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MANIPULATION OF CROWDING STRESS IN CORN

A Dissertation Presented

by

ABOLHASSAN HASHEMI-DEZFOULI

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I lovingly dedicate this thesis to my wife, Zohreh, and my children Ali, Sara, and Arash.

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ABSTRACT

MANIPULATION OF CROWDING STRESS IN CORN

SEPTEMBER, 1990

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Competition in corn crop was studied through manipulation of crowding (density and spacing) and assimilate supply in several experiments conducted in 1986-1988.

Growth and yield responses of 2 hybrids differing in maturity period and prolificacy were studied in a wide range of densities. Under favorable condition, Agway 584S (single-ear, late maturity) out yielded Cornell 281 (multiple-ear, early maturity). Higher yield in Agway 584S was attributed to heavier kernels compared to Cornell 281, which resulted from a longer grain filling duration.

Growth analysis indicated that crop growth rate as well as net assimilation rate were greater in Cornell 281 than in Agway 584S. Higher crop growth rate in Cornell 281, however, was directed toward tiller production with no fertile ears. Agway 584S maturing later had longer growth duration contributing to its higher yield than Cornell 281.

Intensity of competition was quantified by comparing the grain yield and its components to "isolated" plants.

Yield per plant decreased 75% and 80% compared to isolated plants in Agway 584S and Cornell 281 respectively, as density increased from 3 to 12 plants m^{-2}. Number of kernels per row in Agway 584S and number of productive ears per plant in Cornell 281 were found to be the most sensitive yield components.

The timing of competitive stress was investigated by removal of alternate plants at different stages of growth. Most of the competition within the corn canopy occurred during the period between vegetative stage and anthesis. Adjustment in grain yield in response to releasing the competition pressure occurred primarily through increase in kernel number in Agway 584S and number of productive ears per plant in Cornell 281.

Artificial shading (50% light reduction) showed that reduction in yield in high densities is due to reduction in photosynthesis rate caused by mutual shading and also by lengthening of the intervals between anthesis and silking.

Density-light relationships in six corn hybrids having different leaf orientation indicated that hybrids with upright leaves had some yield advantages over horizontal leaf hybrids in favorable climatological conditions when high densities are used.

Results supported the model proposed by Duncan (Crop Sci., 1984) that a linear relationship exists between the logarithm of yield per plant and crowding.

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LITERATURE REVIEW

Competition and Yield

In any given environment, the yield of a crop is determined by the level of available resources and genetic potential of the crop to exploit that environment. Growing plants in crop communities introduces competition.

Justus von Liebig (1840) represented the "limiting factor" concepts in his " Law of the minimum", whereby plant growth is limited by the essential factor which is in shortest supply. Later, Clements (1903, in Donald 1963), defined the competition on the basis of "supply and demand":

> " When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins."

The definition has been confirmed by other researchers (Donald, 1963; Odum, 1971). However, plant competition is highly interactive and is too complex to be viewed as a purely physical process.

Bleasdale (1960) proposed a different approach to defining and quantifying competition. He avoided defining competition in terms of supply and demand for factors:

> " Two plants are in competition with each other when the growth of either one or both of them is reduced or their form modified as compared with their growth or form in isolation."

Bleasdale viewed plant weight as indicating the accumulated effect of competition.

The main growth factors that plants usually compete for can be identified as light, nutrients, moisture, and CO_2. Among these growth factors, light has a unique status. It is the driving force for all vital processes within the plant and is available as a "passing stream" to be intercepted or not (Donald, 1963). Radiation interception by a crop is thought to limit productivity when other environmental factors are not limiting (Loomis and Williams, 1963; Monteith, 1981).

Plant density has long been recognized as a major factor in influencing the degree of between-plant competition within a crop canopy. As plant density increases, intensity of interplant competition increases and therefore yield per plant declines. However, the yield per unit area is a function of yield per plant multiplied by the number of plants per unit area. Thus, total yield per unit area may increase with density increase. Holliday (1960), generalized the yield-density relationships into two responses. First, there may be an asymptotic relationship where, with increase in density, yield rises to plateau (Fig. 1.1). This yield plateau presumably occurs when light interception by the canopy is essentially complete and thus little if any dry matter increase per unit area would be possible (Duncan, 1975).

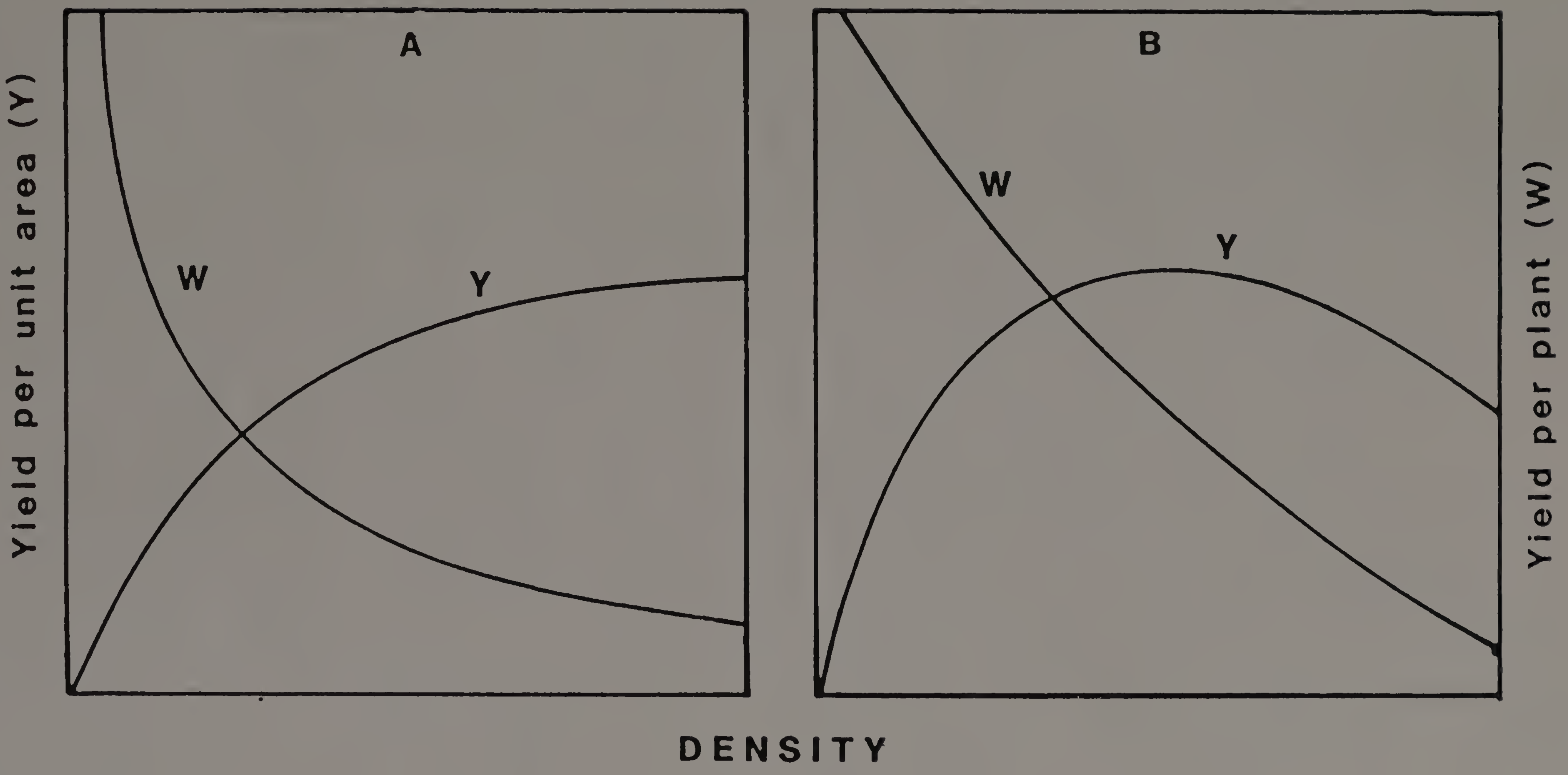

Figure 1.1. General responses of yield to density increase (A) asymptotic and (B) parabolic. Idealized data from Holiday (1960) (graph A, giant rape), and Lange et al. (1956) (graph B, corn grain).

Second, a parabolic response may occur when yield increases to a maximum but declines at higher densities. More favorable environmental conditions would result in a higher optimum plant density (Donald, 1963). The response of corn grain yield to increased density has been shown to be parabolic. (Downey, 1971; Prior and Russel, 1975; Tetio-Kagho and Gardner, 1988b). Many researchers suggested that the decline in grain yield after a maximum is reached is chiefly due to barren plants (Duncan, 1973; Buren et al., 1974; Iremiren and Milbourn, 1980). Duncan (1975) stated that if the yield decrease started at densities lower than those needed for maximum light interception, that is factors other than light are more limiting, then the yield-plant density curve would have a sharp maximum rather than a plateau condition. When growth factors other than light are not optimal, then barrenness would occur at lower densities (Duncan, 1954; Lang et al., 1956).

Many workers have tried to quantify the relationships between density and crop yield. The simplest reason to do this is prediction of optimum density that gives the maximum yield (Willey and Heath, 1969). The mathematical relationship between plant density and grain yield also, could be used to compare genotypes that are different in tolerance to competition as well as comparison between different cropping patterns and practices.

Willey and Heath (1969) have reviewed several different mathematical methods used to quantify the yield-density relationship. Among these methods, the exponential equation proposed by Duncan (1958) will be examined. Duncan derived his model by fitting a linear regression of the logarithm of yield per plant on density. The proposed equation was therefore:

$$\text{Log } y = \text{Log } K + bP \quad \text{or} \quad y = K\,10^{bP}$$

where: y is the yield per plant, K is a constant (the intercept on the y axis), b is the slope of the regression line (always negative), and P is the density.

The yield per unit area (Y), thus is the product of the average yield per plant and the number of plants per unit area:

$$Y = yP \quad \text{and} \quad Y = PK10^{bP}$$

He suggested that since the relationship was linear, only two densities would be needed to determine maximum yield and the whole yield-density curve.

However, density has two components, the number of plants and planting pattern. Yield per unit area, therefore, is dependent not only on the number of plants per unit area (plant density) but also on the spatial arrangement of those plants or rectangularity. Plant rectangularity is an index of unevenness and can be defined as the largest distance between plants divided by the shortest distance (in row crops, the between-row spacing divided by the within-row spacing). A value of 1 indicates a uniform or square pattern while values larger than 1 indicate the degree of rectangularity, the larger the value the more rectangular the spacing. The extent to which rectangularity may effect the yield of a crop is dependent on the plasticity of the individual plant (Willey and Heath, 1969). Theoretically, yield per unit area gradually declines with increasing rectangularity. Some studies have shown that corn grown in more equidistant plant-spacing patterns (narrower row width) has yielded more grain per unit area of land than that grown in wider row widths (Lutz et al., 1971; Karlen and Camp, 1985; Karlen et al., 1987; Bullock et al., 1988; Ottman and Welch, 1989). However, other studies have shown no effect, or little yield differential from alteration of spatial arrangement (Nunez and Kamprath, 1969; Putnam, 1986).

In many yield-density equations, the yield effect of density is confounded with the effect of planting patterns. Duncan (1972 in Caldwell, 1984) gave a general assessment of research on the response of corn to plant arrangement:

> " Surely the first scientific problem that came up after <u>when</u> to plant corn was <u>how many</u> seed to plant and <u>how</u> to space it. Coming down through time I wonder if any subject pertaining to corn has given of as many field experiments" (p.159).

Nevertheless, Duncan felt a clear understanding of the influence of plant arrangement on corn was missing. He reasoned that with a fixed number of plants per unit area, yield would be obviously different if rows were 1, 5, or 20 meters apart (Duncan, 1984).

Duncan (1984) proposed a model (theory) which was a continuation of his earlier equation (Duncan, 1958). In his new model, the spacial arrangement of the plants in planting pattern was taken into account. He stated that the amount of yield reduction for a given environment and pattern depends on how near and how numerous the neighboring plants are. He used the term of crowding (C) for all forms of interplant competition and this was defined for crowding between <u>two</u> plants (c_i) as:

$$c_i = SF^{ALPHA}$$

Where: SF = [(DMAX - Separation) / DMAX]. SF = Separation fraction computed for each surrounding plant. DMAX is the minimum distance at which competition is negligible. The crowding relationship for individual plants is shown in Figure 1.2.

The value of c_i is between zero at DMAX (isolation) to a value of one at zero separation (two plants per hill). When two widely spaced plants are moved closer together, crowding increases in a curvilinear pattern. The curvature is determined by ALPHA and was computed practically using the data set of Kohenke and Miles (1951). Duncan (1984) calculated the value of ALPHA as equal to 4.0 (at DMAX = 3.0). However, the ALPHA value of 3.06 (at DMAX = 2.5) differed little in its precision in predicting yields for these sets of data.Crowding for the crop community is:

$$C = \sum_{p_1}^{p_i} c_i$$

Where: p_1 to p_i = Plants within the circle with radius DMAX of a chosen center plant (the target plant).

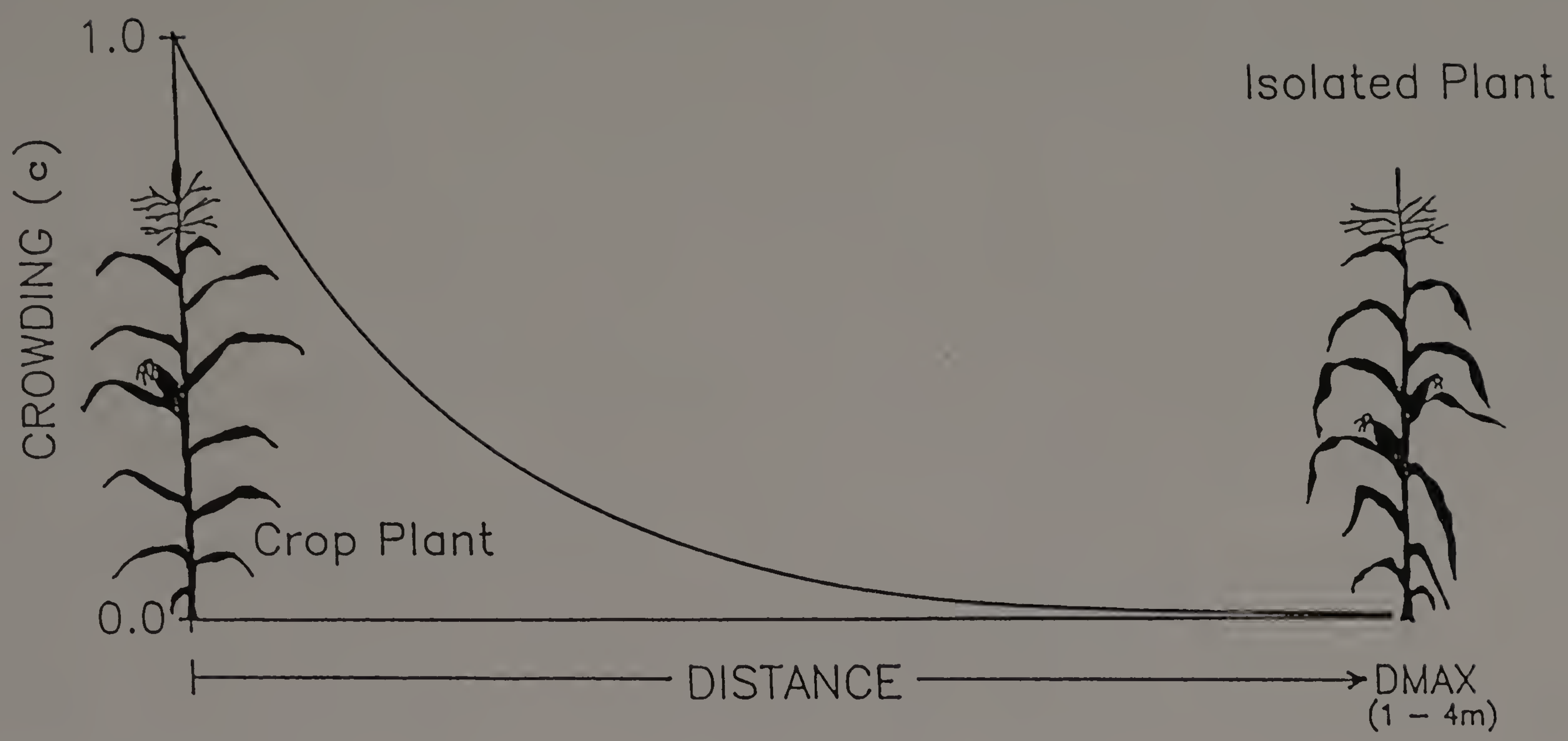

Figure 1.2. Relationship between Crowding (c_i) of an individual plant and Distance as derived from the model of Duncan (1984). DMAX is the minimum distance at which competition is negligible.

Duncan's new competition model (Duncan, 1984) based on crowding instead of density can be computed as:

$$\mathrm{Ln}y = \mathrm{Ln}\ y_0 + EC$$

Where: y and y_0 are yield per plant in crop and isolation, respectively. C is total crop crowding and E, which is negative, is defined as effect of crowding on yield. This changes the yield per plant a fixed fraction for every change in crowding. The values of E and y_0 are constants for any given environment and genotype and must be determined experimentally.

By using crowding values instead of absolute plant densities, yield per plant can be calculated more precisely showing the effect of planting pattern and row width. The competition model predicts that in any given environment and genotype, yield per plant will be the same if the C value is the same regardless of plant density or spatial arrangement. Thus, any planting pattern that includes more plants at a given C value would produced a higher yield per unit area. Practically, a square planting pattern is the highest yielding spatial arrangement for any given density. For any other spacing at the same density the C value will be higher. The model is useful for the evaluation of the row width effects on corn plant yield. Increased row spacing will increase the C value and reduce yields compared to a square planting pattern.

Competition and Yield Components

The grain yield of a corn plant can be expressed in terms of its components i.e. number of ears per plant, number of rows per ear, number of kernels per row, and weight per kernel. The effect of competition on these components is not similar and depends on environmental conditions and availability of resources, genotype, and the stage of growth and development in corn plant.

The efficient utilization of assimilates by different plant parts appears to be limited by many complex physiological and biochemical processes. For example, the ratios of carbon to nitrogen and rates of assimilate translocation were reported to be dependent on genotype as well as environmental conditions (Evans and Wardlaw, 1976; Below et al., 1981; Swank et al., 1982; Shannon, 1982; Jones and Simmons, 1983). Distribution and utilization of assimilates in the corn plant and probably in many other crops are controlled by the assimilate demands of distant metabolic sinks (Mondal et al., 1978; Gifford and Evans, 1981; Bagnara and Daynard, 1982; Jones and Simmons, 1983; Jones et al., 1985), which might change with ontogenetic development or in response to environmental signals originating from biochemical mechanisms in leaves (Geiger and Giaquinta, 1982). Competition among multiple plant sinks, therefore, affects the distribution and utilization of the assimilates in a corn plant.

In a corn plant each axillary bud at lower nodes has the potential of developing into either a tiller or an ear. The size and the number of ears at anthesis is dependent on genotype and is also strongly influenced by light and deficiencies of other growth factors. Ottman and Welch (1988) reported a 25% increase in ear number when the lower periphery of the corn canopy received supplemental radiation from fluorescent lamps. Increase in production of secondary and tertiary ears have been reported by many investigators at low densities (Prior and Russell, 1975; Tetio-Kagho and Gardner, 1988b). The term "prolific" has been given to the hybrids with strong tendency to produce more than one ear at low densities. While corn plant breeding has mostly directed toward selection of single ear genotypes, prolific hybrids have shown to have some advantages in unfavorable and stressed conditions (Collins et al., 1965; Russell, 1968; Buren et al., 1974; Prior and Russell, 1975).

For different hybrids growing with the same environmental conditions high negative correlation has been found between the number of ears at silking with the number of kernels per ear (Duncan, 1975). It has been observed that even though fertilization is accomplished the fertilized embryos may never start development (Daynard and Duncan, 1969; Iremiren and Milbourn, 1980). Undeveloped embryos are usually located in the apical portion of the ear (Tollenaar and Daynard, 1978a,b,c; Frey, 1981; Reed et al., 1988; Mozafar, 1990). Ear tip kernels, which would normally abort, continue to develop when transferred to an *in vitro* culture medium (containing sucrose) soon after pollination (Hanft et al., 1986). This suggests that carbohydrate supply may be limiting development at the ear tip. Abortion of kernels is a complex phenomenon and some studies suggested that assimilate supply to the ear may not play a direct role in kernel abortion. Tollenaar and Daynard (1978a) reported that sugar concentrations in aborting and nonaborting kernels were similar during flowering. Mozafar (1990) showed that the concentration of many elements was not lower in the nubin ear than in the normal ear thus, an insufficient supply of the mineral elements was ruled out as a cause of kernel abortion. Also, it has been shown that kernels at the ear tip can be induced to abort by ethylene treatment (Dill et al., 1987). In prolific cultivars undeveloped kernels are found in tertiary and secondary ears rather than the uppermost ear (Tetio-Kagho and Gardner, 1988b).

Manipulation of assimilation through light enrichment, shading, or defoliation has shown that yield adjustments most often take place through number of kernels per ear and number of ears per plant (Poneleit and Egli, 1979; Baenziger and Glover, 1980). Plant competition during ear development can cause second ear abortion (Harris et al., 1976; Poneleit and Egli, 1979). Weight per kernel and especially the number of rows per ear usually show a high degree of stability to assimilate manipulation (Hall et al., 1981; Schoper et al., 1982; Tetio-Kagho and Gardner, 1988b).

The timing of competition stress may also be important. Some studies indicate that competition after flowering has more detrimental effects on grain yield than does competitive pressure during vegetative growth.

The period 2 weeks before and after silking are suggested to be the most critical in establishing the percentage of potential ears and kernels which will develop to maturity (Prine, 1971; Evans and Wardlaw, 1976; Tollenaar, 1977; Frey, 1981). Assimilate supply during this period appears to be the dominant factor controlling final kernel number (Egharvba et al., 1976; Edmeads and Daynard, 1979). Water-soluble carbohydrates of the stem usually continue to accumulate until 2-3 weeks after silking (Campbell, 1964; Williams et al., 1968; Campbell and Hume, 1970) and often decline during the grain filling period (Daynard et al., 1969; Adelana and Milbourn, 1972; Fairey and Daynard, 1978). This observation led several workers to suggest that a part of the dry matter in grain especially during stressed periods and in short season environments, comes from reserved materials in corn stalk and husk (Duncan et al., 1965; Genter et al., 1970; Palmer et al., 1973; Fairey and Daynard, 1978; Jones and Simmons, 1983; Barnett and Pearce, 1983; Salvador and Pearce, 1988). Yield potential for a corn plant soon after pollination represents potential capacity that may or may not be translated into final grain yield (Duncan, 1975; Jones and Simmon, 1983; Kiniry et al., 1990).

The weight per kernel is a function of grain growth rate and duration of grain filling period or grain dry matter accumulation. The differences in kernel weight in different environmental conditions and also between genotypes have been attributed to both components. Poneleit and Egli (1979) concluded that final kernel weight is more closely related to duration of grain filling. Similar results reported by other workers (Daynard et al., 1971; Cross, 1975; Daynard and Kannenberg, 1976). However, others have shown that the difference in grain growth rate is the primary cause for variations in the weight per kernel among hybrids and with assimilate manipulation (Hanway, 1969; Tollenaar and Daynard, 1978a).

Labelling studies have shown that less than 10% of grain yield is attributable to assimilates formed before silking (Swank et al., 1982; Simmons and Jones, 1985). However, assimilated carbohydrate before silking may establish sink capacity (Tsai, et al., 1978) and thus, may be quite important in determining the final yield. Grain yield potential at anthesis is a function of the prior growth of the plant. Therefore, plants grown under less competition (low densities) have higher potential yields than those from dense plantings (Duncan, 1975). Plant stress may increase the contribution of pre-silking assimilates to yield (Allison and Watson, 1966).

Canopy Architecture and Yield

Visible light, making up about 40-50% of the incident solar radiation, is the fundamental source of energy required for photosynthesis and carbohydrate production in all green plants (Luxmoore et al., 1971; Rosenberg et al., 1983). The visible band is made up of that part of the solar spectrum from 400-700 nm and is referred to as photosynthetically active radiation (PAR) and is measured as photosynthetic photon flux density (PPFD) (Gallo and Daughtry, 1986). The PPFD is the number of photons in the PAR wave band that are incident on a unit surface in a unit time (Shibles, 1976). Like most plants, corn has a low photosynthetic efficiency, which is defined as the fraction of energy fixed biochemically by the plant to that energy incident on the plant as measured in the PAR band, or in the total solar spectrum (Loomis and Williams, 1963). Lemon (1969) found the energy fixed in annual dry matter production for corn to be equivalent to only one or two day's typical solar radiation intercepted by the corn canopy. For the best farming practices available at the time, he estimated photosynthetic efficiency for typical corn crops to be no greater than 1%. Even with such low efficiencies, many researchers have found positive correlations of intercepted solar radiation and/or PAR with total dry mater production and final grain yield (Pendleton et al., 1967; Linvill et al., 1978; Monteith, 1981; Ottman and Welch, 1988 and 1989; Muchow et al., 1990).

Tollenaar and Bruulsema (1988) reported that when nutrient and moisture are not limiting to crop growth, a linear relationship occurs between PAR and crop dry matter accumulation and the slope of the linear relationship (i.e. the efficiency of conversion of solar radiation into plant material) varies with crop species and phase of crop development.

The interception of PAR by a corn canopy is associated mainly with the leaf area index (LAI) (Hunter, 1980) and the orientation of leaves, collectively referred to as canopy architecture (Duncan, 1971 and 1975). The effect of canopy architecture on radiation penetration and distribution in the canopy is also thought to be a major determinant of photosynthetic efficiency and growth (Williams et al., 1968; Ottman and Welch, 1989).

