 1975. The genetics of photosynthesis and rational means of breeding highly productive plants. In Nasyrov, Yu. S., and Z. Sestak (ed.) Genetic Aspects of Photosynthesis. pp. 315-341. Dr. W. Junk B. V. Publishers, The Hague.

Ondok, J. P. and J. Kvet. 1971. Integral and differential formulae in growth analysis. Photosynthetica 5: 358-363.

Peet, M. M., A. Bravo, D. H. Wallace and J. L. Ozbun. 1977. Photosynthesis, stomatal resistance and enzyme activities in relation to yield of field-grown dry bean varieties. Crop Sci. 17: 287-293.

Radford, P. J. 1967. Growth analysis formulae. Their use and abouse. Crop Sci. 7: 171-175.

Richards, F. J. 1969. The quantitative analysis of growth. In Steward, F. C. (ed.) Plant physiology - A Treatise. Vol. 5A. pp. 3-76. Academic Press, NY.

Ross, J. K. and T. A. Nilson. 1967. The spatial orientation of leaves in crop stands and its determination. In A. A. Nichiporovich (ed.) Photosynthesis of Productive Systems. pp. 86-99. Tranlated by Israel Prog. Sci. Transl. Jerusalem.

Salazar, J., J. Wiersma and M. W. Adams. 1977. IKI-starch status in bean varieties at three stages of seed-development. Ann. Rpt. Bean Imp. Coop. pp. 24-27.

Subhadrabandhu, S. 1976. Control of abscission of flowers and fruits of Phaseolus vulgaris L. Ph.D. Thesis. Michigan State University. E. Lansing, Michigan.

Wallace, D. H., M. M. Peet and J. L. Ozbun. 1975. Studies of CO_2 metabolism in Phaseolus vulgaris L. and applications in breeding. In Burris, R. H. and C. C. Black (ed.) CO_2 Metabolism and Plant Productivity. pp. 43-58. University Park Press, Baltimore.

Watson, D. J. 1952. The physiological basis of variation in yield. Adv. in Agron. 4: 101-144.

Williams, W. A., R. S. Loomis, W. G. Duncan, A. Dovrat and F. Nunez. 1968. Canopy architecture at various densities and the growth and yield of corn. Crop Sci. 8: 303-308.

Wit C. T. de. 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. No. 663. Center Agri. Publ. Doc. Wageningen. 57 p.

CHAPTER 3

CANOPY ARCHITECTURE AND PHOTOSYNTHESIS OF TWO DRY BEAN (*Phaseolus vulgaris* L.) PLANT TYPES

ABSTRACT

Two dry bean genotypes were selected on the basis of their different growth habits. They were: a) Seafarer, a normal bush type (CIAT type I), and b) NEP-2, a narrow erect, short vine type (CIAT type II). The azimuth and the inclination of all bean leaflets at every 10 cm plant height (plant strata) up to the top of the canopy were measured weekly by the use of a compass and an inclinometer. Carbon dioxide uptake of bean leaves, by plant strata, were measured using a $^{14}CO_2$-technique modified from the one proposed by McWilliam *et al.* (1973). Two light environments (full and 50% full sunlight) were used to modify crop architecture and photosynthesis.

Seafarer and NEP-2, due to their leaf inclination functions, could be classified as erectophile and planophile foliar structure, respectively, by using de Wit's system (1965). Leaf area distribution as a function of leaf inclination and average leaf angle showed that the leaf angle changed with plant strata and time of the day. The shade environment reduced the average leaf angle of Seafarer and NEP-2 by 22.54% and 23.22%, respectively. Neither Seafarer nor NEP-2, under both light environments, had leaves oriented with more frequency for any azimuth. Leaf area indexes of both cultivars were increased by the shade

environment, primarily by affecting leaf size. Photosynthetic rates increased from the bottom to the top leaves, for both cultivars. Maximum CO_2 uptake rates for each plant stratum were observed at inital pod filling. Seafarer had higher rates of uptake at all canopy levels than NEP-2. During the stage of maximum CO_2 uptake, the shade environment reduced the uptake rates of Seafarer and NEP-2 by 55.19% and 30.54%, respectively. Starch, measured by IKI, started to accumulate in roots and stems of both cultivars after flowering. At final harvest starch disappeared in both roots and stems of Seafarer but was still present in NEP-2. The shade environment reduced the amount of starch but not the ontogenetic patterns.

INTRODUCTION

The primary productivity of plant communities is initially dependent upon photosynthesis. The pattern of leaf display at each level of a community can be related to light interception, canopy photosynthesis, and hence, to production. Results obtained by experimental research and modeling with grasses indicate that leaf inclination is an important characteristic of plant architecture for light penetration in the plant canopy. The results with dry bean (Chapter 2) also identified leaf inclination as an important morphological characteristic.

The objectives of this study were to measure photosynthesis in different plant strata and to better characterize the canopy architecture of two dry bean plant types during their ontogenetic development. Light environments (full and 50% sunlight) were used to modify canopy architecture and photosynthesis.

MATERIALS AND METHODS

This experiment was conducted at the Michigan State University Crop Science Farm, E. Lansing, on a soil clasified as a Miami-Conover Loam.

Two dry bean genotypes were selected on the basis of their different growth habits. They were: a) Seafarer, a normal bush type (CIAT type I), and b) NEP-2, a narrow erect, short vine type (CIAT type II). Both cultivars were seeded in 70 cm rows oriented north-south, with 5 cm between plants within rows. Two light environments were

imposed on each cultivars: 1) full sunlight during the whole growing season (hereafter termed sun environment), and 2) shade environment 30 days after planting (hereafter termed shade environment). For the shade environment, incoming Photosynthetically Active Radiation (PAR) was reduced 50% by using a plastic screen raised 150 cm from the ground. The light treatments were not randomly allocated to the plots due to physical limitations in the construction of the support system for the plastic screen. However, the cultivars were randomly allocated in the experimental plots. The plots were distributed in a randomized complete block design with three replications. Each plot consisted of six rows, each 5.8 m long. Planting date was on June 8, 1977. One week before planting 500 Kg/ha of 18-16-0 plus 4% Mn and 2% Zn fertilizer were broadcast and incorporated on the experimental area. All plots received supplemental sprinkler irrigation when necessary.

The four central rows of each plot were used for periodic collection of data. All the plants in a .5 m sample or row were harvested at weekly intervals for 7 consecutive weeks starting 30 days after planting (dap). The sample for the final harvest was taken from 2.0 m of row. At each harvest date the plants were separated into stem and petioles, flowers, pods, and leaves, and then dried in a forced air dryer at 45 to 50° C to a constant dry weight. For specific leaf dry weight (SLDW) determinations, a sample of five central leaflets was randomly choosen from the harvested leaves in each plot and their area was measured with a portable leaf area meter (Lambda Instruments Model LI-300). The leaves were dried like the other plant parts to obtain their dry weights. The Leaf Area Index (LAI) of each plot was determined by multiplying its respective SLDW by its corresponding leaf dry weight.

Figure 1. Plots under shade environment. The plastic screen was raise 150 cm about the ground leve.

Figure 2. Metal structure used to separate the crop canopy by heights (10 cm each).

Figure 1.

Figure 2.

The azimuth and the inclination of all bean leaflets at each 10 cm plant height up to the canopy in a .5 m row were measured weekly between 11:00 a.m. and 1:00 p.m. EDT. The azimuth of each leaflet was determined with a compass and then was classified into one of eight different 45° intervals. The inclination of each leaflet was measured with an inclinometer constructed by drilling a small hole in the center of a broad protractor base, inserting a thread through the hole, and fastening two small lead weight on both ends of the thread. The base of the protractor was placed parallel to the adaxial surface of the leaflet to determine the angle of leaf inclination with a horizontal line. The leaflets were grouped into inclination classes with 10° intervals.

Carbon dioxide uptake of bean leaves were measured using a $^{14}CO_2$ technique modified from the one proposed by McWilliam _et al_. (1973). This method has been suggested for measurement of apparent photosynthetic rates by various researchers (Austin and Longden, 1967; Shimsi, 1969; Incoll and Wright, 1969; Bravdo, 1972; McWilliam _et al_., 1973; Neylor and Teare, 1975). The usual technique consists of three operations: 1) exposing leaves to a known $^{14}CO_2$ activity for a given time interval, 2) obtaining a leaf sample form the exposed area, and 3) measuring the amount of $^{14}CO_2$ which has been taken up.

The apparatus used in this experiment (Figures 3 and 4) to expose a leaf segment to $^{14}CO_2$ can be divided into:

A) $^{14}CO_2$ gas supply: The radioactive gas was obtained in 54 lts compressed-gas bottle from Matheson Gas Products, East Rutherford, NJ; 340 ppm $^{14}CO_2$ (with a specific activity of 10 µCi/l), 21% of O_2, and the balance N_2.

B) Photosynthesis chamber: The one used was similar to the one described by McWilliams _et al_. (1973), and consisted of an aluminum

Figure 3. Apparatus used to expose leaves to $^{14}CO_2$ labelled CO_2. A) $^{14}CO_2$ gas syookuer: 54 lts bottle, B) gas regulator, C) flowmeter, D) hose to the aluminum handpiece, and E) aluminum support.

Figure 4. Closeup of the aluminum handpiece. A) photosynthetic chamber, B) gas regulator, C) inlet gas conduct, D) inlet tube, E) outlet tube, F) trigger, G) clamping lever, and H) soda-lime container.

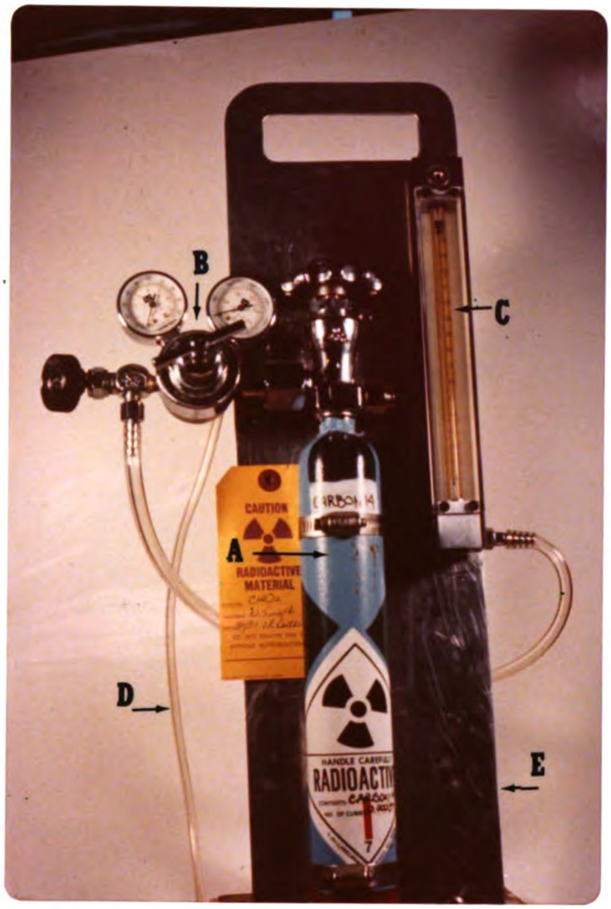


Figure 3.

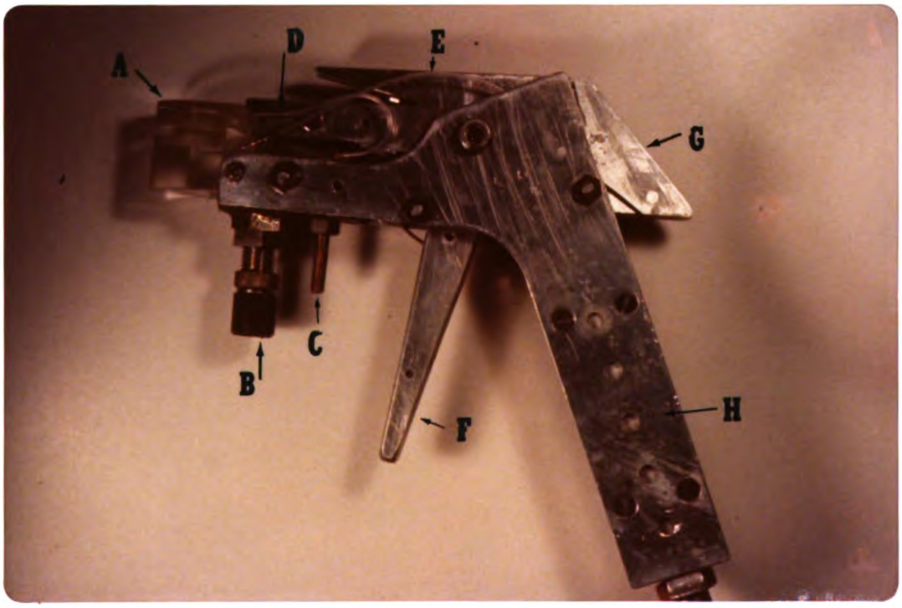


Figure 4.

Figure 5. The apparatus used for $^{14}CO_2$ uptake measurements under field conditions. A) aluminum support with the $^{14}CO_2$ bottle, B) aluminum handpiece, C) light sensor (PAR), and D) light meter.

