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MODELING 'YIELD - POPULATION' RELATIONSHIPS IN SOYBEAN

A Dissertation Presented

by

JOMOL P. MATHEW

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2001

Department of Plant and Soil Sciences

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MODELING 'YIELD - POPULATION' RELATIONSHIPS IN SOYBEAN

A Dissertation Presented

by

JOMOL P. MATHEW

Approved as to style and content by:

10

Stephen J. Herbert, Chair

Wesley R. Autio, Member

Stephen Simkins, Member

Daniel R. Cooley, Member

liam J. Bramlage, Department Head

William J. Bramlage, Department Head Department of Plant and Soil Sciences

DEDICATION

To my Father

ACKNOWLEDGMENTS

First and foremost I would like to thank Dr. Stephen J. Herbert for being a wonderful mentor in every sense of the word. I owe my development as a scientist to his enthusiasm and encouragement through out my stay. His commitment to science will always be an example for me to live by.

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ABSTRACT

MODELING 'YIELD - POPULATION' RELATIONSHIPS IN SOYBEAN MAY 2001 JOMOL P. MATHEW, B.Sc(Ag)., KERALA AGRICULTURAL UNIVERSITY M.Sc(Ag)., KERALA AGRICULTURAL UNIVERSITY Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Stephen J. Herbert

Our objectives were to evaluate the seed yield of soybean, and Duncan's model with respect to relationship between seed yield and plant population, and analyze the response of soybean seed yield components to light enrichment initiated at different growth stages. Duncan coined the term crowding to include the effects of density and planting pattern. Duncan's model states that there is a linear relationship between natural logarithm of yield plant⁻¹ and crowding. Results of the studies fitting Duncan's model to the data obtained from different soybean cultivars planted at different densities and planting patterns indicated that the model can predict the changes in yield with changing densities and planting pattern especially if the variability in the data is low.

In order to analyze the response of soybean seed yield components to non destructive light enrichment initiated at different growth stages, light enrichment was imposed on the indeterminate soybean cultivar Evans by installing wire mesh fencing on either side of the center row to push the adjacent rows aside at different growth stages. Fences prevented plants in the neighboring rows from encroaching on the growing space of the center row plants. Pod number per plant and to a lesser extent seed size

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accounted for variation in seed yield. Light enrichment initiated at late vegetative or early flowering stages increased seed yield 217%, mainly by increasing pod number, while light enrichment beginning at early pod formation increased seed size 23%, resulting in a 115% increase in seed yield. Responses to light enrichment occurred proportionately across all node positions despite the differences in the time (15 to 20 days) of development of yield components at the different node positions. Although maximum seed size may be under genetic control in soybean plants, our results suggested seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. It indicates that plants are able to redistribute the available resources to components not yet determined, in an attempt to maintain or improve yield.

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CHAPTER I

INTRODUCTION

Understanding the quantitative relationships between plant density and crop yield has been of great interest to Agronomists. Such knowledge helps in explaining and evaluating the characteristics of 'optimum density' and 'maximum yield', and facilitate comparisons between different cropping situations. Deriving equations relating yield and population helps agronomists in fitting yield population curves easily and accurately from minimum data (Willey and Heath, 1969). Many equations relating population and yield have been put forth by scientists.

Holliday (1960) suggested that the total dry matter produced follows an asymptotic relationship with density, while reproductive forms of yield exhibits a parabolic relationship. Even though some exceptions have been reported to this rule (de Wit, 1959; Bleasdale, 1966; Bruinsma, 1966; Campbell and Viets, 1967; Farazdaghi, 1968), it holds true for most crops.

Among the many mathematical equations that have been put forth to define the biological relationships between population and crop yield, some propose a direct relationship between 'yield per unit area' and density while the majority propose a basic relationship between 'mean yield per plant' and density.

<u>Yield - Density Equations</u>

Polynomial equations

<u>Hudson</u>

Hudson (1941) described the relationship between grain yield and seed rate of winter wheat as

 $y = a + b\rho + c\rho^2$

where y is the grain yield in kg/ha, ρ is the density in plants/ha, and

a, b and c are constants, c being negative.

As reviewed by Willey and Heath in 1969, this equation gives little flexibility in fitting yield/density relationships and it is not suitable for the asymptotic situations. For parabolic situations, the accuracy is restricted to a narrow range of density around the point of maximum yield. It assumes a value 'a' and not the 'origin' corresponding to zero density and has an unrealistically sharp decline in yield at high densities.

Sharpe and Dent

Sharpe and Dent (1968) proposed

$$y = a + b\rho + c\rho^{1/2}$$

where y is the grain yield in kg/ha, ρ is the density in plants/ha, and a, b, and c are constants, b being negative.

Again, this equation is unsuitable for asymptotic situations. It has a slightly more gradual decline in yield at higher densities and hence is slightly better than the previous equation for parabolic situations. However, it also assumes a value 'a' for the zero density.

However, due to the above mentioned shortcomings, yield predictions using polynomial equations might lead to values very much different from actual yields especially at lower and higher densities.

Exponential equations

Duncan

Duncan (1958) proposed an exponential equation relating grain yield and density as

 $\log y = \log K + b\rho$

or

$$y = K \ 10^{b}$$

Where y is the yield per plant in kg, K is a constant (the y intercept), and b is the

slope of the regression line (negative), ρ is the density in plants per ha.

This equation can also be expressed as

 $Y = \rho K 10^{b\rho}$

where Y is the yield in kg/ha.

Carmer and Jackobs

Carmer and Jackobs (1965) proposed an analogous equation

 $Y = \rho AK^{\rho}$

Where A and K are constants.

The exponential equations, compared to the polynomials are much more flexible and give a good fit for the parabolic situations. Unlike the polynomial equations, the curves pass through the origin, and at high densities the curves do not cut the density axis, but more realistically, only gradually approaches it. However they still do not give a good fit for the asymptotic situations (Willey and Heath, 1969).

Since Duncan's equation is based on a linear regression, it is possible to construct the line, using the yield from two densities. However, as pointed out by Duncan (1958) himself, the accuracy depends on the distance between the two points on the line. Duncan suggested that the farther apart the two densities, the more accurate will be the regression line.

Geometric equations

<u>Warne</u>

Warne (1951), while studying the effect of density on root yield of beet, parsnip and carrot, proposed a linear relationship between root yield per plant and the logarithm of the distance between plants in a row where row width was constant.

$$Log w = log A + b log(s)$$

or

$$w=A(s)b$$

where w is the root yield per plant, s is the space available per plant, and A and b are constants.

If we consider 'yield per unit area' instead of 'yield per plant' and include 'density' rather than 'space', the equation becomes

$$y = A(\rho)^{1-b}$$

Kira et al

Kira *et al.*(1953) proposed a linear relationship between the logarithm of total yield and the logarithm of density in soybeans as

 $\log w + a \log \rho = \log K$

or

or

$$w \rho^a = K$$

where 'a' known as 'competition-density index' and K are constants. The only type of yield density curve which this equation can describe is one where yield is still increasing even at the highest density (Willey and Heath, 1969). Failure of the equation to describe the leveling off of yield per plant at densities too low for competition to occur is another disadvantage (Shinozaki and Kira, 1956).

Reciprocal equations

These equations describe the mathematical relationships between the reciprocal of mean yield per plant and density.

Shinozaki and Kira

Shinozaki and Kira (1956) assumed a linear relationship between the reciprocal of yield per plant as

$$l/w = a + b\rho$$

where a and b are constants.

Even though Shinozaki and Kira (1956) found that the equation holds true for many asymptotic situations, it could not be used for parabolic situations.

Shinozaki and Kira suggested a modification in their equation to account for the constancy of yield at lower densities where competition is negligible as

$$1/W = a + b(\rho + \delta)$$

where δ is a value chosen depending on the maximum yield per plant (when there is no competition), so that at high densities δ will be negligible compared to ρ and could be discarded, and at lower densities δ would become meaningful..

However, the term δ was introduced to increase the goodness of fit at lower densities and has no biological meaning and its value also has to be determined experimentally (Willey and Heath, 1967).

<u>Holliday</u>

Holliday (1960) proposed an equation identical to Shinozaki and Kira's equation. Later, identifying that his equation could not account for a constant yield per plant at low densities where there is no competition, he proposed a modified equation beginning at the density where competition starts as

$$1/W = a' + bm$$

where $m = \rho - n$ (n is the density at which competition starts), b is a constant and a' is experimentally determined for each cropping situation.

However, as mentioned by Willey and Heath(1967), Holliday himself admitted that the practical use of the equation would be limited as a' would have to be experimentally determined for each cropping situation.

Holiday also proposed a parabolic yield density equation as

$$1/w = a+b\rho+c\rho^2$$

where a, b, and c are constants.

This equation produces a curve which is not symmetrical about its point of maximum yield and flattens off realistically at high densities.

De Wit

De Wit and Ennik(1958) proposed an equation as

$$1/y = a+bd$$

where a and b are constants and d is the row width (row width = distance between plants in a row).

Like in the case of Shinozaki and Kira's, de Wit's equation can only be applied to asymptotic yield - density situations.

Bleasdale and Nelder

Bleasdale and Nelder (1960) proposed the reciprocal equation representing asymptotic conditions as

$$1/w^{\theta} = a + b\delta^{\theta}$$

where a, b and θ are constants.

They also proposed that if slightly modified, the equation can be used for parabolic conditions also. The modified equation is

$$1/w^{\theta} = a + b\rho^{\phi}$$

where θ and ϕ are parameters having constant values for any one set of data (Bleasdale, 1966b; Bleasdale and Thompson, 1966; Bleasdale, 1967). When yield is asymptotic, $\theta = \phi$; and when yield is parabolic, $\theta < \phi$.

Bleasdale (1967) also suggested that the ratio of θ to ϕ is more important than their absolute values and that for practical purposes, it is adequate to take ϕ as unity. Thus the equation becomes

$$1/w^{\Theta} = a + b\rho$$

Farazdaghi and Harris

Farazdaghi and Harris (1968) proposed the yield-density equation as

$$1/w=a+b\rho^{\gamma}$$

For asymptotic situations $\gamma = 1$ and for parabolic situations $\gamma > 1$. According to them, this equation can predict the yield in both asymptotic and parabolic situations.

'Crowding' vs 'density' in yield - population modeling

Even though most of the above equations, especially the reciprocal equations express the relationship between density and yield, they do not account for the fact that plant population can not be defined just in terms of number of plants per unit area. Population involves number of plants and planting pattern or rectangularity of plant spacing. Rectangularity of plant spacing is the longest distance between plants divided by shortest distance. A square planting pattern has rectangularity of 1 while a wide row width with close intra row spacing has high rectangularity. As competition between plants growing in 'communities' depends on the number of plants and planting pattern, considering rectangularity would give more biological meaning to the yield-population equations.

Recognizing the significance of the interaction of density with spacial arrangements of plants, Duncan (1984) suggested that all forms of interplant competition can be combined into a single term 'crowding' (C) in which he included the effects of plant population (density) and planting pattern. Accordingly Duncan stated that the maximum crowding (C = 1) occurs when two plants are grown together in essentially the same space. As the distance between the plants increases, crowding decreases and becomes zero at D_{max} which is the least separation at which competition is considered negligible. To calculate crowding, the deviation of the plant from D_{max} is expressed as a fraction of D_{max} and is termed the 'Separation Fraction' (SF). Duncan calculated SF as

 $SF = (D_{max} - separation)/D_{max}$

The rate of change of crowding with separation is obtained by raising SF to a power of

alpha. Crowding between two plants then is $C = SF^{alpha}$. The total crowding for a community of plants is

$$C = \sum_{p=1}^{p=n} SF^{alpha}$$

where, p = 1 to p = n includes all plants in the planting pattern within the distance D_{max} from the center plant. The total crowding in a planting pattern, is the sum of crowding experienced by all the individual plants and it is a constant for a particular planting pattern. Figure 1 illustrates the competition between two plants in terms of their separation.

Based on this concept of crowding, Duncan proposed a crowding model to express the relationship between crowding and yield in a mathematical form. According to the model,

dy/dC = Ey

where, y is yield/plant; C is crowding and E is a constant which defines the

effect of crowding on yield.

This can also be written as:

$$dy/y = EdC$$

By integrating,

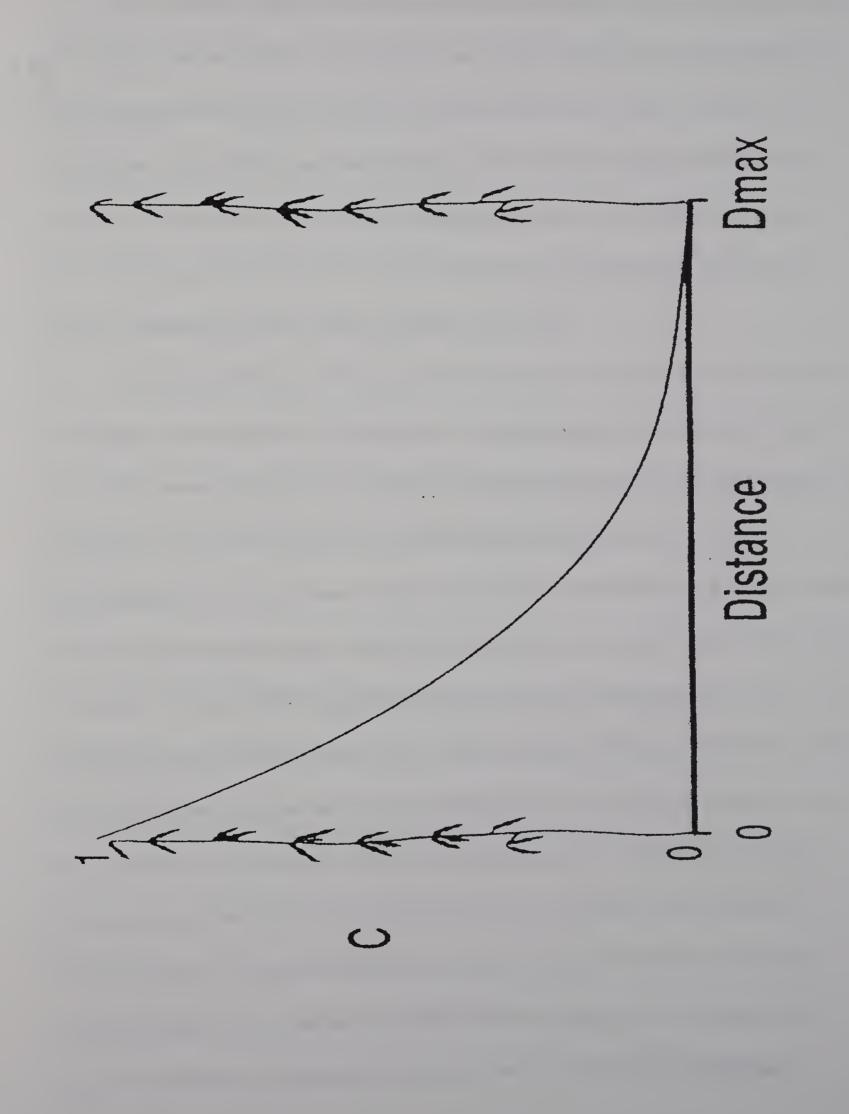
$lny = lny_0 + EC$

When a plant is grown in isolation, separation $\ge D_{max}$, and SF equals zero. Crowding therefore equals zero and thus $\ln y_0 = \ln y$. Thus y_0 can be defined as the maximum yield of a single plant at zero crowding.

Figure. 1. Crowding (C) between two plants as proposed in Duncan's model.

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Responses of seed yield components to changes in growth environment

Environmental conditions prevailing during the growth period, especially intensity and quality of solar radiation intercepted by the canopy, are important determinants of yield components and hence the yield of soybean (Taylor *et al.*, 1982; Willcott *et al.*, 1984; Myers *et al.*, 1987; Board and Harville, 1992 & 1996). Light enrichment using lamps or reflectors increased the yield of soybean (Johnston *et al.*, 1969; Schou *et al.*, 1978). Shading (49-20% of ambient light) resulted in lengthening of internodes and increased lodging in soybean plants (Ephrath *et al.*, 1993).