High density crops intercept more light energy at an earlier growth stage than sparse stands because of a greater leaf surface (Williams et al., 1968). The higher leaf area of dense stands is the result of a greater leaf number per unit area while both leaf number per plant and area per leaf may decrease at high densities (Williams et al., 1965; Eik and Hanway, 1965; Nunez and Kamprath, 1969; Allison, 1969; Bonaparte and Brown, 1976; Edmeades and Daynard, 1979). The reduction in leaf area per plant, however, is not inversely proportional to plant density increase. Therefore, LAI of a corn canopy can be controlled within wide limits by the density of planting (Duncan, 1975). In early growth stages most of the leaf area may be effective in dry matter production, but at the time when canopies become essentially closed, the effectiveness of the leaf area declines because of mutual shading of leaves. The more rapid canopy closure and higher LAI in dense plantings induces competition for light at an earlier stage. Critical LAI, has been defined as the area of leaves at which a crop canopy reaches its maximum growth rate and this is the time when 95% of incident light is intercepted (Brougham, 1956). A large variation has been reported for critical LAI in corn, depending on genotype, density and environmental condition (Watson, 1958; Nunez and Kamprath, 1969; Duncan, 1971; Hunter, 1980; Bullock et al., 1988).

In densely planted corn, the upper one-third of the canopy intercepts almost all incoming solar radiation, while the lower leaves are shaded (Ottman and Welch, 1988). The light interception in high densities might be similar to those in less dense stands, but the efficiency of conversion may be less due to less uniform distribution of light in the dense canopy. Manipulation of canopy architecture to aid greater light penetration, especially in high densities, can increase the efficiency of dry matter production (Pendeleton, 1968).

Substantial increases in grain yield have been reported by supplemental radiant energy at the lower periphery of the corn canopy using reflectors (Pendleton et al., 1967; Winter and Pendleton, 1970; Tollenaar and Daynard, 1978b; Schoper et al., 1982) and artificial lighting (Graham et al., 1972; Ottman and Welch, 1988). More uniform distribution of solar radiation inside the corn canopy, thus, allows higher densities to be used. Higher grain yield in narrower rows (less rectangularity) has been attributed to the more efficient distribution of radiation (Scarsbrook and Doss, 1973; Ottman and Welch, 1989). Use of hybrids having vertical leaves compared to those with horizontal leaves also has been suggested to result in a more uniform distribution and therefore, higher grain yield (Pendleton et al., 1968; Duncan, 1971; Bunting, 1973; Pepper et al., 1977).

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CHAPTER 2

MANIPULATION OF COMPETITIVE PRESSURE IN CORN

I. GROWTH RESPONSE

Abstract

Growth analysis techniques can be used to compare patterns of dry matter accumulation in field crops. Two corn hybrids were planted in two years at 6 densities (0.25, 3, 4.5, 6, 9, and 12 plants m^{-2}), the lowest density being considered "an isolation density". These densities (except for isolation) were factorially combined with 4 removal treatments (control and 3 removal), consisting of removal of alternate plants in rows at different growth stages. Growth analysis descriptors were estimated from regression equations fitted to the relationships between the measured plant total dry weight, leaf dry weight and leaf area over time. Both hybrids reached their maximum leaf area index 60 days after emergence, however, only densities greater than 9 plants m^{-2} produced sufficient leaf area to intercept 95% of incident light. Optimum LAI's were 3.5 in Agway 584S and 4.2 in Cornell 281, were provided by 6 and 9 plants m^{-2} respectively. Crop growth rate was greater in Cornell 281 and increased to maximum then declined in both hybrids as density increased. Relative growth rate and net assimilation rate steadily decreased in both hybrids as density increased and the season progressed. Net assimilation rate was greater in Cornell 281 up to density of 9 plants m^{-2} compared to Agway 584S. Leaf area ratio decreased over time and this was mainly due to decrease in leaf weight ratio. Plant removal at 38 DAE did not change the pattern of "responses of growth descriptors" over time. Crowding values were computed for removal treatments from a competition model and indicated that competition at the time of 50% tassel emergence had the greatest influence on yield reduction.

Introduction

Plant density has long been recognized as a major factor influencing the degree of inter-plant competition in a corn stand. Many experiments have been conducted to determine optimum plant density and to describe changes in yield components and growth associated with increased densities (Duncan, 1958; Willey and Heath, 1969; Brown et al., 1970; Fery and Janick, 1971; Karlen and Camp, 1985; Tetio-Kagho and Gardner, 1988b).

The rate of dry matter production is dependent on the area of assimilatory organs, mainly leaves (Allison, 1969; Hunter, 1980). Percent light interception and rate of dry matter production increase with leaf area development (Williams et al., 1965; Scarsbrook and Doss, 1973; Tetio-Kagho and Gardner, 1988a; Bullock et al., 1988). Since the number of leaves in corn within a specific genotype and environment is relatively constant, the normal and easy technique used to increase leaf area is increasing the number of plants per unit area. Increasing density, however, increases the competition between the individual plants for light energy. The extent of light interception and distribution through the profile of a plant community has a major role in determining crop productivity (Williams et al., 1968). Much of the radiant energy is intercepted at the upper part of canopy. While the upper leaves may become light saturated, leaves lower in the canopy may receive insufficient light for maximum photosynthesis.

Duncan (1984) proposed a model to evaluate the competition effects in a corn stand. In this model, plant number (density) as well as spatial arrangement (pattern) were taken into account and collectively were described as crowding. Crowding will increase with increased density and/or sub-optimal plant arrangement. Effect of crowding on yield per plant is described by the following equation:

$$LnY = LnY_0 + EC \quad \text{(Duncan, 1984)}$$

Where: LnY is the natural logarithm of yield per plant; Y_0 is the predicted maximum yield per plant at zero crowding (isolated plant); E is an environment-genotype constant which determines the amount of reduction in yield due to the sum of all forms of competition that occur between the plants, and C is the crowding value which varies according to the established plant density and spatial arrangement. The predicted Y_0 and E are constant for any given genotype and environment.

Higher yield in erectophylle genotypes and also dominancy of equidistant planting (narrower row widths) over conventional planting pattern have been attributed to the greater availability of radiant energy at the lower region of the corn canopy (Scarsbrook and Doss, 1973; Bullock et al., 1988; and Ottman and Welch, 1989).

To further understanding of the physiological basis of competition relationships in different densities, we applied growth analysis techniques (Radford, 1967). Using plant dry matter and leaf area at different growth stages, various growth descriptors were quantified. The light profile within the canopy was also examined as densities were increased. In this experiment, the effect of reduction in competition pressure (crowding) through thinning of alternate plants at critical stages of growth was also investigated.

A detailed account of grain yield and yield components as a function of plant density and manipulation of competition pressure through plant removal is discussed in chapter 3.

Materials and Methods

Cultural Practices

A two year field study was conducted in 1986 and 1987 in the Connecticut River Valley at the University of Massachusetts Agricultural Experiment Station Farm in Deerfield, Massachusetts. The soil type was a Hadley fine sandy loam (Typic Udifluvent, coarse-silty, mixed, nonacid, mesic). In both years the experimental site received 36 Kg N ha^{-1}, 16 Kg P ha^{-1} and 13 Kg K ha^{-1} broadcast prior to planting and 75 Kg N ha^{-1} as side dressing. Weeds were controlled by spray pre-emergence cyanazine (2-{[4-chloro-6-(ethylamino)-S-triazin-2-yl]amino}-2-methylporpionitrile), and alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide) at the rates of 1.8 and 2.2 kg a.i. ha^{-1}, respectively. Plots were planted in a north-south direction on May 9 and May 8 in 1986 and 1987 respectively. Tillage practices were mold board plowing and disking prior to planting. No irrigation was found necessary during entire period of the growing season in either year. Soil moisture measured gravimetrically during both seasons showed no differences among treatments.

Experimental Treatments

The design of the experiment was a split plot with 3 replications. The main plots were 2 hybrid cultivars; Agway 584S (single-ear, late maturity), and Cornell 281 (semi-prolific, early maturity). Five-row sub-plots were used with rows 91 cm apart and 7.30 m long. The final harvest area for measurement of grain and stover yields at maturity was 3 m^2 taken from the central row. Sub-plots were 5 plant densities; 3, 4.5, 6, 9, and 12 plants m^{-2} combined with 4 removal treatments where alternate plants were cut at the soil surface at 3 critical stages of growth. These were, no removal (R_0), removal during vegetative growth {38 days after emergence (DAE)=R_1}, removal at 50% tassel emergence (59 DAE for Cornell 281 and 73 DAE for Agway 584S=R_2), removal at early grain filling time (80 DAE for Cornell 281 and 88 DAE for Agway 584S=R_3). One larger sub-plot for each hybrid in each replication was allocated to widely spaced or "isolated plants", which were separated by 2 m between plants (0.25 plants m^{-2}). All plots were over-seeded and hand-thinned initially using templates that were marked for proper spacings. Thinning was done 10 DAE in both years.

Measurements and Samplings

Light Interception and Growth Analysis. Measurements of photosynthetically active radiation (PAR) were taken above, within, and below the canopy for 5 plants in each plot. Due to time constraints only Cornell 281 was sampled. Measurements were obtained between 1045 to 1315 h with a Li-Cor line quantum sensor (LI-188B) placed across the inter row space. Readings were taken on days when clouds caused no interference. All readings were integrated over 1 meter and 10 seconds. In 1986, the first reading was taken 33 DAE at 3 levels, i.e., above the canopy, at the soil surface and 30 cm above the ground. The second measurement was taken 53 DAE at above the canopy, soil surface, 30 and 70 cm above the ground. The third and fourth readings were obtained 69 and 89 DAE at 6 different heights; above the canopy, soil surface, 70, 120, 150, and 180 cm above the ground. In 1987, only one measurement (69 DAE) which coincided with early anthesis in Cornell 281 was obtained. Number of leaves between each two consecutive heights and also total number of leaves per plant were also counted. Percent light available at a given height (% of above canopy) was calculated:

$$\% \text{ Light available} = L_i / L_a \times 100$$

where L_i and L_a are light read at any given height and above the canopy respectively.

Three growth samples were taken (35, 60 and 77 DAE in 1986 and 37, 61 and 80 DAE in 1987) from each plot during the growing season. Each sample was taken from a row adjacent to the central row of the plot and consisted of one square meter (equal to 1.1 m of row) taken one meter in from the ends of the plot. In this way no plants were removed from areas adjacent to the final sampling area of the central row. Each sample was separated into leaf and shoot (leaf sheath, stem, tassel and ear when present) fractions. Leaf area was measured using a Li-Cor area meter (LI-3100). Leaf and shoot were then dried to a constant weight in a forced-air oven at 80°C. Primary data for total dry weight (TDW) and leaf area (LA) were $\log_e$ transformed, thus making the variances more independent of the means. Second degree polynomials, $\log_e W = a + bt + ct^2$ and $\log_e A = a' + b't + c't^2$ were fitted by the least squares method to express the weight (W) and area (A) as functions of time (t). Relative Growth Rate (RGR) at any instant in time was derived directly by differentiation:

$$RGR = d(\log_e W)/dt = b + 2ct \text{ (Buttery, 1969)}$$

Leaf area ratio is the ratio of leaf area to total plant dry weight:

$$LAR = e^{(a'-a) + (b'-b)t + (c'-c)t2}$$

Since RGR = NAR × LAR, where NAR is Net Assimilation Rate then:

$$NAR = (b+2ct)e^{(a-a')+(b-b')t+(c-c')t2}$$

$$CGR = NAR \times LAI$$ (Watson, 1958)

where CGR and LAI are Crop Growth Rate and Leaf Area Index, respectively. Values for other growth descriptors were obtained by performing the specific mathematical operations using the following equations:

LAR = LAI/TDW

SLA = LAI/LDW

SLW = LDW/LAI

LWR = LDW/TDW

where LAR=Leaf Area Ratio, SLA=Specific Leaf Area, LDW=Leaf Dry Weight, SLW=Specific Leaf Weight, and LWR=Leaf Weight Ratio (Warren Wilson, 1981; Herbert and Litchfield, 1984; Fitter and Hay, 1987; Bullock et al., 1988; Tollenaar, 1989).

Differences observed in the growth descriptors in different treatments were only judged significant when the differences observed in TDW and LAI (which were used to derive the growth descriptors) were found to be statistically significant. This indirect inference was necessary because normal measures of statistical significance are difficult, if not impossible, to obtain when derivatives of the various growth equations are used to calculate growth analysis descriptors (Clawson et al., 1986).

Final Harvest

Grain harvesting was completed 118 DAE for Cornell 281 and 137 DAE for Agway 584S in 1986 after physiological maturity. In 1987, grain harvesting was completed 110 DAE for Cornell 281 and 131 DAE for Agway 584S. The first and second ears (when present) of all plants in the final harvest area were hand-picked and kept separate. For all sub-plots, ears and stover were weighed in the field. All ears were then dried in a forced-air oven at 80°C for one week. Dry weight for stover was determined, using the 3 plant sub-samples. Using a hand-sheller, all the ears were shelled, and cobs and kernels were dried again and weighed separately.

Results and Discussion

Interception of PAR

The plant canopy was divided into different strata to provide more information about which part(s) of the canopy intercept most of the incoming light.

At 50% tassel emergence, total light interception was not significantly different in the 2 years and was about 95, 90 and 85 % in high, medium, and low density respectively (Fig. 2.1). Light available at the ear position also differed among densities. In the highest density only 20 and 25% of maximum available light reached to the ear position in 1987 and 1986 respectively. The results are very consistent with those reported in Chapter 4. In the lowest density (3 plants m^{-2}) percent light available was 45 and 55 in 1987 and 1986 respectively. Lower availability of light at ear level in 1987 compared to 1986 could be attributed to the higher number of leaves above the ear in 1987 compared to 1986 ($p=.044$)(Table 2.1). Total leaf number, however, was very similar in the 2 years. In both years the number of leaves above the ear increased as density increased up to 9 plants m^{-2} and then decreased (Table 2.1). An increase in the concentration of leaves at the top of the plant with increased density was also reported by Williams et al. (1965). In medium and high densities about 50 and 65% of light was intercepted by the top 1/3 of the canopy in 1986 and 1987, respectively.

Comparison between light interception at 69 and 89 DAE showed that light interception reached its maximum by 69 DAE and no significant difference was found between the two sampling dates for interception by the canopy above the ear position at all densities (Fig. 2.1). However, the lower portions of the canopy received more light at early anthesis (69 DAE) compared to grain filling stage (89 DAE). Since the leaf number as well as LAI reached their maximum values by 69 DAE the results, therefore, suggest that leaf angle and configuration changed between the two sampling periods.

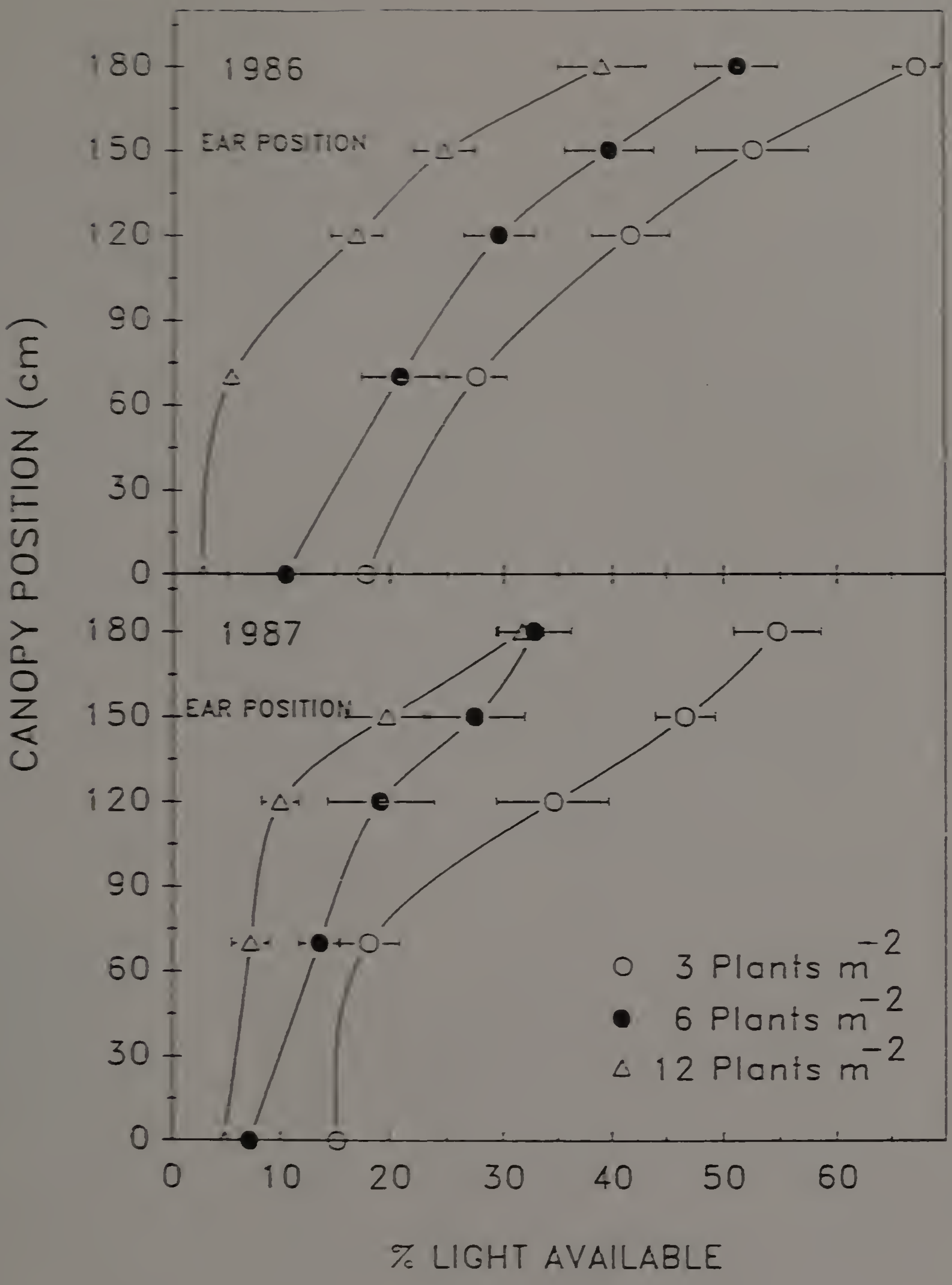

Figure 2.1. Light distribution within canopies of three densities in Cornell 281 at early anthesis in 1986 and 1987. Horizontal lines represent standard error of means.

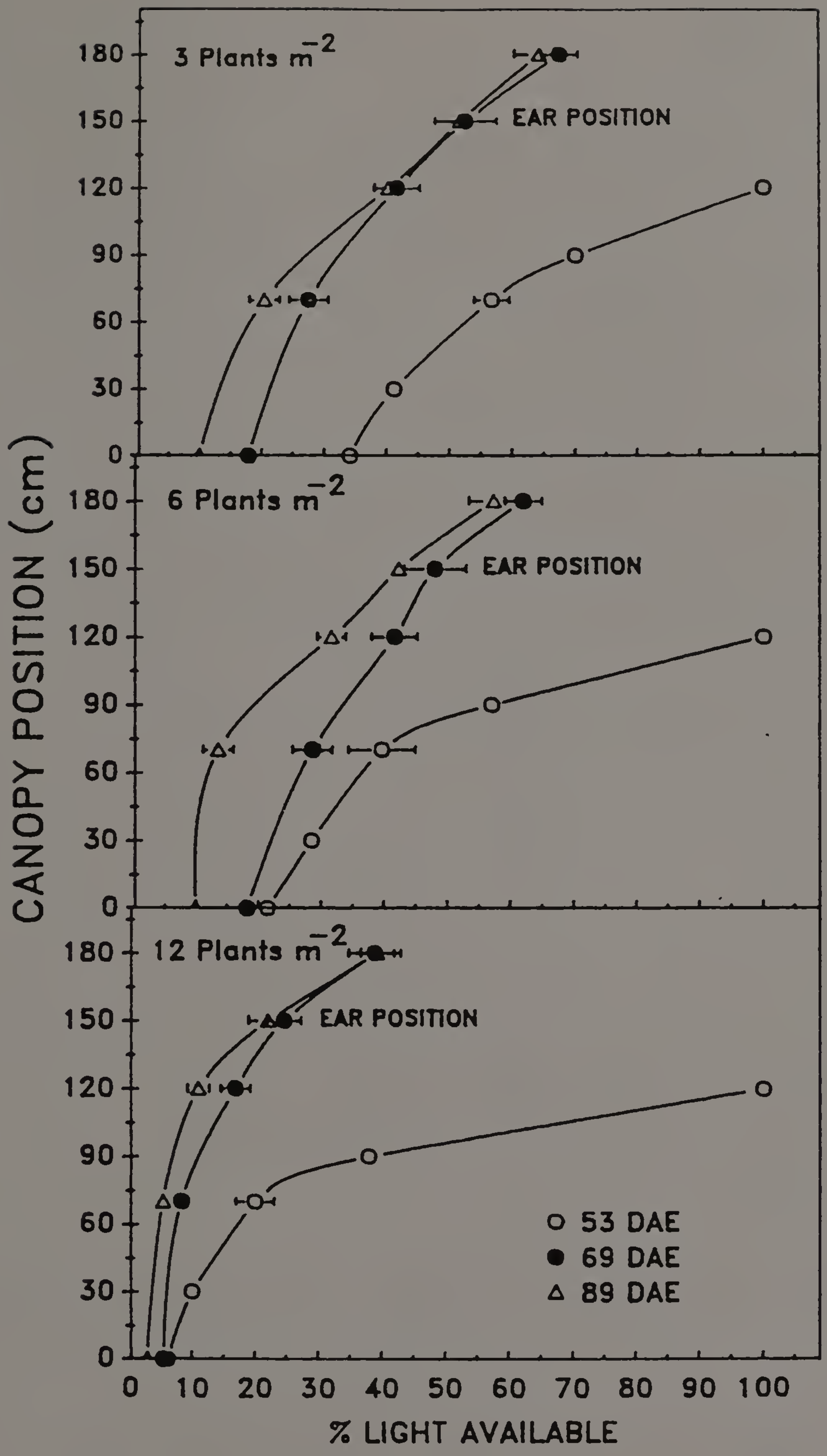

Figure 2.2. Light distribution within canopies of three densities at different stages of growth of Cornell 281 in 1986. Horizontal lines represent standard error of mean.

Table 2.1. Number of leaves above the ear and total leaf number as influenced by plant density.

Density	Leaf number above ear		Total leaf number	
plants m^{-2}	1986	1987	1986	1987
3	3.8	5.4	12.9	13.5
4.5	5.0	5.9	13.5	13.9
6	5.2	6.4	13.6	13.4
9	5.7	6.3	14.1	13.5
12	4.9	4.6	13.6	12.8
Mean	4.9	5.7	13.5	13.4
F-test significance				
Density				
L†	.021‡	.245	.025	.091
Q	.001	.010	.014	.354
C	.936	.816	.593	.972
CV, %	20.2	23.6	5.6	7.7

† Significance of linear (L), quadratic (Q), and cubic (C).

‡ probability of a greater F value by chance.

Growth Analysis

Leaf Area Index. Leaf area index increased linearly with increased plant density (Fig. 2.3). However, the comparison between the 3 harvests showed a asymptotic response, that is no significant difference was found between the LAI at 60 and 80 DAE. At 60 DAE only high densities (9 and 12 plants m^{-2}) could intercept 95% or more of the incident light. Maximum LAI values for the lowest and highest density were 1.8 and 6.4 inAgway 584S and 1.9 and 5.7 in Cornell 281 respectively. Early removal had no effect on LAI, but later removal (early anthesis), showed a trend towards lower LAI.

Dry Matter Acumulation. No interaction was shown between either year × treatment or year × hybrid for accumulation of dry matter. The influence of density on accumulation of dry matter for both hybrids averaged over 2 years for each harvest is shown in Figure 2.4. While the relationship between dry matter accumulation and density was linear for the first two harvests, a quadratic response was found at 80 DAE. Densities greater than 6 and 9 plants m^{-2} in Agway 584S and Cornell 281 respectively, did not result in a greater production of dry matter. Partitioning of dry matter changed as the plants developed. The ratio of leaf dry weight to total dry weight (LWR) when averaged over

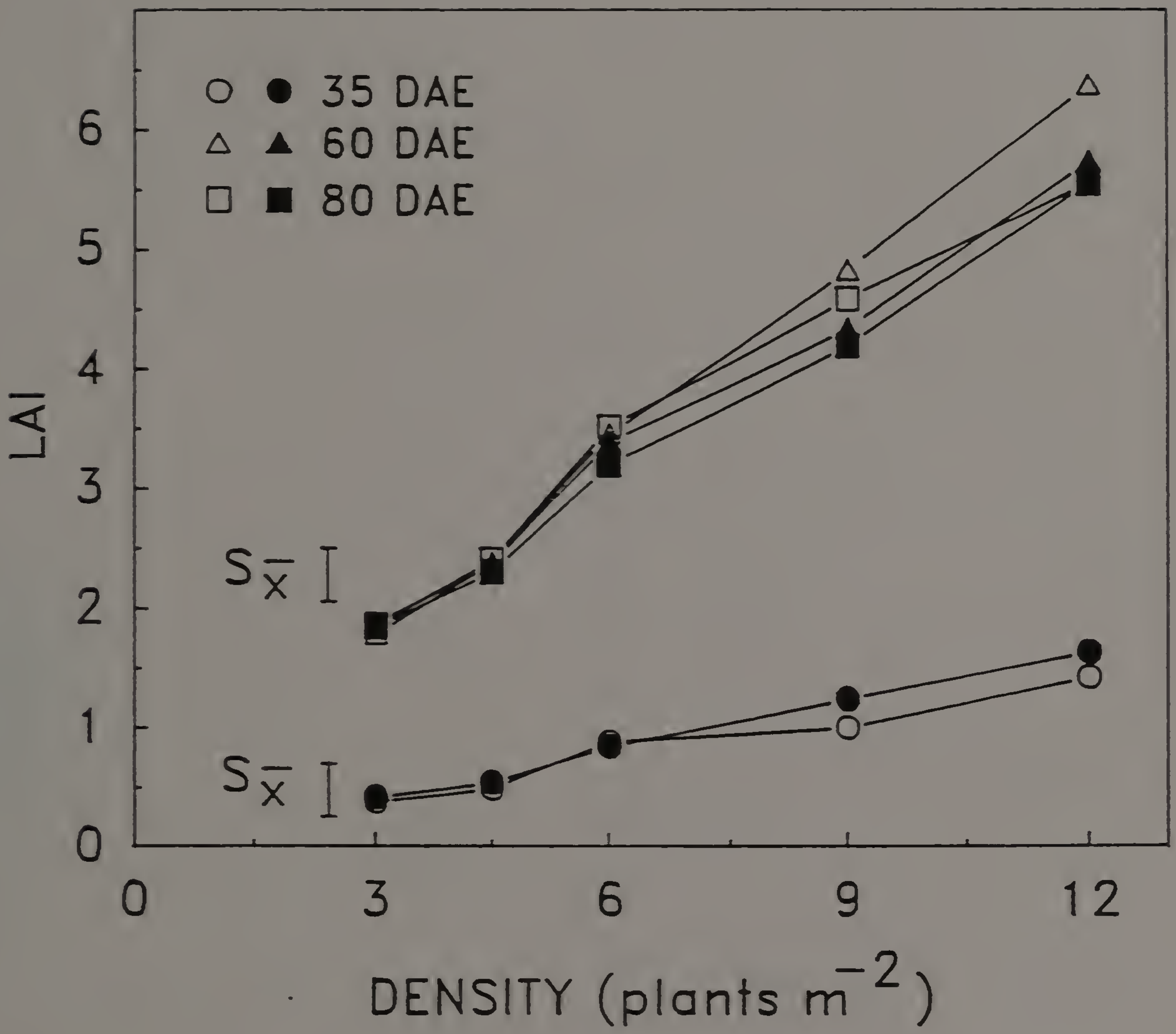

Figure 2.3 Effect of plant density on leaf area index at 3 stages of growth. Agway 584S (unfilled) and Cornell 281 (filled); average of 1986 and 1987.

density was 50, 42, and 26 percent in Agway 584S and 50, 36, and 23 percent in Cornell 281 in first, second, and third harvests respectively. At 60 DAE, the LDW's in both hybrids and in all densities reached their maximum values. However, TDW's in both hybrids and in all densities were still in the phase of rapid dry matter accumulation at 80 DAE. This resulted in a decrease in LAR as the season progressed.