Figure 6. Some of the complementary materials used in the $^{14}CO_2$ uptake determination in the field. A) 22 ml scintillation vials containing 1 ml of NCS., B) black plastic, C) glass with a zinc-oxide glycerol mixture, D) stopwatch, and E) notebook.

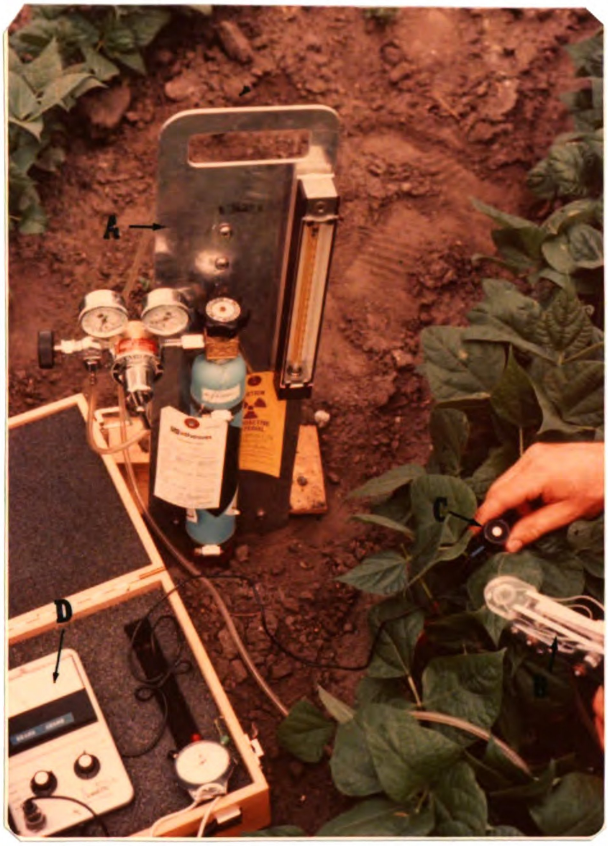


Figure 5.

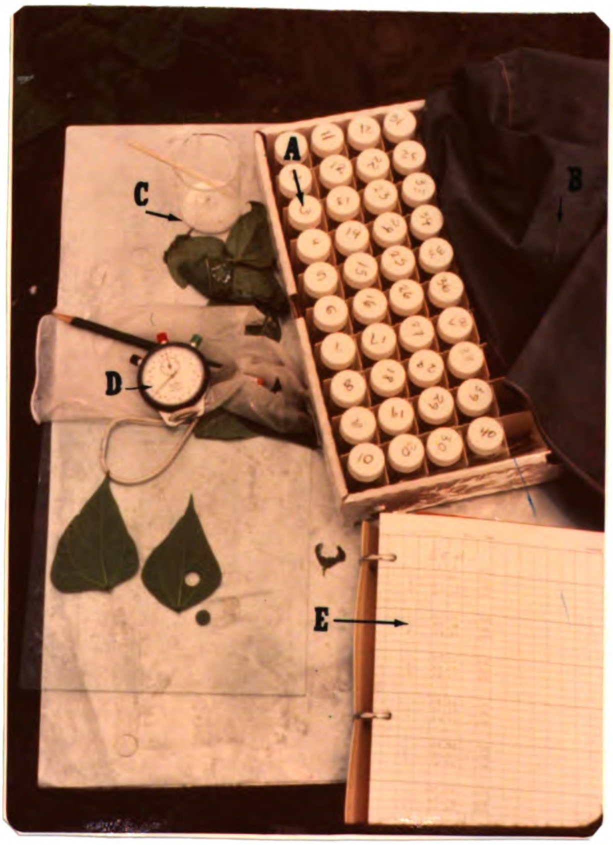


Figure 6.

pistol grip, two transparent plexiglass jaws (which house a valve to regulate the flow rate, and two photosynthesis chamber gaskets), a lock-release trigger, and a soda-lime absorbing column. The chamber was 9.5 mm in diameter and 5 mm in height.

A leaf section of the central leaflet of a fully expanded leaf was exposed to $^{14}CO_2$ by attaching the leaf chamber to the leaf and allowing the gas to flow on both sides of the leaf. In preliminary experiments, it was found that a flow rate of 130 ml min^{-1} and an exposure time of 20 seconds produced optimum photosynthetic rates.

The exposed area of the leaf was marked by putting a zinc oxide-glycerol mixture on the lower gasket before placing the leaf in the chamber. A leaf-disc punch of the same diameter as the chamber was used to punch out the exposed leaf area. The leaf disc was placed in a 22 cm scintillation vial containing 1 ml of NCS, a commercial solubilizer (a solution of a quaternary ammonium base in toluene) from Amersham-Searle Corp., Arlington Heights, Illinois. The vials were protected from the direct sunlight for any appreciable length of time in the field by covering them with black plastic. The samples were allowed to digest for 48 hours in the laboratory. After digestion was complete, the solution was bleached with 1 ml of saturated solution of benzoyl peroxide (1 ml of benzoyl peroxide in 5 ml of toluene). Eighteen ml of scintillation fluid (6 gr/l PPO and 75 mgr/l POPOP) were added to the vial. The samples were counted for two minutes in a scintillation counter (Beckman LS-100).

Carbon dioxide uptake by the bean leaf was calculated by using the following formula

$$BPs = \frac{(C-B).\alpha.\ K}{E.Spa.\beta.R.t}$$

where:

BPs = CO_2 uptake (mg dm^{-2} hr^{-1})

C = sample counts per minute

B = background counts (leaf sample without exposure $^{14}CO_2$)

α = conversion factor from µmoles to mg CO_2 (.44)

K = constant to change seconds to hours and cm^2 to dm^2 (3.6×10^{-5})

E = efficiency of the counting process (.80 to .85)

Spa = specific activity of the labeled gas (.75 µCi · $µmole^{-1}$)

β = leaf sample area (.95 cm^2)

R = conversion factor for dpm to µCi (2.2×10^6 dpm $µCi^{-1}$)

t = $^{14}CO_2$ exposure time (20 sec)

Carbon dioxide uptakes rates of both cultivars under the two light environments were usually measured between 11:00 a.m. and 1:00 p.m. EDT at selected levels of plant height during the growing season. For each $^{14}CO_2$ uptake sample the PAR was measured by placing the light sensor in the same orientation as the leaf (hereafter termed leaf PAR).

Starch status in the roots (ground level) and stems (every third internode of main axis) was determined by using an iodine-potassium iodide starch-indicator (IKI) solution (.3 gr of iodine; 1.5 gr potassium iodide; and 100 ml water; Johansen, 1940). In each plot five plants were randomly chosen and starch accumulation was estimated on a visual scal of 1 to 5 (Salazar et al., 1977) from fresh sections to each of which had been applied 3 to 4 drops of IKI.

RESULTS AND DISCUSSION

Leaf inclination

The results obtained in the experiment of 1976 (Chapter 2) indicated that leaf inclination (leaf angle) is a very important factor which affects light penetration in the bean plant canopy. Therefore, more careful measurements of this parametere were made in the present experiment.

Measurements of leaflet area were necessary for the estimation of leaflet orientation. For this purpose leaflet length and width were taken simultaneously with leaflet inclination and azimuth. At 40 dap, 100 leaflets from each of Seafarer and NEP-2, growing in the sun environment, were sampled. For each leaflet, width and length were measured and the area determined with a leaf area meter (Lambda Instruments Model LI-300). These data were used to calculate regression equations to estimate Seafarer leaflet area (Leaflet area = 1.7884 + 0.8455X, $R^2 = .9214$) and NEP-2 leaflet area (Leaflet area = 1.1700 + .9604X, $R^2 = .9433$) by knowing the length X width of the leaflet (X in the above equations in cm^2).

Leaf area distributions as a function of leaf inclination of Seafarer and NEP-2 grown under the sun environment are presented in Figure 7. The canopy of Seafarer was found to have a greater frequency of vertical leaves, while NEP-2 had a greater frequency of horizontal leaves. Seafarer and NEP-2, according to their leaf angle distributions, could be calssified as erectophile and planophile foliar structures respectively, using de Wit's system (1965).

At 49 dap, leaf inclination measurements of Seafarer grown under the sun environment were made at 8:30 a.m. 12:00 a.m. and 3:00 p.m. EDT. PAR above the plants at these times were 800, 3,200, and 3,600 $\mu E\ cm^{-2}\ sec^{-1}$, respectively. The results are presented in Figure 8A. In the morning, Seafarer had a planophile foliar structure which changed to different degrees of erectophile as the light intensity increased during the day. At each sampling time (at 49 dap) leaf inclination data were

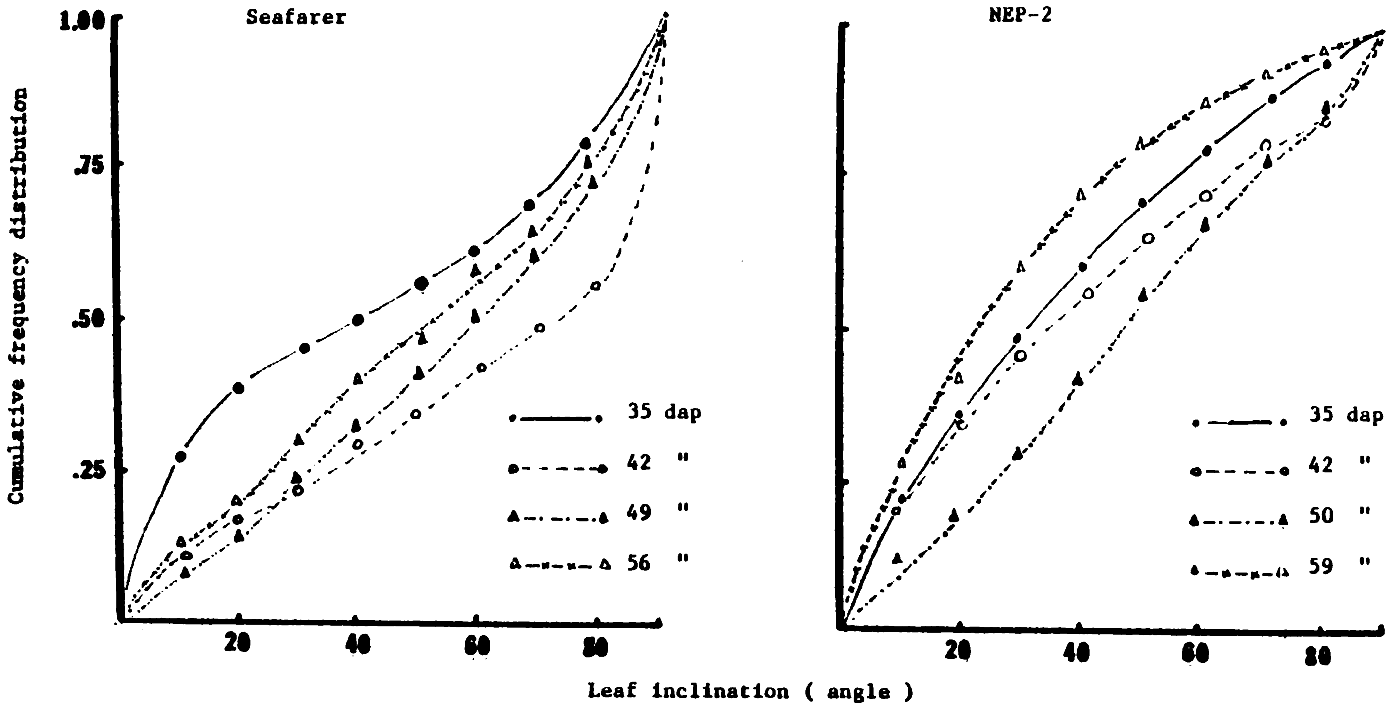


Figure 7. Leaf area distribution as a function of leaf inclination of Seafarer and NEP-2 during the growing season and under the sun environment.