Hardman and Brun (1971) proposed that the yield of soybean is controlled by the availability of photosynthates during the post flowering stage of development. Schou et al. (1978) observed that light levels during late flowering to mid-pod formation stages of growth are more critical than during vegetative and late reproductive periods in determining the yield of soybean. Taylor et al. (1982) concluded that pod abortion caused by lack of photosynthate supply late in the growing period is a major factor limiting yield of soybean. Duncan (1984) suggested that light intercepted during and after seed initiation is a major determinant of yield. Jiang and Egli (1993) reported that shade during R₁ to R₅ period of the reproductive stage reduces flower production and increases flower and pod abscission resulting in reduced pod number and yield. They also found that canopy photosynthesis during flowering and pod set are important determinants of seed m⁻², and that the impact of shading on seeds m⁻² depends on duration of shading (Jiang and Egli, 1995). Sharma et al. (1996) observed anthesis to be the most critical stage during which low light intensity can cause severe yield reduction in soybean.

Board *et al.* (1992) and Board and Harville (1996) suggested that the increased seed yield of soybean from planting in narrow rows (less than 50 cm) reported by many researchers (Lehman and Lambert, 1960; Costa *et al.*, 1980; Herbert and Litchfield, 1982; Willcott *et al.*, 1984), can be attributed to the increased light interception during vegetative and early reproductive periods (first flowering to seed initiation). In most of the above studies, changes in yield was mainly brought about by changes in pod and seed number. However an increase in seed size so as to compensate for the decreased pod load has been observed in source - sink manipulation studies (Mc Alister and Krober, 1958; Schonbeck *et al.*, 1986).

Herbert and Litchfield (1982) noticed that pod number per plant was the most important component responsible for differences in soybean yield between different row widths and densities within a particular year, while a change in seed size resulted in the yield difference between two consecutive years. Thus, there is a differential response of yield components to changes in environmental conditions. However, the exact nature of response to the timing of light enrichment has not been identified yet. Also most of the studies conducted so far on differential response achieved increases in light interception indirectly by removal of leaves and thereby modifying the source strength.

Objectives

The objectives of the research are:

1) To evaluate the seed yield of soybean, and Duncan's model with respect to the relationship between seed yield and plant population in soybeans.

2) To determine the influence of nondestructive light enrichment imposed at different growth stages on seed yield and the nodal development of seed yield components.

CHAPTER II

YIELD POPULATION MODELING

Introduction

Genotype and environment as determinants of 'maximum yield'.

Crop plants carry all the genetic information acquired during evolution and breeding in their chromosomes in the cells. By changing or incorporating specific genes controlling certain traits, scientists have developed cultivars that are more adapted to the local environment, tolerant to stresses, and resistant to specific pests and diseases. Donald (1968) proposed that 'ideotypes' of crop plants can help in improving productivity. The ideotype for intensively cropped wheat plants is characterized by short stiff straw, minimum number of erect leaves(erect at the top, gradually becoming horizontal towards the bottom the lower most leaf becoming perfectly horizontal), and a large spike.

'Environment' as defined by De Vries (1965) is "the entire complex of physical, chemical and biological factors met by a plant or other living entity". The principal physical and chemical factors that affect growth and yield of crops include climatic factors like radiation, cloudiness, precipitation, wind, air temperature, humidity, CO₂ content of the air, air pollution etc.; and edaphic factors like soil structure and texture, soil temperature, soil moisture, soil aeration, organic matter content, soil reaction and soil fertility.

Climate is a major determinant of the geographic distribution of both natural and cultivated crops. Each plant species has certain climatic requirements for optimum growth, and the success or failure of the crop is based on how well each of these particular requirements is met (Watson, 1965, Buck, 1961).

Environmental factors effecting potential yield of crops

Solar radiation

The ultimate source of energy for earth is 'solar radiation'. The solar radiation reaching the outer edge of earth's atmosphere is 1.39 kWm⁻². However only 47% of it reaches the earth surface after reflection by clouds, refraction and diffraction in the atmosphere, and scattering and absorption by clouds and suspended particles. The ecosphere (part of the atmosphere that supports life) receives solar radiation at wavelengths 290-3000 nm. About 40-50% of the solar energy falls in the spectral region of 390-780 nm (visible light). Of the visible light that falls on the leaves about 6-12% is reflected. About 70% of the photosynthetically usable radiation (PAR 400-700 nm) entering the mesophyll is absorbed by the chloroplast. Photoreceptors involved in photosynthesis are chlorophylls with an absorption maxima of red and blue along with accessory plastid pigments (carotin and xanthophylls) that absorb the blue and UV regions.

In crop stands, photosynthesis occurs in a stacked arrangement of leaves. The incident light is absorbed progressively as it passes through the leaf layers. This attenuation of radiation depends mainly on the density of foliage called the leaf area index (LAI - Watson, 1947), and the arrangement of leaves. Monsi and Saeki (1953), have shown that

$I = I_0 e^{-k.LAI}$

where, I is the intensity of radiation at a certain distance from the top of the plant canopy, I_0 is the radiation incident on the top of the canopy and k is the extinction coefficient for the plant community. The LAI above the level at which I is estimated is used in the

equation. Extinction coefficient indicates degree of light attenuation within a canopy for a given LAI. In grain crops where leaves have an upright orientation (more than 3/4 of the leaves at an angle of more than 45[°] from horizontal), k is less than 0.5 and in stands with broad horizontal leaves (e.g. Clover or sunflower), k is greater than 0.7. Studies on the net photosysnthesis of grain plants in stands indicated that, within a stand, because of the angle at which light strikes at the leaf surface and because of the shading of leaves by one another, light saturation is not reached even under strong irradiation (Boysen-Jensen, 1932).

Photosynthesis and hence yield are influenced by intensity and quality of solar radiation, and crops differ in their light requirements. He *et al.*(1996), conducted experiments on the influence of irradiance on photosynthesis under natural conditions using *Heliconia* spp. The results indicated reduced photosynthetic capacities and lowered chlorophyll content when the plants were grown under full sunlight compared with those grown under intermediate and deep shade. Experiments by Sanchez, in 1989 on lettuce showed that shading reduces growth and yield especially when done at the heading stage of development. Potential productivity of maize in temperate regions was found to be limited by the amount of solar radiation available around silking (Otegui *et al.*, 1995).

Plants exhibit environmental and genetic modifications to the prevailing quality and quantity of radiation. Plants adapted to intense light have more efficient axial system, several layers of mesophyll cells with abundant choroplasts, and hence produce more dry matter. Those adapted to shade develop extensive leaf surfaces with high concentration of chlorophyll and accessory pigments in the chloroplasts and are distinguished by comparatively lower dry matter production and low respiration. Depending on anatomy and CO_2 fixation mechanism, plants have been described as C_3 , C_4 and CAM plants. Comparison of the light dependence curves showing dependence of net photosynthesis on light showed that C_4 plants like maize and millet are not light saturated i.e.,reach maximum photosynthesis, even at high light intensities, and at intermediate irradiance they operate more efficiently than C_3 plants. C_3 plants on the other hand are much less efficient and hence light saturate at lower intensities. Studies by Kephart *et al.* in 1992 using C_3 and C_4 perennial grasses indicated that responses of C_4 grasses in terms of herbage yield, shoot dry weight and crop growth rate to irradiance were two to three times greater than for C_3 grasses.

Temperature

Plants vary in their tolerance to temperature. Most plants can live in the temperature range of 5°C to 50°C. However, biological activities are limited at lower temperatures by freezing of water and at upper temperatures by denaturation of protein. Chilling and freezing injury occurs in plants at low temperatures. This results in damage to bio - membranes and breakdown of metabolism of nucleic acids and proteins. Certain crops on the other hand, have a chilling requirement for their growth. Winter annuals and biennials, as well as buds of certain woody plants require a cold winter season (chilling requirement) in order to flower normally in the spring. They do not flower until after they have been exposed for weeks to temperatures between -3°C to 13°C. This acquisition or enhancement of the ability to flower by exposure to cold is called vernalization. Excessive heating also results in the death of plants by denaturing the enzymes and breakdown of metabolism. Temperature resistance mechanisms in plants vary according to the genetic

adaptations (Levitt ,1958). Photosynthesis has been shown to be extremely sensitive to air temperature. Studies on the performance of the photosynthetic apparatus using the third leaves of maize seedlings showed a reduction in photosynthetic rate as temperature decreased from 25-4°C (Haldimann *et al.*, 1996). Based on experiments to study the effects of high light and temperature stress on structure and function of the photosynthetic apparatus of wheat, Mishra and Singhal (1992) reported a decrease in the electron transport activity of chloroplast isolated from photoinhibited and heat stressed leaves. Photosynthetic rates of wheat seedlings declined gradually after temperature increased from 22 to 42°C (Al Khatib and Paulsen, 1989). Studies on the seasonal changes in growth of 'titan' red raspberry indicated that photosynthetic rates of primocane and floricane leaves was very sensitive to temperature exhibiting a decline from 15-40°C (Massacci *et al.*, 1995).

Temperature range suitable for dry matter production, growth and development depends on thermal climate of the region in which the species grows. For example, extension of shoot growth of temperate plants begins as soon as the temperature rises a few degrees above zero whereas in tropical plants growth does not begin until 12-15°C is reached. For each plant, there is a minimum, optimum, and maximum range of temperature called 'cardinal temperature' for each stage of the crop.

Carbon dioxide content of the atmosphere

Impact of increased CO₂ on physiology, growth and yield of crops has been an issue of debate among scientists (Kubiske and Pregitzer, 1996; Koike *et al.*, 1996; Jones *et al.*, 1996; Conroy *et al.*, 1994; Acock, 1990; Nederhoff and Vegter, 1994; Pearson *et al.*,

1994; Seddigh *et al.*, 1994). Positive effects of high CO_2 on wheat grain yield were observed by (Tubiello *et al.*, 1995). Elevated CO_2 was found to increase dry matter accumulation and pod yield in ground nut (Clifford *et al.*, 1993). However experiments by Chen, in 1990, indicated improvement in production of marketable seeds in groundnut only when CO_2 enrichment was combined with depegging which helped to prevent excessive sink load. In many other studies also, response to increased CO_2 by different crops were found to be influenced by interactions with other environmental factors (Allen, 1990; Sengupta and Sharma, 1993; Teramura *et al.*, 1990; Wheeler *et al.*, 1991).

<u>Wind</u>

Wind is shown to have both favorable and unfavorable effects on crop production. Mild wind assists in pollination of many crops [fir (El Kassaby *et al.*, 1993), corn (Johnson and Hayes, 1932)], and helps in air mixing replenishing CO_2 in the crop canopy depleted by photosynthesis. Unfavorable effects include lodging of crops (Jones and Mitchell, 1992), desiccation of fruits and vegetables, mechanical damage to leaves (Eckstein *et al.*, 1996), and branches, increased transpiration rates etc. These can severely reduce crop yields or in extreme cases result in complete devastation of crops.

Apart from these direct influences, wind affects crop growth indirectly by causing substantial soil erosion (Schillinger, 1996; Johnston *et al.*, 1995). Wind velocities and direction often influence the spread of pests and diseases (Montandon *et al.*, 1993) and application efficiencies of fertilizers (Viets, 1950; Sogaard and Kierkegaard, 1994).

Precipitation

Yet another factor that decides crop productivity is water availability. About 75 - 95% of the weight of plants is contributed by water. The roles of water in plants include: being a structural constituent of proteins and nucleic acids, involvement in biological reactions and temperature regulation.

Rainfall is the direct source of most of the water used by crops. Amount and distribution of rainfall in a region influences the growth and distribution of plants as water is essential for all biological reactions from germination to senescence. Crops differ in critical stages during which a deficiency of water will result in yield reductions (e.g. tasseling and silking in corn, pod filling in soybean). Certain plants are genetically adapted to growing in regions with low water availability. They often possess morphological features like pubescent leaves, rolling of leaves, bloom on stem and leaf (white powder in sorghum), number and distribution of stomata, cutinized epidermal cells, sunken stomata etc. Plants also differ in their water use efficiency (WUE=Dry matter production/water consumption (g DM. $I^{-1} H_2O$). Millets, corn etc are the most efficient water users followed by cereal grains which are intermediate in water requirements and forages (e.g. alfalfa) have a relatively high water requirement.

In addition to playing these direct roles, rainfall controls crop growth and yield indirectly by influencing surface runoff soil erosion(Razavian, 1990), and availability of nutrients.

Humidity

Relative humidity influences crop growth directly and/or indirectly. Leaf growth rate and turgor was found to be sensitive to relative humidity in experiments by (Metcalfe *et al.*, 1991). Humidity during grain filling has been shown to influence wheat protein quality (Graybosch *et al.*, 1995) and wheat yield (Kobata *et al.*, 1992). Relative humidity influences incidence of diseases [early leaf spot of peanut (Wu *et al.*, 1996)] and insects [(cabbage maggot on broccoli and chinese cabbage (Matthews Gehringer and Hough Goldstein, 1988)]. Calcium uptake by sorghum was found to be slowed down at high relative humidity due to decreased transpiration which reduced the Ca mobility (Murtadha *et al.*, 1989). Humidity influences application efficiency of agricultural chemicals (Singh and Das, 1939; Wills and Street, 1988).

Environmental pollution

Atmospheric and water pollution and its impact on crop production has gained significance in the recent past. Atmospheric pollutants particularly dangerous to plants are SO₂, hydrogen halides (HF, HCl) ozone and peroxy-acetyl nitrates (PAN). Nitrogen oxides, ammonia, hydrocarbons, tar fumes, soot and dust are also dangerous. Plants growing in water are damaged by poisonous chemicals in sewage (cyanides, chlorine, and hypochlorite, phenol and benzol derivatives, heavy metal compounds etc.), detergent additives (sulfonates, phosphates) and by seepage from sewage plants, garbage dumps, and cultivated fields. The effects of many pollutants is decided by their concentration and period of exposure. Below the concentration threshold there are no observable changes even after prolonged exposure (Kohut *et al.*, 1988; Lesser *et al.*, 1990; Sommerville,

1989). Exposure to high concentration (e.g. greater than 1 cm³ SO₂/m³ air) causes acute injury to plants. Chlorophyll bleaching, leaf discoloration, necrosis of tissue and organs or death of entire plants results. At low concentrations (e.g. 0.05 to 0.2 cm³ SO₂/m³), there is no externally visible poisoning initially, but chemical, biochemical or structural and functional changes might occur (e.g. enolase inhibition and enhance peroxidase activity under HF stress). However certain crops like lavender can tolerate the effect of pollutants and can be grown without threat of contamination of economic parts (Zheljazkov and Nielsen, 1996)

Edaphic factors

Edaphic factors play crucial roles in determining crop yield. Soil texture has been shown to be one of the factors that cause yield differences among landscape positions (Brubaker *et al.*, 1993). Texture influences water infiltration (Gulick *et al.*, 1994), erodibility of the soils (Burroughs *et al.*, 1992) and availability of plant nutrients (Davis *et al.*, 1996; Yadvinder *et al.*, 1994).

Management practices that help to maintain good soil structure have been shown to facilitate proper aeration of soil and increase yield of crops (Glenn and Welker, 1989; Pezzarossa *et al.*, 1995; Bell *et al.*, 1995). Studies by Meyer *et al.* (1985) on cotton, Mukhtar *et al.* (1988) on corn, Bushnell (1935) on potato and Kosaka *et al.* (1981) on sugarbeet have stressed the significance of soil aeration as an important factor affecting performance of crops. Soil temperature was reported to control root growth (Teasdale *et al.*, 1995) and yield of crops (Shuler and Hannaway, 1993). Soil moisture is another important edaphic factor that is critical for the growth, yield and quality of crops (Haddock, 1949; Hunter et al., 1950; Awada et al., 1967; Cullen, 1971; Kamara, 1976; Kolderup, 1975; Kosaka et al., 1981; Morris and Sims, 1985; Carlson, 1990).

Voluminous research data are available on the influence of *soil organic matter* (Bauer and Black, 1994) and nutrients on growth and yield of crops (Mooso *et al.*, 1995; Odland and Allbritten, 1950; Fageria and Baligar, 1995; Lynd and Ansman, 1995, and Saxena *et al.*, 1996).

Soil reaction influences crop growth (Sundling *et al.*, 1932), quality (Stark, 1924) and yield by controlling incidence of diseases [for example, higher soil reaction (6.1) was found to decrease yield and increase scab incidence in potato (Odland and Allbritten, 1950)], and nutrient availability (Ensminger and Cope, 1947; Warden and Reisenauer, 1991).