The CGR was greater for Cornell 281 than for Agway 584S in both years. This is shown in Figure 2.5a where CGR for each density at 60 DAE is plotted against LAI at the same date. Maximum CGR's in both hybrids were obtained by the highest densities (39.3 and 37.7 in Cornell 281 and Agway 584S respectively). Maximum CGR values were reached at about 62 DAE.

The LAI's in both hybrids were similar at 60 DAE except at the high density where LAI was greater in Agway 584S than Cornell 281 (Fig. 2.3). Since CGR = NAR × LAI (Watson, 1958), the higher CGR in Cornell 281 resulted from higher NAR values compared to those for Agway 584S (Fig. 2.5b). The increased CGR due to increased density resulted from their greater LAI's since NAR's decreased as density increased. Maximum CGR in isolated plants was obtained at 65 DAE in both hybrids and was 39.0 and 21.6 g m^{-2} day^{-1} in Cornell 281 and Agway 584S respectively. The difference between the 2 hybrids was mainly due to the potential for tiller production in Cornell 281 compared to Agway 584S. Isolated

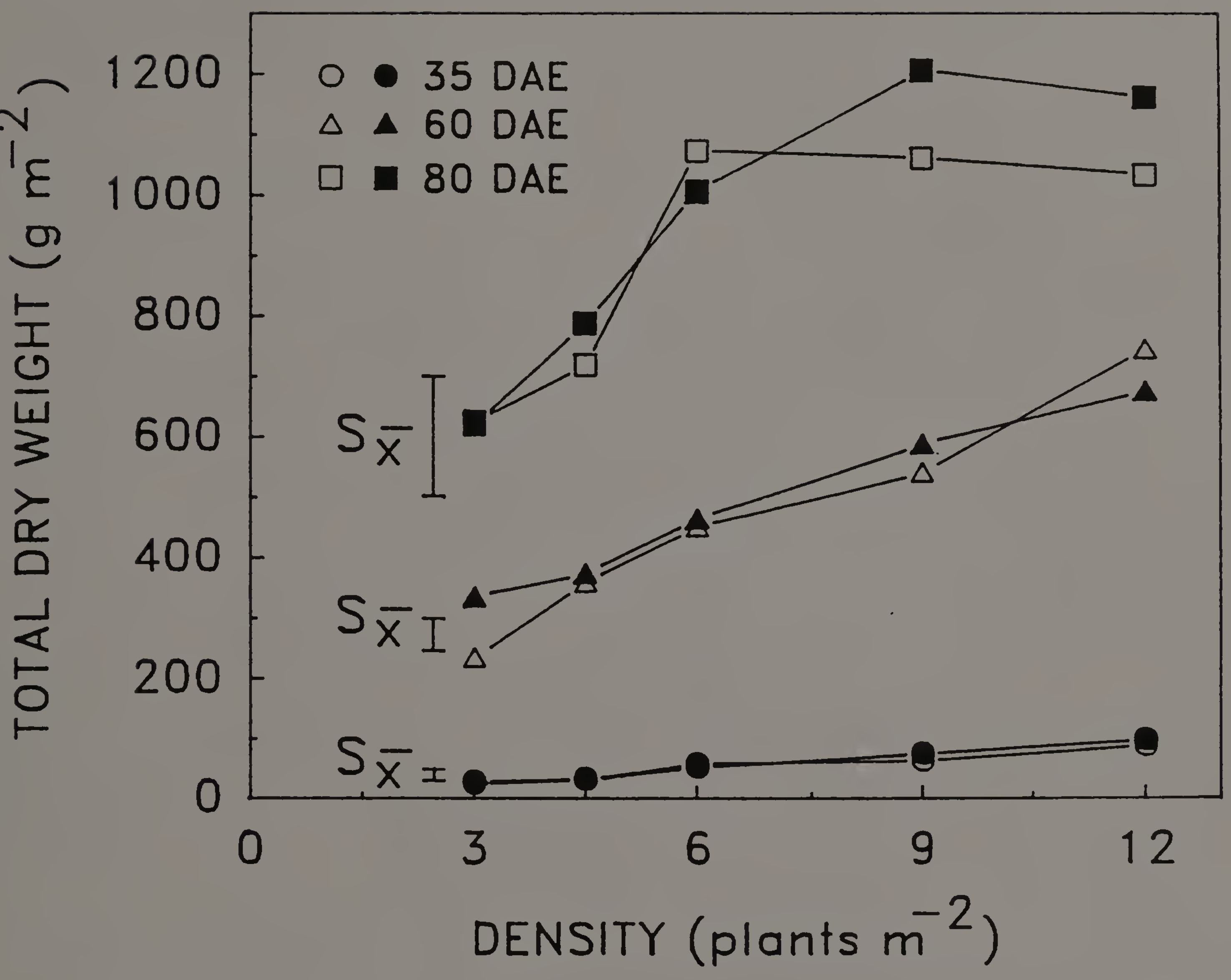

Figure 2.4 Effect of plant density on total dry matter accumulation at 3 stages of growth. Agway 584S (unfilled) and Cornell 281 (filled); average of 1986 and 1987.

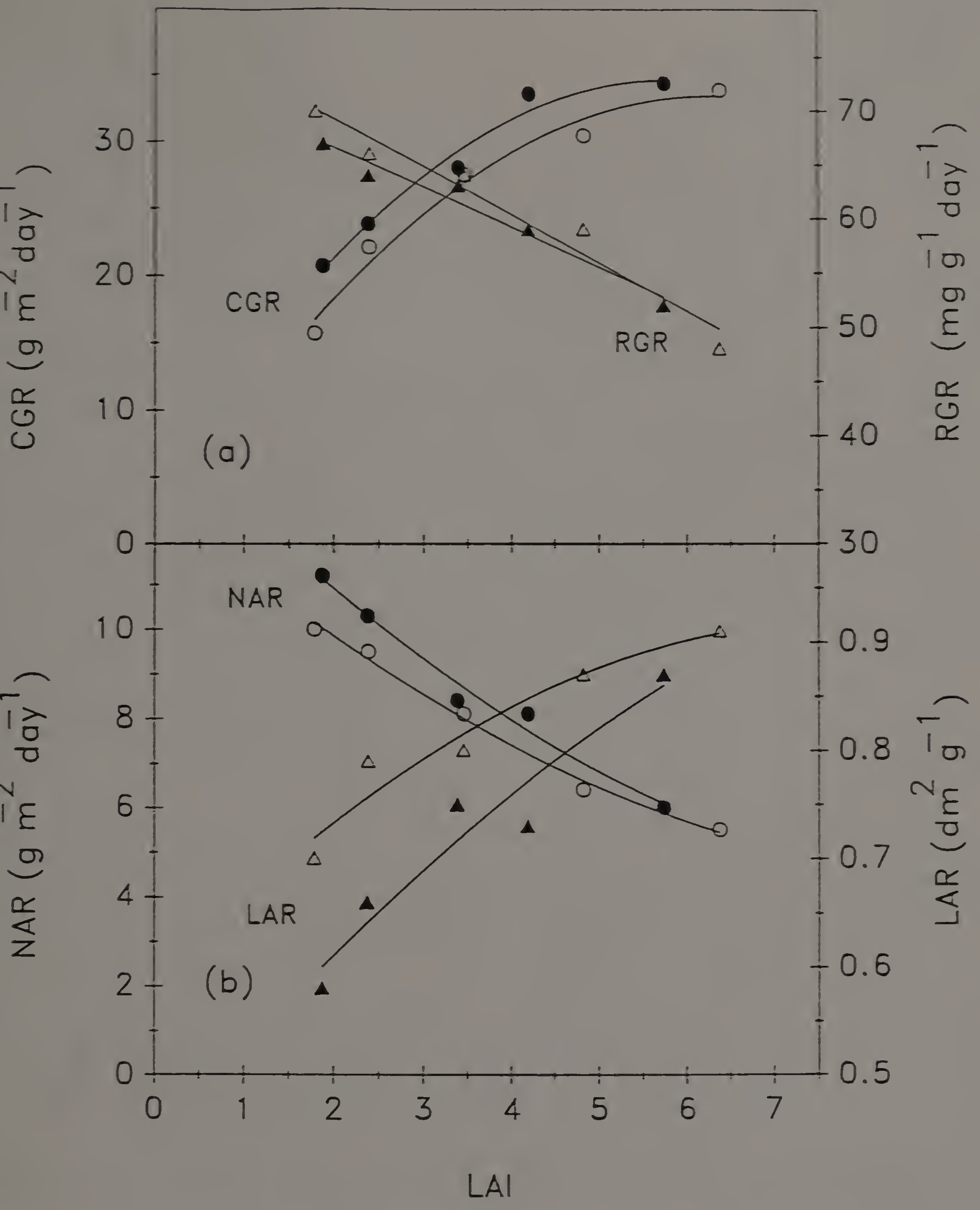

Figure 2.5. Crop growth rate and relative growth rate (a) and net assimilation rate and leaf area ratio (b) plotted against mean LAI for densities ranging from 3 to 12 plants m^{-2}. Agway 584S (unfilled) and Cornell 281 (filled); average of 1986 and 1987.

plants in Cornell 281 produced as many as 12 tillers compared to maximum of 3 tillers in Agway 584S.

The RGR was similar for both hybrids and decreased linearly as LAI (and density) increased (Fig. 2.5a). The decline in RGR's and also the efficiency of dry matter production (net assimilation rate i.e. NAR) (Fig. 2.5b) with density (LAI) is the usual response to increased mutual shading of leaves. The LAI for isolated plants were 2.9 and 2.1 for Cornell 281 and Agway 584S respectively. The RGR of isolated plants compared to their LAI's fitted the regression line derived from the higher densities (Fig. 2.5a). Competition for light is the major factor inducing morphological changes in plants when plant density is increased. This is reflected in lower NAR at high densities (Fig. 2.5b). Low densities in Cornell 281 more efficiently utilize intercepted light as indicated by the higher NAR's compared to Agway 584S (Fig. 2.5b). This capability may be due to the greater tiller production in Cornell 281 at low densities.

Leaf area ratio (LAR) decreased for all plant densities in both hybrids over the time period (data not shown). However, at any point, LAR (Fig. 2.5b) and its components i.e. LWR and SLA, increased linearly with density increase. The increase in LAR (the ratio of assimilatory area to total biological dry weight) and SLA (the ratio of leaf area to leaf dry weight) indicate that as density increased, the leaves became wider and thinner.

We have shown (Chapter 4) that the chlorophyll concentration and rate of photosynthesis decreased substantially as density increased from 3 to 12 plants m^{-2}. Therefore, production of a larger assimilatory area, while the LAI was supra-optimal induced more shading which in turn lowered the efficiency of conversion of solar radiation into the plant dry matter. Alternately, it could be argued that thinner leaves reduced the amount of chloroplasts and therefore, reduced the rate of dry matter production. Brougham (1960) reported a positive correlation between the chlorophyll content and the thickness of the leaves in corn and clover. He also found a high correlation between chlorophyll content of the leaves above the 95% light interception and maximum growth rate.

Dornhoff and Shibles (1970) and Beuerlein and Pendleton (1971) reported that soybean leaves with high SLW (low SLA) had high apparent photosynthesis rates. Several other researchers also have shown that the low SLW (high SLA) of leaves in various crops could be related to lower light penetration into the canopy at higher plant densities (Brandes et al., 1973; Beuerlein et al., 1971; Herbert, 1977a).

Harvest Yield

No significant differences in grain yield or above ground biomass yield were shown between 1986 and 1987 (Table 2.3). The interaction of year × hybrid as well as year ×

treatment for biomass yield were also not significant. The interaction of year × treatment for grain yield was small, therefore, the results of two years have been merged and are presented in Table 2.2 and Table 2.3. Both grain and biomass yield of Agway 584S were significantly higher than Cornell 281. The superiority of Agway 584S in producing biomass was related to its longer growing season. Cornell 281 was physiologically mature 114 DAE whereas Agway 584S reached physiological maturity 134 DAE (numbers are average of two years). The harvest indices (grain yield/total biomass yield) (HI) indicate that Agway 584S partitioned more dry matter to grain yield than Cornell 281 (Fig. 2.6) (Table 2.2 and 2.3). Also Agway 584S had a higher grain filling rate compared to Cornell 281 (Chapter 3).

Maximum grain yield can be obtained when the crop canopy produces just enough leaf area to intercept maximum available radiant energy. Grain yields of the two hybrids plotted against mean LAI of the different densities are presented in Figure 2.6. Both hybrids showed a quadratic response with an optimum LAI of 3.5 and 4.2 in Agway 584S and Cornell 281 respectively. These LAI's coincided with lowest densities for near maximum light interception (Fig. 2.1). Beyond the optimum LAI, no increase in grain yield was obtained. This can be attributed to mutual shading of leaves. These values of LAI for maximum grain yield of corn are consistent to those reported earlier (Loomis et al., 1968; Nunez and Kamprath, 1969; Scarsbrook and Doss, 1973;

Table 2.2. Density and plant removal effects on total grain yield, total biomass, and harvest index of 2 hybrids averaged over 2 years.†

Density at harvest	Agway 584S				Cornell 281			
	R_0‡	R_1	R_2	R_3	R_0	R_1	R_2	R_3
Plants m^{-2}								
	Total grain yield (Mg ha^{-1})							
3	5.71	6.02	5.45	5.01	4.77	4.85	4.34	3.87
4.5	7.15	7.34	6.15	5.89	5.83	5.81	5.11	4.49
6	9.59	8.96	5.93	5.36	7.50	7.12	5.86	4.71
9	9.36				8.28			
12	9.30				6.82			
	Total Biomass (Mg ha^{-1})							
3	12.20	12.84	11.78	11.40	13.60	12.60	10.92	9.87
4.5	14.55	14.87	13.02	11.60	14.40	13.55	12.07	10.99
6	19.23	17.07	13.28	11.95	16.68	16.19	13.77	11.78
9	19.47				18.67			
12	20.98				17.43			
	Harvest index (%)							
3	46.8	46.9	46.3	43.9	35.1	38.5	39.7	39.2
4.5	49.1	49.4	47.2	50.8	40.5	42.9	42.3	40.9
6	49.9	52.5	44.7	44.9	45.0	44.0	42.6	40.0
9	48.1				44.3			
12	44.6				39.1			

† Analysis of variance with singel degree of freedom comparisons are presented in Table 2.3.

‡ R_0, R_1, R_2, and R_3 are no removal, removal at 38 DAE, 50% tassel emergence, and early grain filling time respectively.

Table 2.3. Analysis of variance showing the F-test significance for the effect of density and removal on grain yield, biological yield, and harvest index of 2 hybrids in 1986 and 1987.

Source of variation	Total grain yield	Biomass yield	Harvest index
Year (Y)	.654[†]	.776	.274
Hybrid (H)	.001	.084	.001
Y × H	.095	.216	.409
Treatment (T)	.001	.001	.001
Dens in R_0 L[‡]	.001	.001	.884
Dens in R_0 Q	.001	.001	.001
Dens in R_0 C	.920	.570	.347
Dens in R_1 L	.001	.001	.001
Dens in R_1 Q	.604	.475	.606
Dens in R_2 L	.015	.011	.599
Dens in R_2 Q	.458	.871	.197
Dens in R_3 L	.118	.119	.473
Dens in R_3 Q	.171	.941	.004
R_0 vs Removal	.001	.001	.632
R_1 vs R_2 & R_3	.001	.001	.005
R_2 vs R_3	.014	.014	.521
Y × T	.042	.076	.539
H × T	.010	.272	.157
CV, %	10.1	9.8	7.3

[†] Probability of a greater F value by chance.

[‡] L = linear, Q = quadratic, and C = cubic trends, respectively.

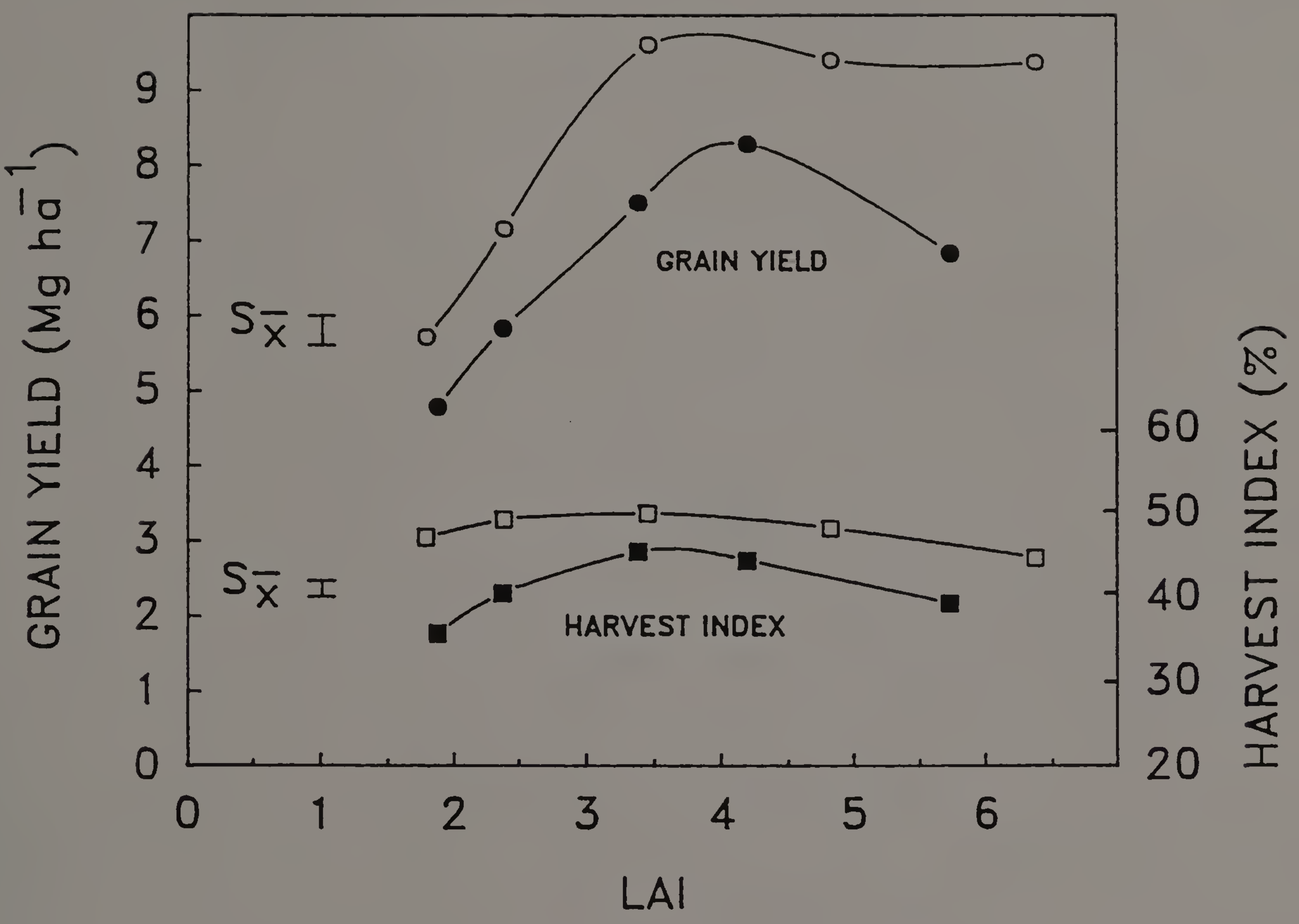

Figure 2.6. Grain yield and harvest index plotted against mean LAI for densities ranging from 3 to 12 plants m^{-2}. Agway 584S (unfilled) and Cornell 281 (filled); average of 1986 and 1987.

Tetio-Kagho and Gardner, 1988a). Agway 584S showed more tolerance to higher densities (LAI) than Cornell 281. In Cornell 281, HI increased up to the density of 6 plants m^{-2} before declining at higher densities, which indicates suppression of tillering improved partitioning of assimilates towards grain production. The effect of plant removal (Table 2.2) at different stages of growth on grain yield is discussed fully in Chapter 3.

Estimation of Crowding within Removal Treatments

Since the number of plants in removal treatments was halved at different stages of growth, estimation of competition through the entire growing period is difficult. Two densities are involved; initial density and final density, and the competition crowding values would be expected to fall somewhere in between crowding values for the initial and final densities. It is possible to estimate crowding values for removal treatments, however, from observed yields of unthinned plots (R_0) by using the prediction equation proposed by Duncan (1984) to establish values of E, the environment-genotype constant and Y_0, the maximum predicted yield in isolation. The predicted value for C would then be:

$$C = (LnY - LnY_0) / E$$

where: C is the predicted crowding value for the removal treatment, LnY_0 and E are constants calculated from the non-thinned plots established with different crowding values, and LnY is the natural logarithm of the yield observed in the removal treatment. The computed values for crowding before and after thinning (based on planted and final densities) and the predicted values of crowding from the yields after the removal averaged over 2 years for each hybrid are shown in Table 2.5 and Table 2.6.

The difference between predicted crowding values for any final density in removal treatments and crowding values for the same density in unthinned plots (R_0) is equal to the crowding competition prior to thinning. Therefore, the later the thinning, the greater the difference. The results indicate that the period between seed emergence and 50% tassel emergence (R_2) caused the highest increase in crowding value. Competition during the vegetative stage was less than later stages as shown by the smaller increase in crowding values for the R_1 treatment (Table 2.5). This indicates crowding competition during the first 38 days had little or no effect in determining yield. Crowding competition was also important between early anthesis (R_2) and the early grain filling stage but less so than crowding prior to early anthesis. This suggests crowding competition at anthesis and during ear development is important in determining yield and grain yield components. In Chapter 3 ear number per plant, and kernel number per row are shown to be greatly affected by increasing density. Weight per kernel was less affected and row number per ear least affected by density.

Table 2.4. Effect of plant removal at different stages of growth on the estimated value of C using the model of Duncan (1984).

Hybrid	Density		C_{R0}†		Total grain yield			Biomass yield		
	Planted	Final	Planted	Final	C_{R1}	C_{R2}	C_{R3}	C_{R1}	C_{R2}	C_{R3}
	Plants m^{-2}		Computed		Predicted					
Agway 584S	6	3	10.7	4.9	4.7	6.3	8.4	3.6	5.1	6.2
	9	4.5	16.5	7.8	8.4	11.3	11.7	8.9	10.9	13.1
	12	6	22.4	10.7	10.4	18.0	18.9	12.3	17.1	18.2
Cornell 281	6	3	10.7	4.9	5.4	7.0	9.2	4.8	7.0	8.8
	9	4.5	16.5	7.8	8.7	11.2	13.5	9.8	11.9	13.4
	12	6	22.4	10.7	10.9	13.4	17.4	12.3	14.1	16.7
Mean			16.5	7.8	8.1	11.2	13.2	8.6	11.0	12.7

† C_{R0}, C_{R1}, C_{R2}, and C_{R3} are crowding values for no removal, removal at 38 DAE, 50% tassel emergence, early grain filling time, respectively.

Table 2.5. Analysis of variance showing the significance of the effect of density and removal on the estimated value of C, using the model of Duncan (1984) for 2 hybrids in 1986 and 1987.

Source of variation	C_{TG}†	C_{BIOL}
Year (Y)	.146‡	.462
Hybrid (H)	.806	.643
Y × H	.206	.246
Density (D)	.007	.003
Linear	.004	.001
Quadratic	.955	.147
Removal (R)	.003	.011
R_0 vs R_1	.605	.276
R_1 vs R_2 & R_3	.002	.008
R_2 vs R_3	.022	.067
Y × D	.209	.672
Y × R	.709	.793
H × D	.076	.184
H × R	.537	.975
R × D	.141	.161
CV, %	15.8	15.8

† C_{TG}, and C_{BIOL} are crowding values for total grain yield and biomass yield, respectively.

‡ Probability of a greater F value by chance.

Summary

Total grain production in Agway 584S exceeded that of Cornell 281 by approximately 17% averaged over densities. Application of growth analysis techniques to curves of TDW, LDW, and LA showed that CGR as well as NAR was even greater in Cornell 281 than those of Agway 584S. However, the amount of dry matter accumulated in the grain fraction was higher in Agway 584S than in Cornell 281. Production of higher dry matter in Cornell 281 was directed toward tiller production, which usually failed to produce a fertile ear. The optimum LAI in Agway 584S was less than in Cornell 281, but Agway 584S showed more tolerance to higher density than Cornell 281.