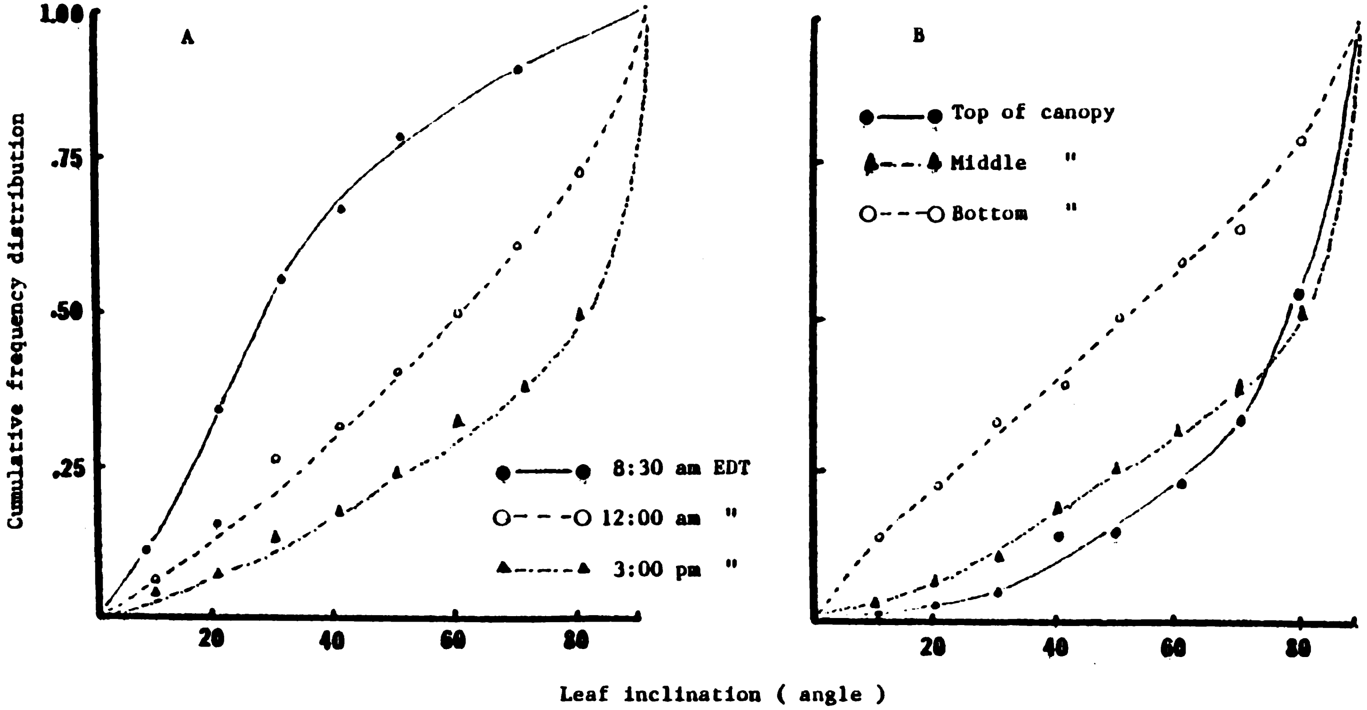


Figure 8. Leaf area distribution of Seafarer at 49 dap and under the sun environment: A) as a function of leaf inclination during the day, and B) as a function of leaf inclination and canopy height at 3:00 p.m. EDT.

Table 1. Average leaf angle by plant strata of Seafarer at 45 dap grown under the sun environment.

Time	Plant strata (cm)				
	0 - 10	10 - 20	20 - 30	30 - 40	Mean
8:30 a.m.	16.95	29.30	35.70	39.32	31.20
12:00 a.m.	42.82	52.64	62.24	60.84	54.71
3:00 p.m.	47.61	64.92	66.66	67.29	63.86

also taken by plant strata. The results at 3:00 p.m. are presented in Figure 8B. Similar trends in leaf inclination were observed at the other sampling times. Figure 8B shows that the degree of erectophile structure increased from the bottom to the top of the plant canopy. In Table 1 is presented the average leaf angle by plant strata of Seafarer at 49 dap grown under the sun environment. These date indicate that leaf inclination of Seafarer changed during the day and increased fromthe bottom to the top of the plant canopy.

Average leaf angles of Seafarer and NEP-2 in the sun and the shade environments, during the growing season, are presented in Table 2. Both cultivars showed similar trends, however, Seafarer had higher average leaf angles than NEP-2. Their values increased and then decreased during the growing season. The average leaf angle increased from the bottom (0 - 10 cm) to the top of the plant canopy (40 - 50 cm) for both cultivars on all sampling dates. A similar trend was observed for the leaf angle values at any plant height. The shade environment reduced the average leaf angle of Seafarer and NEP-2 by 22.54% and 23.22%, respectively.

Leaf area distribution as a function of leaf inclination and average leaf angle clearly showed that the leaf angle changed during the day. It increased from the morning to the afternoon and from the bottom to the top of the plant canopy.

Maximum photosynthesis of the plant canopy is found when leaf inclination changes gradually from 90^{o} degrees at the top layer to 0^{o} degrees at the lowest layer of the canopy (Loomis and Williams, 1969; Kuroiwa, 1970). The higher phtosynthesis is caused by the more uniform distribution of light over the leaves and the curvilinear nature of the photosynthetic light response curve. Verhagen <u>et al</u>.

Table 2. Average leaf angle of canopy profile of Seafarer and NEP-2 during the growing period.

Date	Plant strata (cm from the bottom)											
dap	0-10	10-20	20-30	30-40	40-50	Mean	0-10	10-20	20-30	30-40	40-50	Mean
	Seafarer: sun env.						Seafarer: shade env.					
35	46.98	50.09	50.13			48.93						
42	48.78	59.82	69.70			62.06						
49	42.82	52.64	62.24	50.84		54.46	34.68	38.09	42.84	47.39		41.40
56	43.66	44.54	55.81	62.68		51.67	33.51	46.34	47.70	49.58		40.77
63*	20.53	21.08	22.50	32.21		23.71	20.54	20.11	22.26	23.64		22.13
	NEP-2: sun env.						NEP-2: shade env.					
35	25.12	33.68	32.28			32.28						
42	25.18	37.77	40.53	40.63		36.03						
50	25.56	40.20	40.81	42.78		37.34	19.01	21.68	32.41	32.53		26.41
59	25.54	28.75	31.53	37.80	32.31	31.19	22.14	25.82	30.26	31.47	20.14	25.97
64		20.65	27.18	32.07	34.02	28.50		20.63	20.34	20.48	25.60	21.76

* cloudy day

(1963) stated that the "ideal foliage" consists of layers with continuously changing inclination so that available light is evenly spread over all available leaf area. Under this consideration Seafarer has a better plant canopy structure than NEP-2 because it has higher leaf inclination and allows more light penetration in the canopy than NEP-2.

Leaflet orientation depends on the relative turgor of motor cells on dorsal and ventral sides of the pulvinus, an organ at the base of the leaflet (Satter et al., 1970a). Potassium (K^+) flux is involved in turgor changes in Mimosa pudica (Allen, 1979), Albizzia julibrissin (Satter et al., 1970b), and Trifolium repens (Scott et al., 1977). Phytochrome has been suggested to be the mechanism for K^+ flux and K^+ movement is at least partly the result of changes in membrane permeability and/or transport of K^+ in the motor cells of the pulvini (Satter and Galston, 1971; Setty and Jaffe, 1972). Breeding for efficient and uniform light distribution in a bean canopy would have to be conducted with consideration given to leaf inclination.

Leaf azimuth

Simultaneous measurements of leaf inclination and leaf azimuth were made during the growing season. The results of the X^2 (Chi-square) Test, using the number of leaflets as variable, for random azimuthal distribution for Seafarer and NEP-2 under both light environments are presented in Table 3. Neither Seafarer nor NEP-2 had leaves oriented more frequently for any particular azimuth. Leaf area distribution (% of total) as a function of azimuth angle for Seafarer and NEP-2, after 49 and 50 dap, respectively, is presented in Table 4. Figure 9 represents graphically the data of Table 4 for Seafarer under the sun environment. Apparently leaves of Seafarer under the sun environment

Table 3. X^2 (Ch-square) Test for random aximuth leaf orientation for Seafarer and NEP-2 during the growing season.

Date (dap)		Light env.	X^2	p
35	Seafarer	sun	4.4789	.900
35	NEP-2	sun	7.3104	.500
42	Seafarer	sun	4.3724	.900
42	NEP-2	sun	7.1136	.500
49	Seafarer	sun	5.7959	.900
49	Seafarer	shade	3.1305	.900
50	NEP-2	sun	2.9168	.900
50	NEP-2	shade	2.7109	.900
56	Seafarer	sun	.6432	.995
56	Seafarer	shade	3.2593	.900
59	NEP-2	sun	6.0993	.750
59	NEP-2	shade	.5995	.995
64	NEP-2	sun	2.8540	.900
64	NEP-2	shade	.7174	.995

Table 4. Leaf area distribution (% of total) as a function of azimuth for Seafarer and NEP-2 after 49 and 50 dap, respectively.

	Seafarer				NEP-2	
	sun			shade	sun	shade
Azimuth	8:30 am	12:00 am	3:00 pm	1:00 pm	12:00 am	1:00 pm
0- 45	17.05	15.34	17.84	9.39	12.98	14.96
45- 90	17.21	20.25	17.54	18.01	10.62	10.51
90-135	8.51	12.44	13.85	15.79	12.99	15.30
135-180	9.21	8.40	14.95	16.58	13.06	14.02
180-225	11.04	10.00	9.82	11.13	12.77	11.16
225-270	5.61	8.17	6.26	9.75	12.31	11.57
270-315	14.84	14.03	13.19	8.56	12.78	10.78
315-360	12.49	10.39	6.56	10.78	12.99	11.70
X^2	3.3110	5.7959	10.4307	3.1305	2.9168	2.7109
P	.900	.500	.250	.900	.900	.900

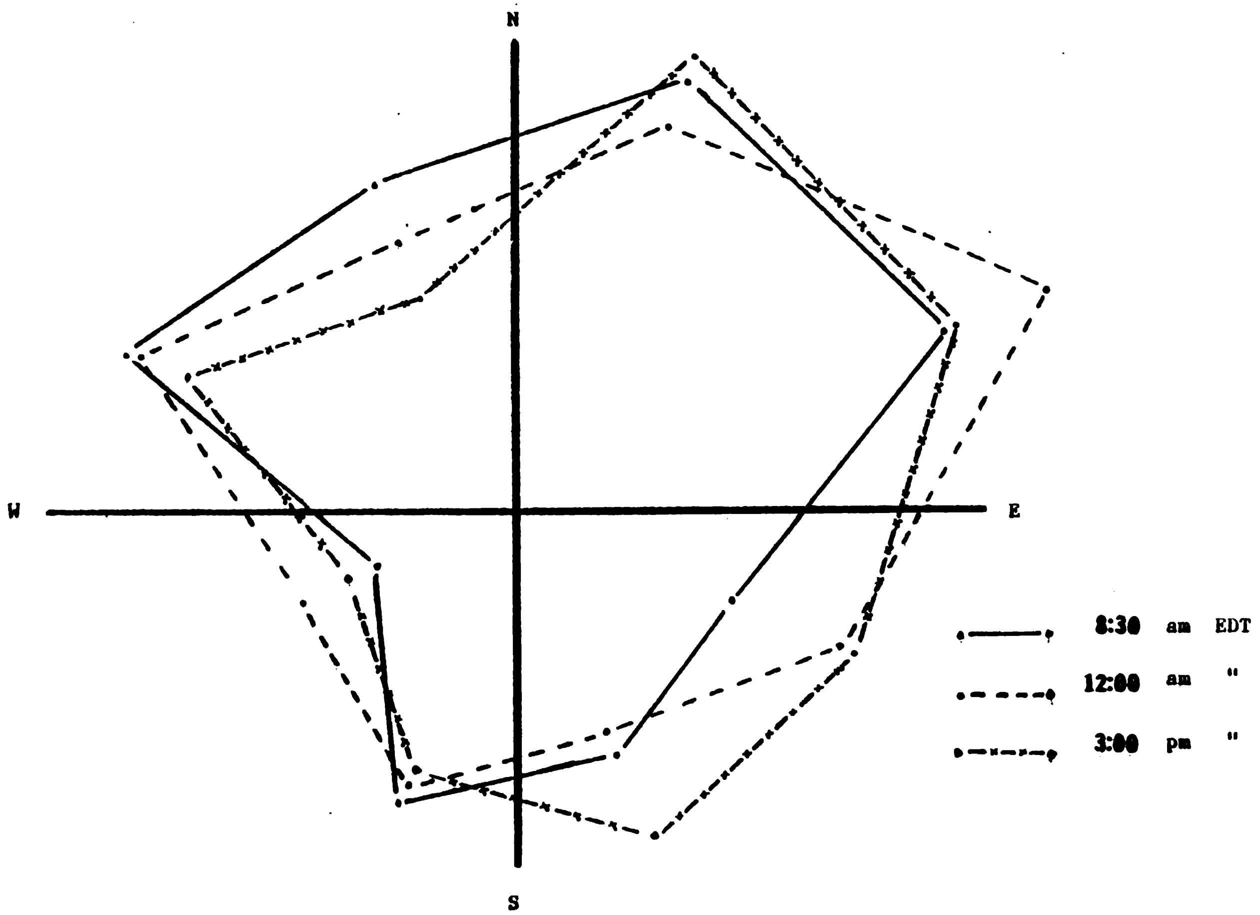


Figure 9. Azimuthal density functions of Seafarer under the sun environment at 49 dap.

had more leaves oriented in the northeastern azimuth which became more prominent in the afternoon. This could be due to the direction of the prevailing winds. But no statistical significance was found for any azimuth orientation.

Shell *et al.* (1974) observed that bean leaves had a northeasterly azimuth in the morning which changed to a northerly azimuth in the afternoon. But they did not give any explanation for this behavior. However, all four plant species observed by them (sunflower, beans, cucumbers, and peppers) showed preference for a northeasterly azimuth orientation. Soybean plants have a random azimuthal distribution (Blad and Baker, 1972; Lemeur, 1973), as well as broad beans (Ross and Nilson, 1967). Corn plants have a marked preference for azimuthal direction perpendicular to the row (Ross and Nilson, 1967; Loomis and Williams, 1969; Lemeur, 1973). Sunflower plants have three preferential directions due to the spiral phyllotaxy of the leaves which is equal to 120° (Lemeur, 1973).