Duncan's Model

The foregoing discussion clearly indicates that the potential yield of a crop is very specific to the genotype and the environment in which it is grown. According to Duncan's model -

$\ln y = \ln y_0 + EC$

Thus, y in Duncan's model (Duncan, 1984) is decided by genotype, growing environment and competition from neighboring plants (crowding) for the available environmental resources. The extent to which competition affects the yield, E in the model, is a measure of the interaction between genotypes and environmental factors. This means that if there is no resource limitation, the impact of crowding on yield will be the least and yield will be dependent mostly on genetic potential. This dependence of E on environmental factors is well demonstrated in experiments by Lang *et al.*(1956) and Rhodes and Stanley (1984) as cited by Duncan (1984). If so, y_0 can be thought of as the theoretical 'maximum yield' that can be attained by a specific genotype under a particular environment when there is absolutely no competition from any other plant for the available resources. The current study was conducted with the objective of evaluating the seed yield of soybean, and Duncan's model with respect to the relationship between seed yield and plant population in soybeans.

Materials and Methods

A three - year field study was conducted in 1995, 1996 and 1998 at the University of Massachusetts research farm in South Deerfield. The soil at the experimental site is a Hadley fine sandy loam (Typic Udifluvent). In all years, seeds inoculated with commercial, powdered, peat - based granular *Bradyrhizobium* were used for planting, and other normal cultural practices were followed. A pre-emergence mixture of 0.85 kg (ai) ha⁻¹ Linuron [3-(3,4-dichlorophenyl)-1-methoxy-1-methylurea] and 1.75 kg (ai) ha⁻¹ Alachlor (2chloro-2',6'-diethyl-N-(methoxymethyl) acetanilide) were used for weed control in all years.

In 1995 and 1996, a complete randomized block design of four soybean cultivars NK 0066, NK1990, PIONEER 9071, and PIONEER 9111, grown at three different densities was used. The densities were 25 plants m⁻² planted at a distance of 25cm between rows and 16cm within row, 50 plants m⁻² planted at a distance of 25cm between rows and 8cm within row, and 75 plants m⁻² planted at a distance of 25cm between rows and 5.3cm within row. The plots were 7m long with 8 rows per plot. In 1998, a complete randomized block design of three soybean cultivars PIONEER 9071, NK 0066 and PIONEER 9111, grown at six different densities and row spacing was used. The different densities used in the experiment included 83 plants m⁻² planted at a distance of 25cm between rows and 4.826cm within row, 41 plants m⁻² planted at a distance of 50cm between rows and 4.826cm within row, 43 plants m⁻² planted at a distance of 25cm between rows and 9.525cm within row, 21 plants m⁻² planted at a distance of 50cm between rows and 9.525cm within row, 57 plants m⁻² planted at a distance of 25cm between rows and 9.525cm within row, 57 plants m⁻² planted at a distance of 50cm between rows and 7.112cm within row, and 23 plants m⁻² planted at a distance of 75cm between rows and 5.842cm within row. Each plot was 2.25m wide and 7.5m long.

Each year, in addition to the above mentioned treatments, uniformly spaced ('isolated') plants were grown at 50cm x 50cm, 75cm x 75 cm, 100cm x 100cm, and 150cm x 150cm spacings.

Yield was determined by harvesting plants in one square meter from each plot and recording the seed dry weight after drying the samples to constant weight at 60°C in a forced dry air oven. This sample was used to calculated yield m⁻² and the number of plants m⁻². For yield component analysis, 15 plants, were harvested at maturity from each treatment. For each group of plants, data were recorded on pod number, seed number, and seed dry weight.

Statistical analyses of the data was performed using the SAS analysis of variance and regression procedures (SAS, 1995).

Determination of crowding

Crowding for each cultivar and planting pattern was calculated following the procedure outlined by Duncan(1984).

- a) D_{max} , the distance at which crowding becomes zero or negligible, was determined by growing soybean plants at different spacings and plotting the yield per plant against density of uniformly spaced (rectangularity = 1) plants.
- b) Deviation of the plant from D_{max} was expressed as a fraction of D_{max} termed the Separation fraction(SF) as SF = (D_{max} separation)/ D_{max}).
- c) Alpha, the power to which SF is raised to get an appropriate curve relating crowding and separation distance was calculated by fitting different arbitrary values and testing them with several years of data.
- d) Crowding value for the given planting pattern was calculated using a computer program written using C++ programming language (Appendix A) as

Crowding (C) =
$$\sum_{p=1}^{p=n} SF^{alpha}$$

where, p=1 to p=n includes all plants in the planting pattern within the distance D_{max} from the center plant.

Crowding remains constant for a particular planting pattern but increases with increasing plant number and increasing plant rectangularity at the same planting density.

Calculation of y₀ and E

 y_0 and E were calculated as follows :

- a) Different genotypes of soybean were grown in the given environment at two populations spanning as wide a range of plant populations as feasible.
- b) C values for each of these populations were calculated as described above.
- c) Yield per plant from each of these populations was calculated from the harvest data on yield.
- d) Regression analysis of ln of y (measured) against C value was done as suggested by Duncan(1984) as $lny = lny_0 + EC$ where lny_0 is the isolated plant yield at zero crowding and E is a measure of the effect of cultural and environmental factors in influencing the rate of change in yield with a change in crowding.

Testing the prediction lines using two crowding values

Regression equation fitted using the lowest crowding value and the highest crowding value was compared to an equation fitted using all data points to see if there is a statistically significant difference between the slopes and intercepts of the lines.

Results and Discussion

Yield per square meter

Results showed significant difference in yield m⁻² among cultivars in all years (Table 1). In both 1995 and 1996, PIONEER 9071 produced the highest yield and was closely followed by NK 1990. NK 0066 gave the lowest yield m⁻². In 1998, PIONEER 9111

Table 1. Yield component analysis of soybean varieties for 1995, 1996 and 1998.

	Variety	1995	1996	1998
Yield m ⁻²	NK 0066	580.01c [‡]	329.39c	482.50b
(g m ⁻¹)	NK 1990	675.81a	396.07ab	-
	PIONEER 9071	685.06a	425.50a	495.61b
	PIONEER 9111	634.18b	340.28bc	636.33a
Plants m ⁻²	NK 0066	52.00	47.00	42.56
(No m ⁻¹)	NK 1990	57.33	46.33	-
	PIONEER 9071	48.22	47.89	42.94
	PIONEER 9111	47.22	44.77	40.00
Yield plant ⁻¹	NK 0066	12.70c	9.74b	20.01b
(g plant ⁻¹)	NK 1990	15.43a	13.81a	-
	PIONEER 9071	14.25ab	12.87a	19.17b
	PIONEER 9111	12.95bc	12.65a	26.95a
Pods plant ⁻¹	NK 0066	29.27	20.94c	55.80
(No plant ⁻¹)	NK 1990	29.56	23.02bc	-
	PIONEER 9071	34.29	32.46a	57.39
	PIONEER 9111	28.96	25.43b	63.39
Seeds pod ⁻¹	NK 0066	2.32b	2.37	2.25
(No pod ⁻¹)	NK 1990	2.54a	2.78	-
	PIONEER 9071	2.41b	2.41	2.41
	PIONEER 9111	2.38b	2.40	2.35
Seed size	NK 0066	192.89b	198.95b	159.56b
(mg seed ⁻¹)	NK 1990	209.02a	229.52a	-
	PIONEER 9071	175.28c	166.08c	140.46c
	PIONEER 9111	190.34b	203.93b	181.17a

[‡]Means not followed by the same letter are significantly different at the 0.05 probability level.

Mean separation was done using DMRT.

gave significantly higher yield compared to PIONEER 9071 and NK 0066. Statistically similar yield m⁻² was recorded for PIONEER 9071 and NK0066 in 1998.

Differences among the densities with regard to yield m⁻² were significant in 1995 and 1998 (Tables 2 and 3). Among the three densities used in the experiments in 1995 and 1996, the highest yield in both years was recorded by the highest density of 75 plants m⁻². In 1998, a density of 83 plants at 25 cm between the rows gave the highest yield. There was no significant difference in yield m⁻² between densities of 43 and 57 plants m⁻² at 25 cm row spacing, and density of 41 plants m⁻² at 50cm row spacing. Lowest yield m⁻² was recorded by a density of 23 plants m⁻² at 75 cm row spacing and this was statistically similar to that of 21 plants m⁻² at 50 cm row spacing.

Thus, it can be summarized that narrow row planting at a density of 75 - 83 plants m⁻² gives the maximum yield m⁻² among the different cultivars and densities studied in these experiments.

Yield components

Yield plant⁻¹

Significant difference in yield plant⁻¹ was observed among different cultivars in all years (Table 1). In 1995 and 1996, NK 1990 and PIONEER 9071 recorded the highest yield plant⁻¹ across all densities. The lowest yield plant⁻¹ was recorded by NK 0066. Just as in the case of yield m⁻², in 1998, PIONEER 9111 gave significantly higher yield plant⁻¹ compared to the other two cultivars. Statistically similar yield plant⁻¹ was recorded by PIONEER 9071 and NK0066.

 Table 2. Yield component analysis of soybean grown at different densities in 1995

 and 1996.

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	Density	Row Spacing	Crowding at Dmax 120 and Apha 2	1995	1996
Yield m ⁻²	25	25	20.20	626.34	363.78
(g m ⁻¹)	50	25	39.08	621.18	373.69
	75	25	58.32	683.77	380.95
Plants m ⁻²	25	25	20.20	28.33	23.83
(No m ⁻¹)	50	25	39.08	52.58	45.42
	75	25	58.32	72.67	70.25
Yield plant ⁻¹	25	25	20.20	19.13	19.10
(g plant ⁻¹)	50	25	39.08	12.60	10.16
	75	25	58.32	9.78	7.54
Pods plant ⁻¹	25	25	20.20	44.52	40.23
(No plant ⁻¹)	50	25	39.08	27.17	21.10
	75	25	58.32	19.88	15.06
Seeds pod ⁻¹	25	25	20.20	2.40	2.47
(No pod ⁻¹)	50	25	39.08	2.41	2.41 · ·
	75	25	58.32	2.44	2.59
Seed size	25	25	20.20	181.52	194.51
(mg seed ⁻¹)	50	25	39.08	194.30	200.43
	75	25	58.32	199.83	203.91

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Table 3. Yield component analysis of soybean grown at different densities in 1998.

	Density	Row Spacing	Crowding at Dmax 120 and Apha 2	1998
Yield m ⁻²	83	25	64.26	689.00
(g m ⁻¹)	41	50	31.61	593.89
	21	50	33.11	449.89
	43	25	15.85	540.22
	57	25	43.86	558.78
	23	75	17.60	397.11
Plants m ⁻²	83	25	64.26	77.89
(No m ⁻¹)	41	50	31.61	41.56
	21	50	33.11	21.78
	43	25	15.85	38.11
	57	25	43.86	51.67
	23	75	17.60	20.00
Yield plant ⁻¹	83	25	64.26	13.51
(g plant ⁻¹)	41	50	31.61	20.09
	21	50	33.11	29.61
	43	25	15.85	21.64
	57	25	43.86	17.67b
	23	75	17.60	29.75
Pods plant ⁻¹	83	25	64.26	34.82
(No plant ⁻¹)	41	50	31.61	54.72
	21	50	33.11	80.21
	43	25	15.85	58.32
	57	25	43.86	45.92
	23	75	17.60	79.18
Seeds pod ⁻¹	83	25	64.26	2.29
(No pod ⁻¹)	41	50	31.61	2.28
	21	50	33.11	2.36
	43	25	15.85	2.35
	57	25	43.86	2.38
	23	75	17.60	2.36
Seed size	83	25	64.26	167.30
(mg seed ⁻¹)	41	50	31.61	160.21
	21	50	33.11	156.33
	43	25	15.85	158.64
	57	25	43.86	162.89
	23	75	17.60	157.00

Differences among the densities with respect to the yield plant⁻¹ were statistically significant in all years (Tables 2 and 3). In both 1995 and 1996, the highest yield plant⁻¹ was recorded by the lowest density of 25 plants m⁻² and the lowest yield plant⁻¹ was recorded by the highest density of 75 plants m⁻² which gave the highest yield m⁻². In 1998, the highest yield plant⁻¹ was given by the lowest densities of 23 plants m⁻² at 75 cm row spacing and 21 plants m⁻² at 50 cm row spacing. Significantly lowest yield plant⁻¹ was observed at the highest density of 83 plant⁻¹ at 25 cm row spacing. The other densities were statistically similar to each other with respect to yield plant⁻¹.

The results thus indicate that as the density increases yield plant⁻¹ decreases. This can be attributed to the increase in competition for the available resources, mainly solar radiation and water.

Pods plant⁻¹

Pods plant⁻¹ showed significant difference between cultivars only in 1996, when PIONEER 9071 recorded the highest followed by PIONEER 9111 and NK 1990 (Table 1). The lowest number of pods plant⁻¹ was given by NK 0066 which gave the lowest yield plant⁻¹.

Pods plant⁻¹ was the component that was the component most affected by changes in density and there for also competition for available resources in our experiments (Tables 2 and 3). Results on changes in pods plant⁻¹ with density were similar to that of yield plant⁻¹. Differences among the densities were statistically significant in all the years. In both 1995 and 1996, the most pods plant⁻¹ was recorded for the lowest density of 25 plants m⁻² and the lowest pods plant⁻¹ was recorded for the highest density of 75 plants m⁻². In 1998, the highest pods plant⁻¹ was given by the lowest densities of 21 plants m⁻² at 50 cm row spacing and 23 plants m⁻² at 75 cm row spacing. Significantly lowest pods plant⁻¹ was observed at the highest density of 83 plant⁻¹ at 25 cm row spacing. Like in the case of yield plant⁻¹ the other densities gave statistically similar number of pods plant⁻¹.

Seeds pod⁻¹

No statistically significant difference in the number of seeds pod⁻¹ between cultivars could be observed in all years except 1996 when NK 1990 recorded a slightly higher seed number per pod compared to the other varieties (Table 1).

Densities showed no significant difference in seeds pod⁻¹ in all the years indicating that seeds per pod is the component that is least affected by the growing environment (Tables 2 and 3).

Seed size

Seed size seed⁻¹ was significant in all years between the cultivars. NK 1990 recorded the highest seed size and POINEER 9071 recorded the lowest seed size in both 1995 and 1996 (Table 1). In 1998, POINEER 9071 had the lowest seed size and PIONEER 9111 had the highest seed size. There was no statistically significant difference between varieties PIONEER 9111 and NK 0066.

Just like in the case of seed number per pod, seed size did not show any statistically significant difference between densities in any year (Tables 2 and 3).

D_{max}, alpha and crowding

Analysis of the yield plant⁻¹ from isolated plants (Table 4) revealed a significant difference between seed yield between cultivars. NK 1990 had the highest yield plant⁻¹ in both 1995 and 1996. In 1998, among the three cultivars grown, PIONEER 9111 and PIONEER 9071 had similar yield plant⁻¹. NK 0066 had the lowest yield plant⁻¹ in all the ...

There was a significant difference in yield plant⁻¹ between the different separation distances in all years (Table 5). Yield plant⁻¹ increased as the separation distance increased from 50 cm to 100 cm between plants following a 2nd order polynomial each year. The data showed that the yield was similar for separation distances of 100cm and 150cm between plants. There was no significant interaction between cultivars and separation distance in any year.

As the separation distance increased yield plant⁻¹increased and then plateaued. NLIN procedure (SAS, 1995) was used to determine the point at which the relationship plateaus for each cultivar in each year thus determining D_{max} (Figure 2 to 5). Most cultivars reached plateau between 112cm to 120cm separation distance. The extreme low value of 85cm for PIONEER 9111 in 1996 may be due to the damage to plants due to Japanese beetle attack and the relatively higher values of 137 for NK0066 in 1995 and 135 for PIONEER 9071 in 1998 may be due to increased number of weeds and the resulting lower yields at higher separation distances.

Data were combined for each different variety across years (Figure 6), for all varieties within a year (Figure 7) and all varieties and all years (Figure 8) to examine the consistency of the predicted plateau points. All combinations suggested that 120cm was a

Table 4. Yield plant⁻¹ from different cultivars of isolated plants grown from 1995 to 1998.

Variety	Yield Plant ⁻¹ (g)			
	1995	1996	1998	
NK 0066	56.55c [‡]	55.12c	47.66b	
NK 1990	165.47a	147.19a	-	
PIONEER 9071	62.90c	65.09b	60.47a	
PIONEER 9111	87.83b	61.51bc	60.92a	

[‡]Means within columns not followed by the same letter are significantly different at the 0.05 probability level. Mean separation was done using DMRT.