Estimation of crowding values (C) for removal treatments, using the Duncan (1984) model showed that early competition up to 38 DAE had no effect in determining biomass or grain yield. The highest effect of competition on grain yield was determined to be near the time of pollination and fertilization.

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CHAPTER 3

MANIPULATION OF COMPETITIVE PRESSURE IN CORN

II. YIELD AND YIELD COMPONENTS

Abstract

Plants grown at non-competitive densities (isolated plants) can be used to estimate competitive pressure on yield and yield components in higher densities. Two corn hybrids were planted in two years at 6 densities (0.25, 3, 4.5, 6, 9, and 12 plants m^{-2}), the lowest density being considered an isolation density. These densities (except for isolation) were factorialy combined with 4 removal treatments (control and 3 removal), consisting of removal of alternate plants in rows at different growth stages. Intensity of competition was quantified by comparing grain yield and its components of plants grown in non isolated densities to those components on isolated plants. Agway 584S is a single-ear late maturity hybrid while Cornell 281 is semi-prolific with early maturity in Massachusetts. Total kernel yield per plant decreased 75% and 80% compared to isolated plants in Agway 584S and Cornell 281 respectively, as density increased from 3 to 12 plants m^{-2}. The reduction in kernel yield in both hybrids was primarily due to the reduction in number of productive ears per plant and number of kernels per row. The response of these components to density increase was linear in Agway 584S and quadratic in Cornell 281. Weight per kernel was also reduced significantly as density increased and the decline was greater in Agway 584S than in Cornell 281. The results from removal treatments indicated that early competition had no significant effect on final yield. Plant competition between the vegetative stage and anthesis had the greatest effect with 18% and 13% yield reduction (averaged over densities) for Agway 584S and Cornell 281 respectively. Adjustment in grain yield in response to increasing assimilate supply by removing the plants occurred primarily through increase in kernel number per row in Agway 584S and number of productive ears per plant in Cornell 281. Number of rows per ear and weight per kernel did not change significantly in response to plant removal. No significant difference was obtained in grain growth rate of the 2 hybrids. Increasing density decreased grain growth rate while plant removal showed no significant influence and mean grain growth rate adjusted to the new density. Kernels at the middle and tip showed 3% and 11% slower grain growth rate than basal kernels. The respective average grain filling period for the 2 hybrids was 40.2 and 28.7 days in Agway 584S and Cornell 281 and was not significantly changed by density and plant removal. The higher yield of Agway 584S was attributed to heavier kernels than Cornell 281.

Introduction

Competition for resources such as light, water and nutrients has long been viewed as an important consideration in the growth and yield of plants. Plant density has been recognized as a major factor determining the degree of competition between plants.

Yield per plant decreases as the density per unit area increases. The rate of yield decrease in response to decreasing light available to each plant is also affected by such factors as fertility, level of water availability and genotype (Duncan, 1954; Lang et al., 1956; Duncan, 1958; Brown et al., 1970). Reduction in yield may be the result of lower number of ears (barrenness) (Lang et al., 1956; Prine, 1971; Bunting, 1973), fewer kernels per ear (Baenziger and Glover, 1980; Karlen and Camp, 1985; Tetio-Kagho and Gardner, 1988b), lower kernel weight (Poneleit and Egli, 1979) or a combination of these components. In dense populations, many grains may not develop. This occurs in some genotypes due to poor pollination resulting from prolonged silking compare to tassel emergence (Bunting, 1973; Iremiren and Milbourn, 1980) and/or due to limitation in assimilate supply that cause kernel and ear abortion (Iremiren and Milbourn, 1980; Karlen and Camp, 1985).

Grain yield per unit area is the product of grain yield per plant and number of plants per unit area. The response is usually parabolic, as the density increases. At low densities, grain yield is limited by the number of plants, whereas at higher densities it declines due to increase in number of aborted kernels and barren stalks. Therefore, finding the optimum densities that produce the maximum yield per unit area under different environmental conditions and/or genotypes has been the major concern in many investigations.

Research indicates that assimilate supply may be limiting yields, especially in short-season regions. Light enrichment due to reflectors and fluorescent lamps (Tollenaar and Daynard, 1978b; Schoper et al., 1982; Ottman and Welch, 1988) and/or plant removal (Baenziger and Glover, 1980; Schoper et al., 1982) has been shown to increase final grain yield. Artificial shading (Struik, 1983; Kiniry and Ritchie, 1985; Reed et al., 1988) and defoliation (Egharevba et al., 1976; Tollenaar and Daynard, 1978c; Barnett and Pearce, 1983) have resulted in a decrease in grain yield .

The timing of competitive stress may also be important. Many studies indicate that competition after flowering has more detrimental effects on grain yield than competitive pressure during vegetative growth. Labelling studies also have shown that less than 10% of grain yield is attributable to assimilates formed before silking (Swank et al., 1982; Simmons and Jones, 1985). However, assimilated carbohydrate before silking may establish sink capacity (Tsai et al., 1978) and thus may be quite important in determining the final yield. Plant stress may also increase the contribution of pre-silking assimilates to yield (Allison and Watson, 1966).

The research described in this study uses isolated plants as a model, to provide a quantitative estimate of the extent of competition taking place on any measured variable in the crop community. The effect of time of reduction in competition pressure at different stages of corn development on kernel development and final grain yield was also investigated.

Materials and Methods

Cultural Practices

A 2 year field study was conducted 1986 and 1987 in the Connecticut River Valley at the University of Massachusetts Agricultural Experiment Station Farm in Deerfield, Massachusetts. The soil type was a Hadley fine sandy loam (Typic Udifluvent,coarse-silty, mixed, nonacid, mesic). In both years the experimental site received 36 Kg N ha^{-1}, 16 Kg P ha^{-1} and 13 Kg K ha^{-1} broadcast prior to planting and 75 Kg N ha^{-1} as side dressed when corn was approximately 40 cm high. Weeds were controlled with a pre-emergence application of cyanazine (2-{[4-chloro-6-(ethylamino)-S-triazin-2-yl]amino}-2-methylporpionitrile), and alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide) at the rates of 1.8 and 2.2 kg a.i. ha^{-1}, respectively. Plots were planted in a North-South direction on May 9, 1986 and May 8, 1987. Tillage practices were mold board plowing and disking prior to planting. No irrigation was found necessary during entire period of growing season in both years. Soil moisture measured gravimetrically during both seasons showed no differences among treatments.

Experimental Treatments

The design of the experiment was a split plot with 3 replications. The main plots were 2 hybrid cultivars; Agway 584S (single-ear, late maturity) and Cornell 281 (semi-prolific, early maturity). Five-row sub-plots were used with rows 91 cm apart and 7.30 m long. The final harvest area for measurement of grain and stover yields at maturity was 3 m^2 taken from the central row. Sub-plots were 5 plant densities; 3, 4.5, 6, 9, and 12 plants m^{-2} combined with 4 removal treatments where alternate plants were cut at the soil surface at 3 critical stages of growth. These were, no removal (R_0), removal during vegetative growth {38 days after emergence (DAE)=R_1}, removal at 50% tassel emergence (59 DAE for Cornell 281 and 73 DAE for Agway 584S=R_2), removal at early grain filling time (80 DAE for Cornell 281 and 88 DAE for Agway 584S=R_3). One larger sub-plot for each hybrid in each replication was allocated to widely spaced or "isolated plants", which were separated by 2 m between plants (0.25 plants m^{-2}). All plots were over seeded and hand-thinned initially using templates that were marked for proper spacings. Thinning was done 10 DAE in both years.

Grain Filling. In order to determine the grain growth rate (GGR) and grain filling period (GFP), ear samples were taken 4 times in 1986 at 5 day intervals starting at 84 DAE for Cornell 281 and 89 DAE for Agway 584S. In 1987, 4 samples for Cornell 281 and 7 samples for Agway 584S were taken, starting at 87 DAE for both varieties. First ear (the uppermost ear when more than one ear was present) of 3 plants in the rows next to the central harvest row were randomly sampled and dried in a forced air oven at 80^0C. After drying, a complete ring of kernels from each of the 3 ears at the base (8th kernel from the bottom), middle (19th kernel from the bottom), and tip (29th kernel from the bottom) was taken and kept separate according to ear position. The number and weight of kernels at each position was then determined. Grain growth rate (GGR) was determined by linear regression of weight per kernel verses sampling date. Grain filling period (GFP) was calculated by dividing final weight per kernel by GGR.

Final Harvest. Grain harvest occurred after physiological maturity and was completed 118 DAE for Cornell 281 and 137 DAE for Agway 584S in 1986. In 1987, grain harvest was completed 110 DAE for Cornell 281 and 131 DAE for Agway 584S. The first (uppermost) and second ear (when present) and ears on tillers when present of all plants in the final harvest area were hand harvested and kept separate. Total weight of ears and stover were measured in the field. All ears were then dried in a forced-air oven at 80^0 C for one week. Moisture content of stover was determined from a 3 plant sub-sample in each sub plot. Number of productive (ears having at least one complete circle of kernels) and nubbin ears was recorded. Length of all ears and number of rows in each ear, were then measured. All the ears were shelled, using a hand-sheller, cobs and kernels were dried again and weighed separately. Weight per kernel was determined from 1000 kernel sub-samples.

Results and Discussion

Yield and Yield Components

Year and the interaction of year with treatment and hybrid were not significant for any yield component (Table 3.1). Results presented are the average of the two years.

Density Effect. Total grain yield for non removal plots reached a maximum of 9.6 Mg ha^{-1} at 6 plants m^{-2} for Agway 584S and 8.3 g ha^{-1} at 9 plants m^{-2} for Cornell 281 (Fig. 3.1).

Plants grown in "isolated" densities (0.25 plants m^{-1}) were used as models to determine the relative level of competition for each yield component. The yield of the plant in isolation represents the full yield potential of the genotype at this location in these years.

Yield components were analyzed to determine how the yield per individual plant in these two hybrids was adjusted to density increase. The significance of the treatment effects and results of the single degrees of freedom comparisons for kernel yield per plant and all dependent variables were determined (Table 3.1). Hybrid and the interaction of hybrid and plant density showed a highly significant differences in all components. This indicated different types of response to competition increase in the two hybrids.

Total kernel yield per plant decreased 75% and 80% compared to isolated plants in Agway 584S and Cornell 281 respectively, with increased density (Fig. 3.2). Competitive effects of density for each yield component for both hybrids as a proportion of the isolated plant component are also shown in Figure 3.2. The relative impact of density on each yield component can be determined by comparing the position and slopes of the regression lines. In single-ear genotype (Agway 584S), all yield components for both total ears and first ear showed a linear response over the density range when treatment was partitioned into single degree of freedom comparisons in the analysis of variance. In semi-prolific hybrid (Cornell 281), however, the response was more complicated. When only first ear was considered, kernel yield per plant, productive ear number per plant and kernel number per row indicated a quadratic relationship. When all ears were taken into account, the components, ear number per plant and kernel number per row indicated a quadratic response.

Table 3.1. Analysis of variance showing the F-test significance for the effect of treatment (density and removal) on the yield and the components of yield in 1986 and 1987.

Source of variation	Grain yield		% Yield plant^{-1}		% Ear plant^{-1}		% Row ear^{-1}		% Kernel row^{-1}		% Weight kernel^{-1}	
	F[†]	T	F	T	F	T	F	T	F	T	F	T
Year (Y)	.559[‡]	.654	.192	.305	.298	.217	.904	.418	.291	.342	.119	.107
Hybrid (H)	.001	.001	.001	.001	.012	.006	.001	.001	.001	.001	.001	.001
Y × H	.052	.095	.042	.093	.131	.221	.053	.077	.504	.557	.001	.001
Treatment (T)	.001	.001	.001	.001	.001	.001	.048	.085	.001	.001	.001	.001
Y × T	.031	.042	.051	.040	.688	.197	.148	.239	.105	.448	.669	.694
H × T	.001	.003	.001	.001	.001	.001	.408	.048	.001	.001	.001	.001
Y × H × T	.312	.237	.087	.052	.107	.175	.824	.786	.721	.884	.068	.120
CV, %	10.1	10.1	8.5	8.5	5.0	8.6	3.7	3.8	6.5	7.7	3.6	3.7

[†] F and T are represent first ear and total ears respectively.
[‡] Probability of a greater F value by chance.

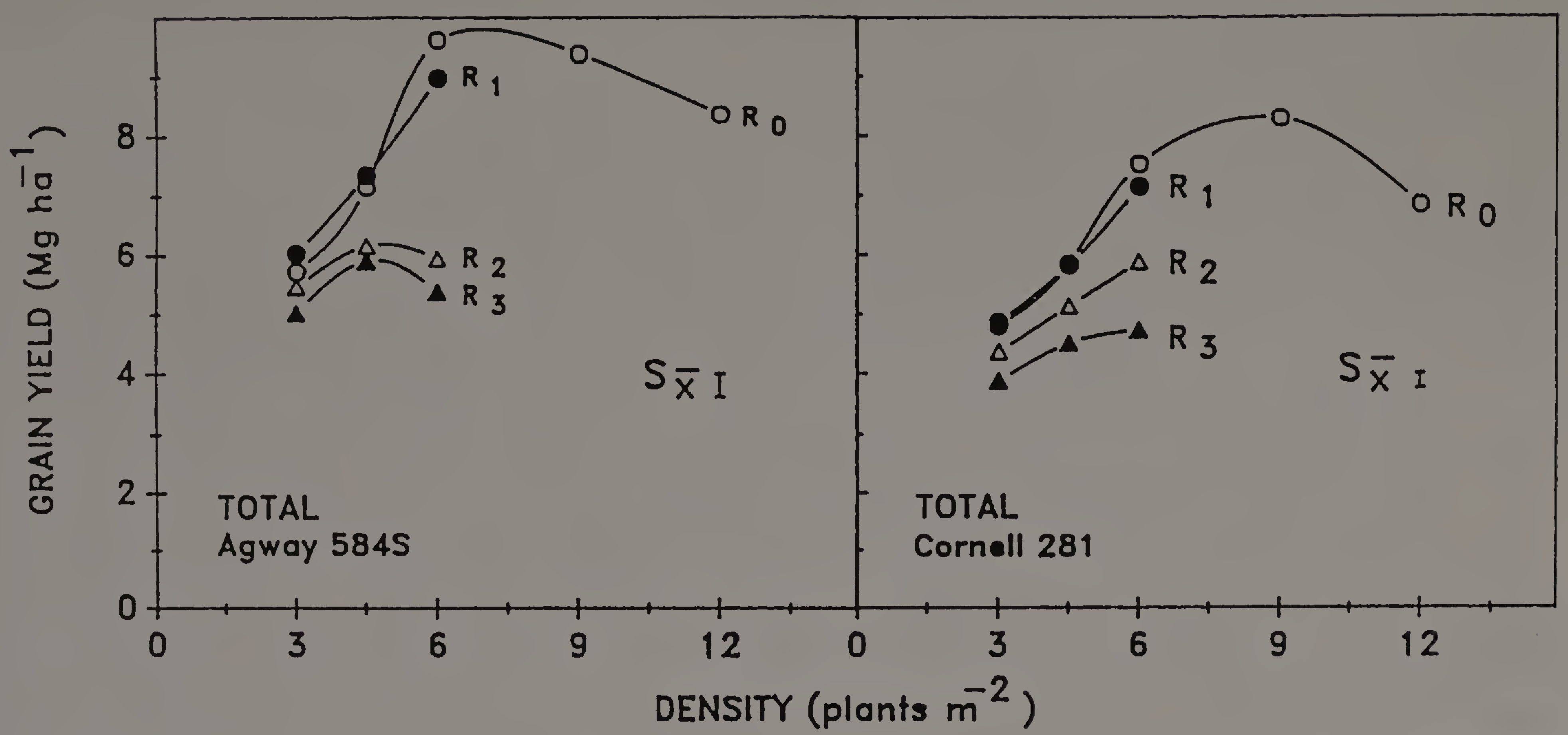

Figure 3.1. Effect of plant density and removal on total kernel yield of 2 corn hybrids. R_0=unthinned, R_1=removal of alternate plants 38 DAE, R_2= removal at 50% tassel emergence, R_3=removal at early grain filling. Average of 2 years.

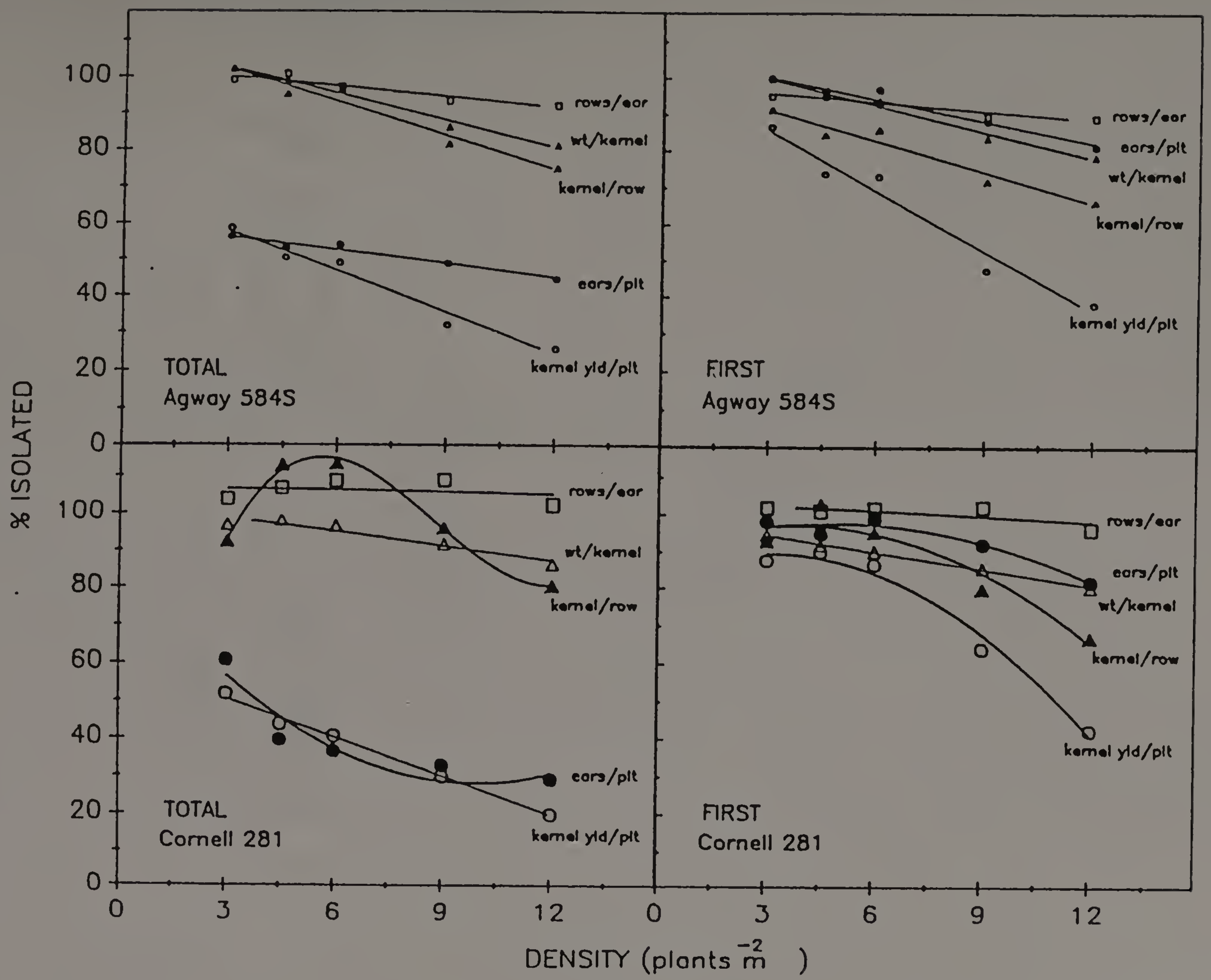

Figure 3.2. Effect of density on total and first ear yield components as a proportion of isolated plants for 2 corn hybrids. (average of 2 years).

The reduction in total kernel yield in both hybrids was mostly due to the reduction in number of productive ears per plant. For Cornell 281 the reduction was almost 50% between the high and low densities. This component in Cornell 281, showed a similar trend to kernel yield reduction as density increased. When only first ears were considered, the number of productive ears in Cornell 281 decreased more slowly withincreasing density (quadratic trend p=0.019) than the linear decrease (P<0.01) for Agway 584S. Cornell 281 was a more prolific hybrid in isolation than Agway 584S. Earlier findings of Lang et al.(1956) and Tetio-Kagho and Gardner (1988b) have indicated that prolific hybrids are more resistant to barrenness as the competition among the crop plants increases. In Agway 584S, the number of both total and first ears per plant decreased linearly as density increased.

Agway 584S had a greater number of kernels per row than Cornell 281 (35.7 vs 29.6 averaged over densities). Number of kernels per row decreased as the density increased. Cornell 281 showed a quadratic response (P=0.013). This being a result of secondary and tiller ears on isolated and the lowest density plants having far fewer kernels per row than first ears at low and medium densities. In Agway 584S kernel number per row decreased throughout the density range. Kernel number per row was the largest contributing component to reduction in first ear yield at high densities in both hybrids (all densities for Agway 584S).

Comparing the weight of individual kernels, showed that the kernels in Agway 584S were heavier than Cornell 281 (307 vs 238 mg, averaged over densities). This contributed greatly to the increased yield of Agway 584S compared to Cornell 281 (Figure 3.1). Both hybrids showed a decrease in weight per kernel as density increased. The decline in weight per kernel with density was greater in Agway 584S than in Cornell 281. The reductions were 21% and 11% when weight per kernel in the highest density was compared to that in the lowest density.

Among the yield components, number of rows per ear showed the highest degree of stability and this component contributed the least to the yield reduction per plant with increased density. Agway 584S showed a small (6%) linear decrease in number of rows per ear but this was not significant in Cornell 281 as the density increased. The results are consistent with other research which showed that this component rarely has any adjusting role in grain yield. When all ears were considered, Cornell 281 showed an increase in number of rows per ear compared to isolated plants. This is again due to more secondary and tiller ears produced in isolated plants which had fewer row numbers than first ears (data not shown). Tetio-Kagho and Gardner (1988b) did not find a significant difference in row numbers in first and secondary ears, but found a significant decrease in tertiary ears.

Removal Effect. A comparison of unthinned plants with thinned plants having the same density after thinning is shown in Figures 3.1 and 3.3. In this way, the effect of competition between the period of seed emergence and time of thinning can be determined.

Plants remaining after early thinning (R_1) had a similar yield at harvest as unthinned plants (Fig. 3.1 and 3.3a, b). This indicates that eny competition during early vegetative growth had no significant effect on final yield. Plant competition between the periods of R_1 (vegetative stage) and R_2 (anthesis) had the greatest influence on yield. Reduction in yield (averaged across densities) between these two periods, was 18% and 13% for Agway 584S and Cornell 281 respectively (Fig. 3.3a). The yield loss was greater in high densities than low densities (Fig. 3.1). For example, in Agway 584S the competition in high density during this period resulted in a 30% reduction in grain yield. The results, differ however, from the findings of Baenziger and Glover (1980), who found less effect of removal on grain yield per ear in higher densities than in lower densities. The competition between R_2 and R_3 (completion of silking), had a stronger effect in Cornell 281 than Agway 584S. For Cornell 281 there was an additional 12% reduction in grain yield compared to 4% for Agway 584S (Fig. 3.1 and 3.3a). The yield pattern of plants thinned at R_2 and R_3 in Agway 584S and R_3 in Cornell 281 was more similar to the yield pattern of R_0 plants at the initial density for these removal treatments (Fig. 3.1).

When compared to their initial densities, the amount of yield compensation with removal of alternate plants was greatest the earlier the removal occurred. The average increase in grain yield compared to plants grown at the initial non thinned density (R_0) was 65, 29 and 19 percent in Agway 584S and 59, 37 and 16 percent in Cornell 281 for R_1 , R_2 and R_3 respectively. These results are consistent with those reported earlier by Schoper et al. (1982). Density also showed a significant interaction with removal. The higher the density, the more increase in grain yield with plant removal. Compared to plants grown at the initial unthinned density (R_0), plants remaining after thinning increased their yield by 15, 31, and 67 percent for the initial densities of 6, 9, and 12 plants m^{-2} respectively.