Leaf area distribution with plant height

Light models of plant communities require the distribution of LAI with plant height. Leaf area distributions for Seafarer and NEP-2 as a function of plant height are presented in Figures 10 and 11, respectively. Leaf area distributions with height for Seafarer and NEP-2 under the sun environment for this experiment were similar to those observed in the previous experiment (Chapter 2). Seafarer had its maximum leaf area at approximately the middle of the plant height with equal leaf area toward the bottom or the top of the plant canopy; NEP-2 had its maximum leaf area at higher levels and more leaf area in the top than in the bottom of the canopy. Both cultivars, when grown under the shade environment, showed 60% less leaf area in the lower layers. This

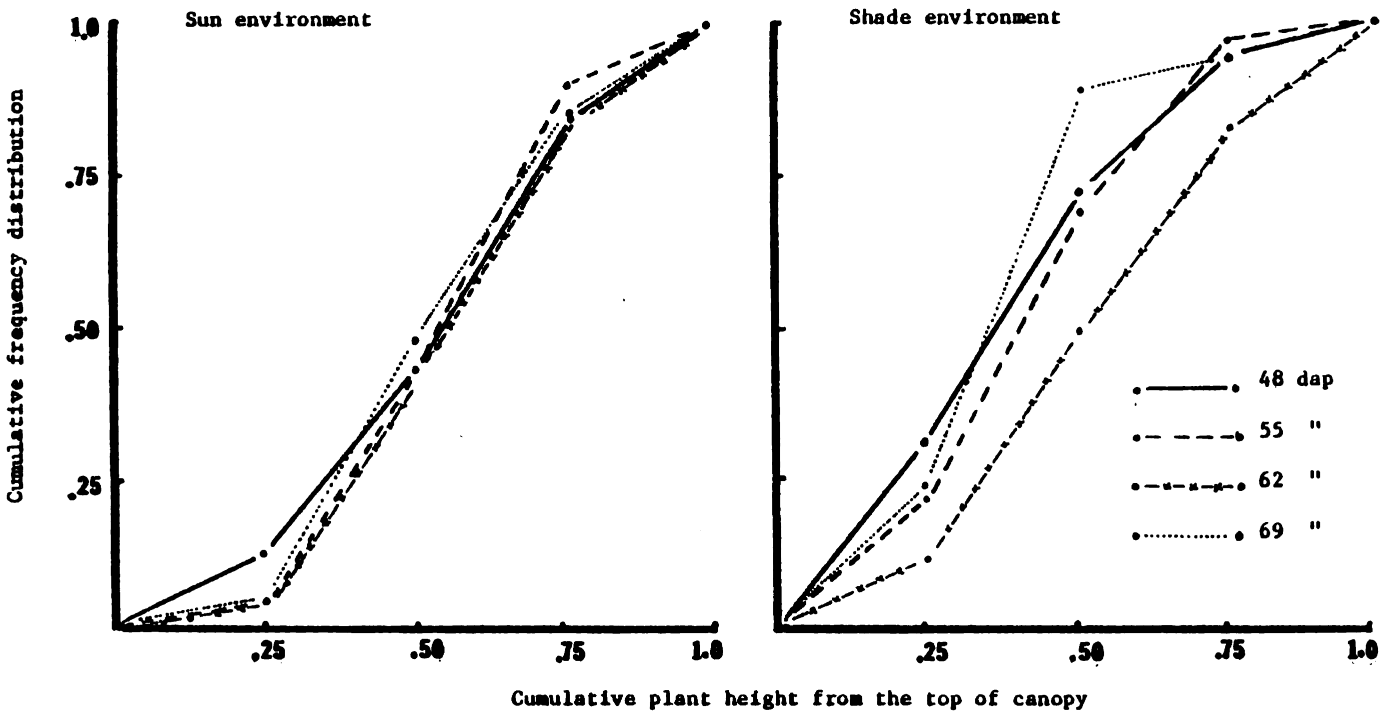


Figure 10. Leaf area distribution with plant height for Seafarer.

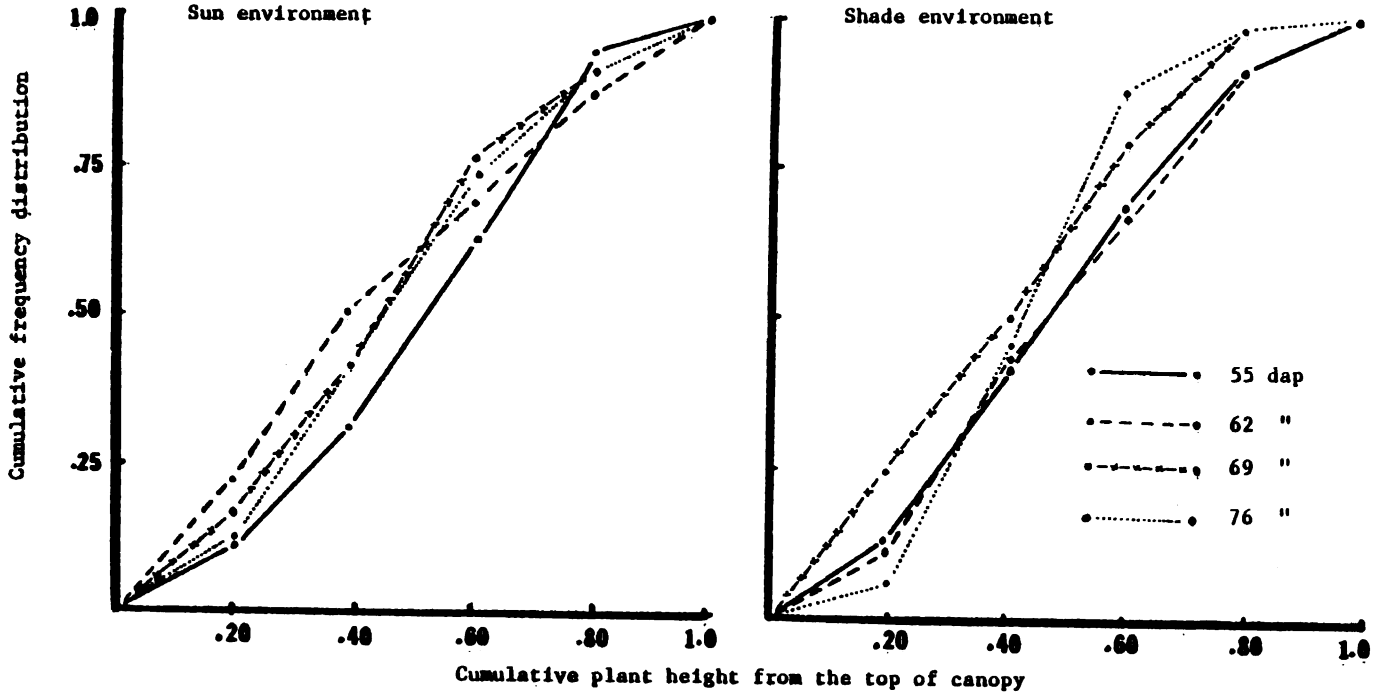


Figure 11. Leaf area distribution with plant height for NEP-2

is visualized by higher values of leaf accumulation at .75 and .8 values of cumulative leaf area for Seafarer and NEP-2, respectively.

Leaf area

The time courses of development of LAI for Seafarer and NEP-2 are presented in Figure 12. Both cultivars had lower LAI's than in the previous year (Chapter 2). The shade environment increased the LAI of both cultivars, primarily by affecting leaf size (Figure 13A and Table 5), since the number of branches and number of nodes were not affected. The bean plants were shaded 30 dap when they had formed branches and the number of nodes had been determined by the genetic potential of each cultivar.

Dale (1964) observed that the pattern of growth at the stem apex of bean plants was highly determinate and the number of leaf primordia produced was independent of environmental factors. Dale also found (1965) that leaf size and the rate of leaf unfolding was a parabolic function of light intensity. This may explain why, in this experiment, an increase of bean leaf size was found under shaded field conditions; Crookston *et al*., (1975) observed a decrease in bean leaf size due to shading, working in crontrolled-environment chambers. Segovia and Brown (1978) found that under field conditions, soybean leaf area increased under 50% of sunlight. There was an effect of the shade environment on the expansion of the bean leaf. This could originate either from a diverson of more material to the leaves under the shade conditions or from the development of a larger leaf area from the same amount of dry matter, i.e., by alteration of the specific leaf dry weight (SLDW). Table 6 shows that the shade environment did not affect the amount of leaf dry matter in relation to the whole plant; however, the SLDW was reduced in both cultivars by the shade environment (Figure 13B and Table 7).

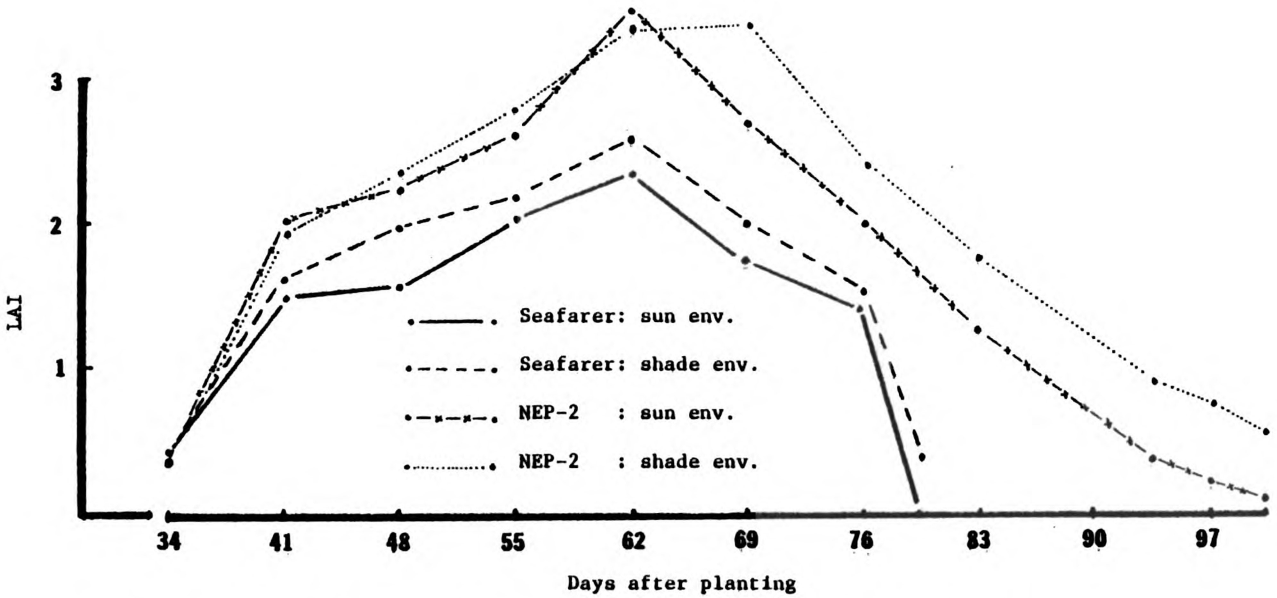


Figure 12. LAI of Seafarer and NEP-2 during the growing season at two light environments.

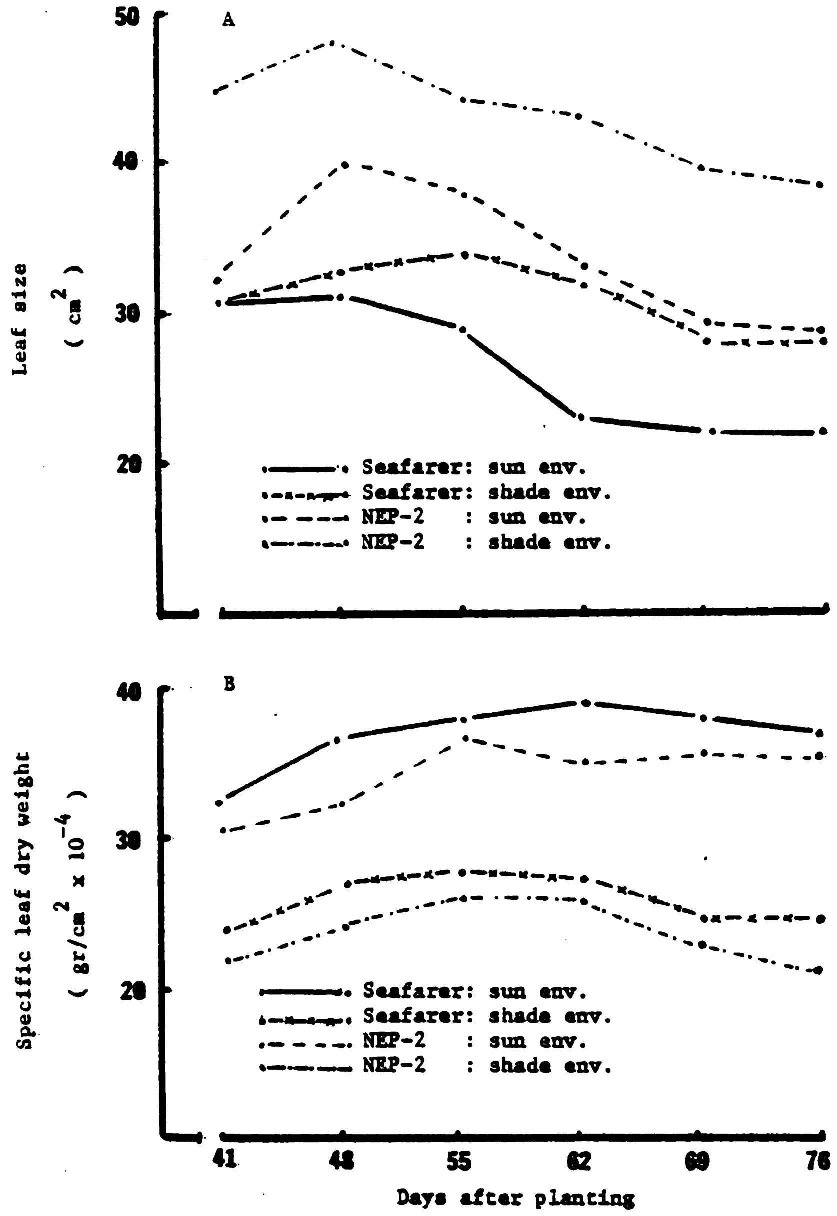


Figure 13. Size of the central leaflet (A) and specific leaf dry weight (B) of Seafarer and NEP-2 during the growing season at two light environments.