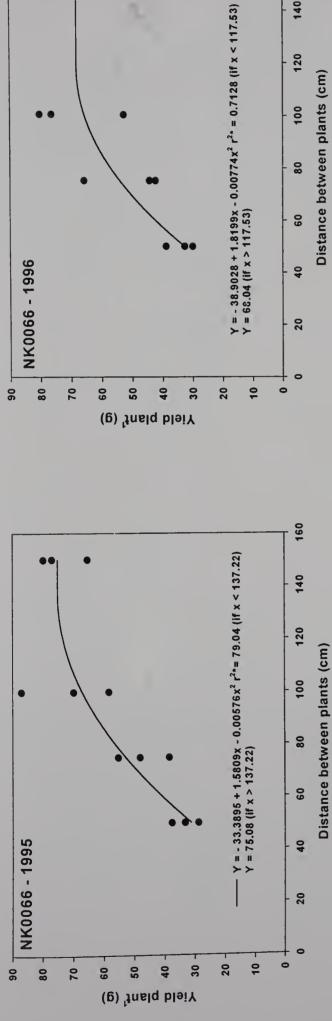
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Table 5. Yield plant⁻¹ from isolated soybean plants grown at different separation distances from 1995 to 1998.

Separation		Yield Plant ⁻¹ (g))
Distance	1995	1996	1998
50cm X 50cm	68.44	54.66	27.49
75cm X 75cm	87.10	78.36	48.55
100cm X 100cm	100.52	98.07	78.87
150cm X 150cm	108.69	97.83	70.48
Trend	Quadratic + Plateau	Quadratic + Plateau	Quadratic + Plateau

Figure 2. Relationship of distance between plants to yield plant⁻¹ of NK 0066.

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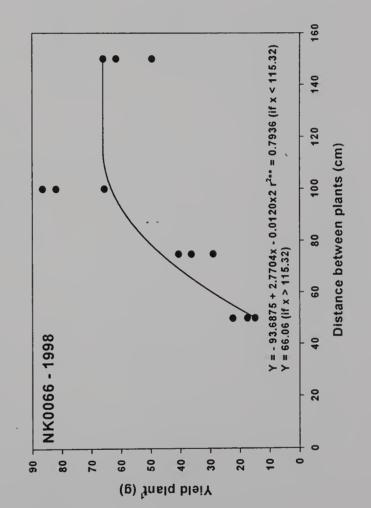


Figure 3. Relationship of distance between plants to yield plant⁻¹ of NK 1990.

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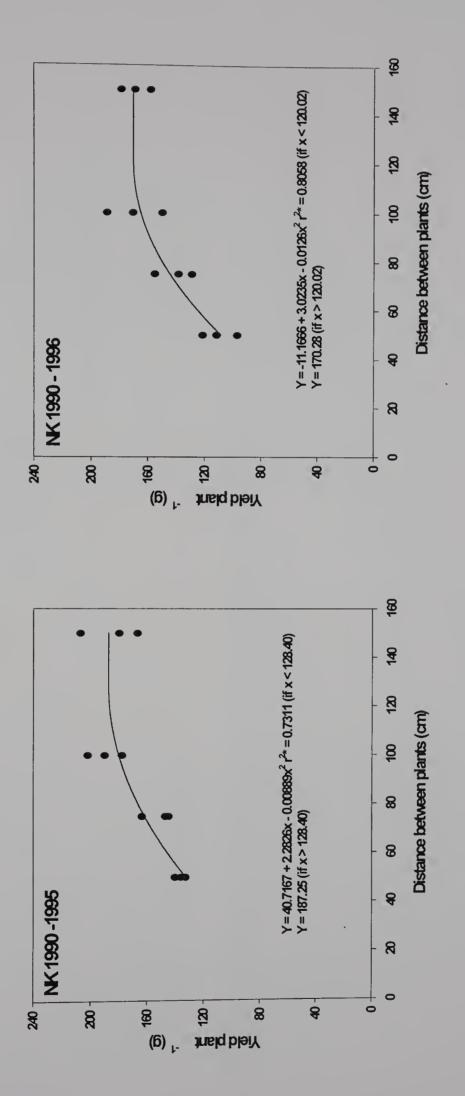
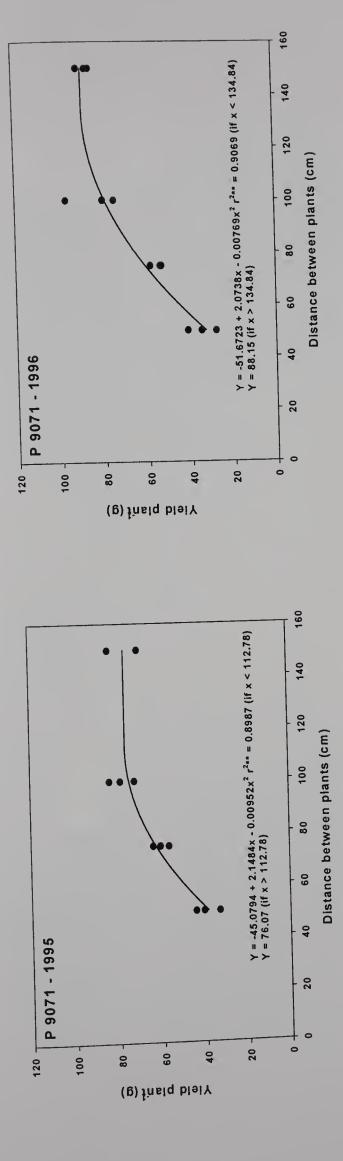


Figure 4. Relationship of distance between plants to yield plant⁻¹ of PIONEER 9071.



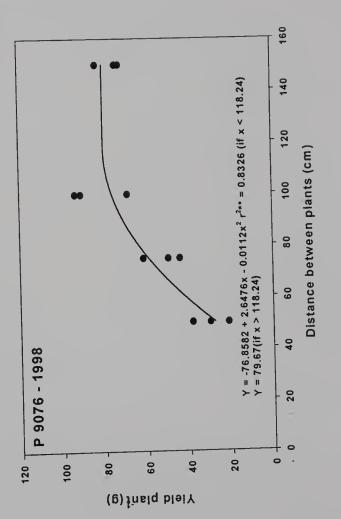
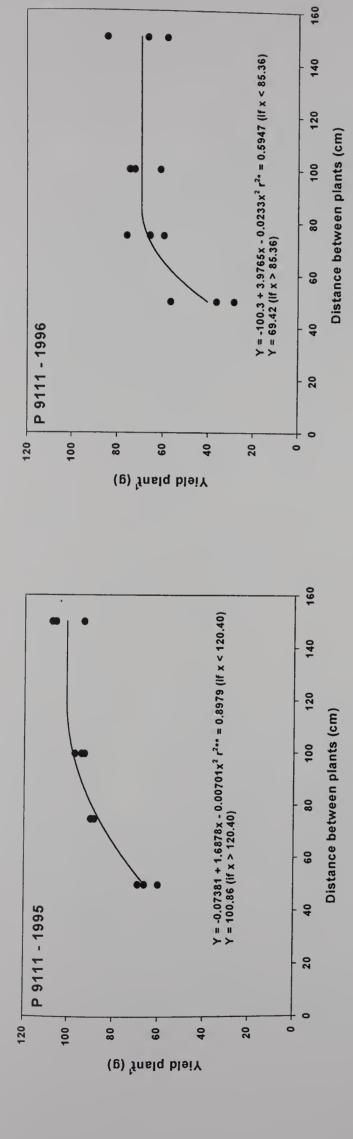


Figure 5. Relationship of distance between plants to yield plant⁻¹ of PIONEER 9111.



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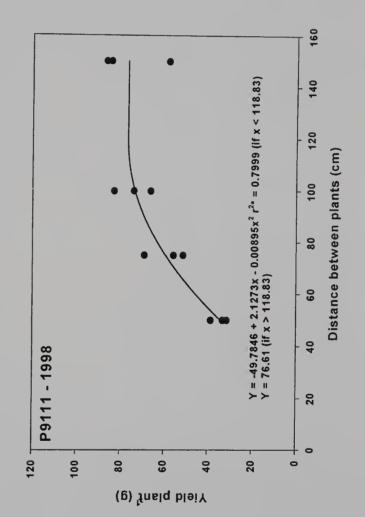




Figure 6. Relationship of distance between plants to yield plant⁻¹ of different varieties combined over the years (1995-1998).

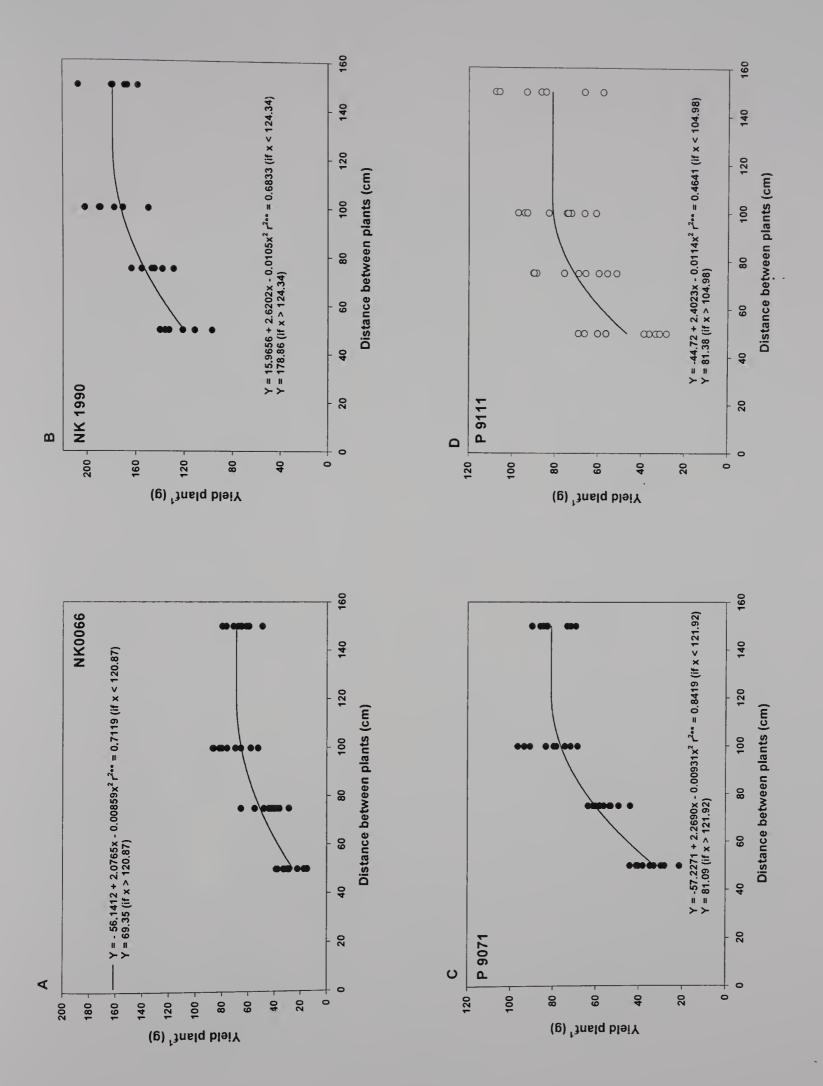
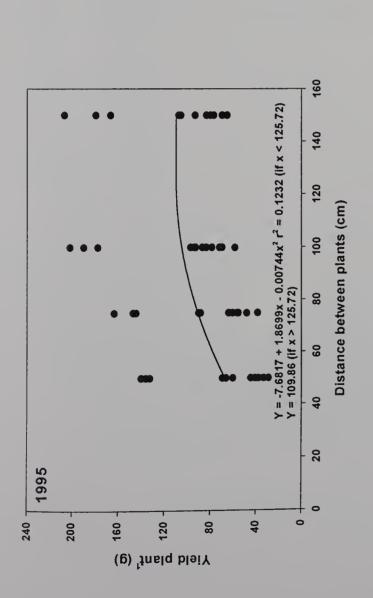
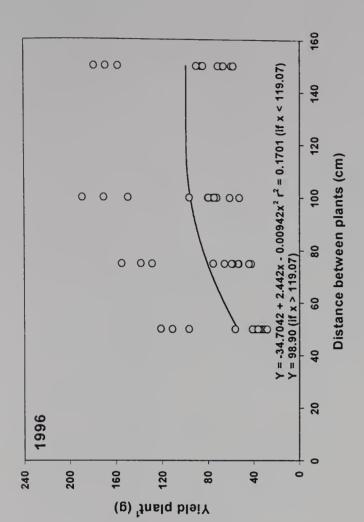


Figure 7. Relationship of distance between plants to yield plant⁻¹ of varieties combined per year.

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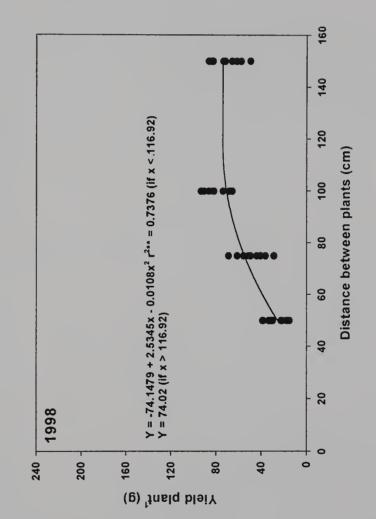
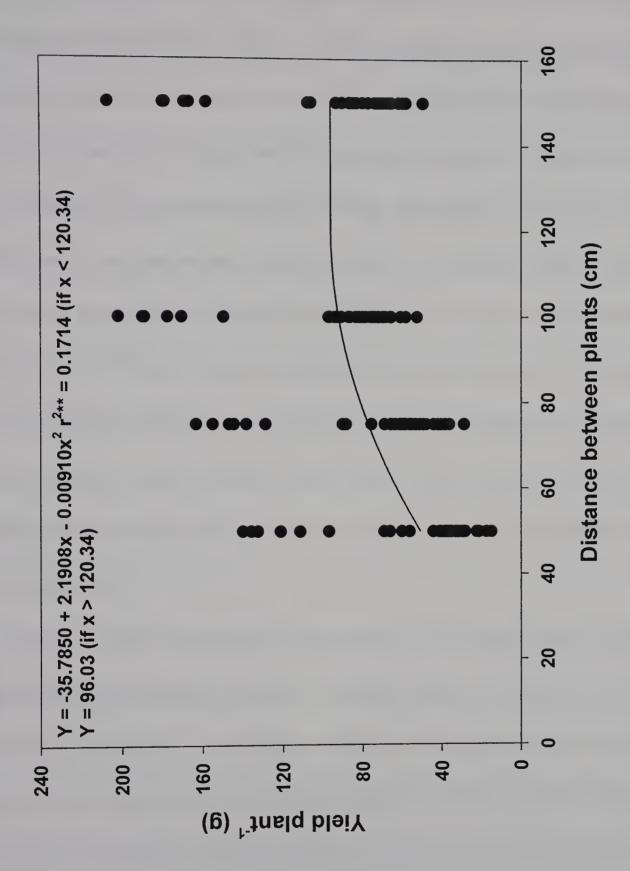


Figure 8. Relationship of distance between plants to yield plant⁻¹ of all varieties combined over all the years (1995 - 1998).



good approximation of plateau point. The lower value of 105cm for P9111 (Figure 6D) resulted from the lower value for this variety in 1996 as explained before. The analysis of yield plant⁻¹ from uniformly spaced (isolated) plants thus began to decrease at separation distances below approximately 120cm suggesting that a D_{max} of 120cm would be suitable for calculating crowding values. Duncan (1984) suggested using D_{max} values of 3m for corn which was equal to the mature height of Corn Belt cultivars. In the case of soybean, it has been shown that the roots grew across the inter-row space of 102cm rows by the R2 (full bloom) stage of development and the average plant height for soybean is 79 to 119cm at R6 (full seed) development stage (Herman, 1985). In the case of the varieties used in our experiment, mature plant height exceeded 100cm. This might be the reason for yield stabilization above 120cm of separation distance between the plants. Competition for available resources like light, water and nutrients might be negligible or practically zero when the distance between two plants is more than 120cm, because, any possibility of competition due to mutual shading or due to overlapping roots is negligible at such separation distances.