Genetic factors also might have a significant influence on response to the removal. With prolific hybrids the later the time of removal, the less opportunity to produce secondary or tiller ears. Yield components in the two hybrids did show different responses to increasing assimilate supply through thinning (Fig. 3.3c-f). Row number per ear and weight per kernel showed the least response and are thus not presented. In Agway 584S plant removal had a significant effect on all yield components. However, the component affected most was the number of kernels per row (Fig. 3.3e). Plants thinned at anthesis (R_2) had about 10%

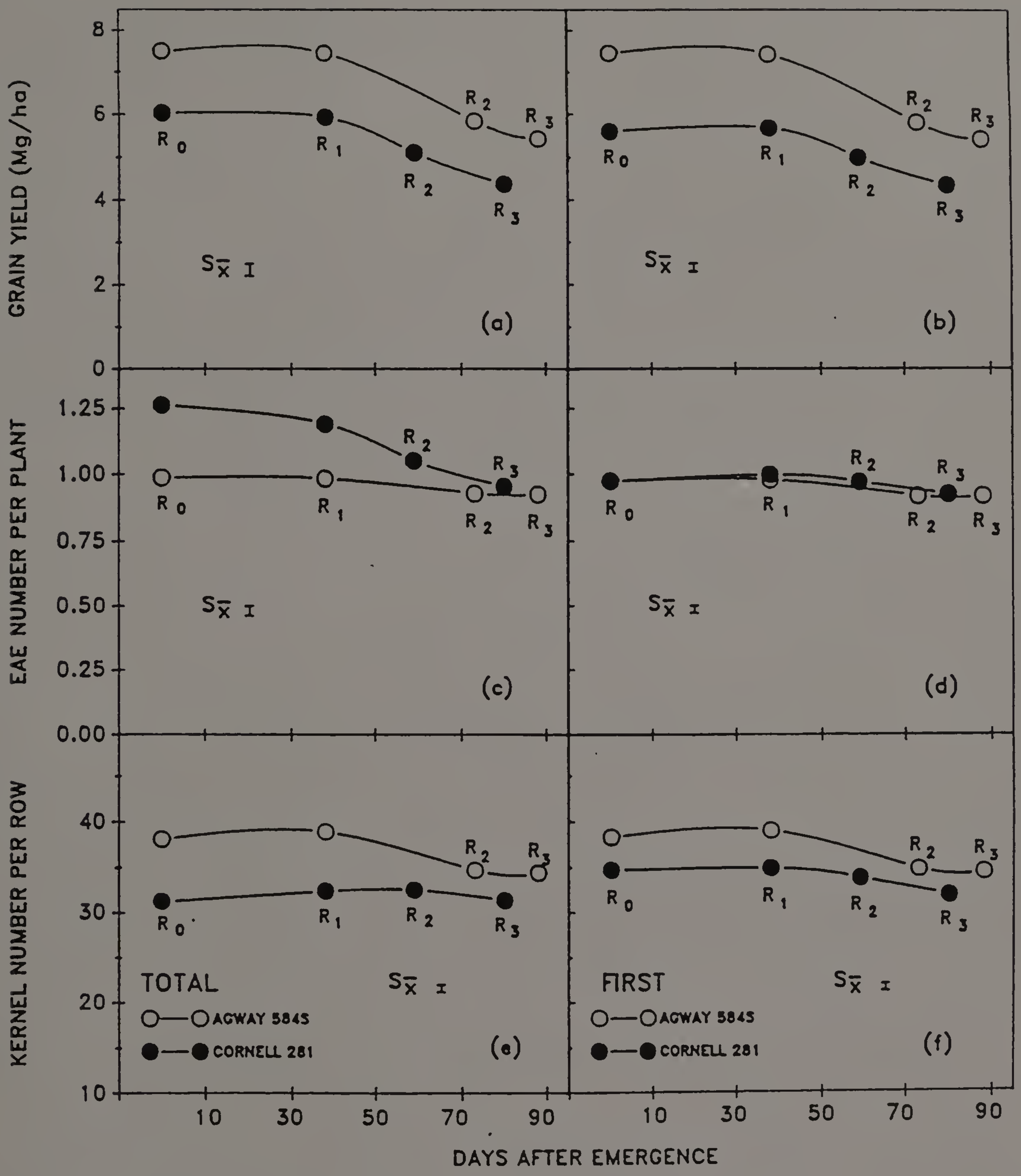

Figure 3.3. Effect of plant removal on grain yield and yield components for two corn hybrids. (Average of 2 years).

fewer kernels per row than those in unthinned plots (averaged over harvest densities). Plant removal did not increase the number of ears per plant in Agway 584S, except in high density and only when this was done early (R_1). In this case it showed a 20% increase compared to the initial density which indicates a partial neutralization of the high density effect on barrenness. Removal at later stages did not show such compensation. For Agway 584S contribution from secondary ears was negligible hence total and first ear yield and yield components show similar trends.

In Cornell 281 none of the yield components in thinned plots, except the number of ears per plant (Fig. 3.3c), wassignificantly different from those in unthinned plots at equivalent harvest densities. This indicates that kernel number per row and weight per kernel, which decreased at high densities in unthinned plots (Fig. 3.2), responded to thinning even at the later stages of growth. There was a large interaction between density and removal date for Cornell 281. However, the main effect for removal on kernel number per row when averaged over densities was not significant (Fig. 3.3e). The highest density plants showed a significant reduction in kernel number per row, as the time of removal approached the harvest time. Medium density plants had little reduction and low density showed an increase in kernel number per row when compared to non thinned densities as the time of removal approached the harvest time. This interaction is due to the role of secondary and tillers ears. Low population plants in unthinned plots produced secondary and tiller ears while the plants in removal plots which were initially planted twice as dense than unthinned plots, produced few secondary and tillers ears especially when removal was delayed to silking or grain filling. Since the number of kernels per row in tiller and secondary ears was less than first ears (data not shown) and production of these ears was more sensitive to density increase than the main ear (Fig. 3.2) (Tetio-Kagho and Gardner, 1988b), the delay in removal in reducing secondary and tiller ears resulted in the increase in kernel number per row in the low density. In high densities secondary and tiller ears were not produced thus late removal resulted in kernel number per ear showing a reduction as occurred in Agway 584S (non prolific hybrid) and unthinned high density plant in Cornell 281.

Frey (1981) reported that thinning at 50% silking had no effect on number of kernels that already showed some growth. However, enhancement of assimilate supply through thinning at this stage of growth resulted in more developed kernels. Baenziger and Glover (1980), also reported no significant differences for weight per kernel in thinnings at different times. Wilson and Allison (1978), reported late removal at the grain filling stage had little effect on weight per kernel but increased the weight per kernel when done before or at about flowering. Schoper et al. (1982), using reflectors concluded that increase in assimilate supply 4-6 weeks after silk emergence had a significant effect on kernel size while earlier than that had no significant effect.

Plant removal also had no significant effect on number of rows per ear in Cornell 281 and little effect in Agway 584S. This is also consistent with the results obtained by Schoper et al. (1982), who found no effect in row number when assimilate supply was increased by either reflectors or plant removal. Number of rows seems genetically controlled and environmental factors have little effects on it. In Chapter 4 we have reported that the effect of high density and artificial shade (50% reduction in ambient light), reduced the row numbers by less than 10%. Tetio-Kagho and Gardner (1988b) concluded that in prolific hybrids, number of rows in secondary and tertiary ears may have a greater adjusting role in grain yield.

Seed Development

Growth Rate. The overall means of growth filling rate in Cornell 281 and Agway 584S were 8.4 and 8.0 mg/kernel/day respectively. This difference was not significant (p=.37). However, the density showed a significant effect. Increasing density decreased kernel growth rate (Fig. 3.4). The mean kernel growth rate in isolated plots was lower than at the low density in both hybrids. This indicates that some within plant competition occurred when tiller and secondary ears

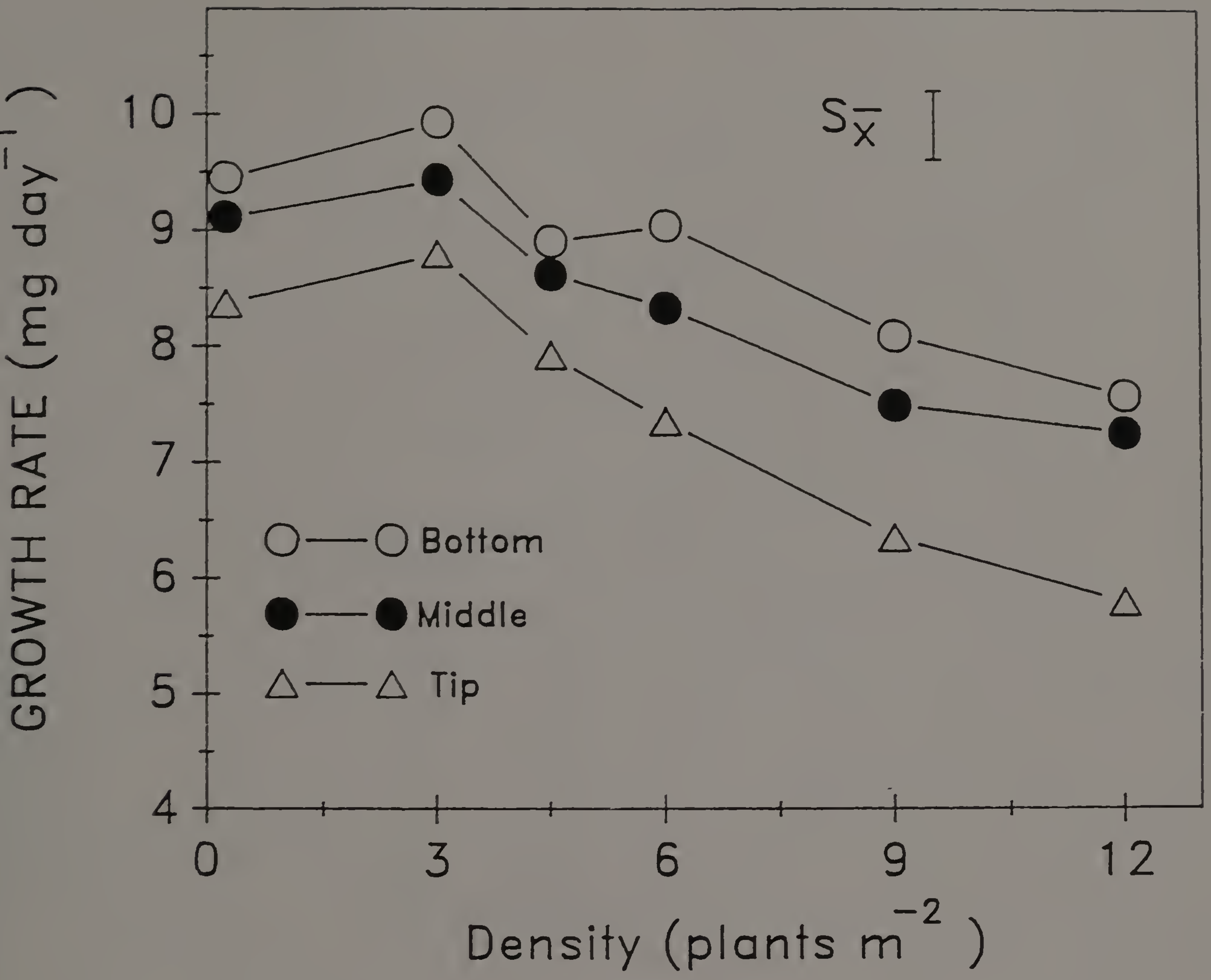

Figure 3.4. Effect of density on grain growth rate at 3 positions in the ear. Values are the average of the 2 hybrids and 2 years.

were produced. Poneleit and Egli (1979) had reported that the kernel growth rate was not affected by plant density. This difference, however, might be due to moderate densities they used in their study.

Growth rate also varied in different positions within the ear. Kernels at the middle of the ears had a 3% slower growth rate than basal kernels, while tip kernels showed an 11% reduction compared to basal kernels. The results are consistent with the earlier reports by Frey (1981) and Tollenaar and Daynard (1978a) that tip kernels have slower growth rate than basal kernels.

Removal at either vegetative or early reproductive stages of growth did not change the kernel growth rate significantly (data not shown). Many reports also have shown that source-sink alterations through defoliation had littleor no effect on kernel filling rate (Duncan et al., 1965; Egharevba et al., 1976; Jones and Simmons, 1983).

<u>Filling Period.</u> The average seed filling periods for Agway 584S and Cornell 281 were 40.2 and 28.7 days, respectively, and were significantly different (p=.017). Neither density nor plant removal showed a significant effect on duration of seed filling. This agrees with the results obtained by Schoper et al. (1982). They reported that increase in photosynthate per plant through thinning had no effect on grain filling period. Poneleit and Egli

(1979), however, reported a 2.5 day reduction in filling time in high density compared to low density.

Summary

In summary, isolated plants were used to index the yield potential relationship with density. The data from these experiments indicate that the hybrids showed different responses to competition pressure. Number of kernels per row in Agway 584S and number of productive ears per plant in Cornell 281 were found to be the most sensitive yield components. They showed the greatest decline as the density increased and increased more than any other components when the competition pressure was released through plant removal.

The greater mass of kernels in Agway 584S compared to Cornell 281 was due to longer filling duration.

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CHAPTER 4

INTENSIFYING PLANT DENSITY RESPONSE OF CORN WITH ARTIFICIAL SHADE

Abstract

Competition among corn plants for interception of photosynthetically active radiation (PAR) at high density usually results in a severe reduction in kernel number or complete ear barrenness. The response of field corn to long term shading as density increased was investigated during 1987 and 1988. A single-ear hybrid (Agway 584S) was grown in Agricultural Experiment Station Farm, University of Massachusetts, at 3 densities of 3, 7.5, and 12 plants m^{-2}. Shading factorially combined with density and was provided by using black polypropylene fabric with 50% light penetration installed 44 days after emergence. The rate of photosynthesis in ear leaves was reduced significantly by both increased density and shading. The reduction was attributable to reduced PAR in higher densities and shaded plots and to the decreased chlorophyll concentration in leaves of high density plants in both ambient light and shaded plots. Tassel emergence was slightly delayed in high density and shaded plots. However, the time of silking was delayed significantly due to both high density and shading. Nine days after 100% tasseling, 10% of plants in high densities and 50% of plants in shaded plots had no silk. Response of grain yield per unit area in ambient light to increasing density was quadratic. With shade, no increase in yield was obtained with density increase. Shade reduced number of productive ears per plant together with a reduction in number of kernels per row which resulted in 23% and 66% yield reduction in low and high densities respectively, when compared to ambient light. Weight per kernel was reduced 28% with increased density. Shading did not intensify the response. Number of rows per ear was least sensitive to both density increase and shading.

Introduction

Use of high plant densities is the primary technique used to increase the yield per unit area. While yield per plant decreases with increased density, total light interception by the canopy is maximized and total yield is increased. The response of grain yield to increase in densities is parabolic (Kohnke and Miles, 1951; Duncan, 1958; Bunting, 1973; Karlen and Camp, 1985). Reduction in grain yield at high densities is partly due to an increase in ear barrenness (Lang et al., 1956; Moss and Stinson, 1961; Woolley et al., 1962; Buren et al., 1974; Daynard and Muldoon, 1983), and/or decrease in number of kernels per ear (Iremiren and Milbourn, 1980; Tetio-Kagho and Gardner, 1988b). A reduction in the number of kernels per ear may result from fewer flower initials being formed prior to flowering, from poor pollination due to desynchronization of tasseling and silking, and from abortion of kernels after fertilization. Although reduction in number of fully developed florets has been reported (Wilson and Allison, 1978; Iremiren and Milbourn, 1980) it seems that the effect of high population densities on extension of the tasseling-to-silking interval (Woolley et al., 1962; Bunting, 1973; Buren et al., 1974; Daynard and Muldoon, 1983) and lack of kernel filling are more detrimental.

Artificial shading may have effects similar to those of high densities. Reduction of incident light, particularly during reproductive growth, causes a severe reduction in grain yield mainly through a decrease in kernel number (Early et al., 1967; Kiniry and Ritchie, 1985; Reed et al., 1988). Kernel number or sink size is established during silking (Tollenaar, 1977). Therefore, any stress such as water deficit (Herrero and Johnson, 1981; Grant et al., 1989), artificial shading (Moss and Stinson, 1961; Early et al., 1967) or defoliation (Cloninger et al., 1974; Singh and Nair, 1975; Tollenaar and Daynard, 1978; Kiniry and Ritchie, 1985) that delays silking, may cause abortion of kernels at the ear tip and complete barrenness (Stinson and Moss, 1960; Buren et al., 1974; Karlen and Camp, 1985).

No study we are aware of has examined the relationship in corn between plant density and long term shading. This is of interest for a greater understanding of the response of corn to decreasing light availability to each plant as density increases. In this study the effect of density and shading were examined for forage and grain yield, and grain yield components.

Materials and Methods

Cultural Practices

A 2-year field study was conducted 1987 and 1988 in the Connecticut River Valley at the University of Massachusetts Agricultural Experiment Station Farm in Deerfield, Massachusetts. The soil type was a Hadley fine sandy loam (Typic Udifluvent, coarse-silty, mixed, nonacid, mesic). In 1987, the experimental site received 2200 kg ha^{-1} lime and a basal application of 66-30-23 kg ha^{-1} of N-P-K broadcast prior to planting and 100 kg N ha^{-1} as a side dressing four weeks after planting. In 1988, the experimental site tested high for P and K, thus only N supplied as NH_4NO_3 was added; 75 kg N ha^{-1} preplant plus 95 kg N ha^{-1} sidedress. In both years, weed control consisted of 1.8 kg a.i. ha^{-1} cyanazine (2-{[4-chloro-6-(ethylamino)-S-triazin-2-yl]amino}-2-methylporpionitrile), and 2.2 kg a.i. ha^{-1} alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide) pre emergence. Tillage practices were mold-board plowing and disking prior to planting. Irrigation was not needed in either year.

A single-ear late maturity corn hybrid (Agway 584S) was planted on 7 May 1987 and 4 May 1988. The experiment was arranged in a randomized complete block design with 3 replications. Five-row plots were 6 m in length with a row spacing of 76 cm. The final harvest area for measurement of grain and stover yields at maturity was 3 m^2 taken from the central row. All plots were over-seeded and thinned to desired densities of 3, 7.5 and 12 plants m^{-2}, 15 days after emergence (DAE).

Each density was factorially combined with two light regimes; ambient light intensity (full light) and a shade treatment. Shade was provided by using black polypropylene fabric with 50% light penetration. The shade cloths were kept in place above the plants using metal wires attached to wooden posts. The shade cloths were installed 44 DAE and were kept approximately one meter above the plants by moving the cloths up every week.

Measurements and Samplings

Interception of Photosynthetically Active Radiation.

Measurements of available photosynthetically active radiation were taken above, within, and below the canopy for all plant densities in both light regimes. Measurements were obtained with a Li-Cor line quantum sensor (LI-188B), at 1045 to 1315 h on days when clouds caused no interference. All readings were integrated over 1 m and 10 s. Inter-row light readings were taken with the light sensor placed across the inter-row space, at 0, 70, 120, 150, and 180 cm above the ground, and above the canopy. Readings from three adjacent plants in each plot were taken at early anthesis (July 27) and early grain fill (August 12). Number of leaves between each 2 consecutive heights were also counted.

Photosynthesis. The rate of photosynthesis was measured at the early grain fill stage on August 8, 1988, using a LI-COR 6000 portable photosynthesis system. For this measurement, ear leaves of 3 consecutive plants in a row adjacent to the final harvest area were randomly selected. Measurements were replicated twice for the low and high densities, and were made on a day when clouds caused no interference.

Chlorophyll Concentration. The concentration of chlorophyll in each ear leaf was determined immediately after photosynthesis measurements were taken using the procedure reviewed by Bruinsma (1963). Starting from the edge of the leaf blade, 1 cm^2 disks were cut from the middle of each ear leaf that had been used for the photosynthesis measurement. Disks were macerated with a mortar and pestle and extracted with 80% (v/v) acetone. Extracts were refrigerated at 5°C in darkness until analysis. Total chlorophyll (a and b) content was determined using a Coleman model 124D double beam spectrophotometer (Coleman Instruments, Maywood, IL), with optical density at 663 and 645 nm (MacKinney, 1941; Arnon, 1948).

Tasseling and Silking. The number of plants with tassels (fully exposed tassels still with closed flowers) and with silks (visible silks emerged out of the husks) were recorded from July 26 to August 8, 1988 (70-83 DAE) for all plants in the final harvest area of all plots.

Final Harvest. Grain harvesting occurred after physiological maturity; 130 and 134 DAE in 1987 and 1988 respectively. The ears of all plants in the final harvest area were hand-picked and length and number of rows in each ear were measured. All ears were shelled, using a hand-sheller. Cobs and kernels were dried in a force-air oven at 70^0C for at least 72 hours and weighed separately. Weight per kernel was determined from 1000 kernel sub-samples which were dried again then weighed. Stover dry weight, was measured by harvesting all plants (minus harvested ears) in the final harvest area. A 3-plant sub-sample was chopped in the field before drying to determine moisture content.

Results and Discussion

Interception of PAR

Light measurements showed that as density increased from 3 to 7.5 plants m^{-2}, available light at the soil surface was decreased by about 20% throughout the canopy in both shaded and ambient light conditions (Fig. 4.1). However, with shading further increase in density up to 12 plants m^{-2} had no significant effect on canopy interception of available photosynthetically active radiation (PAR). Relative PAR at the ear position as a percentage of above the unshaded canopy PAR decreased from 48% in the low density to 15% in high density in the ambient light regime (Fig. 4.2). Average ear height in ambient light was approximately 150 cm. These results are consistent with an earlier report by Tetio-Kagho and Gardner (1988a). With shading, average ear height was decreased to 130 cm. In shaded plots, only 22% of the full ambient light was available at the ear position and that decreased to 5% at the high density.

The number of leaves per plant averaged 13.6 and was unaffected by density or light regime.

Photosynthesis

Ear leaf photosynthesis rate measured at the early grain filling stage decreased greatly, as the density increased from low to high (Table 4.1). The reduction was 48 and 58 percent for 1987 and 1988, respectively. Shading caused a 39% reduction in photosynthesis.

Chlorophyll

Chlorophyll content was also decreased significantly as density increased (Table 4.1). The reduction in rate of photosynthesis was attributed to greater mutual shading in

Table 4.1. Effect of density and shading on photosynthesis rate and chlorophyll content of the ear-leaf during early grain filling.

Treatment	Density	Rate of Photosynthesis 1987	Rate of Photosynthesis 1988	Chlorophyll content 1988
	plants m^{-2}	mg s^{-1} m^{-2}		ug cm^{-2}
Shaded	3	0.619	0.719	6.34
	7.5	-	-	5.72
	12	0.273	0.279	5.54
Ambient	3	0.918	1.157	7.96
	7.5	-	-	6.16
	12	0.532	0.490	5.75
Source of variations				
Light (L)		.001†	.001	.002
Density (D)		.001	.001	.001
L × D		.765	.141	.026
CV, %		19.3	12.1	10.1

† Probability of a greater F value by chance.

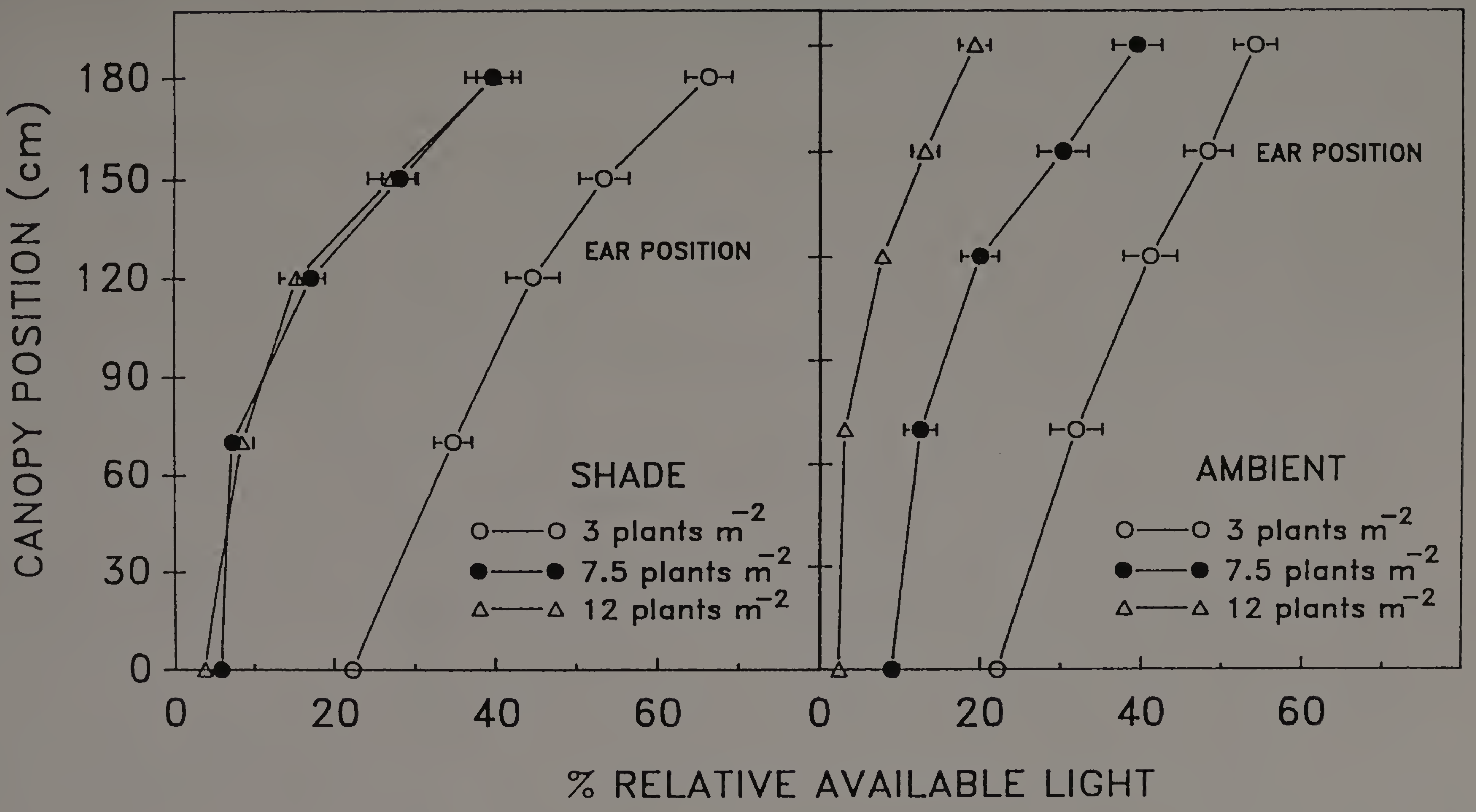

Figure 4.1. Light distribution within canopies of shade and ambient light treatments. Average of readings at or above ground taken on two separate days in each of two years at silking. Horizontal lines represent standard error of mean.