Table 5. Analysis of Variance (ANOVA) for leaf size during the growing session.

Source of variance	df	MS	F
Treatments (T)	3	776.3767	78.63**
sun vs. shade	1	1088.5948	110.25**
Sea sun vs. Sea shade	1	213.5372	21.62**
NEP-2 sun vs. NEP-2 shade	1	1027.0396	104.01
Replications	2	1.9845	
Error (a)	6	9.8736	
Date of sampling (D)	4	121.3975	15.26**
D X T	12	10.9124	1.42
Error (b)	32	7.6538	

** Significant at the 1% level

Table 6. Leaf dry weight/Plant dry weight ratio of Seafarer and NEP-2 during the growing season.

Date	Seafarer		NEP-2	
dap	sun env.	shade env.	sun env.	shade env.
	Leaf d. w / Plant d. w			
34	.69	.69	.67	.67
41	.68	.67	.57	.61
48	.58	.59	.54	.56
51	.50	.54	.49	.48
62	.35	.39	.45	.45
69	.27	.30	.32	.31

Table 7. Analysis of Variance (ANOVA) for specific leaf dry weight (SLDW) during the growing season.

Source of variance	df	MS	F
Treatments (T)	3	530.3466	44.52**
sun vs. shade env.	1	793.4200	66.61**
Sea. sun vs. Sea. shade	1	456.5358	38.32**
NEP-2 sun vs. NEP-2 shade	1	341.0841	28.63**
Replications	2	14.2682	
Error (a)	6	11.9110	
Date of sampling (D)	4	18.6434	3.25**
D X T	12	11.6180	2.02
Error (b)	32	5.7329	

** Significant at the 1% level

Canopy photosynthetic profiles

Photosynthetic rates, measured by the $^{14}CO_2$ techniques as CO_2 uptake rates, of Seafarer and NEP-2 canopy profiles are presented in Table 8. All plant strata were sampled in each cultivar with the exception of those leaves at the upper most strata, because only fully expanded leaves were considered and to have uniform number of strata for comparison purposes among cultivar and light environments. A general trend can be observed. Carbon dioxide uptake rates at all sampling dates increased from the bottom to the top of the plant for both cultivars. Maximum CO_2 uptake rates for each plant stratum were observed at the time of initial pod filling, 58 and 71 dap, for Seafarer and NEP-2, respectively. Seafarer generally had higher rates of uptake at all canopy levels than did NEP-2. The shade environment affected CO_2 uptake rates of both cultivars, i.e., during maximum CO_2 uptake, the shade environment reduced the CO_2 uptake rates of Seafarer and NEP-2 by 55.19% and 30.54%, respectively. This resulted in a significant cultivar X treatment interaction (Table 8). There were significant statistical differences between Seafarer and NEP-2 canopies, light environments, and plant strata in the rate of CO_2 uptake in all sampling dates (Table 9). Some interactions were also significantly different from zero.

In general, the observed photosynthetic rates were in the range of previously reported values for bean leaves (Howe, 1962, 1964; Charter *et al.*, 1970; Austin and MacLean, 1972; Crooksten *et al.*, 1974; Sestak *et al.*, 1975; Peet *et al.* 1977). Frazer and Bidwell (1974) observed in beans a pattern of photosynthesis with age that is repeated in each leaf. Apparent photosynthesis of individual bean leaves rose to a maximum and then slowly declined with time. However, it increased with

Table 8. Photosynthetic rates of canopy profiles of Seafarer and NEP-2 during the growing season.

Genotype	Treatment	Plant strata	Days after planting					
			43	50	58	65	71	79
			---- CO_2 uptake (mg CO_2 dm^{-2} hr^{-1}) ------					
Seafarer	sun env.	20 - 30 cm		12.90	16.31	11.19		
		10 - 20	11.01	11.84	13.99	11.17		
		0 - 10	11.72	11.26	12.13	9.92		
	shade env.	20 - 30			9.37	8.63		
		10 - 20	8.07		6.70	8.58		
		0 - 10	6.87		3.39	3.28		
NEP-2	sun env.	30 - 40					11.53	9.40
		20 - 30		8.43	6.23	10.29	10.44	6.81
		10 - 20	8.69	8.50	5.78	10.11	10.77	5.75
		0 - 10	7.90	7.67	5.43	7.00	6.35	5.28
NEP-2	shade env.	30 - 40				8.50	9.53	5.81
		20 - 30			5.00	8.66	7.89	5.27
		10 - 20	7.32		2.38	7.56	7.85	4.59
		0 - 10	5.89		0.95	2.61	1.89	1.63
	$LSD_{(.05)}$		1.20	0.65	1.34	1.13	0.69	0.83

Table 9. Analysis of variance (ANOVA) of photosynthetic rates of Seafarer and NEP-2 during the growing season.

Source of variability	Days after planting					
	43	50	58	65	71	79
	F Test					
Cultivar (I)	22.55**	272.47**	269.54**	12.58**		
Treatment (II)	47.95**		201.82**	115.95**	166.78**	86.91**
Plant strata (III)	3.40	9.10	36.29**	65.84**	152.92**	42.69**
I X II	8.64**	1.16	32.99**	3.18		
I X III	1.52		5.07**	1.45		
II X III	3.53		4.59	11.89**	6.32*	6.62*
I X II X III	31.92**		11.40**	1.04		
Error MS	.9337	.2389	1.24	.88	.3149	.4524

the appearance of a new leaf or during flowering. They concluded that photosynthesis was, to a large extent, controlled by or dependent on intrinsic factors in each leaf and by extrinsic events in other parts of the plant. Neales and Incoll (1968) suggested that the rate of photosynthesis is regulated by the interactions of the accumulation of assimilates within the leaf, the rate of transpiration from the leaves, and the demand of assimilates in other parts of the plant. Ormrod (1963) observed that net carbon dioxide exchange rates of bean leaves also increased in the linear phase of increase in pod dry weight. Woodward and Rawson (1976) found similar net photosynthesis patterns with age for soybean leaves. Peet _et al_. (1977) reported that photosynthetic rates of bean leaves were highest at early pod development and differences between cultivars were observed. Victor _et al_. (1977) found that leaf apparent photosynthesis rates of inbred, hybrid and open-pollinated corn plants were affected by leaf position and declined as plants aged.

The observations reported here are in keeping with results reported by the above authors. The CO_2 uptake rates were highest at the upper most measured strata of the bean plants which was probably the result of younger leaves and higher demand for assimilates since most of the pods are located in these levels. Under the shade environment, similar CO_2 uptake rate patterns were observed, although the uptake behavior may indicate that the shade environment induced quantitative changes of the photosynthetic mechanism of the bean leaves and/or lower demand for assimilates.

Relationship between photosynthesis and leaf PAR

Photosynthetic rates of Seafarer and NEP-2 canopies as a function of the incident PAR on the leaves (leaf PAR) are shown in Figure 14 to

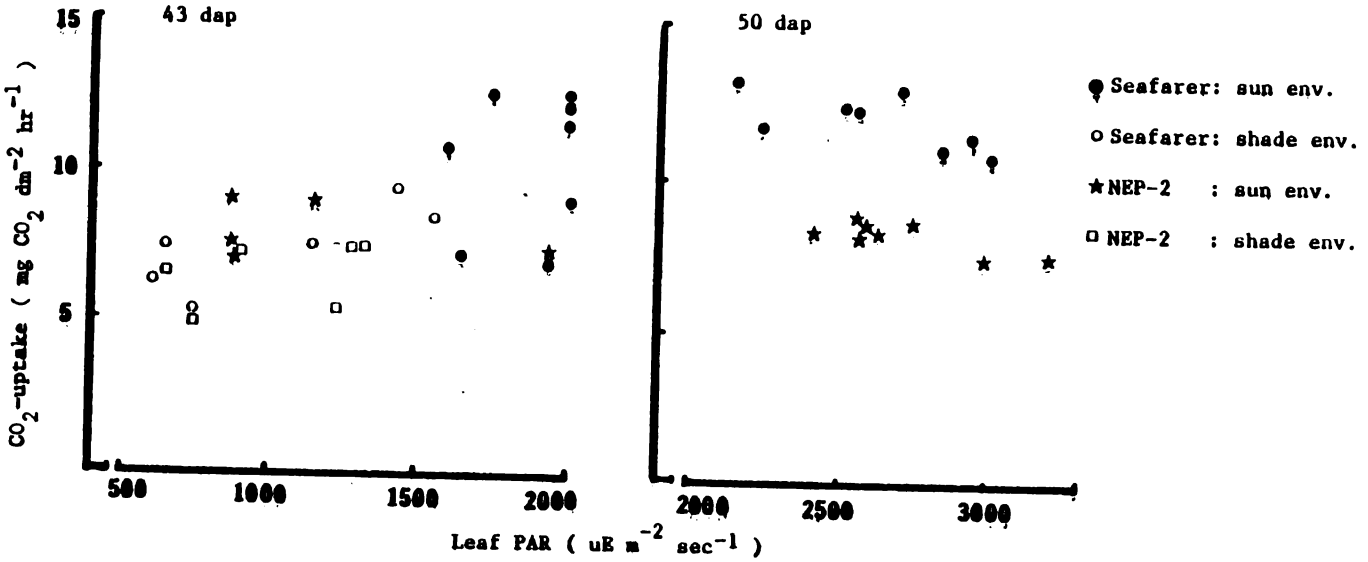


Figure 14. Photosynthetic rates of Seafarer and NEP-2 canopies as a function of leaf PAR.

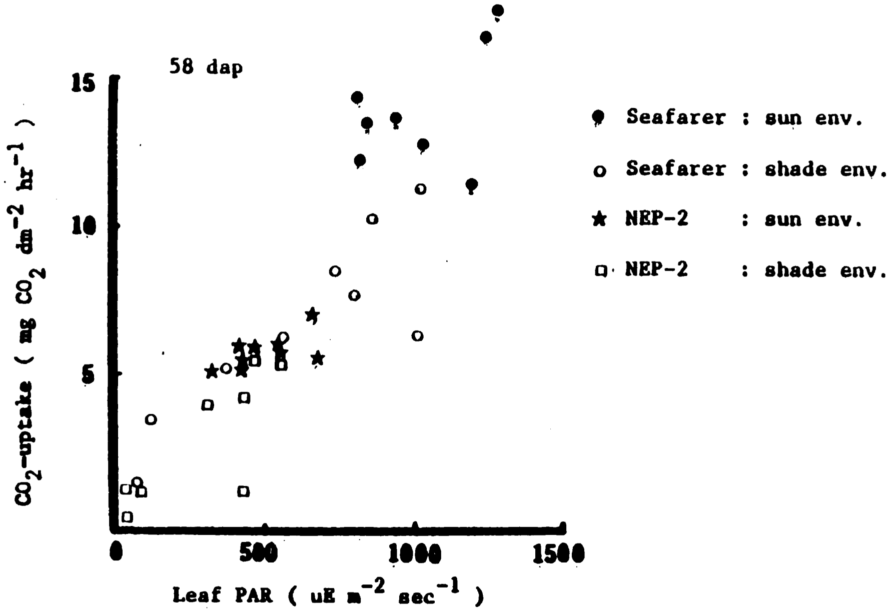


Figure 15. Photosynthetic rates of Seafarer and NEP-2 canopies as a function of leaf PAR at 58 dap.