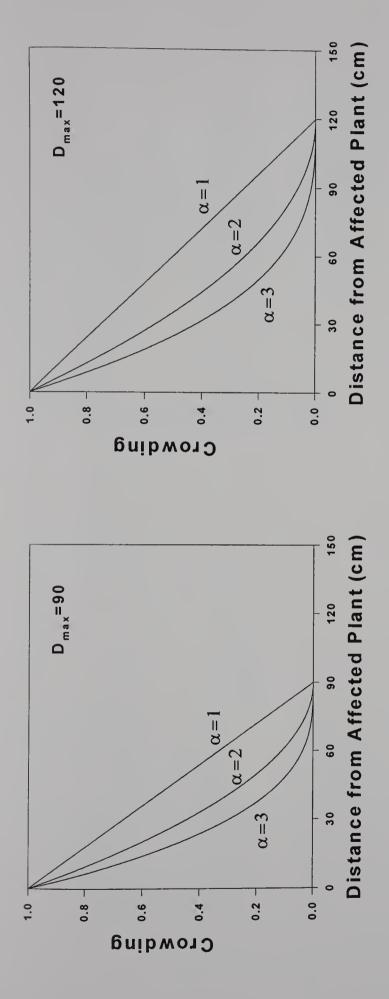
When two widely separated plants are planted increasingly closer together, crowding becomes measurable when the separation distance is equal to or less than D_{max} (120cm in our experiment). Crowding increases at an increasing rate and reaches the maximum value of one when the plants are brought in contact with each other. The function used to calculate C, defined as alpha by Duncan, should be one that allows the value of C to rise from zero at D_{max} to one at zero separation. The quadratic relationship between separation distance and yield plant⁻¹ until the plateau point suggested that using an alpha value of 2 would give good prediction lines.

The generated relationship between yield plant⁻¹ and the separation distance suggested as the with varying ALPHA's and D_{max} 's indicated that, for a given D_{max} and separation distance, competition at any given point decreases with increase in alpha (Figure 9). Also, as evident from Figure 9, as D_{max} increases, the competition experienced at a particular separation decreases and hence a corresponding alpha value that signifies this reduction in competition has to be chosen while calculating crowding. This means that if the C value increases too rapidly (ie. alpha is low) as the separation distance decreases from D_{max}, the effect of more distant plants is exaggerated and if it increases too slowly (ie. alpha is high), the relative influence of near-by plants on the target plant is over emphasized. Also, it appears that rather than the absolute values of alpha or D_{max} , it is an appropriate combination of both that controls the accuracy of predictions using the model. Duncan (1984) also stated that precise determination of alpha and D_{max} were not necessary. However, it may be important that if a higher value of D_{max} is chosen, then a correspondingly higher alpha value should be chosen or vice versa so that the total crowding of the system is not altered. A comparison of crowding relationship shown in Figure 9 for the different varieties, with the reduction in yield per plant⁻¹ suggested that an alpha of 2 would best approximate the change in yield plant⁻¹ with separation.

Prediction lines

By fitting a linear regression of these C values corresponding to a D_{max} of 120 and alpha value of 2, and experimental per - plant yields, $\ln Y_0$ and E were calculated. In the case of most cultivars and years, these gave significant regression lines (Figures 10 to 13). To check the validity of the assumption that, rather than the absolute values of alpha or

Figure 9. Relationship between crowding and separation distance between two plants.



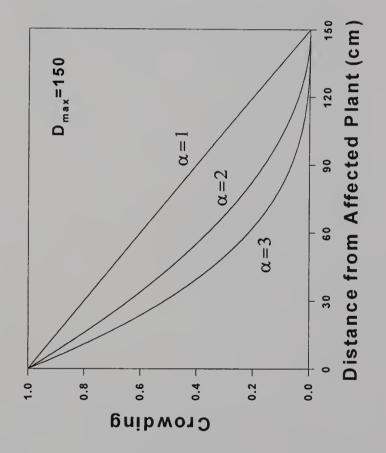
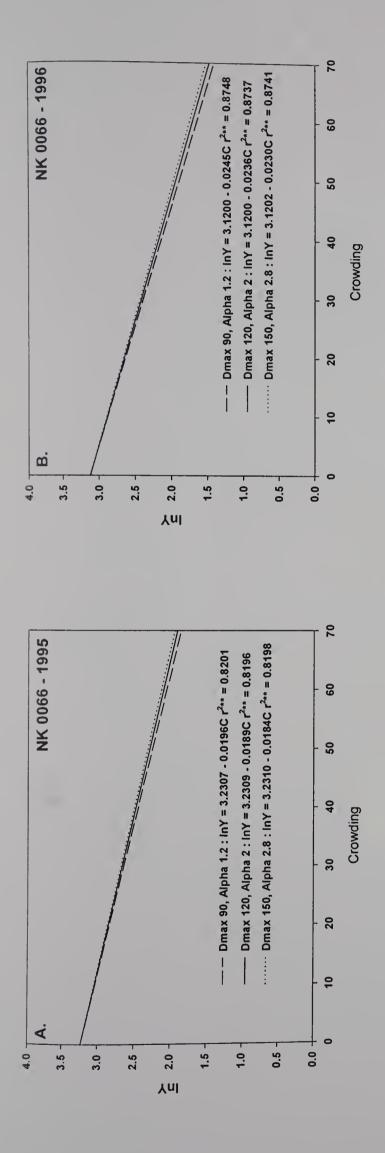
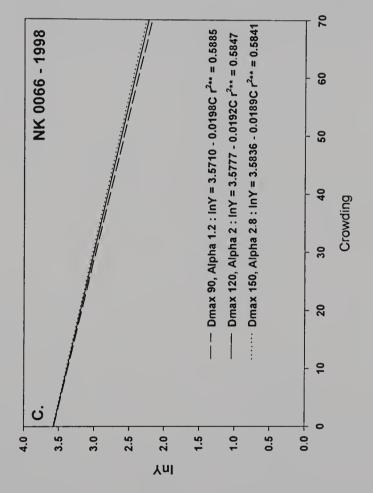


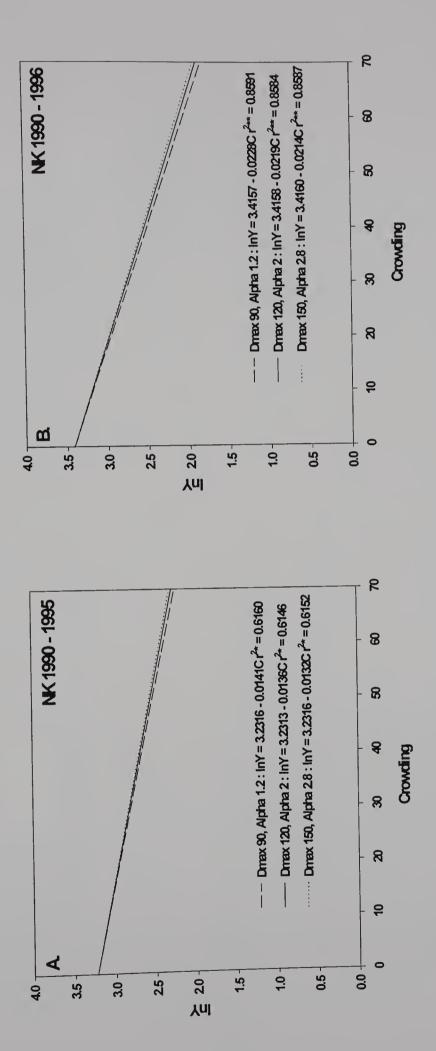
Figure 10. Effect of crowding on lnY for NK 0066.





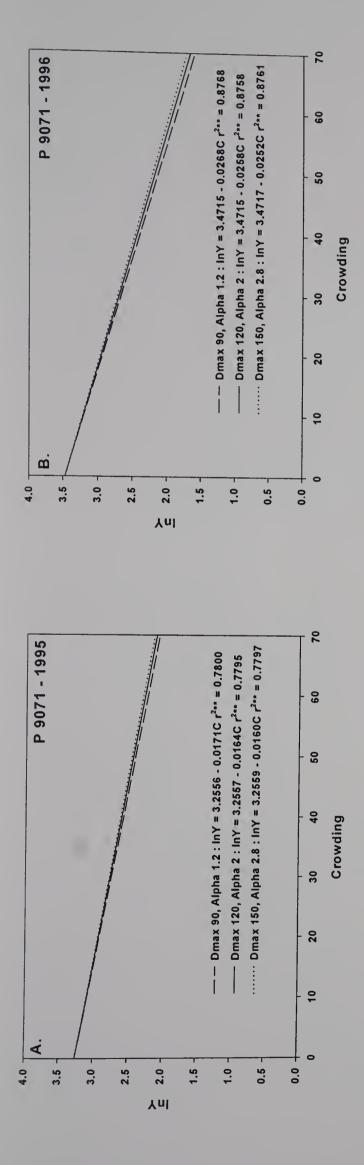
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Figure 11. Effect of crowding on lnY for NK 1990.



ς.

Figure 12. Effect of crowding on lnY for PIONEER 9071.



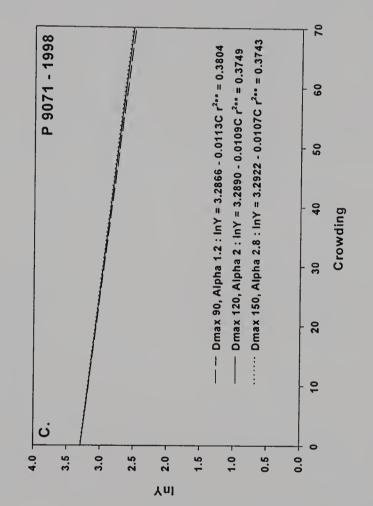
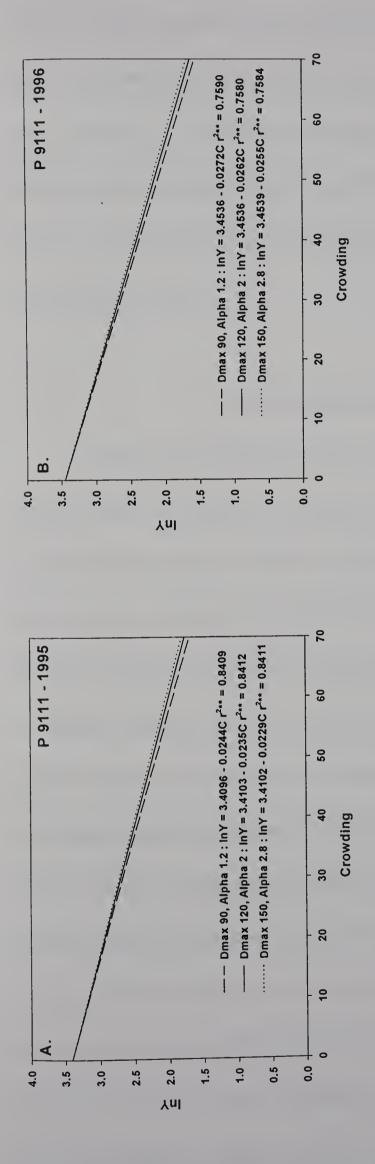
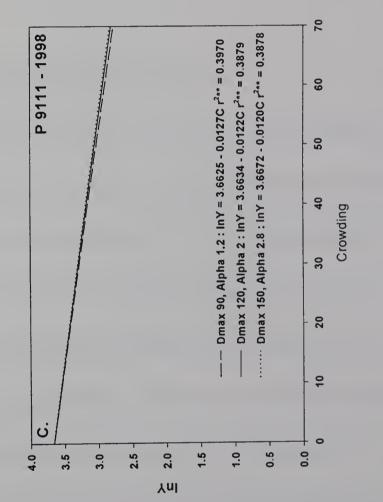


Figure 13. Effect of crowding on lnY for PIONEER 9111.







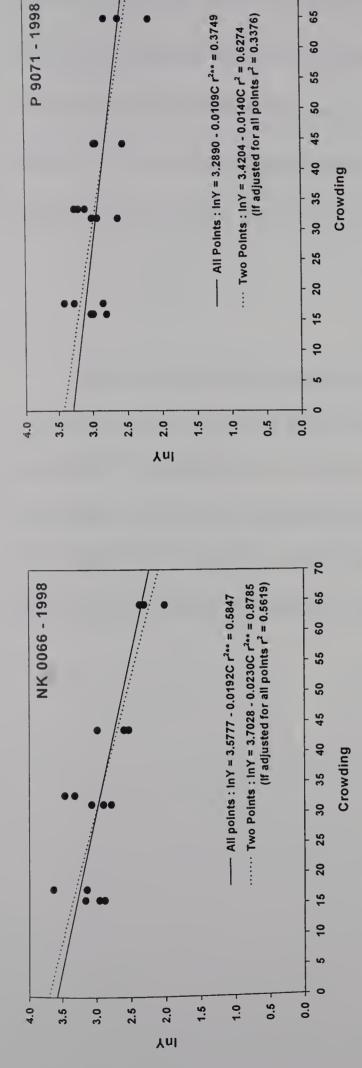
 D_{max} , it is an appropriate combination of both that controls the accuracy of predictions using the model, predicted yields obtained for D_{max} set at 90, 120 and 150 cm with different alpha values were tested. As shown in the Figures 10 to 13, combinations of D_{max} and alpha 1.2 and D_{max} 150 and alpha 2.8 gave lines that were statistically similar in slope and intercept to those obtained from D_{max} 120 at alpha 2. Also the regression was significant in each case indicating that any of the chosen D_{max} and alpha combinations will give good fitting regression lines.

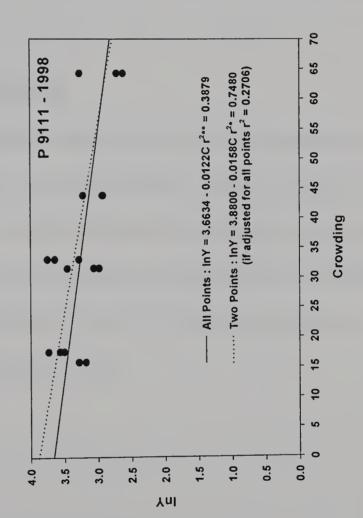
Prediction lines using two crowding values

Comparison of regression lines obtained by fitting regression equations obtained from the lowest and highest crowding values the one obtained using all data points revealed no statistically significant difference between the lines (Figure 14). For all the cultivars, regression lines obtained from all points accounted for a significant amount of variation. However, in the case of P9071 even though the regression obtained from all points was significant, regression using two points was not significant. This can be attributed to the greater variation in the data points which is evident from the error bars. There was no statistically significant difference between the regression lines using all points and those using the GLM procedure (SAS, 1995). In the case of NK 0066, the regression line obtained from two crowding values(17.6 and 64.3) when optimized over all points, had an r^2 value of 0.5619 which was close to the r^2 of 0.58, obtained by using all points. However, In the case of PIONEER 9071, the regression line obtained from two crowding points (17.6 and 64.3) when optimized over all points, the r^2 was 0.3376 compared to an r^2 of 0.3749 obtained by using all points. For PIONEER 9111, regression line obtained from

γ.

Figure 14. Effect of crowding on lnY obtained by using two crowding values.





two crowding points(17.6 and 64.3) when optimized over all points, had an r^2 value of 0.27 compared to an r^2 of 0.39, obtained by using all points. This shows that if the variability in the data is small, the model can effectively predict the changes in yield with crowding using a regression equation obtained using two crowding values. However, great emphasis has to be given to all experimental practices that would help in attaining less variability among replicates. This includes using proper seeding techniques which ensures the correct plant population and adequate weed control to prevent competition (crowding) from weeds.

Conclusion

Density and spatial arrangement of plants together determine the competition for available resources especially solar radiation, water and nutrients. These two factors are represented by 'crowding' in the model. The results indicated that the model can predict the changes in yield with changing densities and planting pattern especially if the variability in the data is low. Thus, this model shows promise as a tool for evaluating planting patterns for soybean as was suggested by Duncan for corn.