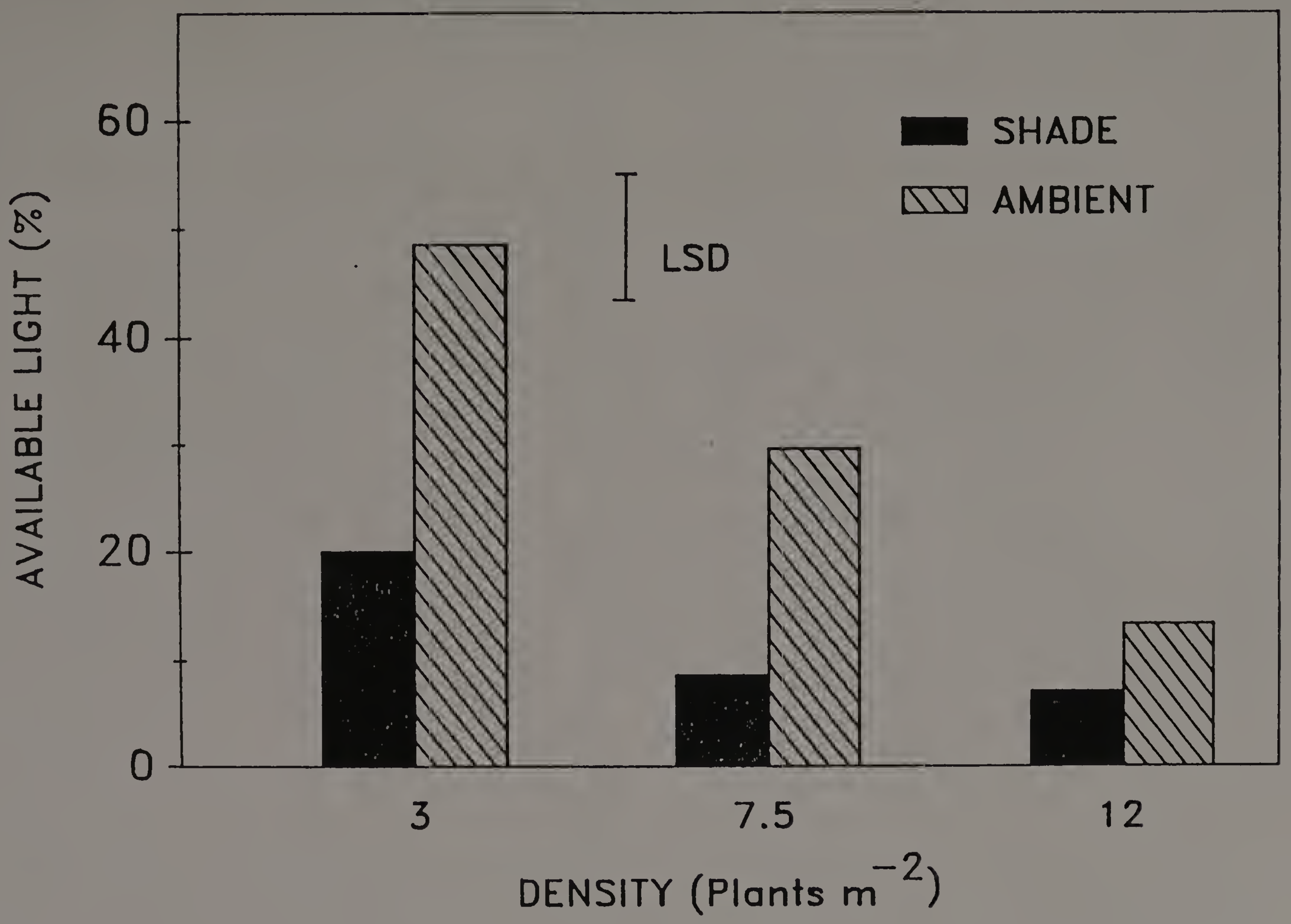

Figure 4.2. Light available (%) at the ear position relative to ambient light above the canopy. Average of readings taken on two separate days in each of two years at silking.

higher densities and to the decrease in chlorophyll content of ear leaf. A high correlation (r=0.62) was found between chlorophyll content and rate of photosynthesis. These effects were intensified by shading.

Silking Pattern

Tassel emergence was slightly delayed in high density and shaded plots (Fig. 4.3). However, all treatments had 100% tassel emergence 86 days after planting (DAP). Plants at low densities in shade and ambient light reached 100% silking 2-3 days after 100% tassel emergence (Fig. 4.4). The time for 100 percent silking in ambient light was delayed by up to 5 days as the density increased from 3 to 7.5 plants m^{-2}. In the high density, about 10% of the plants did not show any silk 9 days after 100% tassel emergence. With shade, 9 days after 100% tasselling, 25% and 50% of plants in medium and high densities, respectively, had no silk. Plants without silks for this length of time after 100% tassel emergence would remain barren even if silking occurred later, due to desynchronization between pollen shed and silking (Buren et al., 1974; Daynard and Muldoon, 1983). Such desynchronization can be related to the decrease in kernel number per ear, number of barren plants, and therefore, to the change in total grain yield.

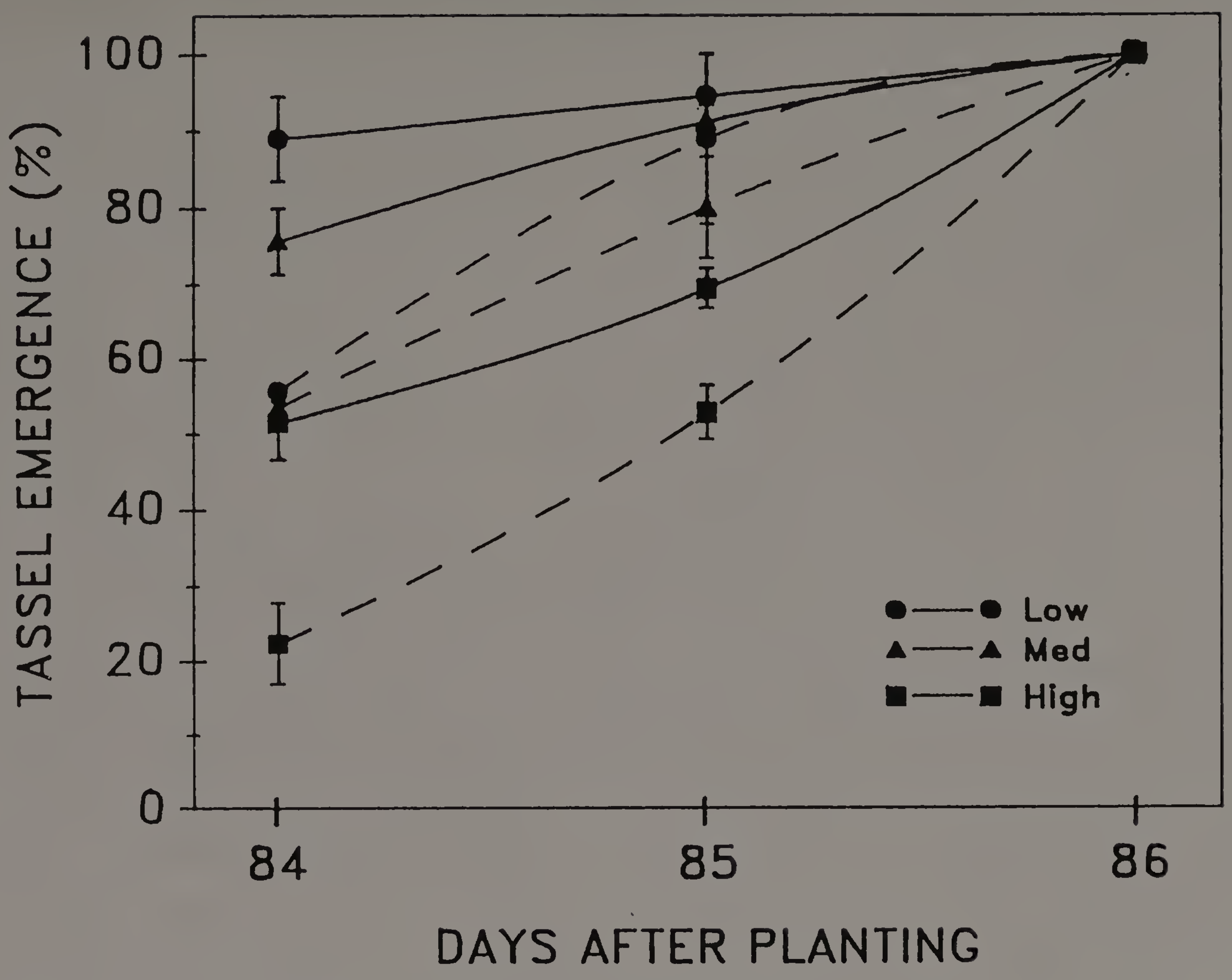

Figure 4.3. Pattern of tassel emergence for light (ambient solid, shade dash) and density treatments. Vertical lines represent standard error of mean.

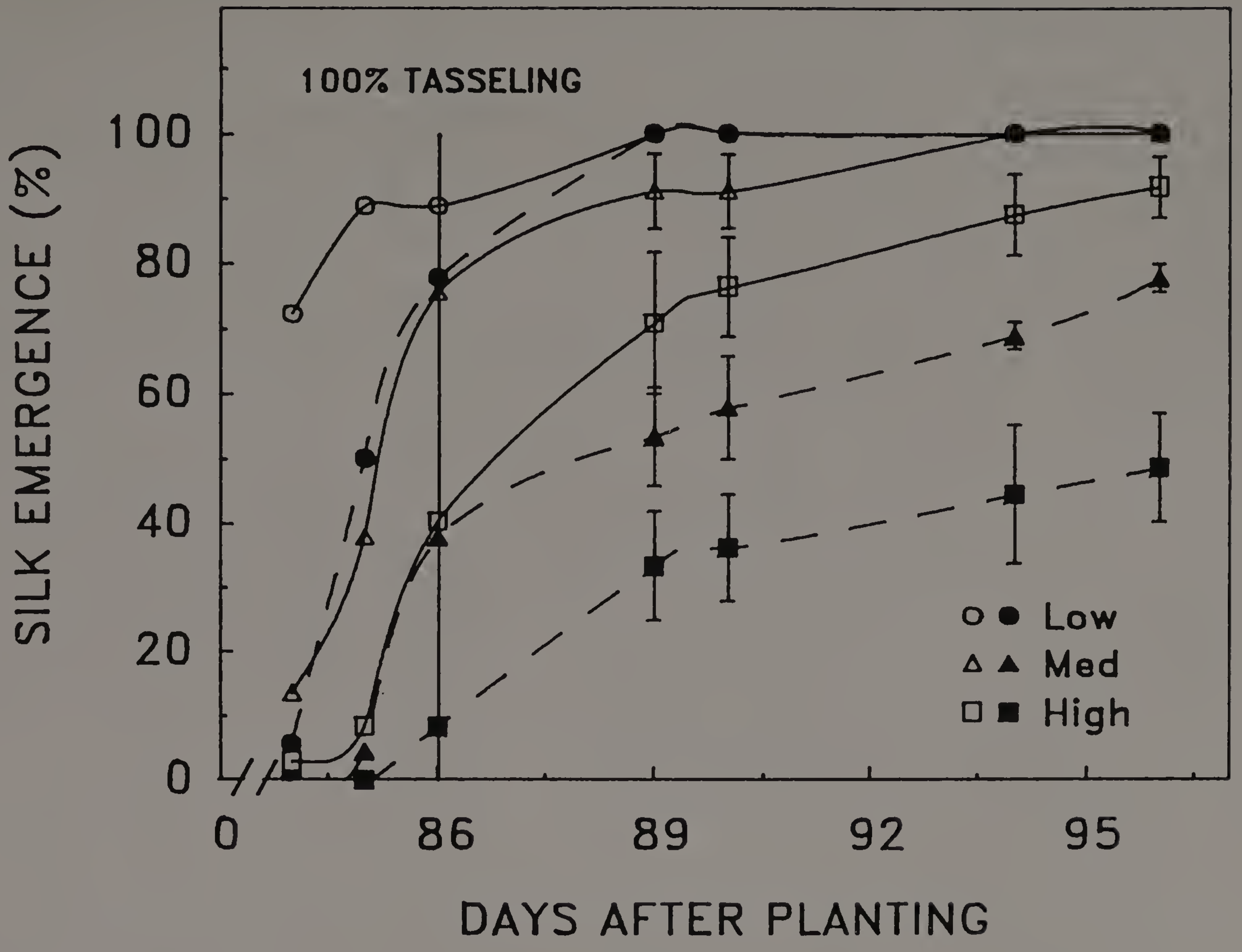

Figure 4.4. Pattern of silk emergence in relation to 100% tasseling (86 DAP) for light (ambient solid, shade dash) and density treatments. Vertical lines represent standard error of mean.

Yield and Yield Components

Total dry matter increased with increasing density in ambient light. However, yield was unaffected by density for shaded treatments. Response of grain yield in ambient light to increasing density was quadratic (Table 4.2). However, in shade, no increase in yield was found with increasing density. At low density, grain yield was reduced by 23% with shaded compared to low density ambient light. In high density grain yield was reduced by 66%. The reduction in grain yield per plant with increased density was partly due to an increase in barrenness (Table 4.2). At low density each plant developed an ear in both ambient light and shade. However, the number of barren stalks increased linearly as the density increased. Shading intensified this effect. In ambient light 15% of the plants were barren at high density compared to 51% in shaded high density plots. These results are consistent with the pattern of silking in relation to time of pollen shed at tassel emergence. At high density, silk emergence was delayed (Fig. 4.3) leading to increased barrenness and reduced average grain yield per plant (Table 4.2). Other studies have shown that the length of interval between pollen shedding and silking greatly influenced barrenness (Woolley et al., 1962; Buren et al., 1974; Karlen and Camp, 1985). In our study shading intensified this response.

Kernel number per row was also greatly reduced with increased density and this was intensified with shading

Table 4.2. Interactive effect of shading and density on yield and yield components. Results are average of 2 years.

Light Treatment	Density	Grain yield	Kernel yield	Ear plant^{-1}	Row# ear^{-1}	Kernel# row^{-1}	Weight kernel^{-1}
	Plants m^{-2}	kg ha^{-1}	g plant^{-1}				mg
Shaded	3	4812	160.4	1.00	14.1	38.4	298
	7.5	4418	58.9	0.76	13.2	17.3	259
	12	3165	26.4	0.49	12.6	8.7	247
Ambient	3	6223	207.4	1.00	13.9	43.5	344
	7.5	10098	134.6	0.97	13.7	37.6	266
	12	9214	76.8	0.85	13.0	23.9	246
Source of variations							
Year		.203†	.264	.020	.311	.831	.008
Treatment		.005	.001	.041	.005	.007	.053
Shd vs Ambient		.001	.001	.039	.179	.007	.284
Dens w/in Shd (L)‡		.171	.001	.007	.001	.002	.091
Dens w/in Shd (Q)		.651	.034	.903	.558	.247	.548
Dens w/in Amb (L)		.034	.001	.255	.010	.016	.010
Dens w/in Amb (Q)		.045	.558	.686	.261	.457	.220
CV, %		16.4	14.2	8.4	3.8	14.4	4.4

† Probability of a greater F value by chance.
‡ L = linear and Q = quadratic trends, respectively.

(Table 4.2). High density plants in ambient light had 45% fewer kernels per row compared to low density plants. With shade this reduction was 77%. Poor pollination due to a prolonged interval between pollen shed and silking would contribute to this reduction in kernel number per row. Reduced assimilate supply resulting from the light reduction in high density and shaded plots would also contribute to this reduction in kernel number per row. Reduced assimilate supply causes abortion of kernels especially at the ear tip (Reddy and Daynard, 1983).

Weight per kernel was also significantly decreased by density, more so than row number per ear but less than kernel number per row and ear number per plant. Weight per Kernel reductions in ambient light were 23 and 28% in medium and high densities respectively. Shading caused a 13% reduction in weight per kernel at low density. However, it did not cause further reduction in weight per kernel in medium and high densities when compared with weight per kernel for these densities in the full light condition. Adjustments in kernel number per row perhaps compensated for the light reduction allowing remaining kernels to fill to a similar weight as those in ambient light. Recently, Kiniry et al. (1990) reported that increase in weight per kernel was a result of artificially reducing kernel number (by bagging the ears). This depended on the hybrid and the timing of bagging inducing the kernel number reduction. However, they suggested that a more complex relationship may exist between manipulation of assimilate supply and weight per kernel.

Number of rows per ear showed the least effect under either shading or high density. Shading had no significant effect on row number per ear. Although significant, the reduction in row number per ear was less than 10% between low density and high density.

In summary, the effect of high density and shading on yield components were similar. Shading intensified the density effect. The primary effect of reduction of available light is to reduce photosynthesis. This would then reduce assimilate supply for yield development. However, reduction in light level also decreased the yield through postponing silk emergence which in turn caused a large reduction in kernel number per ear and increase in barrenness.

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CHAPTER 5

EFFECT OF LEAF ORIENTATION AND DENSITY ON YIELD OF CORN

Abstract

Genetic selection for adaptation to different environments has contributed significantly to yield improvements in corn. The mechanism of tolerance to high densities, however, is not fully understood. Six corn hybrids, two each known to have upright, semi-upright, and horizontal leaves were grown at 3 densities in 1987 and 1988. Several morphological and physiological traits as well as yield performance of the hybrids were investigated. Yields in 1988 were greater than 1987. Growing degree days (GDD) and precipitation were greater in 1988. Rate of photosynthesis in ear leaves was not significantly different among the hybrids. This may have been influenced by differences in phenological development and ear height. Highly significant difference in rate of photosynthesis and concentration of chlorophyll were shown between the high and low densities in all hybrids. With increasing density there was a tendency for hybrids to have more erect leaves, an increased the ear height, and reduction in tassel size. In 1987, no significant difference in the grain yield of hybrids averaged over densities was found although there were interactions with density. However, in 1988 upright and semi-upright hybrids out-yielded hybrids with horizontal leaves. The results indicated that the advantage of grain yield in upright leaf hybrids would prevailed only in at favorable climatological conditions and high densities. The number of productive ears per plant was the most sensitive component of yield to increased density where an average of 36 percent reduction was observed. Reductions in kernel number per row and weight per kernel were less affected by density than ears per plant. Row number per ear was least influenced by density.

Introduction

Within a given environment, the productivity of a crop canopy depends on the level of available resources and the genetic potential of the crop to exploit that environment. The productivity of a crop canopy is ultimately determined by the quantity of intercepted photosynthetically active radiation (PAR) , when other environmental factors are favorable. A common practice for maximizing interception of PAR is increasing the plant density. However, not all corn genotypes respond positively to density increase. The response of grain yield to increasing density is parabolic. It declines when the number of plants exceeds the optimum density. Reduction in yield is primarily due to reduction in kernel number (Iremiren and Milbourn, 1980; Tetio-Kagho and Gardner, 1988b) and barrenness (Buren et al.,1974; Daynard and Muldoon, 1983). This is primarily due to inter-plant competition for incoming solar energy. In Chapter 4, it was shown that shading caused a dramatic increase in barrenness. A 50% light reduction at high density resulted in 50% barren stalks. Other researchers also reported that high density had a high correlation with barrenness (Bunting, 1973; Genter and Camper, 1973). The results of detasseling research has shown a decrease in barrenness and an increase in grain yield in higher densities when tassels were removed (Grogan, 1956; Duncan et al., 1967; Hunter et al., 1969). Buren et al. (1974) concluded that the high density tolerant cultivars could be characterized by rapid silking, less pollen shed-silking intervals, prolificacy, and reduced tassel size.

In densely planted corn, the upper one-half of the plant canopy intercepted almost all incoming solar radiation, while the lower leaves are shaded (Chapters 2 and 4). Ottman and Welch (1988) using fluorescent lamps, showed that supplemental radiation at the lower part of the corn canopy resulted in 54% increase in dry matter production. Light penetration to lower region of crop canopy, theoretically, might be increased by altering canopy architecture with the use of upright verses horizontal leaves (Pendleton et al., 1968; Duncan, 1971). Vertical leaves result in a more uniform distribution of light through the canopy area by intercepting less light at the top of the canopy and increasing light penetrating to lower leaves (Bunting, 1973; Pepper et al., 1977). Duncan (1971) showed that a corn canopy with upright leaves at the top and horizontal leaves at the lower parts potentially could tolerate a leaf area index (LAI) value of 10 with no reduction in dry matter production. Using mechanically supporting leaves above the ear in a vertical position as well as use of hybrids with upright leaves showed a substantial increase in grain yield which was attributed mainly to decrease in barrenness (Pendleton et al., 1968; Winter and Ohlrogge, 1973; Pepper et al., 1977). However, Russel (1972) did not find an advantage of upright over horizontal leaf hybrids.

The following experiment examines the interaction of plant density with corn hybrids having different leaf orientations.

Materials and Methods

Cultural Practices

A 2 year field study was conducted 1987 and 1988 in the Connecticut River Valley at the University of Massachusetts Agricultural Experiment Station Farm in Deerfield, Massachusetts. The soil type was a Hadley fine sandy loam (Typic Udifluvent, coarse-silty, mixed, nonacid, mesic). In 1987, the experimental site received 2200 kg ha^{-1} lime and a basal application of 66-30-23 kg ha^{-1} of N-P-K broadcast prior to planting and 100 kg N ha^{-1} as a side dressing four weeks after planting. In 1988, the experimental site tested high for P and K, thus only N supplied as NH_4NO_3 was added; 75 kg N ha^{-1} preplant plus 95 kg N ha^{-1} sidedress. In both years, weeds were controlled with 1.8 kg a.i. ha^{-1} cyanazine

(2-{[4-chloro-6-(ethylamino)-S-triazin-2-yl]amino}-2-methylporpionitrile), and 2.2 kg a.i. ha^{-1} alachlor (2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide) pre emergence. Tillage practices were mold-board plowing and disking prior to planting. Plants were not irrigated during the entire growing seasons of both years.

Six hybrids with different leaf orientation habitats were planted on 21 May 1987 and 5 May 1988. The selection of hybrids was based on their performance in earlier hybrid corn evaluation at this location. The hybrids were (numbers in parenthesis represent the hybrid code):

Upright = Agway 650X (1) and Hytest 650A (2).
Semi-upright = Pioneer 3475 (3) and Hytest 712 (4).
Horizontal = Agway 584S (5) and Funks G4027 (6).

The experiment was arranged in a randomized complete block design with 4 replications in 1987 and 3 replications in 1988. Five-row plots were 5.0 and 6.6 m in length in 1987 and 1988 respectively, with a row spacing of 76 cm. The final harvest area for measurement of grain and stover yields at maturity was 2 m^2 in 1987 and 3 m^2 in 1988, taken from the central row. Each hybrid was factorially combined with 3 densities. All plots were over-seeded and thinned to desired densities of 3, 7.5, and 12 plants m^{-2}, 15 days after emergence (DAE).

Measurements and Samplings

Soil Moisture Content. Soil moisture content in all plots was measured at late vegetative stage of growth 10 days after the last rainfall. Two samples in each plot was taken at 2 depths of 0-20 and 20-40 cm, using an auger. Samples were weighed before and after oven drying. Using the following equation, percent water available at each depth was determined:

$$\% \text{ water} = 100 \text{ X } (\text{sample wet weight} - \text{sample dry weight}) / \text{sample dry weight}$$

Interception of PAR. Measurements of available PAR were taken above, within, and below the canopy for all plant densities and hybrids in 2 replications. Measurements were obtained with a Li-Cor line quantum sensor (LI-188B), at 1045 to 1315 h on days when clouds caused no interference. All readings were integrated over 1 m and 10 s. Inter-row light readings were taken with the light sensor placed across the inter-row space, at 0, 70, 120, 150, and 180 cm above the ground, and above the canopy. Readings from 3 adjacent plants in each plot were taken at completion of tasseling for the latest maturity hybrids i.e. hybrids 2 and 4.

Photosynthesis. Using a LI-COR 6000 portable photosynthesis system, the rate of photosynthesis was measured on August 5 and August 11 which coincided with mid-silking stage of latest hybrids (hybrids 2 and 4). For this measurement, ear leaves of 3 consecutive plants in a row adjacent to the final harvest area were randomly selected. Measurements were replicated 2 times for the low and high densities and were made on a day when clouds caused no interference.

<u>Chlorophyll.</u> The concentration of chlorophyll in each ear leaf was determined immediately after photosynthesis measurements were taken, using the procedure reviewed by Bruinsma (1963). Starting from the edge of the leaf blade, 1 cm^2 disks were cut from the middle of each ear leaf that had been used for the photosynthesis measurement. Disks were macerated with a mortar and pestle and extracted with 80% (V/V) acetone. Extracts were refrigerated at 5°C in darkness until analysis. Total chlorophyll (a and b) content was determined using a Coleman model 124D double beam spectrophotometer (Coleman Instruments, Maywood, IL) with optical density at 663 and 645 nm (MacKinney, 1941; Arnon, 1948).

<u>Plant and Ear Height.</u> In 1988, plant height, tassel length (total height - soil surface to the bottom of the tassels), and ear height of 5 consecutive plants randomly selected within each plot was measured during grain filling period of latest maturity hybrids (hybrids 2 and 4). Number

of barren stalks as well as number of secondary ears in final grain harvest area were determined.

Final Harvest. Grain harvesting occurred after physiological maturity of latest maturity hybrids, 125 and 135 DAE in 1987 and 1988 respectively. The ears of all plants in the final harvest area were hand-picked and length and number of rows in each ear were measured. All ears were shelled, using a hand-sheller. Cobs and kernels were dried in a forced-air oven at 80°C for at least 72 hours and weighed separately. Weight per kernel was determined from 1000 kernel sub-samples which were dried again then weighed. Stover dry weight, was measured by harvesting all plants (minus harvested ears) in the final harvest area. A 3-plant sub-samples was chopped in the field before drying to determine moisture content.

Results and Discussion

Interception of PAR

Light readings at the bottom of canopy as a percent of available light at the above canopy taken at completion of tasseling for the latest maturity hybrids i.e. hybrids 2 and 4, averaged over hybrids were 19, 5, and 3 percent for the 3, 7.5, and 12 plants m^{-2}, respectively (Table 5.2). All hybrids intercepted 95% or more of incident light that penetrated the canopy in medium and high densities. No

Table 5.1. Monthly means of growing degree days (GDD)† and precipitation during the corn growing season of 1987 and 1988‡.

	GDD		Precipitation	
Month	1987	1988	1987	1988
			mm	
May	181	247	29.7	72.1
June	294	272	104.6	28.7
July	401	429	41.7	146.1
Aug	317	391	97.5	140.7
Sept	120	179	108.7	53.6
Total	1313	1517	382.3	441.2

† GDD was calculated by the following equation:
$GDD = [(T_{max} + T_{min})/2] - 10^{\circ}C$ (Shaw, 1977).

‡ Source: Dr. Philip Ives, Dept. of Biology, Amherst College, Amherst, MA.

Table 5.2. Total light available at the bottom of the crop canopy at 3 densities for 6 hybrids. Measured at completion of tasseling in hybrids 2 and 4.