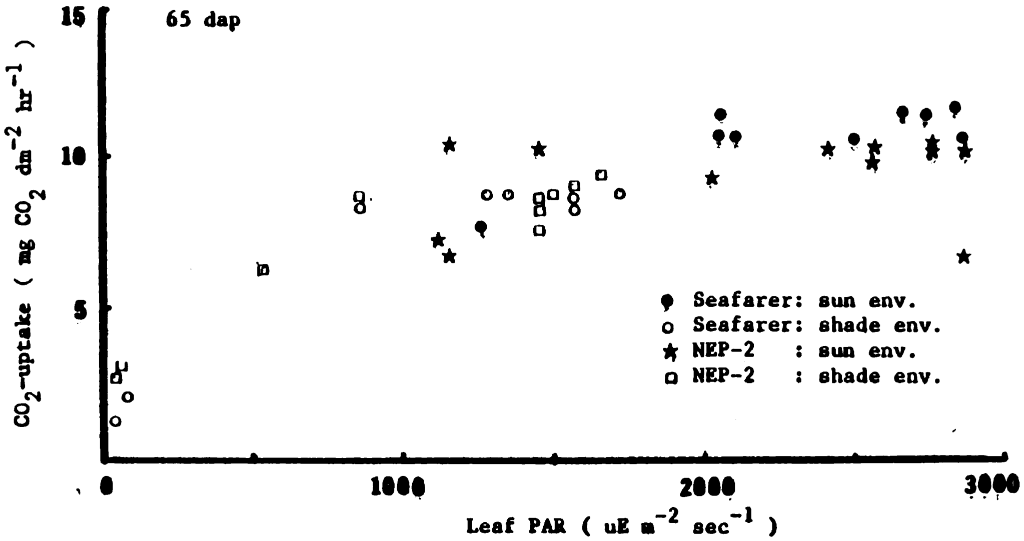


Figure 16. Photosynthetic rates of Seafarer and NEP-2 canopies as a function of leaf PAR at 65 dap.

Table 10. Simple correlation coefficients between CO_2-uptake, plant strata, leaf PAR, and specific leaf dry weight (SLDW) for Seafarer and NEP-2.

Date dap		Seafarer		NEP-2	
		CO_2-uptake	SLDW	CO_2-uptake	SLDW
43	Plant strata	.4504	.2449	.3796	.6133*
	Leaf PAR	.6284*		.3618	
	SLDW	.6516*		.6855*	
50	Plant strata	.6223*	.7877**	.5125	.7872**
	Leaf PAR	.3936		.1417	
	SLDW	.7091**		.6538*	
58	Plant strata	.9287**	.6777**	.8503**	.6794**
	Leaf PAR	.7321**		.7699**	
	SLDW	.8019**		.7158**	
65	Plant strata	.7740**	.7176*	.9114**	.5468
	Leaf PAR	.9010**		.7158*	
	SLDW	.5992		.6662*	
71	Plant strata			.8287**	.4868
	Leaf PAR			.7235*	
	SLDW			.4522	
79	Plant strata			.8859**	.7800*
	Leaf PAR			.8319**	
	SLDW			.5332	

16. Leaf PAR was generally over 700 μE m^{-2} sec^{-1} for leaves of both cultivars under the sun and shade environments, with the exception of the bottom leaves, 58 and 65 dap, which was around 60 μE m^{-2} sec^{-1}. Photosynthesis of bean leaves becomes light saturated at 700 to 900 μE m^{-2} sec^{-1} (Charter *et al.*, 1970; Austin and MacLean, 1972, Crookston *et al.*, 1964). This clearly indicates that enough light for photosynthesis penetrated into the canopy of these cultivars. Neither Seafarer nor NEP-2 canopies completely covered the ground even at maximum LAI. This could explain why the bottom leaves received enough light for photosynthesis, since light came from almost all directions and not only from the top of the plant canopy. However, it is interesting to observe that when PAR was around 1300 μE m^{-2} sec^{-1} over the top of the plants on a cloudy day (Figure 15), the Seafarer canopy had better light penetration than the NEP-2 canopy. Carbon dioxide uptake rates were positively correlated with leaf PAR for both cultivars (Table 10). For calculation of simple correlations of Table 10, both light environment data were considered together in each cultivar. These results suggest that the differences between photosynthetic rates under the sun environment in each cultivar were independent of leaf PAR; however, leaf PAR was an important factor for differences between light environment

Relationship between photosynthesis and SLDW

There was a positive relationship between plant strata and specific leaf dry weight (SLDW) and between plant strata and photosynthetic rates (Table 10). This means that from the bottom to the top of the plant canopy both photosynthesis and SLDW increased. An attempt was made to estimate the relationship between photosynthesis and SLDW. Five central leaflets were sampled for each plant strata for SLDW determinations when CO_2 uptake was measured.

Photosynthetic rates of Seafarer and NEP-2 canopies as a function of LSDW are shown in Figures 17 and 18. In general, plants under the shade environment had lower CO_2 uptake and lower SLDW than under the sun environment. Seafarer under the sun environment had the highest CO_2 and the highest SLDW values, while NEP-2 under the shade environment had the lowest values for both CO_2 uptake rates and SLDW. At 43 and 50 dap, (Figure 17), under the sun environment. Seafarer had both higher CO_2 uptake rates and SLDW than NEP-2. These differences were still shown at 58 dap (Figure 18), but became less apparent at 65 dap (Figure 18). Seven out of the ten simple correlation coefficients between CO_2 uptake rates and SLDW were significantly different from zero at the 5% level (Table 10), which indicates a positive relationship between these two leaf characteristics.

Although genetic differences in apparent photosynthesis rates have been reported, the physiological bases for genotypic variation remains obscure in most species studied. Gaastra (1962) has stated that photosynthesis is influenced by three main processes: 1) a photochemical process, 2) a diffusion process associated with the transport of CO_2 to the CO_2-fixation side, and 3) biochemical process which includes the fixation and chemical reduction of CO_2.

There is some evidence that SLDW might be used in breeding programs for photosynthetic efficiency. Positive correlation between net photosynthesis rates and SLDW has been reported in alfalfa (_Medicago_ _sativa_ L.) Pearce _et_ _al_., 1969; Wolf and Blazer, 1972), soybeans (Dornhoff and Shibles, 1970), oats (_Avena_ spp.) Criswell and Shibles, 1971). Heishel and Musgrave (1969) did find a significant correlation between specific leaf fresh weight and net photosynthesis. Although I found a positive correlation between CO_2 uptake rates and SLDW, further work

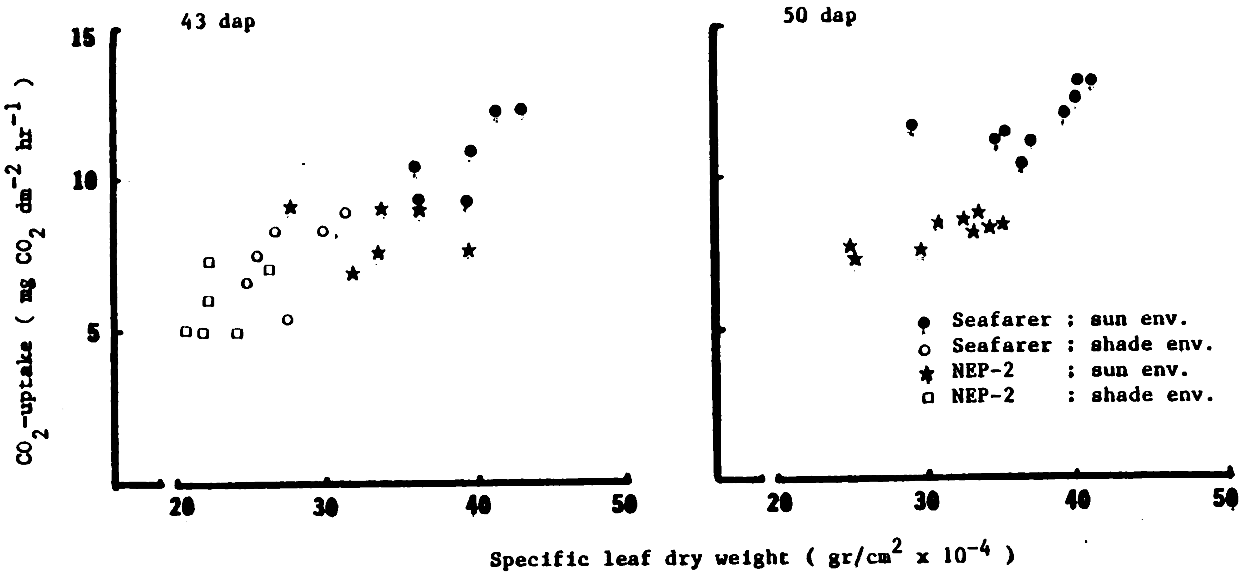


Figure 17. Photosynthetic rates of Seafarer and NEP-2 as a function of specific leaf dry weight.

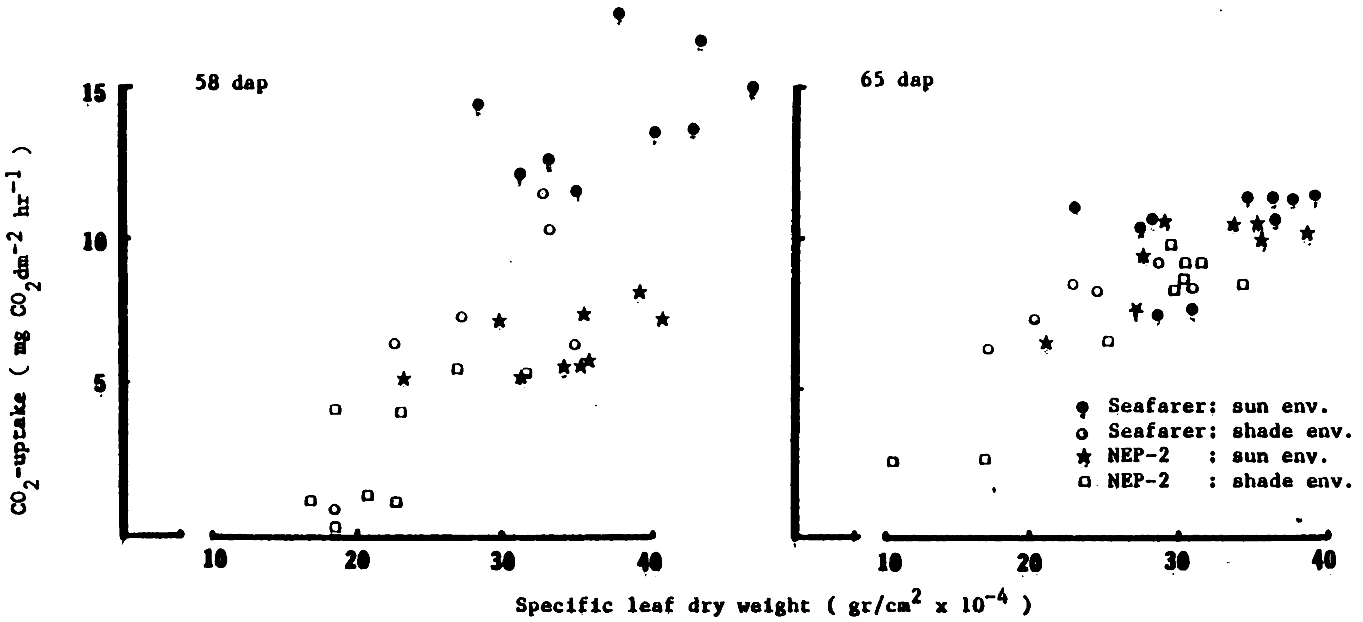


Figure 18. Photosynthetic rates of Seafarer and NEP-2 canopies as a function of specific leaf dry weight.

will be needed in determining the feasibility of SLDW as an index for leaf photosynthetic efficiency in beans because of the limited number of bean genotypes used in this study.

Light intensity during plant growth affects leaf morphology, chloroplast structure, and a number of component processes of photosynthesis. Plants grown at high light intensity have lower mesophyll resistance (r_m), thicker leaves, and greater amounts of the carboxylating enzymes (Boadman, 1977). Crookston _et al_. (1975) working with bean plants grown under two light environments in a growth chamber, found a positive correlation between apparent photosynthesis and leaf thickness. They suggested that the increased intracellular resistance, chloroplast structure and carboxylation enzyme of the shaded leaves was more important in reducing CO_2 uptake than was the increase in stomatal resistance (r_m). Louwense and Zweerde (1977) found, with bean plants grown under different light intensities in field and under growth chamber conditions, a positive correlation between apparent photosynthesis, leaf thickness, and number of chloroplasts per unit leaf area. They suggested that maximum photosynthesis depended on the number of chloroplasts. Nobel _et al_., (1975) reported that the changes in photosynthetic rate induced by various irradiances during leaf development resulted from changes in the mesophyll cell surface area per unit leaf area rather than from changes in CO_2 exchange rate (CER) and that CO_2 residual resistance (r_m) was related to the thickness and cellular volume of the several soybean leaf tissues. They concluded that characteristics internal to the cell, as opposed to CO_2-resistances related to stomata, intercellular space, or cell surfaces, were regulating CER.

Therefore, several factors are modified when plants are grown under selected light intensities, and there is no concensus of opinion concerning any one factor as the prime cause of the altered photosynthetic capacity.

Starch accumulation in roots and stems

The results of the experiment of the previous year (Chapter 2) with respect to changes in stem and pod dry weights, suggested the possible contribution of storage materials in the stem to the final seed and pod dry weights. Adams (1975) reported differences in the amount of carbohydrate stored in stems of Seafarer and NEP-2. In order to relate stem dry weight and starch accumulation, starch levels in the roots and in every third internode (internode immediately above the simple leaf was counted as 1), were determined by using iodine-potassium iodide starch indicator solution (IKI) as suggested by Salazar *et al*. (1977).