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CHAPTER III

DIFFERENTIAL RESPONSE OF SOYBEAN YIELD COMPONENTS TO THE TIMING OF LIGHT ENRICHMENT

Abstract

Solar radiation is an important environmental factor influencing seed yield in soybeans [Glycine max (L). Merr.]. Our objective was to analyze the response of soybean seed yield components to light enrichment initiated at different growth stages. Light enrichment was imposed on the indeterminate soybean cultivar Evans by installing wire mesh fencing on either side of the center row to push the adjacent rows aside at different growth stages. Fences prevented plants in the neighboring rows from encroaching on the growing space of the center row plants. Pod number per plant and to a lesser extent seed size accounted for variation in seed yield. Light enrichment initiated at late vegetative or early flowering stages increased seed yield 217%, mainly by increasing pod number, while light enrichment beginning at early pod formation increased seed size 23%, resulting in a 115% increase in seed yield. Responses to light enrichment occurred proportionately across all node positions despite the differences in the time (15 to 20 days) of development of yield components at the different node positions. Although maximum seed size may be under genetic control in soybean plants, our results suggested seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. It indicates that plants are able to redistribute the available resources to components not yet determined, in an attempt to maintain or improve yield.

Introduction

Environmental conditions prevailing during the growth period, especially intensity and quality of solar radiation intercepted by the canopy, are important determinants of yield components and hence the yield of soybean (Taylor *et al.*, 1982; Willcott *et al.*, 1984; Myers *et al.*, 1987; Board and Harville, 1992, 1996). Light enrichment using lamps or reflectors increased the yield of soybean (Johnston *et al.*, 1969; Schou *et al.*, 1978). Shading (49-20% of ambient light) resulted in lengthening of internodes and increased lodging in soybean plants (Ephrath *et al.*, 1993).

Hardman and Brun (1971) proposed that the yield of soybean is controlled by the availability of photosynthates during post flowering stage of development. Schou et al. (1978) observed that light levels during late flowering to mid-pod formation stages of growth are more critical than during vegetative and late reproductive periods in determining the yield of soybean. Taylor et al. (1982) concluded that pod abortion caused by lack of photosynthate supply late in the growing period is a major factor limiting yield of soybean. Duncan (1984) suggested that light intercepted during and after seed initiation is a major determinant of yield. Jiang and Egli (1993) reported that shade imposed from first flower to early podfill reduced flower production and increased flower and pod abscission, resulting in reduced pod number and yield. They also found canopy photosynthesis during flowering and pod set to be an important determinant of seeds m⁻², and that the impact of shading on seeds m⁻² depends on duration of shading (Jiang and Egli, 1995). Sharma et al. (1996) observed anthesis to be the most critical stage during which low light intensity can cause severe yield reduction in soybean.

Board *et al.* (1992) and Board and Harville (1996) suggested that the increased seed yield of soybean from planting in narrow rows (less than 50 cm) reported by many researchers (Lehman and Lambert, 1960; Costa *et al.*, 1980; Herbert and Litchfield, 1982; Willcott *et al.*, 1984), can be attributed to increased light interception during vegetative and early reproductive periods (first flowering to seed initiation). In most of the above studies, changes in yield was mainly brought about by changes in pod and seed number. However, an increase in seed size compensated for the decreased pod load in some source - sink manipulation studies (McAlister and Krober, 1958; Schonbeck *et al.*, 1986).

Herbert and Litchfield (1982) noticed that pod number per plant was the most important component responsible for differences in soybean yield between different row widths and densities within a particular year, while a change in seed size resulted in the yield difference between two consecutive years. Thus, there is a differential response of yield components to changes in environmental conditions. However, the exact nature of response to the timing of light enrichment has not been identified yet. Also most of the studies conducted so far on differential response achieved increases in light interception indirectly by removal of leaves, thereby modifying the source strength.

Our objectives for conducting these studies were to analyze the differential seed yield response of indeterminate soybean to non-destructive light enrichment imposed at different stages during soybean growth, and to examine the effect of light enrichment on nodal development of seed yield components to determine developmental stages most affected by environmental change.

Materials and Methods

Studies were conducted at the University of Massachusetts during 1995 using Evans of maturity group 0 which matures in approximately 115 days at this location. The soil at the experimental site was a Hadley fine sandy loam (Typic Udifluent).

A randomized block design was used with four replications. There were three light enrichment treatments, no light enrichment, light enrichment initiated 5-7 days prior to first flowering (V_5 stage), and light enrichment initiated at late flower/early pod formation (R_3 stage). In all cases light enrichment, once started, lasted until harvest.. Each plot consisted of 8 rows, planted 25 cm apart. The planting density was 83 plants m⁻². Before planting, the seeds were inoculated with commercial powdered peat based granular Brady Rhizobium. Normal cultural practices were followed. A pre-emergence mixture of 0.85 kg (ai) ha⁻¹ linuron [3-(3,4-dichlorophenyl)-1-methoxy-1-methylurea] and 1.75 kg (ai) ha⁻¹ alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl) acetanilide) was used for weed control. Total rainfall varied from 370mm from May to September. Since soil was near field capacity at planting, water availability was judged as being adequate for growth.

Light enrichment was achieved by installing 90 cm tall wire mesh fencing (mesh hole size 4-5 cm) adjacent to the rows bordering the center sample row, sloping away at a 45^o angle from the center row, in each plot. Fences prevented encroachment of plants from the neighboring rows into the growing space, and thus increased the radiation interception area of the sample row. The fences were inspected periodically (1-3 times per week) and all plants in rows bordering the center row were pushed behind the fences to prevent encroachment on the sample row. Light intensity measurements, using a Licor line quantum

sensor (LI-188B) placed parallel to, and beside the center row plants, during the period from V_5 to R_3 showed that the control intercepted 98.5% and light enrichment treatments intercepted 74.2% of the incoming solar radiation. Thus leaves at the base of the canopy in light enriched plots were receiving more than 25% available light. Light intensity after R_3 was always above 25% available light at the base of the canopy for the light enriched treatments.

Yield was determined by harvesting 3 m of the center treatment row from each plot and recording the seed dry weight after drying the samples to constant weight at 60°C in a forced dry air oven. This sample was used to calculated yield m⁻¹ of the row and the number of plants m⁻¹. Estimates of whole plot yields were not possible since in every plot where plants were light enriched only the center row received the light enrichment treatment and could only be compared on a row equivalent basis. Hence yield is expressed as yield m⁻¹ rather than yield m⁻². For yield component analysis, 15 plants, selected from a random starting point in the center row were harvested at maturity from each treatment. For each group of plants, data were recorded according to node position on the main stem and for each branch corresponding to the main stem node from which it arose. Node one was the unifoliate node, being the first node above the cotyledons. Among the data recorded were pod number, seed number, and seed dry weight. Statistical analysis of the data was performed using the SAS ANOVA procedure (SAS, 1988). Mean separation was done by using Duncan's Multiple Range Test (DMRT).

Results and Discussion

Yield of soybean plants and yield components have been summarized in Table 6.

Yield per unit row length

Light enrichment initiated at both V_5 and R3 increased seed yield m⁻¹ compared to that of the non-light enriched control in all years, and the extent of the increase was higher when light enrichment commenced at V_5 . Light enrichment initiated at R_3 increased yield 115% while there was a 217% increase for light enrichment starting at V_5 over the control.

Light enrichment during flowering and seed fill of soybean increased yield per plant (Johnston *et al.*, 1969; Schou *et al.*, 1978), while shade during seed fill reduced seed yield (Egli *et al.*, 1980). Data obtained from our experiments showed a greater increase in seed yield when light enrichment was initiated at V_5 compared to R_1 suggesting that the period starting from late vegetative stage (V_5) is important in determining the yield of soybean. Improving efficiency of interception of light at this stage through cultural practices and by selecting cultivars with improved efficiency of light utilization could lead to increased yield.

Yield components

In all years, pod number per plant was the yield component most responsible for yield increase from light enrichment initiated at either V_5 (Table 1). Light enrichment initiated prior to flowering (V_5) increased pod number per plant more than light enrichment beginning at early pod formation (R_3). This shows that even though pod formation begins

 Table 6. Yield component analysis of soybean grown under different levels of solar

 radiation during different growth stages

Year	Treatment	1995
Variety		Evans
Yield m ⁻¹	LE ₀ [†]	72.07b
(g m ⁻¹)	LE ₁	228.93a
	LE ₂	155.45a
Plants m ⁻¹ row	LE ₀	21.1
(No m ⁻¹)	LE1	19.9
	LE ₂	20.2
Yield plant ⁻¹	LE ₀	5.17b
(g plant ⁻¹)	LE1	12.02a
	LE ₂	6.63b
Pods plant ⁻¹	LE ₀	13.32b
(No plant ⁻¹)	LE	29.92a
	LE ₂	16.58b
Seeds pod ⁻¹	LEo	2.10
(No pod ⁻¹)	LE ₁	2.20
	LE ₂	2.14
Seed size	LEo	162.1c
(mg seed ⁻¹)	LE	179.43b
	LE ₂	199.63a

[†]LE₀ indicates no light enrichment. Light enrichment, LE₁ initiated at V₅ and LE₂ initiated at R₃. [‡]Means not followed by the same letter are significantly different at the 0.05 probability level. at R_3 , environmental conditions during the period from V_5 to R_3 are more critical in deciding the final pod number than the conditions associated with pod filling and retention prevailing after R_3 . Other studies have also identified pod number per plant as the yield component most influenced by changes in cultural and environmental conditions (Lehman and Lambert, 1960; Dominguez and Hume, 1978; Shou *et al.*, 1978; Herbert and Litchfield, 1982). This suggests that light enrichment imposed during early stages of development of soybean would increase availability of assimilates to the developing reproductive structures, increase flowering, and reduce flower and pod abscission with a resultant increase in final pod number at harvest. Other studies have indicated light interception during vegetative and early reproductive stages to be more critical in determining the yield increase in narrow rows compared to latter stages of growth (Board *et al.*, 1992).

Seed number per pod was least affected by changes in light regime in these experiments (Table 1). No significant changes in seed number per pod were observed among the treatments. As evident from this study, seed number per pod is a minor component determining the yield of soybean. However there was a small tendency for seed number per pod to increase with light enrichment. Similar findings of small or no significant changes in seed number per pod have been reported in other studies (Dominguez and Hume, 1978; Schou *et al.*, 1978; Herbert and Litchfield, 1982).

Light enrichment at both V_5 and R_3 were found to significantly increase seed size compared to that of the control. Light enrichment initiated at R_3 was found to increase seed size more than light enrichment initiated at V_5 . McAlister and Krober (1958) and

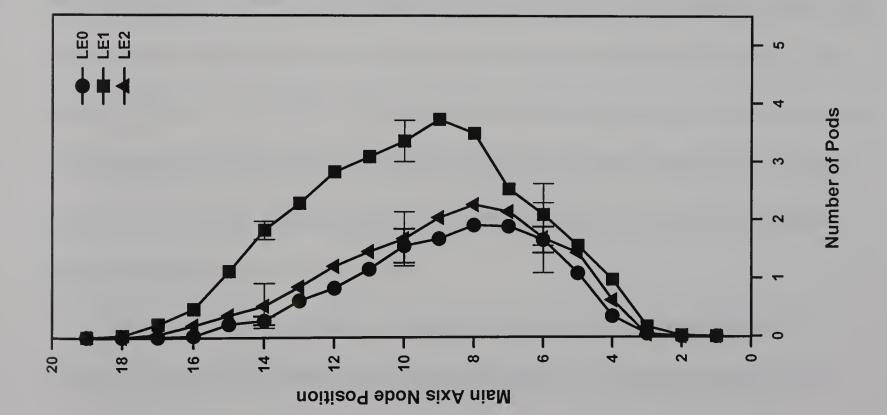
Schonbeck *et al.* (1986) proposed that an increase in seed size is a possible compensation response for the reduction in pod number by pod removal. Egli *et al.* (1978) and Swank *et al.* (1987) indicated that in soybean, seed size was a function of the rate of seed growth and the duration of dry weight accumulation in the seed fraction, and that genetic differences in seed growth rate are controlled by the cotyledon cell number (Egli *et al.*, 1981). Later, based on a source-sink alteration study, Egli *et al.*,(1989) concluded that soybean plants respond to changes in their immediate environment not only by changing the number of pods per plant, but also by altering cotyledon cell number, which correlated with seed size. Cotyledon cell number is one of the two main components determining seed size, the other being cotyledon cell volume or weight. Hence, the increased seed size observed in our experiments in response to light enrichment could be attributed to either an increased number of cells per cotyledon, or an increased dry matter accumulation of cells during the seed filling period.

Nodal analysis

Initiating light enrichment at V_5 increased the number of pods somewhat proportionally across all mainstem nodes (Figure 15). Nodes in the mid-mainstem portion (nodes 4-7) had the largest number of pods, and showed the greatest increase in the number of pods per node. Previous studies (Herbert and Litchfield, 1982; Heindl and Brun, 1984; Jiang and Egli, 1993) also indicated that nodes in the central region of soybean plants have the greatest yield potential among the mainstem nodes. Analysis of pod number per node also revealed that regardless of the treatment, branch pods accounted for

Figure 15. Average number of mainstem pods at each mainstem node of Evans soybean grown under different levels of solar

radiation.



more than 50% of the total pods produced at nodes 1 to 3. Light enrichment initiated at V_5 also increased branching, and thereby increased the number of pods produced from lower nodes, and these branches had 72 to 99% of all pods produced at these mainstem nodes.

Heindl and Brun (1984) reported that in indeterminate soybean, there is only a slight variation in the number of flowers formed at each node, and they suggested that high rate of flower abscission was the major factor determining the pod number per node. Koller (1971) observed that the central nodes had the most leaf area at the time of rapid seed development. Leaves in the middle portion of the plant are also displayed, due to long petioles, much higher and close to the periphery of canopy where light interception is the greatest (Willcott *et al.*, 1984). This appears important for maintenance of yield since most of the photosynthate (60-70%) produced by a soybean leaf during pod filling is ultimately incorporated into pods and seeds borne on the same node or two nodes above and below this node (Stephenson and Wilson, 1977).

Seed number per mainstem pod remained relatively constant across all node positions except for the extreme node positions (Figure 16). Variation in seeds per pod observed at the extreme node positions could be due to the small number of pods borne at these nodes. Whereas seed number per pod for most nodes was averaged over many pods, a smaller number of pods with extreme seed numbers (1 or 4) found at the extreme node positions, would cause variation in the calculation of mean seed number per pod.

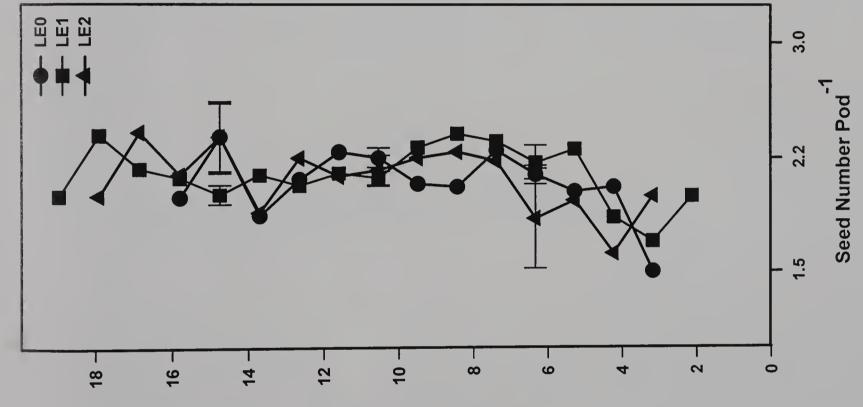
Seed size also was mostly constant across mainstem nodes and seed size response to light enrichment was similar across nodes (Figure 17). In indeterminate soybean vegetative growth continues during reproductive stages. When the lower most nodes

97

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Figure 16. Average number of seeds per pod at each mainstem node of Altona and Evans soybean grown under different

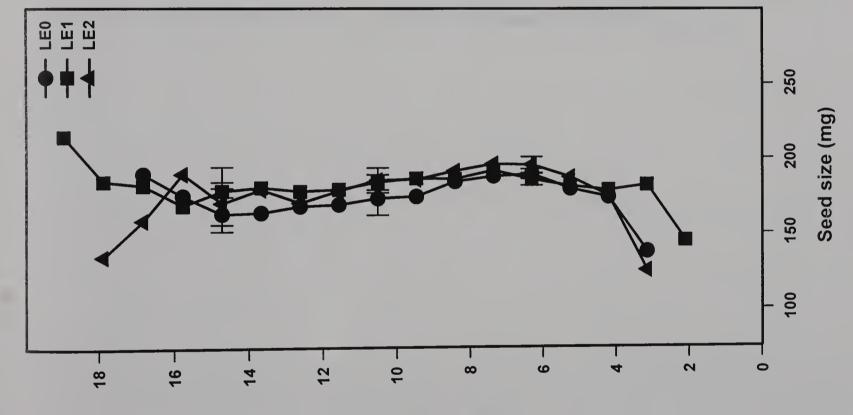
levels of solar radiation.



noitieoq əbo<mark>N</mark> eixA nißM

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Figure 17. Average seed weight at each mainstem node of Evans soybean grown under different levels of solar radiation.



noitiso9 əboN sixA nißM

started filling seeds, the upper most nodes were still producing flowers. However seed size was quite uniform across all node positions in spite of the difference (15 to 20 days) in the duration of seed filling. Egli *et al.* (1981) reported genetic differences in seed growth rates were controlled by the cotyledons not by the supply of assimilate from the plant to the cotyledons. Our data suggests that seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. Soybean seed yield response to changes in light regime, was mostly by changes in pod number per plant, and least by seed number per pod. Responses occurred proportionately across all node positions despite differences in the time of development of yield components.