		Density (plants m^{-2})			
Hybrid	Code	3	7.5	12	Mean[†]
		%			
U[§]	1	21	5	5	10
	2	18	4	3	8
SU	3	20	2	1	8
	4	16	2	2	7
H	5	20	8	5	11
	6	17	4	2	8
Mean[‡]		19	5	3	

[†] Hybrids nonsignificant (P=0.43).
[‡] Density quadratic (P=0.01).
[§] U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids, respectively.

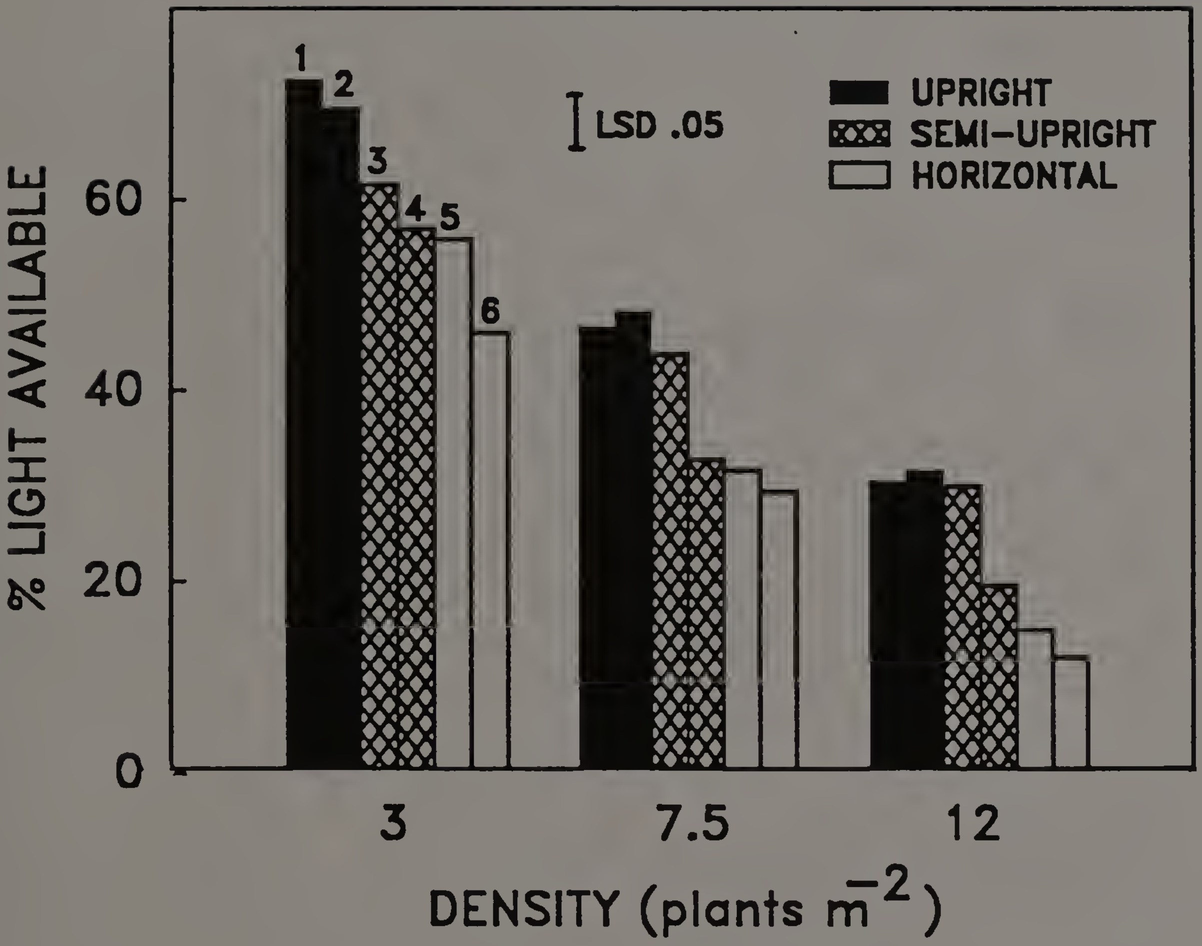

Figure 5.1. Percent light available at ear position of six hybrids at 3 densities. Measured at completion of tasseling in the latest maturity hybrids i.e. hybrids 2 and 4.

Table 5.3. Photosynthesis rate and chlorophyll concentration of the ear leaf at 2 densities[†].

Density	Rate of photosynthesis	Chlorophyll concentration
Plants m^{-2}	mg s^{-1} m^{-2}	ug cm^{-2}
3	1.130a[‡]	8.37a
12	0.661b	5.90b

[†] Averaged over six hybrids and two readings near anthesis.

[‡] Means within columns followed by the same letter are not significantly different at the 5% level of probability using Duncan's Multiple Range Test.

Table 5.4. Photosynthesis rate and chlorophyll concentration of the ear leaf of the six corn hybrids[†]

Hybrid	Code	Rate of photosynthesis	Chlorophyll concentration
		mg s^{-1} m^{-2}	ug cm^{-2}
U[‡]	1	.853a[§]	7.18a
	2	.917a	7.63a
SU	3	.982a	6.34b
	4	.742a	7.59a
H	5	.950a	7.01ab
	6	.979a	7.04ab

[†] Averaged over densities and 2 readings near anthesis.

[‡] U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids, respectively.

[§] Means within columns followed by the same letter are not significantly different at the % level of probability using Duncan's Multiple Range Test.

significant differences was observed (p=.43) between the amount of light available at soil surface of horizontal and vertical leaves. However, light available readings at the ear position of hybrids 1, 2, and 3 were higher than other hybrids (Figure 5.1). These hybrids could be characterized by having near upright or semi-upright leaves.

Photosynthesis and Chlorophyll

Ear leaf photosynthesis rate measured near anthesis were greatly reduced, as density increased from 3 to 12 plants m^{-2} (Table 5.3). Photosynthesis rate for hybrids averaged over densities is shown in Table 5.4.

Dwyer and Stewart (1986) and Dwyer et al. (1989) found a parabolic response of photosynthesis rate in corn with plant age. Maximum rate of photosynthesis was measured at 8-10 weeks after emergence in six corn hybrids. They concluded that comparisons among hybrids differing in development rates should be made at comparable phenological stages. In our study, the 3 highest photosynthetic rates were found among the hybrids which had the earliest tasseling and silking dates. It is also notable that the lowest photosynthetic rates were found among the hybrids with upright or semi-upright leaves (i.e. hybrids 1, 2, and 4). This agrees with the statement of Gardner et al. (1985) that since the photosynthetic response to radiation is curvilinear and radiation efficiency is greatest at low radiation levels, the vertical leaves are more efficient per unit of radiation intercepted. A small reduction in upper leaf photosynthesis because of vertical leaf inclination allows more radiation to penetrate to lower leaves. A reduction of 45% in photosynthetic rate was found as density increased from 3 to 12 plants m^{-2} averaged over hybrids. A similar reduction (50%) has already reported in the shade experiment in Agway 584S (Chapter 4).

Chlorophyll content was significantly different among the hybrids as well as between the densities (Tables 5.3 and 5.4). The hybrids that showed the highest rate of photosynthesis had lower concentrations of chlorophyll. Since the ear height varied among the hybrids, a part of variation in chlorophyll content of different hybrids could be related to the different levels of light received by ear leaves (Brougham, 1960). In the shading study a 50% reduction in radiant energy caused a substantial decrease in chlorophyll concentration especially in high densities (Chapter 4). Figure 5.1 also shows that ear leaves in upright and semi-upright leaf hybrids received higher levels of light compared to more horizontally oriented leaf hybrids. However, this suggests the level of chlorophyll in all hybrids in this study was above the level needed for photosynthesis. Brougham (1960), also suggested that the chlorophyll in species with horizontally displayed leaves could be more effective or efficient in converting CO_2 than that in species with more erect leaves. Our results also confirm such a suggestion. However, this conclusion is based on the results of studies with a relatively limited germplasm and may not, therefore, be representative of other genotypes or other environments.

Plant and Ear Height

Positive relationship between plant height and final grain yield has been reported (Glenn and Daynard, 1974; Daynard and Muldoon, 1983). It has been suggested that density tolerant hybrids might have increased ear height which may result in increased interception of solar radiant by the ear leaf (Buren et al., 1974). The results of our experiment showed plant and ear height generally increased then decreased with increasing density. However, the highest difference averaged over hybrids in both traits did not exceed 8 cm. Similar results already reported by Bunting (1973). Other researchers reported that plant and ear heights especially in short hybrids remained virtually unchanged, as density increased (Genter and Camper, 1973; Voldeng and Blackman, 1974). It is notable that the shortest hybrids also had horizontal leaves, while the tallest hybrids showed either upright or semi-upright leaf orientation. The ratio of ear position to total plant height was not significantly different. There was a tendency to have more erect leaves especially at the upper part of the plant, as density increased. This coincided with an increase in the height of ear (Table 5.5). In all but one hybrid (4),

Table 5.5. Effect of hybrid and density on morphological characteristics measured in 1988.

hybrid	Code	Plant height	Ear height	Tassel size	Mid-silking (week of)
		cm			
U[†]	1	318	165	35	25 July
	2	332	165	51	1 Aug.
SU	3	295	145	36	18 July
	4	365	172	49	1 Aug.
H	5	320	156	36	25 July
	6	267	126	42	4 July
F-test significance					
Hybrid (H)		.001[‡]	.001	.001	
Density (Hybrid)					
H_1 (L)		.299	.074	.211	
H_1 (Q)		.001	.001	.031	
H_2 (L)		.001	.009	.795	
H_2 (Q)		.001	.001	.177	
H_3 (L)		.154	.289	.029	
H_3 (Q)		.315	.705	.714	
H_4 (L)		.002	.002	.184	
H_4 (Q)		.034	.038	.338	
H_5 (L)		.136	.334	.982	
H_5 (Q)		.804	.208	.100	
H_6 (L)		.157	.135	.002	
H_6 (Q)		.129	.004	.006	
CV, %		4.4	7.5	6.6	

[†] U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids respectively.

[‡] Probability of a greater F value by chance.

the tassel size showed a significant linear decrease as density increased.

Grain Yield

Grain yields in almost all hybrids in all densities were higher in 1988 than in 1987 (Table 5.6). This could partly be due to 16 days earlier planting in 1988 compared to 1987 but also could be attributed to the differences in climatic conditions between the 2 years (Table 5.1). In 1988, accumulated growing degree days were higher than in 1987 and were above the norm for this location. Soil moisture measured gravimetrically showed no differences among hybrids and different densities within each season. Average precipitation, especially during the months of July and August, as much higher than those reported for 1987. This coincided with reproductive stages of growth and grain filling period. Highest grain yields in the U.S. Corn Belt have been reported to be associated with above average rainfall during July and average precipitation during the remainder of the year (Thompson, 1969). Other studies also have shown that the reproductive stage, especially mid-silking, is the most sensitive stage to drought (Herrero and Johnson, 1981; Grant et al., 1989).

In both years, superiority of hybrids with more upright leaves was found at higher densities (Table 5.6). With the exception of hybrid 4, upright and semi-upright leaf hybrids showed a linear or asymptotic responses to density increase, while the response of horizontal leaf hybrids was parabolic. The exception of hybrid 4 might be partly due to its high degree of lodging at high density compared to the other hybrids. Yield advantages for genotypes with upright leaves have been observed only at high leaf area indices (Duncan, 1971; Pepper et al., 1977). Gardner et al. (1988) also pointed out that a canopy of vertical leaves needed an LAI of 4 or greater to have a distinctly higher CGR than canopies with horizontal leaves. However, a part of the difference in our study could be attributed to differences in growing season which was coinsidently shorter in the horizontal leaf hybrids compared to more upright leaf hybrids. Variations in other morphological traits, especially in plant and ear height which were higher in upright leaf hybrids, could also have played a role.

Hybrids that produced the highest yields of grain, tended to produce the highest yields of total dry matter (Table 5.7). The exception was again hybrid 4 which showed relatively high dry matter, but lower grain yield. This, confirms that the lower grain yield in this semi-upright leaf hybrid is partly due to sensitiveness to lodging which was more severe in 1987 than 1988.

The comparison between yield components of hybrids averaged over densities indicated that all components responded similar in both years (Table 5.8). The difference in the total kernel yield per plant in the 2 years is primarily due to weight per kernel which was substantially

Table 5.6. Effect of hybrid and density on total grain yield in 1987 and 1988.

		Density (plants m^{-2})						Significant trend	
		3		7.5		12			
Hybrid	Code	87	88	87	88	87	88	87	88
		Mg ha^{-1}							
U[†]	1	7.1	7.0	9.0	10.6	9.7	10.7	L[‡]**	Q*
	2	7.2	7.1	8.7	11.3	10.2	12.4	L**	Q*
SU	3	8.0	7.8	9.3	10.4	8.7	11.3	NS	L**
	4	7.3	6.6	9.1	11.4	6.4	10.0	Q**	Q**
H	5	6.5	6.8	9.9	10.6	8.8	7.4	Q*	Q*
	6	6.6	7.0	9.2	9.3	7.1	8.8	Q**	Q*

[†] U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids, respectively.

[‡] L = linear and Q = quadratic trends, respectively.

*,** Significant at the 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

Table 5.7. Effect of hybrid and density on total biomass yield in 1987 and 1988.

		Density (plants m^{-2})						Significant trend	
		3		7.5		12			
Hybrid	Code	87	88	87	88	87	88	87	88
		Mg ha^{-1}							
U†	1	14.5	16.1	19.8	25.5	20.0	21.7	L$^{\ddagger **}$	Q**
	2	16.1	18.7	18.6	23.6	21.7	24.4	L**	L*
SU	3	14.7	17.7	18.2	21.1	19.5	22.5	L**	L*
	4	14.9	18.3	23.1	22.8	18.8	23.5	Q**	L*
H	5	13.8	15.4	20.2	20.4	22.1	17.4	L**	Q*
	6	11.9	12.4	18.0	16.2	17.3	15.5	Q*	NS

† U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids, respectively.

‡ L = linear and Q = quadratic trends, respectively.

*,** Significant at the 0.05 and 0.01 levels of probability, respectively. NS = Not significant.

heavier in 1988 compared to 1987. This, as indicated before, is probably due to the amount of precipitation available during the critical months of July and August. The total amount of precipitation in these 2 months were 139.2 and 286.8 mm in 1987 and 1988 respectively (Table 5.1). Ouattar et al. (1987) reported that water deficit at mid-silking and early grain filling period reduced the endosperm cell division and thus inhibited the establishment of kernel sink capacity.

The effect of density on yield components (Table 5.8) was mostly similar in both years. The analysis of variance for the interaction between hybrids and density is shown in Table 5.9. Mostly the density response was similar among hybrids which responded either linearly or quadratically. Exceptions were variability in number of rows per ear in hybrids 2, 4, and 5 in 1987 which did not show a significant response to increased density. The number of productive ears per plant was the component affected most as density increased except for hybrid 2 which in 1987 was unaffected by density. The amount of reduction averaged over hybrids and the 2 years was 36% as density increased from 3 to 12 plants m^{-2}. None of the hybrids showed barrenness at either low or medium densities. However, in high density the percent of barren stalk showed a range of 3 to 24%. No relationship was found between the leaf orientation and percent barren stalks. Hybrids 3 and 6 which showed prolific characteristics also showed the least percentage of barren

Table 5.8. Yield components of hybrids in 1987 and 1988.

Hybrid	Code	Ear plant^{-1}		Row ear^{-1}		Kernel row^{-1}		Weight Kernel^{-1}	
		87	88	87	88	87	88	87	88
								mg	
U[†]	1	.98b[‡]	.95b	14.9c	14.9c	40a	40a	240d	266c
	2	.96b	.99b	13.5e	13.9d	39ab	36b	279b	318a
SU	3	1.30a	1.30a	15.3b	15.5b	31d	31cd	251cd	262c
	4	.96b	.94b	15.7a	15.9a	36c	35b	256c	274c
H	5	.98b	.96b	13.9d	14.1d	37bc	32c	290a	304b
	6	1.18a	1.21a	15.6b	15.1bc	30d	30d	241d	242d
Plants m^{-2}									
3		1.40	1.29	15.0	15.4	39.5	39.2	295	316
7.5		0.93	1.01	14.9	15.1	35.6	35.8	254	268
12		0.81	0.86	14.3	14.5	30.4	27.6	225	249
Responses[§]		LQ	L	L	L	L	LQ	L	LQ

[†] U, SU, and H represent upright, semi-upright, and horizontal leaf hybrids, respectively.

[‡] Means within columns followed by the same letter are not significantly different.

[§] L = linear; LQ = Linear and quadratic (significant at $P=0.05$).

Table 5.9. Significance of F-Ratio for the interaction of hybrid and density of the yield components in 1987 and 1988.

	Ear plant^{-1}		Row ear^{-1}		Kernel row^{-1}		Weight Kernel^{-1}	
	87	88	87	88	87	88	87	88
F-test significance								
Hybrid (H)								
Density (hybrid)								
Dens in H_1 L†	.001‡	.002	.037	.001	.001	.001	.001	.001
" H_1 Q	.115	.329	.234	.134	.484	.296	.020	.001
" H_2 L	.006	.247	.151	.002	.001	.001	.001	.001
" H_2 Q	.302	.853	.965	.558	.406	.553	.008	.002
" H_3 L	.001	.001	.001	.001	.001	.237	.001	.001
" H_3 Q	.002	.001	.141	.396	.525	.004	.280	.866
" H_4 L	.001	.001	.134	.149	.001	.001	.001	.001
" H_4 Q	.720	.273	.721	.029	.118	.775	.901	.261
" H_5 L	.019	.001	.117	.001	.001	.001	.001	.001
" H_5 Q	.734	.426	.310	.363	.844	.037	.067	.066
" H_6 L	.001	.001	.001	.001	.645	.001	.001	.001
" H_6 Q	.002	.003	.348	.569	.007	.014	.032	.814
CV, %	14.6	10.0	2.3	2.2	7.7	6.0	5.1	4.2

† L = linear; Q = quadratic.

‡ Probability of a greater F value by chance.

stalks. This is consistent with earlier reports that multiple ear hybrids are more density tolerant than single-eared genotypes (Lang et al., 1956; Collins et al., 1965; Buren et al., 1974; Russel, 1975; Harris et al., 1976; Tetio-Kagho and Gardner, 1988b).

Number of kernels per row and weight per kernel also reduced by 25 and 22 percent respectively due to density increase, averaged over the 2 years and hybrids. Number of rows per ear was the most stable component to density increase and showed only 6% reduction.

Summary

In summary, the upright leaf hybrids showed some advantages in grain yield production over the horizontal leaf hybrids. The difference was higher in 1988 which was climatically more favorable than 1987. The superiority prevailed most in the densest populations. The data obtained in this study suggest density should be one of the factors considered in hybrid evaluations.

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CHAPTER 6

SUMMARY

In the 1986-1988 seasons a number of field experiments were conducted to investigate the competition effects on growth and yield of corn through manipulation of density and assimilate supply.

In the first set of experiments (Chapters 2 and 3), the growth and yield responses of 2 hybrids which differed in maturity period and prolificacy were studied in a wide range of densities. Under favorable condition, Agway 584S (single-ear, late maturity) out yielded Cornell 281 (multiple-ear, early maturity). The higher yield in Agway 584S was attributed to heavier kernels compared to Cornell 281, which resulted from a longer grain filling duration.

Growth analysis indicated that crop growth rate as well as net assimilation rate were greater in Cornell 281 than those of Agway 584S. Higher crop growth rate in Cornell 281, however, was directed toward tiller production with no fertile ears. Agway 584S maturing later had longer growth duration contributing to its higher yield than Cornell 281.

Intensity of competition through increased density was quantified by comparing grain yield and its components to those grown in widely spaced "isolated" plants. The results showed that yield per plant decreased 75% and 80% compared to isolated plants in Agway 584S and Cornell 281 respectively, as density increased from 3 to 12 plants m^{-2}. However, the 2 hybrids showed different responses to competition pressure. Number of kernels per row in Agway 584S and number of productive ears per plant in Cornell 281 were found to be the most sensitive yield components.

Alternate plants were removed at different stages of growth in order to study the compensatory responses of corn hybrids to assimilate alterations. The results indicated that competition between the vegetative stage and anthesis had the greatest effect in yield reduction. Adjustment in grain yield in responses to releasing the competition pressure occurred primarily through increase in kernel number per row in Agway 584S and number of productive ears per plant in Cornell 281.

One of the major factors limiting optimum conversion of light energy into grain dry matter in corn grown at high plant densities is barrenness, the failure of plants to produce fertile ears. Grain yields of many hybrids planted at high densities are markedly reduced most often by barrenness. The reduction of yield in high densities under favorable environmental conditions is primarily due to competition for light interception. A set of experiments was conducted to study light interception-density relationships and factors influencing barrenness and their effects on yield and yield components.

In experiments (Chapter 4) with added shade to reduce available light results showed that reduction in grain yield in high densities is mainly due to an increase in ear barrenness. Artificial shading (50% light reduction) intensified this effect. Shading due to use of high densities and/or artificially induced shade caused a lengthening of the interval between anthesis and silking. Thus, a shorter pollen-shed to silking intervals might be used as a criteria in selection of high density tolerant genotypes.

Another study (Chapter 5) examined density-light relationships in six corn hybrids having different leaf orientations. Results showed the manner of leaf display that allows penetration of light uniformly into the foliage canopy (upright leaves) could have some yield advantages over horizontal leaf hybrids only in favorable climatological conditions and when high densities are used.

The model proposed by Duncan (1984) was used to quantify the release from competition when alternate plants were removed (Chapter 2). Grain yield data fitted to this model for experiments described in Chapters 2 and 3 is shown in Figure 6.1, for Chapter 4 in Figure 6.2, and for Chapter 5 in Figure 6.3. Data from all of these experiments showed a high level of precision when each hybrid in each year was fitted to this model (R^2 ranged from 0.82 to 0.99). This supports Duncan's theory that a linear relationship exists between the logarithm of yield per plant and crowding.

As discussed earlier crowding of one plant on another is influenced by their distance of separation. The closer the two plants are to each other the greater the crowding (maximum crowding for two plants is defined as 1). At a

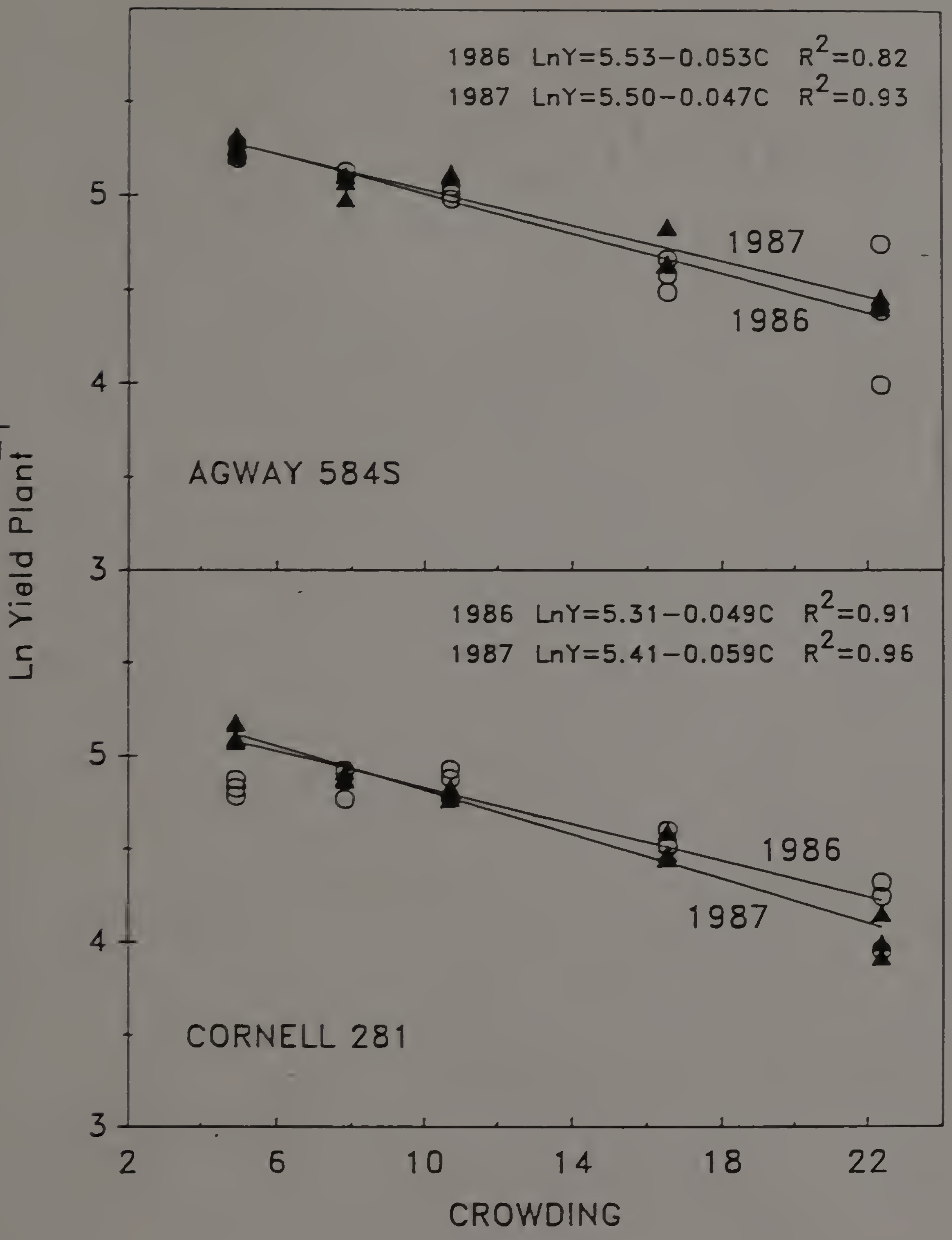

Figure 6.1. Influence of crowding on natural logarithm of grain yield per plant for 2 hybrids discussed in Chapters 2 and 3. Symbols are datum points for individual plots.