IKI determinations in the roots and 3rd internode of Seafarer and NEP-2 during the growing season are shown in Figures 19 and 20. Curves for the other internodes were similar to the 3rd internode in each cultivar. In both cultivars after flowering, greater amounts of starch started to accumulate in the roots than in the stems. Seafarer had maximum IKI values for roots at 62 dap and for stems at 65 dap. After these dates IKI determinations in both roots and stems decreased and reach their lowest values at final harvest (79 dap). NEP-2 had maximum IKI values for roots and stems at 62 dap. Thereafter, IKI determinations started to decrease in both roots and stems with the minimum values of IKI index of 4 and 3, respectively, at final harvest (105 dap). This clearly indicates that starch was present in the roots and stems of NEP-2 and it was not completely remobilized.

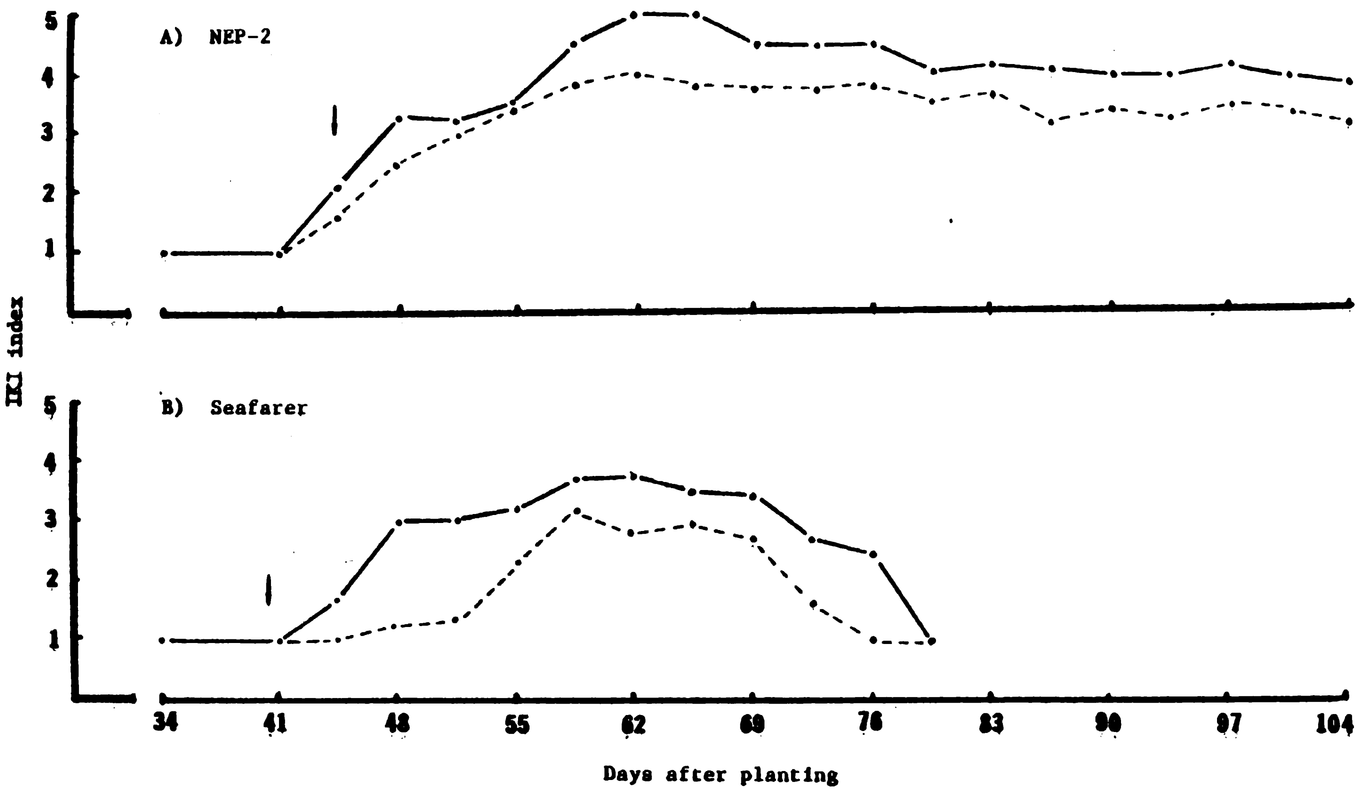


Figure 19. Starch determination on roots of Seafarer and NEP-2 during the growing season in two light environments: the sun environment (.———.) and the shade environment (.------.). Arrow indicates flowering.

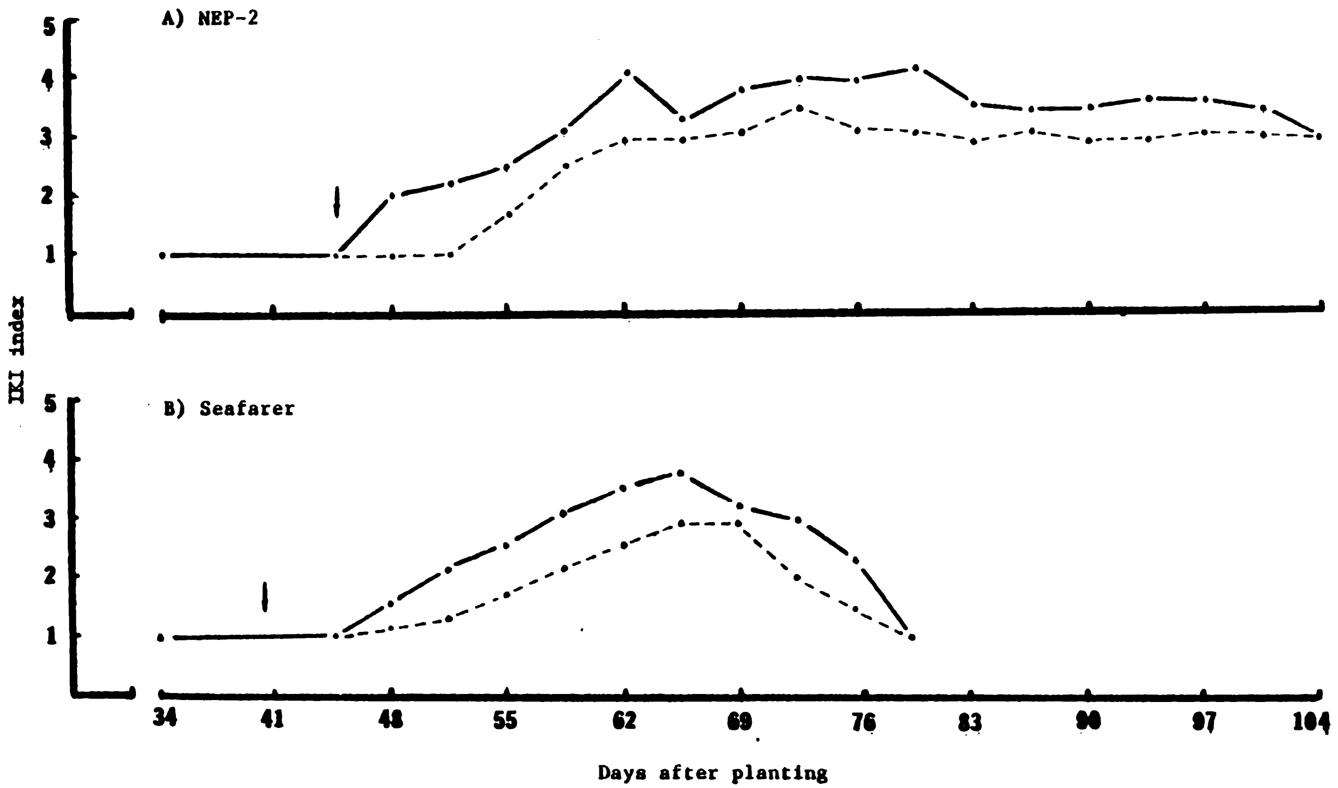


Figure 20. Starch determination on stems at the 3rd internode of Seafarer and NEP-2 during the growing season in two light environments: the sun environment (.▬▬▬.) and the shade environment (.------.). Arrow indicates flowering.

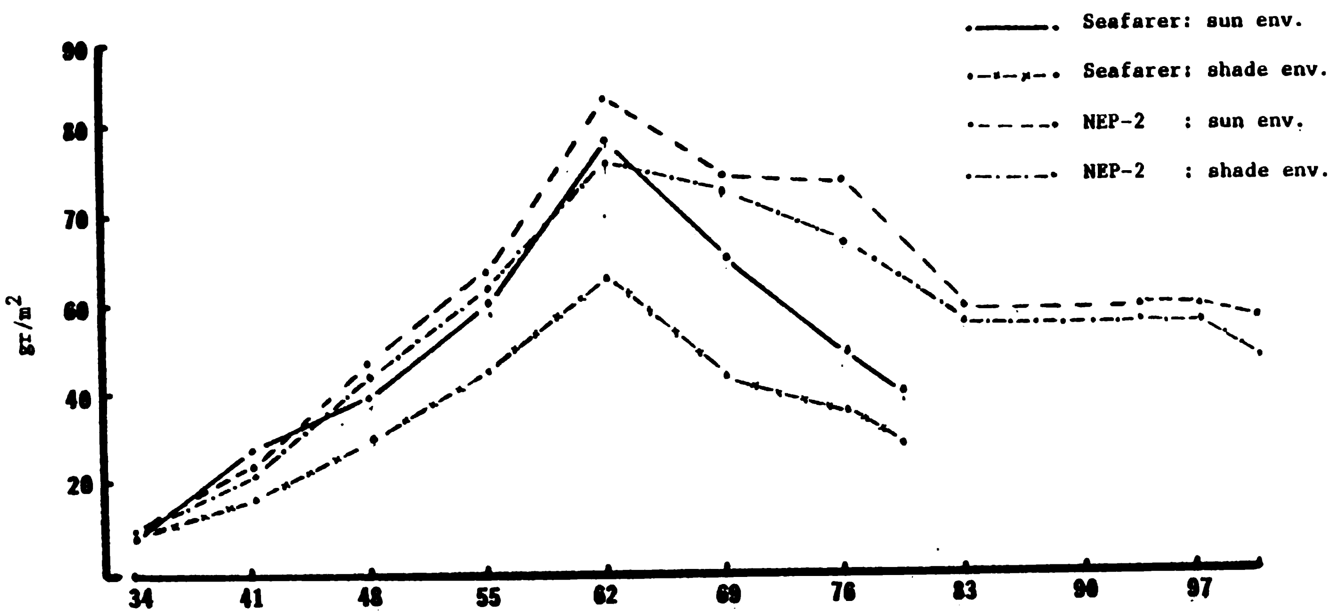


Figure 21. Ontogenetic changes in stem dry weight of Seafarer and NEP-2 during the growing season in two light environments.

The shade environment only reduced the amount of starch in roots and stems of both cultivars and not the patterns of change in IKI values.

Ontogenetic changes in stem dry weight of Seafarer and NEP-2, under both light environments, are presented in Figure 21. Both stem dry weight and starch accumulation in the stems were found to have very similar patterns (Figures 20 and 21). Salazar *et al*. (1977) also reported similar trends of starch accumulation in the roots and stems of Seafarer and NEP-2. Their IKI values were lower than the ones reported here. During the last 3 weeks before final harvest of NEP-2, the plants were exposed to unusual weather conditions of excessive rainfalls. This might have changed the patterns of starch accumulation in NEP-2 at this period. Nevertheless, there appears to be a cultivar X environment interaction in the starch accumulation in roots and stems of bean plants.

REFERENCES

Adams, M. W. 1975. Plant architecture and physiological efficiency in field beans. Ann. Rep. to the Rockefeller Foundation.

Allen, R. D. 1969. Mechanism of the sesismonastic reaction in Mimosa pudica. Plant Physiol. 44: 1101-1107.

Austin, R. B. and P. C. Longden. 1967. A rapid method for the measurement of rates of photosynthesis using 14-CO_2. Ann. Bot. 31: 245-253.

Austin, R. B. and M. S. M. MacLean. 1972. Some effect of temperature on the rates of photosynthesis and respiration of Phaseolus vulgaris L. Photosynthetica 6: 41-50.

Blad, B. L. and D. G. Baker. 1972. Orientation and distribution of leaves within soybean canopies. Agron. J. 64: 26-29.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28: 355-377.

Bravdo, B. 1972. Photosynthesis, transpiration, leaf stomatal and mesophyll resistance measurements by the use of a ventilated diffusion porometer. Physiol. Plant. 27: 209-215.

Chartier, R., M. Chartier and J. Catsky. 1970. Resistances for carbon dioxide diffusion and for carboxylation as factors in bean leaf photosynthesis. Pototsynthetica 4: 48-58.

Criswell, J. G. and R. M. Shibles. 1971. Physiological basis for genetic variation in net photosynthesis of oat leaves. Crop Sci. 11: 550-553.

Crookston, R. K., J. O'Toole, R. Lee, J. L. Ozbun and D. D. Wallace. 1974. Photosynthetic depression in beans after exposure to cold for one night. Crop Sci. 14: 457-464.

Crookston, R. K., K. J. Treharne, P. Ludford and J. L. Ozbun. 1975. Response of beans to shading. Crop Sci. 15: 412-416.

Dale, J. E. 1964. Leaf growth in Phaseolus vulgaris. 1. Growth of the first pair of leaves under constant conditions. Ann. Bot. 28: 127-135.