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CHAPTER IV

SUMMARY

Studies were conducted at the University of Massachusetts to evaluate the seed yield of soybean, and Duncan's model with respect to the relationship between seed yield and plant population in soybeans, and analyze the response of soybean seed yield components to light enrichment initiated at different growth stages. Duncan (1984) suggested that all forms of interplant competition can be combined into a single term 'crowding' (C) in which he included the effects of plant population (density) and planting pattern.

According to Duncan, to calculate crowding, 'Separation Fraction' (SF) has to be calculated as

$$SF = (D_{max} - separation)/D_{max}$$

where SF (Separation Fraction), D_{max} is the maximum distance at which crowding is expereienced. Crowding between two plants then is $C = SF^{alpha}$. The total crowding for a community of plants is

 $C = \sum_{p=1}^{p=n} SF^{alpha}$

where, p = 1 to p = n includes all plants in the planting pattern within the distance D_{max} from the center plant. The total crowding in a planting pattern, is the sum of crowding experienced by all the individual plants and it is a constant for a particular

planting pattern. Based on this concept of crowding, Duncan proposed a crowding model to express the relationship between crowding and yield in a mathematical form. According to the model,

$\ln y = \ln y_0 + EC$

When a plant is grown in isolation, separation $\ge D_{max}$, and SF equals zero. Crowding therefore equals zero and thus $\ln y_0 = \ln y$. Thus y_0 can be defined as the maximum yield of a single plant at zero crowding. The results of the studies fitting the model to the data obtained from different soybean cultivars planted at different densities and planting patterns indicated that the model can predict the changes in yield with changing densities and planting pattern especially if the variability in the data is low. Thus, this model shows promise as a tool for evaluating planting patterns for soybean as was suggested by Duncan for corn.

Solar radiation is an important environmental factor influencing seed yield in soybeans. In order to study the effect of non - destructive light enrichment on yield and yield components in soybean, light enrichment was imposed on the indeterminate soybean cultivar Evans by installing wire mesh fencing on either side of the center row to push the adjacent rows aside at different growth stages. Fences prevented plants in the neighboring rows from encroaching on the growing space of the center row plants. Pod number per plant and to a lesser extent seed size accounted for variation in seed yield. Light enrichment initiated at late vegetative or early flowering stages increased seed yield 217%, mainly by increasing pod number, while light enrichment beginning at early pod formation

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increased seed size 23%, resulting in a 115% increase in seed yield. Responses to light enrichment occurred proportionately across all node positions despite the differences in the time (15 to 20 days) of development of yield components at the different node positions. Although maximum seed size may be under genetic control in soybean plants, our results suggested seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. It indicates that plants are able to redistribute the available resources to components not yet determined, in an attempt to maintain or improve yield.

APPENDIX A

CROWDING CALCULATOR

#include <iostream.h></iostream.h>
#include <conio.h></conio.h>
#include <fstream.h></fstream.h>
#include <stdio.h></stdio.h>
class C
{ private:
struct Cvals
{ float Spacing;
float Width;
float D _{max} ;
float Alpha;
}c;
fstream file;
public:
C()

{ file.open("CVALUE.DAT",ios::binary|ios::app);

if(!file)

{ c.Spacing=c.Width=c.D_{max}=c.Alpha=0.0;

file.write((char*)&c,sizeof(c));

```
}
```

}

```
void show()
{ file.read((char*)&c,sizeof(c));
  cout<<"\nSpacing : "<<c.Spacing;
  cout<<"\nWidth : "<<c.Width;
  cout<<"\nD<sub>max</sub> : "<<c.D<sub>max</sub>;
  cout<<"\nAlpha : "<<c.Alpha;
}</pre>
```

```
void reset()
```

```
{ cout<<"\nEnter new value for Spacing :";
 cin>>c.Spacing;
 cout<<"\nEnter new value for Width :";
 cin>>c.Width;
 cout<<"\nEnter new value for D<sub>max</sub> :";
 cin>>c.D<sub>max</sub>;
 cout<<"\nEnter new value for Alpha :";
 cin>>c.Alpha;
file.write((char*)&c,sizeof(c));
```

}

};

void main()

{ C clas;

// clrscr();

char opt='y';

```
while(opt=='y'||opt=='Y')
```

{ clas.reset();

cout<<"\n\tMore inputs ? (y/n) ";</pre>

cin>>opt;

```
}
```

}

getch();

// Calculate Crowding values
#include <iostream.h>
#include <stdio.h>
#include <stdlib.h>

#include <math.h>

#include <conio.h>

#include <fstream.h>

struct values

{

```
float Spacing,RowWidth,D<sub>max</sub>,Alpha;
```

};

```
void main()
```

{

//clrscr();

system("cls");

values V;

fstream file;

file.open("cvalue.dat",ios::binary|ios::in);

label1:

{

```
cout<<"\nEnter 'C' for calculating C-Values";</pre>
```

cout<<"\nEnter 'Y' for calculating Yield";</pre>

cout<<"\nYour choice :";</pre>

char choice;

cin>>choice;

float Yzero, E, LNYzero;

if(choice=='C'||choice=='c')

112

```
Yzero=0.0;
```

E=0.0;

}

```
else if (choice=='Y'||choice=='y')
```

{

```
cout<<"\n\tEnter value of LNYzero : ";
cin>>LNYzero;
```

```
cout<<"\n\tEnter value of E : ";</pre>
```

cin>>E;

Yzero=exp(LNYzero)/1000;

}

else

```
{
```

```
cout<<"\nInvalid Input !";</pre>
```

```
goto label1;
```

}

```
float Xdist[50][50], Ydist[50][50];
```

do

{

```
file.read((char*)&V,sizeof(V));
```

```
// clrscr();
```

```
// system("cls");
cout<<"\nYzero "<<Yzero<<"\nE
                                      "<<E;
if(V.Spacing==0)
        return;
for(int j=0;j<5;j++)
{
        for(int k=0;k<40;k++)
        {
                Xdist[j][k]=0.0;
                Ydist[j][k]=0.0;
         }
 }
int Xnum=1.0+(2.0*(int)(V.D<sub>max</sub>/V.Spacing));
int Ynum=1.0+(2.0*(int)(V.D<sub>max</sub>/V.RowWidth));
int Xn=V.D<sub>max</sub>/V.Spacing;
int Yn=V.D<sub>max</sub>/V.RowWidth;
int YZ=0;
int XX,YY,XaX;
 for(j=1;j<=Ynum;j++)</pre>
 {
        XX=0;
         YY=Yn-YZ;
```

```
XaX=0;
       for(int k=1;k<=Xnum;k++)</pre>
       {
              if(Xn<XX)
              {
                     Xdist[j][k]=XaX*V.Spacing;
                     XaX++;
                     Ydist[j][k]=YY*V.RowWidth;
              }
              else
              {
                     Xdist[j][k]=(Xn-XX)*V.Spacing;
                     XX++;
                     Ydist[j][k]=YY*V.RowWidth;
              }
       ł
       YZ++;
//cout<<"\n\n\tIYnum "<<Ynum;</pre>
int SFPlant=0;
int count=0;
float Competition=0.0;
```

}

```
for(j=1;j<=Ynum;j++)
{
    for(int k=1;k<=Xnum;k++)
    {
        count++;
        if((Ydist[j][k]<=V.D<sub>max</sub>)&&(Xdist[j][k]<=V.D<sub>max</sub>))
        {
        float
        float
```

```
Hypt=sqrt(pow(Xdist[j][k],2)+pow(Ydist[j][k],2));
```

```
if((Hypt>=0.01)&&(Hypt<=V.D<sub>max</sub>))
```

{

SFPlant++;

float QUAN=(V.D_{max}-Hypt)/V.D_{max};

if(QUAN>0.0)

Competition=Competition+pow(QUAN,V.Alpha);



cout<<"\n\tRow width : "<<V.RowWidth<<" cm";

```
cout<<"\n\tSpacing : "<<V.Spacing<<" cm";
cout<<"\n\tMaximum Distance(D<sub>max</sub>) : "<<V.D<sub>max</sub><<" cm";
cout<<"\n\tAlpha : "<<V.Alpha<<endl;
count=0;
```

```
float Population=10000000/(V.Spacing*V.RowWidth);
cout<<"\n\t\tCompetition = "<<Competition;</pre>
```

```
cout<<"\n\t\tIYnum "<<Ynum;
cout<<"\n\t\tICOUNT "<<count;
cout<<"\n\t\tNumber of plants used for SF : "<<SFPlant;
cout<<"\n\t\tPopulation : "<<Population<<endl;
if(E!=0)
```

```
float EXPON=Competition*E;
float YieldPerPlt=Yzero*exp(EXPON);
float Yield=YieldPerPlt*Population;
cout<<"\n\t\tYield per plant : "<<YieldPerPlt<<endl;
cout<<"\t\tYield per Hect : "<<Yield<<endl;</pre>
```

```
//getch();
```

}

ł

}

APPENDIX B

AGRONOMY JOURNAL PUBLICATION

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Differential Response of Soybean Yield Components to the Timing of Light Enrichment

Jomol P. Mathew, Stephen J. Herbert,* Shuhuan Zhang, Andreas A. F. Rautenkranz, and Gerald V. Litchfield

ABSTRACT

Solar radiation is an important environmental factor influencing seed yield in soybean [Glycine max (L). Merr.]. Our objective was to analyze the response of soybean seed yield components to light enrichment initiated at different growth stages. Light enrichment was imposed on the indeterminate soybean cultivars Altona and Evans by installing wire mesh fencing on either side of the center row to push the adjacent rows aside at different growth stages. Fences prevented plants in the neighboring rows from encroaching on the growing space of the center row plants. Pod number per plant and to a lesser extent seed size accounted for variation in seed yield. Light enrichment initiated at late vegetative or early flowering stages increased seed yield 144 to 252%, mainly by increasing pod number. while light enrichment beginning at early pod formation increased seed size 8 to 23%, resulting in a 32 to 115% increase in seed yield. Responses to light enrichment occurred proportionately across all node positions despite the differences in the time (15-20 d) of development of yield components at the different node positions. Although maximum seed size may be under genetic control in soybean plants. our results suggested seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. It indicates that plants are able to redistribute the available resources to components not yet determined, in an attempt to maintain or improve yield.

ENVIRONMENTAL conditions prevailing during the growth period, especially intensity and quality of solar radiation intercepted by the canopy, are important determinants of yield components and hence the yield of soybean (Taylor et al., 1982; Willcott et al., 1984; Myers et al., 1987; Board and Harville, 1992, 1996). Light enrichment using lamps or reflectors increased the yield of soybean (Johnston et al., 1969; Schou et al., 1978). Shading (49–20% of ambient light) resulted in lengthening of internodes and increased lodging in soybean plants (Ephrath et al., 1993).

Hardman and Brun (1971) proposed that the yield of soybean is controlled by the availability of photosynthates during postflowering stage of development. Schou et al. (1978) observed that light levels during late flowering to midpod formation stages of growth are more critical than during vegetative and late reproductive periods in determining the yield of soybean. Taylor et al. (1982) concluded that pod abortion caused by lack of photosynthate supply late in the growing period is a major factor limiting yield of soybean. Duncan (1986) suggested that light intercepted during and after seed initiation is a major determinant of yield. Jiang and Egli (1993) reported that shade imposed from first flower to early podfill reduced flower production and increased

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flower and pod abscission, resulting in reduced pod number and yield. They also found canopy photosynthesis during flowering and pod set to be an important determinant of seeds m^{-2} , and that the impact of shading on seeds m^{-2} depends on duration of shading (Jiang and Egli, 1995). Sharma et al. (1996) observed anthesis to be the most critical stage during which low light intensity can cause severe yield reduction in soybean.

Board et al. (1992) and Board and Harville (1996) suggested that the increased seed yield of soybean from planting in narrow rows (<50 cm) reported by many researchers (Lehman and Lambert, 1960; Costa et al., 1980; Herbert and Litchfield, 1982; Willcott et al., 1984). can be attributed to increased light interception during vegetative and early reproductive periods (first flowering to seed initiation). In most of the above studies, changes in yield was mainly brought about by changes in pod and seed number. However, an increase in seed size compensated for the decreased pod load in some source-sink manipulation studies (McAlister and Krober, 1958; Schonbeck et al., 1986).

Herbert and Litchfield (1982) noticed that pod number per plant was the most important component responsible for differences in soybean yield between different row widths and densities within a particular year. while a change in seed size resulted in the yield difference between 2 consecutive years. Thus, there is a differential response of yield components to changes in environmental conditions. However, the exact nature of response to the timing of light enrichment has not been identified yet. Also most of the studies conducted so far on differential response achieved increases in light interception indirectly by removal of leaves, thereby modifying the source strength.

Our objectives for conducting these studies were to analyze the differential seed yield response of indeterminate soybean to nondestructive light enrichment imposed at different stages during soybean growth, and to examine the effect of light enrichment on nodal development of seed yield components to determine developmental stages most affected by environmental change.

MATERIALS AND METHODS

Studies were conducted at the University of Massachusetts Agronomy Farm during 1982–1983, 1987–1988. and 1994–1995 using Altona of maturity group 00, which matures in approximately 100 d at this location, and Evans of maturity group 0. which matures in approximately 115 d. The soil at the experimental site was a fine sandy loam (Typic Udifluent).

In each year a randomized block design was used with three replications in 1982 and four in later years. In 1982, a factorial combination of two cultivars (Altona and Evans) with two light levels. light enrichment initiated at flowering [R_1 stage (Fehr and Caviness, 1977)], and a nonenriched control were tested. In all other years there were three light enrichment treatments, no light enrichment, light enrichment initiated 5 to 7 d prior to first flowering (V_5 stage), and light enrichment

Department of Plant and Soil Science, Bowditch Hall, Univ. of Massachusetts, Amherst, MA 01003. This research is based upon work partially supported by the Cooperative State Research Extension. Education Service, USDA, Massachusetts Agric. Exp. Stn., Manuscript 3259. Received 29 Oct. 1999. *Corresponding author (sherbert @pssci.umass.edu).

Yield component		1982		1003		1000		
		Altona	Evans	1983 Average	1987 Evans	1988 Evans	1994 Evans	1995 Evans
Yield m ⁻¹ (g m ⁻¹)	LE₀† LE₁ LE₂	210.0b* 231.1b	212.0b 351.0a	83.0c 203.3a 126.2b	93.0c 230.0a 123.9b	63.0c 178.0a 90.0b	87.2b 306.3a 118.6b	72.07b 228.93a 155.45a
Plants m^{-1} row (No. m^{-1})	LE ₀ LE ₁ LE ₂	27.4 27.5	26.7 27.3	15.0 15.0 15.0	19.0 20.5 21.2	21.4 21.1 20.4	21.0 19.6 17.0	21.1 19.9 20.2
Yield plant ⁻¹ (g plant ⁻¹)		7.7b 8.4b -	7.9b 12.9a -	5.5c 13.6a 8.4b	4.9c 11.2a 5.8b	2.9c 8.4a 4.4b	4.2b 15.6a 7.0b	5.17b 12.02a 6.63b
Pods plant ⁻¹ (No. plant ⁻¹)		20.4b 20.5b	23.9b 36.2a	12.9b 30.7a 16.9b	18.5b 29.7a 15.9b	11.5c 25.2a 15.2b	11.2b 34.0a 15.4b	13.32b 29.92a 16.58b
Seeds pod ⁻¹ (No. pod ⁻¹)		2.23 2.30	2.32 2.33	2.26c 2.39b 2.43a	2.31 2.28 2.27	2.13b 2.28a 2.22ab	2.09b 2.40a 2.23ab	2.10 2.20 2.14
Seed size (mg seed ⁻¹)		168.0b 177.0a	143.0 153.0	188.0b 188.0b 206.0a	180.0b 172.0b 194.0a	1.37.0b 143.0ab 148.0a	164.7b 191.5a 203.0a	162.1c 179.43b 199.63a

Table 1. Yield component analysis of soybean grown under different levels of solar radiation during different growth stages.