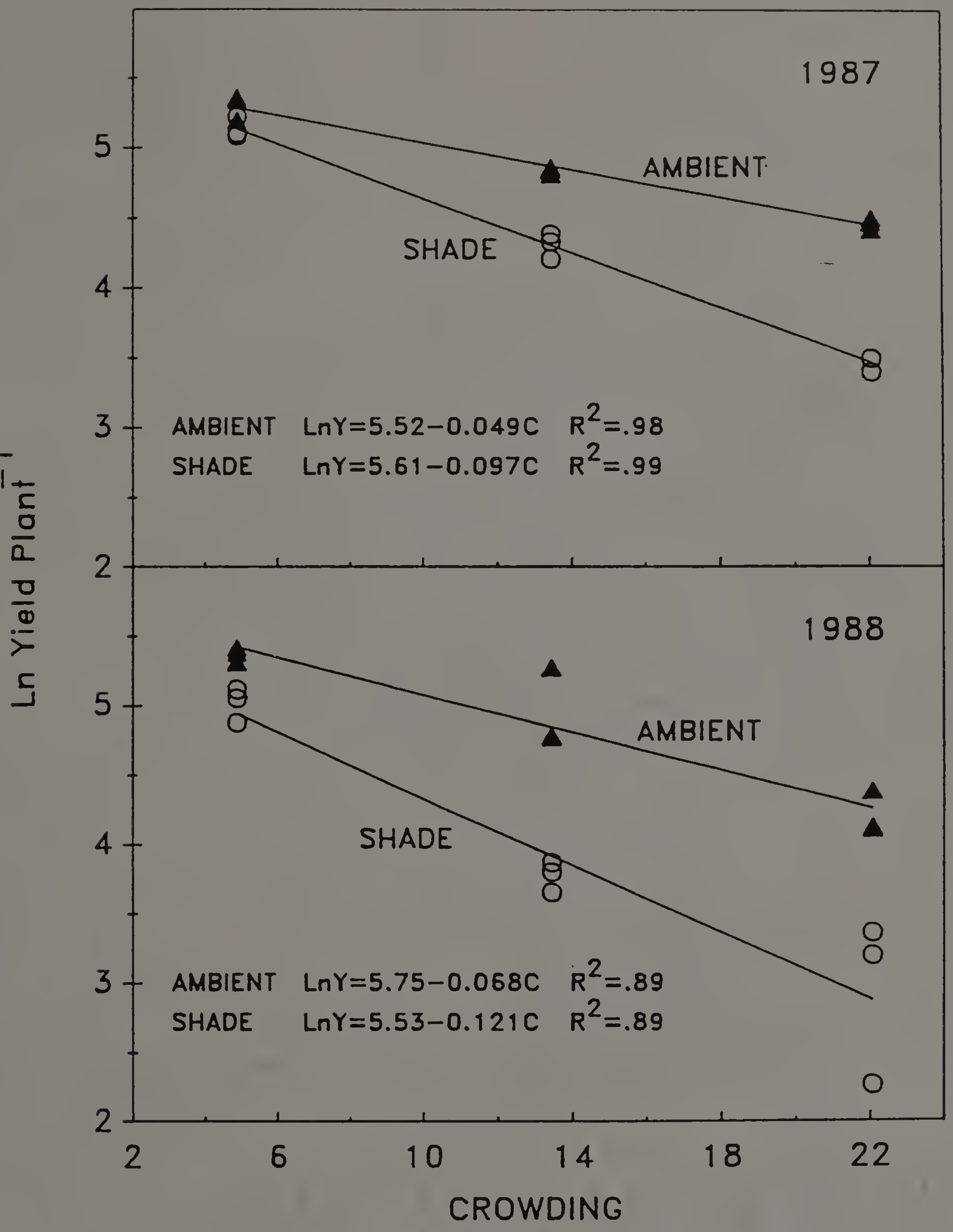

Figure 6.2. Influence of crowding on natural logarithm of grain yield per plant for Agway 584S in ambient and shaded environments as discussed in Chapter 4. Symbols are datum points for individual plots.

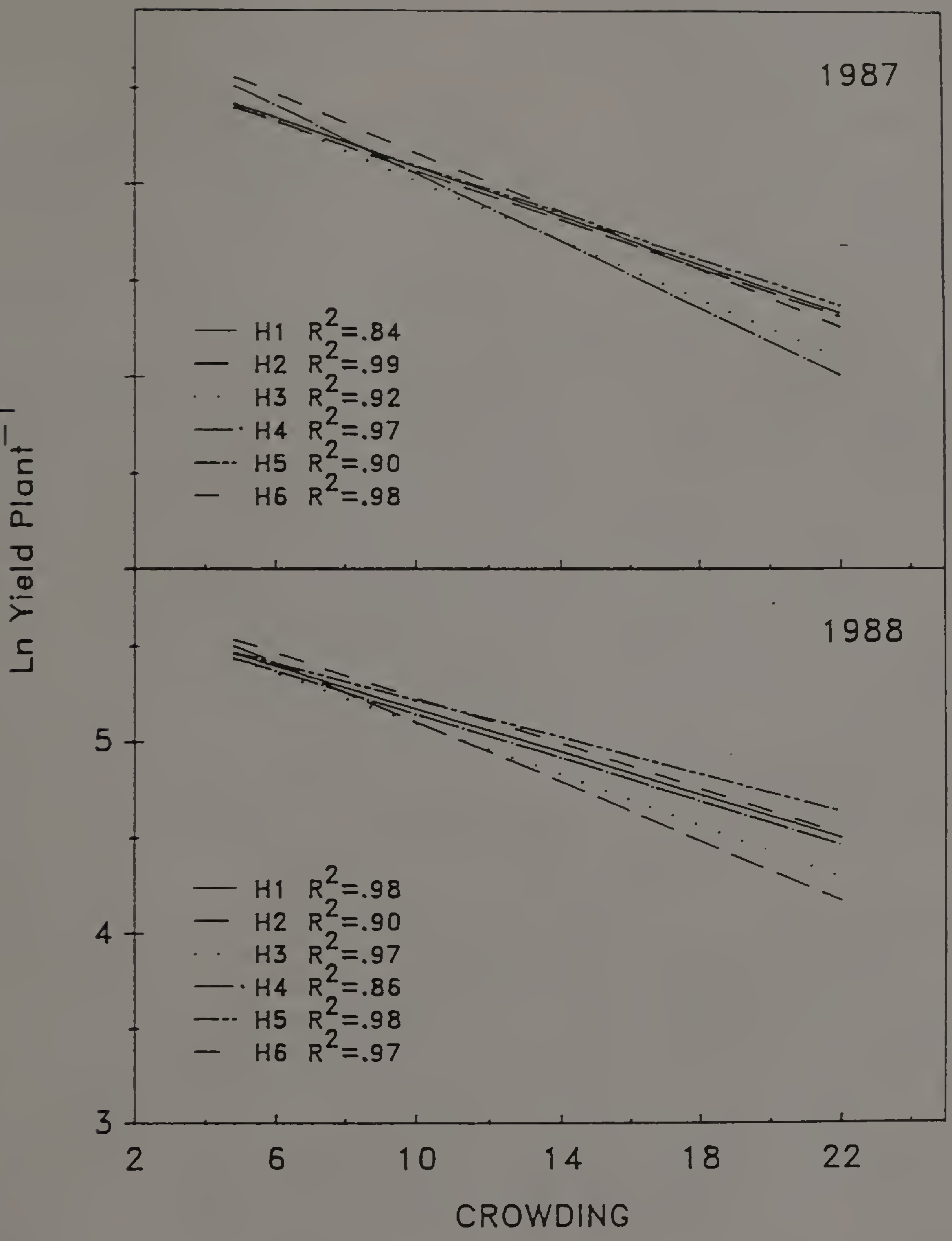

Figure 6.3. Influence of crowding on natural logarithm of grain yield per plant for the 6 hybrids discussed in Chapter 5. Symbols are datum points for individual plots.

distance exceeding Dmax, crowding is said not to occur (zero crowding influence). The nature of the curvilinear relationship between crowding and distance of separation is influenced by Dmax and the power (ALPHA) to which the separation factor (SF) is raised. Duncan (1984) stated precise values for ALPHA and Dmax were not important for a good fitting relationship. In this discussion he used a relatively narrow range of ALPHA's (4 and 3.06) and Dmax's (300 and 250 cm). Figure 6.4 illustrates the relationship between crowding and separation distance with ALPHA ranging from 2 to 6 and Dmax ranging from 150 to 450 cm. The sum of crowding on unit area basis is increased by density and numerically by reducing ALPHA and increasing Dmax (Table 6.1). Even though crowding varies widely depend upon ALPHA and Dmax (e.g. 3.8 to 99 for 12 plants m^{-2}) (Table 6.1), predicted yields show almost no variation within the range of densities tested (3 to 12 plants m^{-2}) for ALPHA ranging from 2 to 6 and Dmax from 150 to 400 cm (Table 6.1).

Yield of isolated plants (plants growing with zero crowding) are not accurately predicted by the model (Figure 6.5). Even when ALPHA and Dmax are varied in the model the isolated yield is under estimated (Figure 6.6). This seems to be especially true for Cornell 281 which was prolific most at low densities, producing both second ears and tiller ears. Agway 584S showed no tillering and had fewer secondary ears.

An examination of the model's predicting power using just 2 densities compared to the full 5 densities in Chapters 2 and 3 is shown in Figure 6.7.

Statistical analysis of the difference between the residuals (actual-predicted) using a paired t-test were conducted for each hybrid in each year. Except for Cornell 281 in 1986 predicted lines from 2 densities (3 replications) were not significantly different from lines predicted from 5 densities (3 replications) (Figure 6.7). This, again confirms the validity of the model proposed by Duncan (1984).

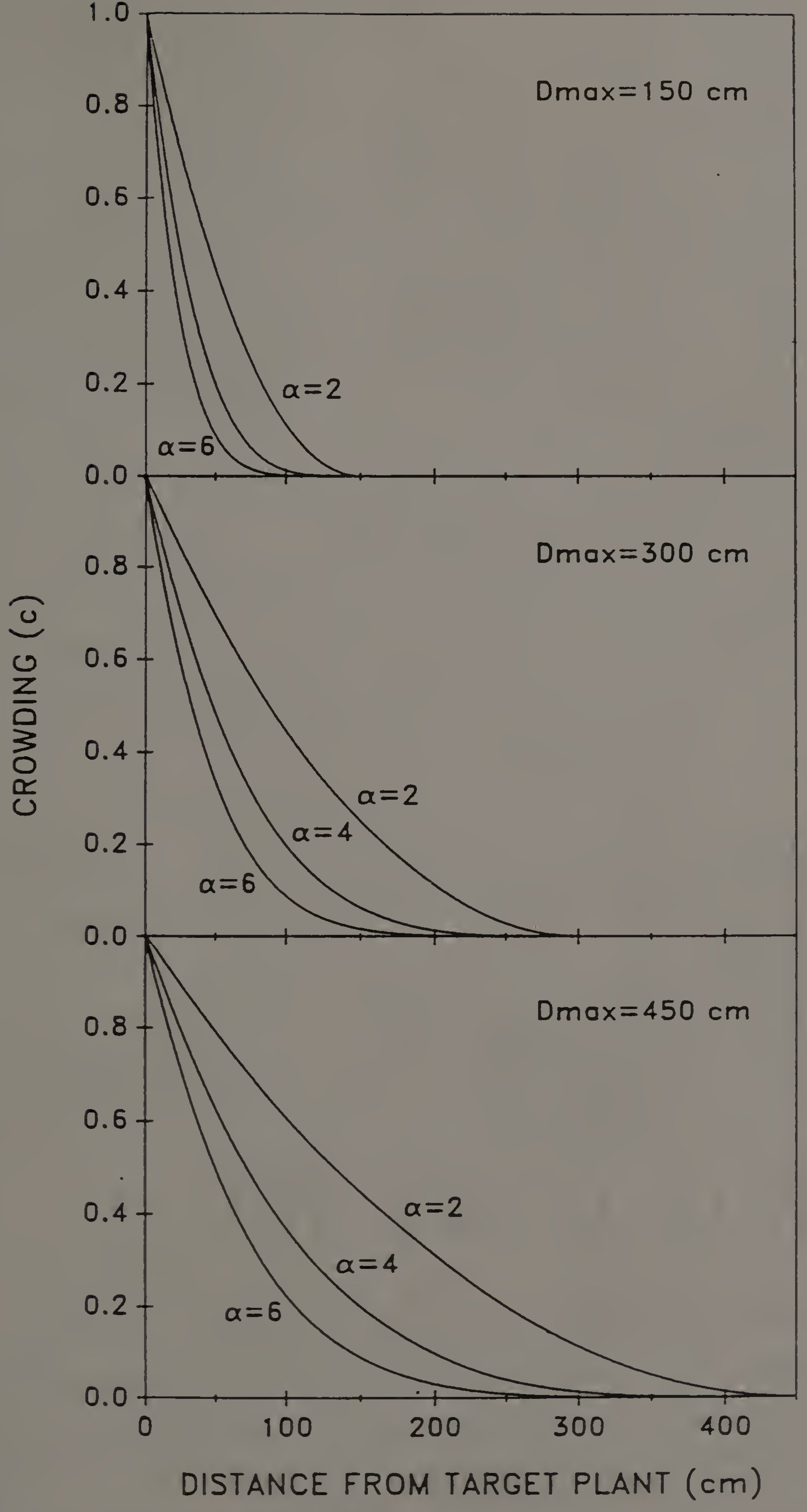

Figure 6.4. Relationship between crowding and the separation distance with varying ALPHA's and Dmax's (distance to isolated plant) according to the model proposed by Duncan (1984).

Table 6.1. Effect of manipulation of ALPHA and Dmax at different densities on crowding and prediction of grain yield per plant by Duncan's model (1984) for 2 hybrids in 1986 and 1987.

				1986				1987			
				AGWAY 584S		CORNELL 281		AGWAY 584S		CORNELL 281	
Density[†]	Dmax	ALPHA	Crowding	A[‡]	P	A	P	A	P	A	P
Plants m^{-2}	cm			g Plant^{-1}							
3	150	2	2.81	188	195	152	160	193	194	166	166
		4	0.92		194		159		193		166
		6	0.42		193		158		192		165
	400	2	24.25		195		160		194		166
		4	9.26		195		160		194		166
		6	4.68		195		160		194		166
6	150	2	6.50	155	143	129	120	165	147	121	117
		4	2.59		144		120		148		118
		6	1.49		144		121		148		118
	400	2	49.44		143		120		147		117
		4	19.43		143		120		147		117
		6	10.23		143		120		147		117
12	150	2	13.86	83	78	66	68	84	85	56	59
		4	6.02		78		68		85		59
		6	3.78		77		67		85		59
	400	2	99.32		78		68		85		59
		4	39.59		78		68		85		59
		6	21.26		78		68		85		59

[†] Row spacing = 91 cm.
[‡] A = Actual and P = Predicted grain yield per plant.

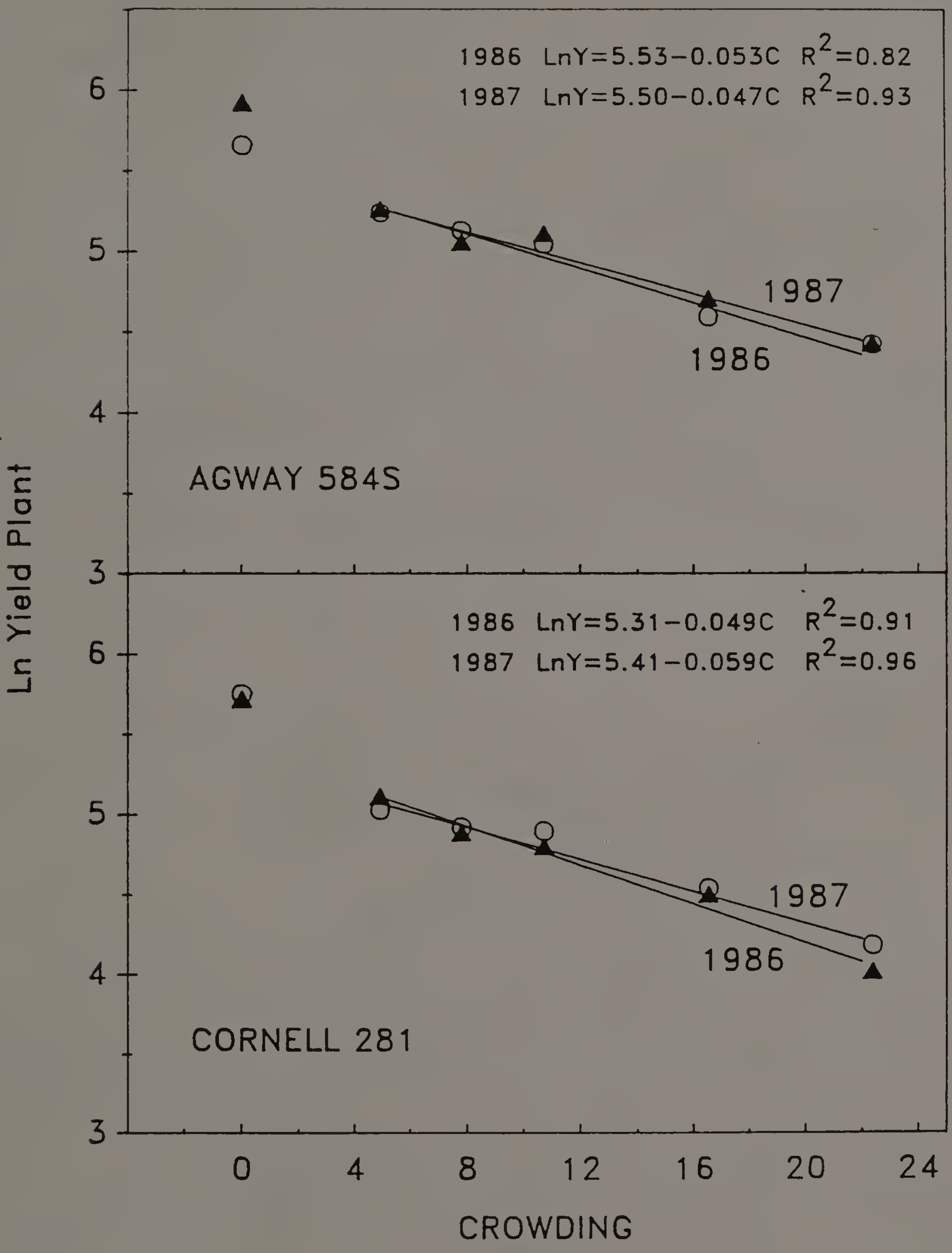

Figure 6.5. Relationship between natural logarithm of grain yield per plant and crowding for densities of 3 to 12 plants m^{-2} (solid line) and for widely spaced plants (zero crowding). Symbols are means of 3 replications at each crowding level.

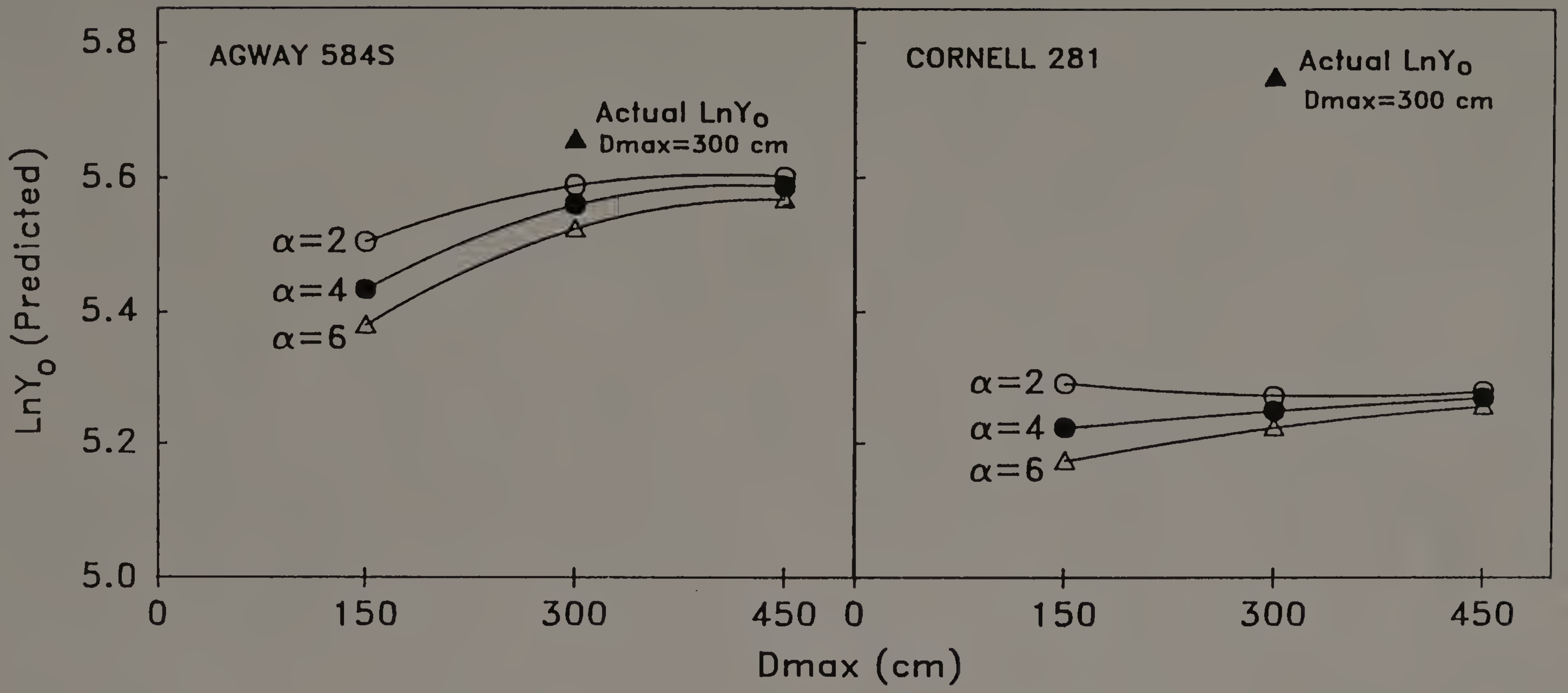

Figure 6.6. Predicted isolated plant yields (LnY_o) with varying ALPHA's and Dmax's. For actual isolated yields a Dmax of 300 cm was selected for field establishment.

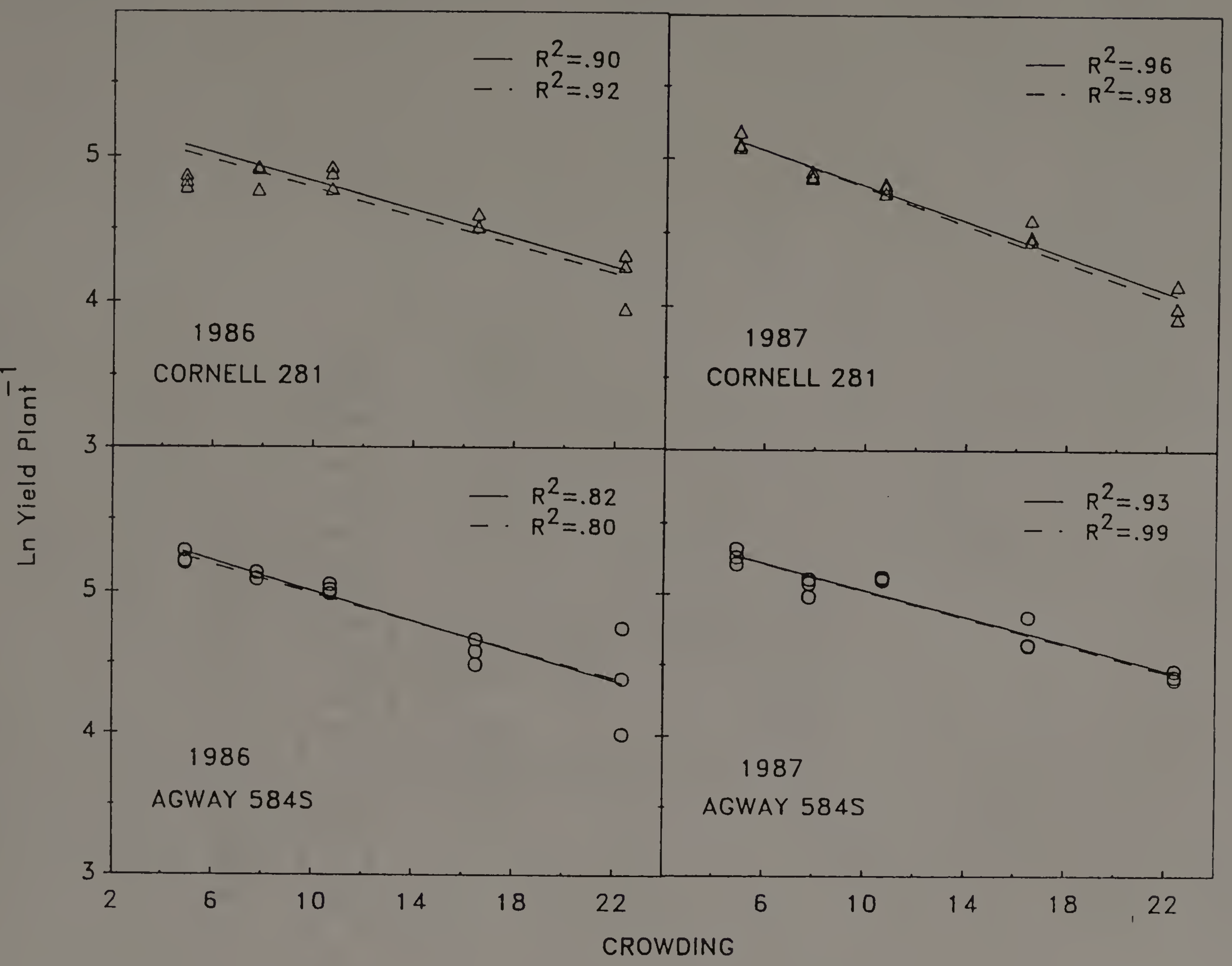

Figure 6.7. Influence of crowding on natural logarithm of grain yield per plant for 2 hybrids in 1986 and 1987. Actual (solid line, 5 densities), predicted (shade, 2 densities).

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