Dale, J. E. 1965. Leaf growth in Phaseolus vulgaris. 2. Temperature effects and the light factor. Ann. Bot. 29: 293-308.

Dornhoff, G. M. and R. M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves.. Crop Sci. 10: 42-45.

Dornhoff, G. M. and R. M. Shibles. 1976. Leaf morphology and anatomy in relation to CO_2-exchange rates of soybean leaves. Crop Sci. 16: 377-381.

Fraser, D. E. and R. G. S. Bidwell. 1974. Photosynthesis and photorespiration during ontogeny of the bean plant. Can. J. Bot. 52: 2561-2570.

Gaastra, P. 1962. Photosynthesis of leaves and field crops. Neth. J. Agric. Sci. 10: 311-324.

Howe, G. F. 1962. Time course of the photosynthetic induction periods in certain higher plants as related to changes in degree of stomatal opening. The Ohio J. Sci. 62: 301-307.

Howe, G. F. 1964. Time course of photosynthetic rhythms in Phaseolus vulgaris L. as related to changes in degree of stomatal opening. The Ohio J. Sci. 64: 378-384.

Incoll, L. O. and W. H. Wright. 1969. A field technique for measuring photosynthesis using 14-carbon dioxide. Special Bulletin Soils XXX/100. Conn. Agri. Exp. Sta. p. 1-7.

Johansen, D. A. 1940. Plant microtechnique. p. 188. McGraw-Hill. New York.

Lemeur, R. 1973. A method for simulating the direct solar radiation regime in sunflower, jerusalem artichoke, corn and soybean canopies using actual stand structure data. Agri. Meteorol. 12: 229-247.

Loomis, R. W. and W. A. Williams. 1969. Productivity and the morphology of crop stands: Pattern with leaves. In Eastin, J. D., F. A. Haskins, C. Y. Sullivan and C. H. M. Van Bavel (ed.) Physiological Aspects of Crop Yield. pp. 27-47. Am. Soc. Agron. Madison, Wisconsin.

Louwerse, W. and W. V. D. Zweerde. 1977. Photosynthesis, transpiration and leaf morphology of Phaseolus vulgaris L. and Zea mays L. grown at different irradiances in artificial and sunlight. Photosynthetica 11: 11-21.

McWilliam, J. R., P. J. Phillips and R. R. Parkes. 1973. Measurement of photosynthesis rate using labeled carbon dioxide. CSIRO. Aust. Div. Pl. Ind. Tech. Pap. No. 31. pp. 1-12.

Naylor, D. G. and I. D. Teare. 1977. An improved, rapid, field method to measure photosynthesis with 14-CO_2. Agron. J. 67: 404-406.

Neales, T. F. and L. D. Incoll. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis. Bot. Rev. 34: 107-125.

Nobel, P. S., L. J. Zaragoza and W. K. Smith. 1975. Relation between mesophyll surface area, photosynthetic rate and illumination level during development for leaves of Plectranthus parviflorus H. Plant Physiol. 55: 1067-1070.

Ormrod, D. P. 1964. Net carbon dioxide exchange rates in Phaseolus vulgaris L. as influenced by temperature, light intensity, leaf area index, and age of plant. Can. J. Bot. 42: 393-401.

Pearce, R. B. and D. O. Lee. 1969. Photosynthetic and morphological adaptation of alfalfa leaves to light intensity at different stages of maturity. Crop Sci. 9: 791-794.

Peet, M. M., A. Bravo, D. W. Wallace and J. L. Ozbun. 1973. Photosynthesis, stomatal resistance and enzyme activities in relation to yield of field-grown dry bean varieties. Crop Sci. 17: 287-293.

Peet, M. M., J. L. Ozbun and D. W. Wallace. 1977. Physiological and anatomical effects of growth temperature on Phaseolus vulgaris L. cultivars. J. Exp. Bot. 28: 57-69.

Ross, Y. K. and T. Nilson. 1967. The spatial orientation of leaves in crop stands and its determination. In Nichiporovich, A. A. (ed.) Photosynthesis of Productive Systems. pp. 86-99. Translated edition. Israel Prog. Sci. Trans., Jerusalem.

Salazar, J., J. Wiersma and M. W. Adams. 1977. IKI-starch status in bean varieties at three stages of seed development. Ann. Rep. Bean Imp. Coop. 20: 24-28.

Satter, L. R., D. D. Sabnis and A. W. Galston. 1970. Phytochrome controlled nyctinasty in Albizzia julibrissin. I. Anatomy and fine structure of the pulvinule. Amer. J. Bot. 57: 374-381.

Satter, R. R., P. Marinoff and A. W. Galston. 1970. Phytochrome controlled nyctinasty in Albizzia julibrissin. II. Potassium flux as a basis for leaflet movement. Amer. J. Bot. 57: 916-926.

Satter, L. R. and A. W. Galston. 1971. Potassium flux: a common feature of Albizzia leaflet movement controlled by phytochrome on endogenous rhythm. Science 174: 518-520.

Scott, B. I., H. F. Gulline and G. R. Robinson. 1977. Circadian electrochemical changes in the pulvinules of Trifolium repens L. Aust. J. Plant Physiol. 4: 193-206.

Segovia, A. J. and R. H. Brown. 1978. Relationship of phoem size to leaf size and position. Crop Sci. 18: 90-93.

Sestak, Z., J. Catsky, J. Solarova, H. Strnadova and I. Ticha. 1975. Carbon dioxide transfer and photochemical activities as factors of photosynthesis during ontogenesis of primary bean leaves. In Nasyrov, Yu. S. and Z. Sestak (ed.) Genetic Aspects of Photosynthesis. pp. 159-167. Dr. W. Junk, N. V. Publishers, The Hague.

Setty, S. and M. J. Jaffe. 1972. Phytochrome-controlled rapid contration and recovery of contractile vacules in the motor cells of *Mimosa pudica* as an intracellular correlate of nyctinasty. Plants 108: 121-131.

Shell, G. S. G., A. R. G. Lang and P. J. M. Sale. 1974. Quantitative measurements of leaf orientation and heliotropic response in sunflower, bean, pepper and cucumber. Agric. Meteorol. 13: 25-37.

Shimsi, D. 1969. A rapid field method of measuring photosynthesis with labeled carbon dioxide. J. Exp. Bot. 20: 381-340.

Victor, D. M., R. P. Ariyanayagam and R. B. Musgrave. 1977. Photosynthetic selection of *Zea mays* L. I. Plant age and leaf position effects and a relationship between leaf and canopy rates. Crop Sci. 17: 567-573.

Wolf, D. D. and R. E. Blaser. 1972. Growth rate and physiology of alfalfa as influenced by canopy and light. Crop Sci. 12: 23-26.

Woodward, R. G. and H. M. Rawson. 1976. Photosynthesis and transpiration in dicotyledoneous plants. II. Expanding and senescing leaves of soybeans. Aust. J. Plant Physiol. 3: 257-267.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Two principal physiological processes can be considered for improvement of crop yields: photosynthate production and photosyntate partitioning to the economically important organs. The aims of this investigation were to obtain information for increasing bean productivity by optimizing the structure of the crop canopy and carbohydrate partitioning. Therefore, it was necessary to define canopy architecture characteristics relevant to light penetration, crop photosynthesis, and ontogenetic carbohydrate partitioning. For these purposes two experiments were conducted: 1) in the summer of 1976 at the B/B Research Farm, Saginaw, Michigan, with four dry bean genotypes representing different growth habits. The genotypes and growth habits were: a MSU experimental line 31908, a narrow bush type (CIAT type I), b) cultivar Seafarer, a normal bush type (CIAT type I), c) cultivar NEP-2, a narrow erect, short vine type (CIAT type II), and d) MSU experimental line 0686, a determinate but very vigorously vegetative type resembling CIAT type III). Plant spacing (47, 20, and 9 plants/m^2) was used to modify the canopy architecture; and 2) in the summer of 1977 at the Crop Science Research Farm, E. Lansing, with two genotypes: Seafarer and NEP-2. Light environments (full and 50% sunlight) were used to modify the canopy architecture. The following conclusions are based on the results of this study.

1. The vertical distribution of the area of green leaves varied during the course of the growing season. Seafarer had its maximum LAI at approximately the same plant height, 10-30 cm from the bottom, during the period of 30 to 72 dap. NEP-2 and Lines 31908 and 0686 had the distribution curves nearly symmetrical with respect to the LAI maximum at the middle of the plant height at 30 to 70 dap, thereafter, the maximum shifted to higher plant layers.

2. All plant parts, independent of plant types, including leaves, stems and pods, develop progressively later toward the top of the plant. However, the difference in growth stage among plant parts was less in the case of pods than for the leaves and stems. Consequently, the time interval between vegetative and pod development was shorter toward the top of the plant.

3. Light distribution in the plant canopy changed with plant height in an exponential manner and fit Bouguer-Lambert's law, with relative illumination as an exponential function of LAI. Relative light interception was closely associated with LAI and both showed similar trends during plant development.

4. Extinction coefficient (k) values at maximum LAI were: .2615, .3396, .4629 and .2993 for Seafarer, NEP-2, Line 31908 and Line 0686, respectively. K values were not significantly affected by plant spacing.

5. Light penetration in the canopy was found to be greater in Seafarer and lower in the Line 31908. NEP-2 and Line 0686 showed intermediate values.

6. LAI, leaf angle, percent of ground cover, and the extinction coefficient were the most important characteristics accounting for 99.22% of the variance in light penetration.

7. The studied plant spacings did not affect either seed yields or yield components of the four plant types.

8. Relative Growth Rate (RGR) was higher for Seafarer and lower for the Line 31908; NEP-2 and Line 0686 had intermediate RGR values. Differences in RGR were due to differences in Net Assimilation Rate (NAR) rather than in Leaf Area Ratio (LAR). RGR was affected by plant spacing.

9. Harvest Index (HI), independent of plant type, was affected by plant spacing with the lowest HI values corresponding to the closest plant spacing.

10. The trends of dry weight distribution suggested a movement of material from leaves to stems and pods. Changes in stem dry weight and pod dry weight were used to estimate the contribution of storage material to the final seed and pod dry weight. There were differences between plant types and plant spacings in the possible contribution of previously stored materials in the stems and petioles to the final pod dry weight. Apparently, the changes in dry weight of the stems were equivalent to the changes in dry weight of the pods at the bottom and top strata of all plant types with the exception of Line 31908 at the lowest strata where pods were not present. Storage material translocation from stems to pods was affected by plant spacing with its highest values at the closest plant spacing.

11. The canopy of Seafarer was found to have a greater frequency of vertical leaves, while NEP-2 had a greater frequency of horizontal leaves. Seafarer and NEP-2 could be classified as erectophile and phanophile foliar structure, respectively, by using de Wit's system (1965). Leaf inclination changed during the day. In the morning Seafarer had a planophile foliar structure which changed to different degrees of erectophile as the light intensity increased and the sun

position changed during the day. With respect to plant strata, the degree of erectophile structure increased from the bottom to the top of the plant canopy. Average leaf angle of Seafarer and NEP-2 showed similar trends during the growing season, however, Seafarer had a higher average leaf angle than NEP-2. Their values increased and then decreased during the growing season. The shade environment reduced the average leaf angle of Seafarer and NEP-2 by 22.54% and 23.22%, respectively.

12. Neither Seafarer nor NEP-2, under either light environment, had leaves oriented with more frequency for any azimuth.

13. The shade environment increased the LAI of Seafarer and NEP-2, primarily by affecting leaf size, since the number of branches and number of nodes were not affected. The bean plants were shaded 30 dap when they had formed branches and the number of nodes had been determined by the genetic potential of each cultivar. There was an effect of the shade environment on the bean leaf, but not on the amount of leaf dry matter in relation to the whole plant, however, the specific leaf dry weight was reduced in both cultivars by the shade environment.

14. Photosynthesis rates, measured by the $^{14}CO_2$ techniques as CO_2 uptake rates, were in the range of previously reported values for bean leaves. They increased from bottom leaves to top leaves for both Seafarer and NEP-2. Maximum CO_2 uptake rates for each plant stratum were observed at the time of initial pod filling, 58 and 71 dap, for Seafarer and NEP-2, respectively. Seafarer generally had higher rates of uptake at all canopy levels than did NEP-2. The shade environment affected the CO_2 uptake rates of both cultivars, i. e. during the maximum CO_2 uptake, the shade environment reduced the CO_2 uptake rates of Seafarer and NEP-2 by 55.19% and 30.54% respectively.

15. There was a positive relationship between plant strata, specific leaf dry weight and photosynthetic rates. This means that from the bottom to the top of the plant canopy both photosynthesis and specific leaf dry weight increased.

16. After flowering, greater amounts of starch started to accumulate in the roots than in the stems of Seafarer and NEP-2. Seafarer had maximum starch accumulation in the roots at 62 dap and in the stems at 65 dap. NEP-2 had maximum accumulation in both roots and stems at 62 dap. Thereafter, starch started to decrease in both roots and stems and disappeared at harvest time for Seafarer, while it was still present in roots and stems of NEP-2. The shade environment only reduced the amount of starch but not the ontogenetic patterns. Similar trends were observed for starch accumulation in the stems and stem dry weight. There appeared to be a cultivar X environment interaction in the starch accumulation in the roots and stems of bean plants.