* Means not followed by the same letter are significantly different at the 0.05 probability level.

+ LE, indicates no light enrichment. Light enrichment, LE, initiated at R, in 1982 and V, in the remaining years: LE, initiated at R, in all years.

initiated at late flower-early pod formation (R₁ stage). In all cases light enrichment. once started, lasted until harvest. In 1983. Altona and Evans were used for the study, and in later years only Evans was grown. Each plot consisted of eight rows. planted 25 cm apart, except in 1982 when each plot had five rows that were 50 cm apart. The planting density was 60 plants m⁻² in 1982 and 1983 and 83 plants m⁻² in later years. Before planting, the seeds were inoculated with commercial powdered peat based granular Brady Rhizobium. Normal cultural practices were followed in all years. A preemergence mixture of 0.85 kg (a.i.) ha⁻¹ linuron [3-(3.4-dichlorophenyl)-1-methoxy-1-methylurea] and 1.75 kg (a.i.) ha⁻¹ alachlor (2chloro-2'. 6'-diethyl-N-(methoxymethyl) acetanilide) was used for weed control in all years. Total rainfall varied from 370 mm (1983 and 1995) to 522 mm (1982 and 1994) from May to September. Since soil was near field capacity at planting, water availability was judged as being adequate for growth.

Light enrichment was achieved by installing 90 cm tall wire mesh fencing (mesh hole size 4-5 cm) adjacent to the rows bordering the center sample row. sloping away at a 45° angle from the center row. in each plot. Fences prevented encroachment of plants from the neighboring rows into the growing space. and thus increased the radiation interception area of the sample row. The fences were inspected periodically (1-3 times per week) and all plants in rows bordering the center row were pushed behind the fences to prevent encroachment on the sample row. Light intensity measurements, using a Licor line quantum sensor (LI-188B) placed parallel to. and beside the center row plants, during the period from V_5 to R_3 showed that the control intercepted 98.5% and light enrichment treatments intercepted 74.2% of the incoming solar radiation. Thus, leaves at the base of the canopy in light-enriched plots were receiving more than 25% available light. Light intensity after R3 was always above 25% available light at the base of the canopy for the light enriched treatments.

Yield was determined by harvesting 3 m of the center treatment row from each plot and recording the seed dry weight after drying the samples to constant weight at 60°C in a forced dry air oven. This sample was used to calculated yield m^{-1} of the row and the number of plants m^{-1} . Estimates of whole plot yields were not possible, because in every plot where plants were light enriched only the center row received the light enrichment treatment and could only be compared on a row equivalent basis. Hence, yield is expressed as yield m^{-1} rather than yield m^{-2} . For yield component analysis, 15 plants, selected from a random starting point in the center row, were harvested at maturity from each treatment. For each group of plants, data were recorded according to node position on the main stem and for each branch corresponding to the main stem node from which it arose. Node 1 was the unifoliate node, being the first node above the cotyledons. Among the data recorded were pod number, seed number, and seed dry weight. Statistical analysis of the data was performed using the SAS ANOVA procedure (SAS Inst., 1988). Mean separation was done by using Duncans multiple range test (DMRT).

RESULTS AND DISCUSSION

Yield of soybean plants and yield components obtained from the six experimental years have been summarized in Table 1.

Yield Per Unit Row Length

Light enrichment initiated at both V_5 and R_3 increased seed yield m⁻¹ compared with that of the nonlight enriched control in all years, and the extent of the increase was higher when light enrichment commenced at V_5 . Light enrichment initiated at R_3 increased yield 32 to 115% while there was a 144 to 252% increase for light enrichment starting at V_5 . In 1982, light enrichment initiated at R_1 increased seed yield m⁻¹ by 38% over the control.

In 1982. a significant cultivar-treatment interaction was observed, with Evans being more responsive to light enrichment than Altona. This could be attributed to the greater plasticity of Evans (Willcott et al., 1984). Evans, a more profusely branching cultivar, exhibited earlier canopy closure compared with Altona, thus enabling greater exploitation of available light. This difference was not obvious in 1983 because the row spacing was reduced from 50 cm in 1982 to 25 cm in 1983, which enabled Altona to attain canopy closure earlier to more fully utilize the available solar radiation. Thus, light enrichment affected both cultivars similarly in 1983 and data was combined.

Light enrichment during flowering and seed fill of

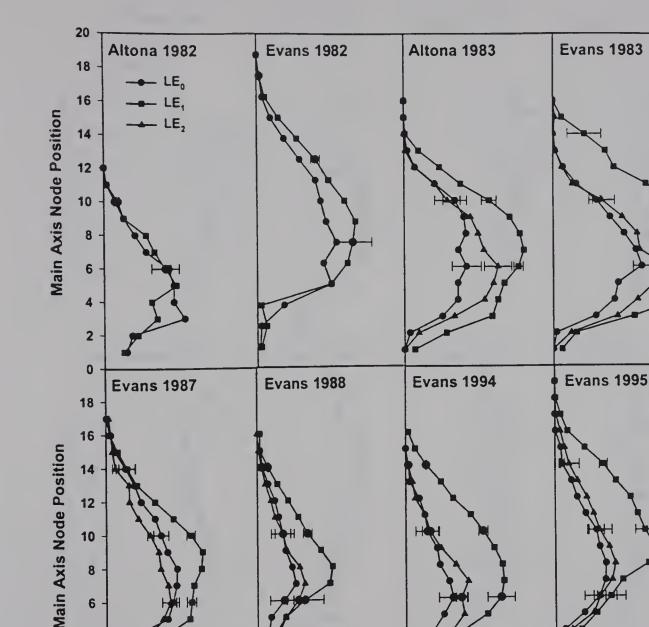


Fig. 1. Average number of mainstem pods at each mainstem node of Altona and Evans soybean grown under different levels of solar radiation. LE, indicates no light enrichment. Light enrichment. LE, initiated at R, in 1982 and V, in the remaining years; LE, commenced at R, in all years. Bars indicate ±1 SE of the mean.

4

2 3

1

5 0

3

5 0

Number of Pods

soybean increased yield per plant (Johnston et al., 1969; Schou et al., 1978), while shade during seed fill reduced seed yield (Egli et al., 1980). Data obtained from our experiments showed a greater increase in seed yield when light enrichment was initiated at V₅ compared with R₁, suggesting that the period starting from late vegetative stage (V_5) is important in determining the yield of soybean. Improving efficiency of interception of light at this stage through cultural practices and by selecting cultivars with improved efficiency of light utilization could lead to increased yield.

8

6

4

2

0

0

Yield Components

In all years, pod number per plant was the yield component most responsible for yield increase from light enrichment initiated at either V_5 or R_1 (Table 1). Light enrichment initiated prior to flowering (V₅) increased

pod number per plant more than light enrichment beginning at early pod formation (R_3) . This shows that even though pod formation begins at R₃, environmental conditions during the period from V₅ to R₃ are more critical in deciding the final pod number than the conditions associated with pod filling and retention prevailing after R3. Other studies have also identified pod number per plant as the yield component most influenced by changes in cultural and environmental conditions (Lehman and Lambert, 1960; Dominguez and Hume, 1978; Shou et al., 1978; Herbert and Litchfield, 1982). This suggests that light enrichment imposed during early stages of development of soybean would increase availability of assimilates to the developing reproductive structures, increase flowering, and reduce flower and pod abscission with a resultant increase in final pod number at harvest. Other studies have indicated light

50

3 A

2

2

3

5

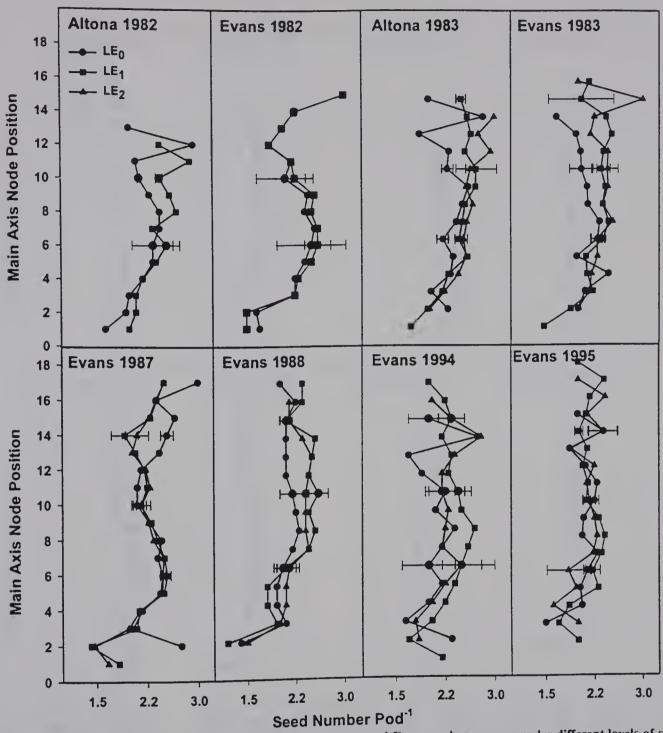


Fig. 2. Average number of seeds per pod at each mainstem node of Altona and Evans soybean grown under different levels of solar radiation. LE_n indicates no light enrichment. Light enrichment, LE₁ initiated at R₁ in 1982 and V₅ in the remaining years; LE₂ commenced at R₃ in all years. Bars indicate ± 1 SE of the mean.

interception during vegetative and early reproductive stages to be more critical in determining the yield increase in narrow rows compared with latter stages of growth (Board et al., 1992).

Seed number per pod was least affected by changes in light regime in these experiments (Table 1). In 1982, 1987. and 1995. no significant changes in seed number per pod were observed among the treatments. However, in 1983, light enrichment initiated at V₅ increased seeds per pod by 6% and late light enrichment initiated at R_3 by 8% over the control. In 1988 and 1994, light enrichment initiated at V₅ increased seed number per pod more than light enrichment initiated at R_3 . As evident from these studies, seed number per pod is a minor component determining the yield of soybean. However, there was a small tendency for seed number per pod to increase with light enrichment. Similar findings of small or no significant changes in seed number per pod have been reported in other studies (Dominguez and Hume, 1978; Schou et al., 1978; Herbert and Litchfield, 1982).

Light enrichment at both V5 and R3 were found to significantly increase seed size in 1994 and 1995 (Table 1). In other years seed weight with light enrichment initiated at V₅ was similar to that of the control. In most years, light enrichment initiated at R3 was found to increase seed size more than light enrichment initiated at V₅. McAlister and Krober (1958) and Schonbeck et al. (1986) proposed that an increase in seed size is a possible compensation response for the reduction in pod number by pod removal. Egli et al. (1978) and Swank et al. (1987) indicated that in soybean, seed size was a function of the rate of seed growth and the duration of dry weight accumulation in the seed fraction, and that genetic differences in seed growth rate are controlled by the cotyledon cell number (Egli et al., 1981). Later, based on a source-sink alteration study. Egli et al. (1989)

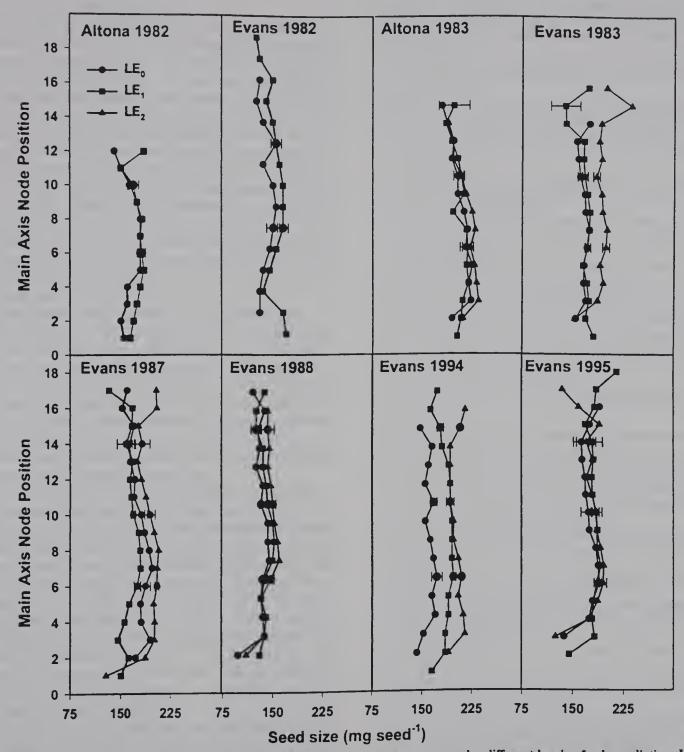


Fig. 3. Average seed weight at each mainstem node of Altona and Evans soybean grown under different levels of solar radiation. LE_0 indicates no light enrichment. Light enrichment, LE_1 initiated at R_1 in 1982 and V_5 in the remaining years; LE_2 commenced at R_3 in all years. Bars indicate ± 1 SE of the mean.

concluded that soybean plants respond to changes in their immediate environment not only by changing the number of pods per plant, but also by altering cotyledon cell number, which correlated with seed size. Cotyledon cell number is one of the two main components determining seed size, the other being cotyledon cell volume or weight. Hence, the increased seed size observed in our experiments in response to light enrichment could be attributed to either an increased number of cells per cotyledon, or an increased dry matter accumulation of cells during the seed filling period.

Nodal Analysis

In each year there were similar responses to nodal distribution of yield components. Initiating light enrichment at V_5 increased the number of pods somewhat

proportionally across all mainstem nodes. Nodes in the midmainstem portion (Nodes 4-7) had the largest number of pods, and showed the greatest increase in the number of pods per node (Fig. 1). The increase in pod number per node with light enrichment was significantly greater in the case of Evans than Altona, again demonstrating plasticity of Evans. Previous studies (Herbert and Litchfield, 1982; Heindl and Brun, 1984; Jiang and Egli, 1993) also indicated that nodes in the central region of soybean plants have the greatest yield potential among the mainstem nodes. Analysis of pod number per node also revealed that, regardless of the cultivar and treatment, branch pods accounted for >50% of the total pods produced at Nodes 1 to 3. Light enrichment initiated at V₅ also increased branching, and thereby increased the number of pods produced from lower nodes, and these branches had 72 to 99% of all pods

produced at these mainstem nodes.

Heindl and Brun (1984) reported that in indeterminate soybean, there is only a slight variation in the number of flowers formed at each node, and they suggested that high rate of flower abscission was the major factor determining the pod number per node. Koller (1971) observed that the central nodes had the most leaf area at the time of rapid seed development. Leaves in the middle portion of the plant are also displayed, due to long petioles, much higher and close to the periphery of canopy where light interception is the greatest (Willcott et al., 1984). This appears important for maintenance of yield since most of the photosynthate (60-70%)produced by a soybean leaf during pod filling is ultimately incorporated into pods and seeds borne on the same node or two nodes above and below this node (Stephenson and Wilson, 1977).

In all the years, seed number per mainstem pod remained relatively constant across all node positions except for the extreme node positions (Fig. 2). Variation in seeds per pod observed at the extreme node positions could be due to the small number of pods borne at these nodes. Seed number per pod for most nodes was averaged over many pods; however, a smaller number of pods with extreme seed numbers (1 or 4) found at the extreme node positions caused variation in the calculation of mean seed number per pod.

Seed size also was mostly constant across mainstem nodes. and seed size response to light enrichment was similar across nodes (Fig. 3). In indeterminate soybean vegetative growth continues during reproductive stages. When the lower most nodes started filling seeds, the upper most nodes were still producing flowers. However, seed size was quite uniform across all node positions in spite of the difference (15-20 d) in the duration of seed filling. Egli et al. (1981) reported genetic differences in seed growth rates were controlled by the cotyledons. not by the supply of assimilate from the plant to the cotyledons. Our data suggests that seed size can still be modified by the environment with some internal control moderating the final size of most seeds in all pods. Soybean seed yield response to changes in light regime was mostly by changes in pod number per plant, and least by seed number per pod. Responses occurred proportionately across all node positions despite differences in the time of development of yield components.

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