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CROP COMPETITION STUDIES:
INTERCROPPING WITH GROUNDNUTS AND
ESTIMATION OF COMPETITIVE EFFECTS IN CORN

A Dissertation Presented

by

DANIEL H. PUTNAM

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

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Department of Plant and Soil Sciences

CROP COMPETITION STUDIES:
INTERCROPPING WITH GROUNDNUTS AND
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Daniel H. Putnam

DEDICATION

This dissertation is dedicated to my parents
Jean and Harold Putnam,
who gave encouragement at the crucial moments.

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I would like to thank my committee memebers, Dr. Stephen J. Herbert, Dr. John Baker, Dr. Prasanta Bhowmik and Dr. John Foster for their guidance and patience and for many helpful suggestions.

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ABSTRACT

CROP COMPETITION STUDIES:INTERCROPPING WITH GROUNDNUTS AND ESTIMATION OF COMPETITIVE EFFECTS IN CORN

SEPTEMBER 1986

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Studies addressing crop competition in two widely different cropping situations are reported. In Hyderabad, India, groudnut was intercropped with sorghum and with sunflower under a wide range of row patterns and intercrop densities in the post-rainy (rabi) and hot (summer) seasons under irrigation using a systematic design. Response surfaces for pattern and density effects on crop component yields and total Land Equivalent Ratios and Staple LERs were calculated. Groundnut yields were supressed in most intercropping treatments compared with sole crops due to competitive effects on pod number and weight. Supression was greater in the sunflower intercrop than under sorghum, and at 1:1 ratios versus 6:1 groundnut:intercrop ratios. Sunflower yields were maintained at 85-90 % of sole crop controls when sunflower occupied only 14% of the intercropped land area, but sorghum yields were reduced to a greater extent with a lower % planted area. Density of the intercrop had little or no effect on groundnut yields or yields of the intercropped species. Total LER potentials of up to 1.46

(sorghum:groundnut intercrop) and 1.60 (sunflower:groundnut intercrop) were indicated by the data. Land-use advantages were consistent across seasons. Increases in land efficiency with wider ratios were found in both seasons in the sunflower intercrop, but the pattern effect on the sorghum intercrop was less consistent across seasons. Percent of the sole crop groundnut yields obtained can be manipulated by changing planted area, not intercropped density. Either system would be advantageous over sole cropping under the two different yield-goal situations.

In Massachusetts, USA, crop competition was studied in a corn stand using the isolated plant as a model. Hybrid Cornell 281 was grown at 3.4, 6.7 and 10 plants m^{-2} and at 2 m distances in a Randomized Block Design (RBD), and in treatments designed to assess the role of time of competition, alternate plants were removed at mid-tasselling and beginning grain fill at the three densities. In a Central Composite Design (CCD), density, time of removal, and nitrogen rate treatments were applied over a wider range. Yield, total dry weight, second ear number, kernel weight and kernel number of first ears, tillering, number of barren plants, and height were effected by density. Removal, but not time of removal effected kernel yield $plant^{-1}$, kernel no. and kernel weight but not other parameters. Competition analysis using the isolated plant as a maximum indicated that competitive effects were greatest on the first ear component of kernel number. Kernel weight and ear number was effected to a lesser extent. Second ear number and tillering were reduced to essentially zero at a discrete density. A competition model of Duncan (1984) fit the data for first ear kernel yield well, but not total kernel yield, because of increased second ear yield at low densities. Row width is predicted to have little effect on yield in this environment. From the removal treatments, most of the competition within a corn stand could be accounted for by the time after beginning grain fill.

Row arrangement, not density was the important yield-determining factor in the intercrop situation. In contrast density, not arrangement was predicted to have the major effect on competition in the corn sole crop.

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CHAPTER I

INTRODUCTION

Within a given environment, the yield of a crop will depend upon the maximum genetic potential of that crop plant, the level of resources available in the environment, and the ability of a crop plant community to exploit that environment. Yield improvements can be made through genetic manipulation via plant breeding and selection, changing the level of the resources available through fertilization or irrigation, or improving the efficiency with which a crop exploits the environment by changing the plant density or arrangement, controlling insect, weed or disease pests, or changing the timing of field practice (ie. time of planting). Crop competition is a phenomenon which encompasses these three aspects of crop yield, and it is this subject which is the topic of this thesis.

This thesis contains three components. The first is a general discussion and literature review about the nature of plant competition in general and the agronomic implications of competition (Chapter 2). A working definition of competition is offered. The second component addresses the idea of groundnut-based intercrops as practiced in the semi-arid regions of the world, especially India. A literature review (Chapter 3) and results of a two season intercropping study (Chapter 4) examining planting pattern and density effects on groundnut-sorghum and groundnut-sunflower intercrops are reported and discussed. The third component addresses the issue of plant competition within a corn stand. A review of equations used to fit plant density responses, as well as the source-sink relationship in maize is presented (Chapter 5). Results of two experiments designed to examine the role of density and stand reduction at different times on corn yield and yield components are reported (Chapter 6). These results are discussed with the use of 1) an indexing method using isolated plants as controls, and 2) the application of a published competition model. Both of these are attempts to quantify competition and competititve effects within a corn stand.

The study of crop competition is of special interest in intercropping because of the magnitude of possible interactions between two or more species and an indication from several studies that intercrops may be more biologically efficient compared with sole crops, due to superior resource use (Willey, 1979). Intercropping is a practice which dates from antiquity. It is defined as a type of multiple cropping in which two or more species are simultaneous for most of the growing season (Andrews and Kassam, 1976). In semi-arid regions with minimal mechanization, intercropping is widely practiced to spread out labor and market risks, decrease disease pest and weed problems and to increase and stabilize yields. Intercropping work in developing regions has increased in recent years with the recognition not only that farmers will continue to intercrop, but that there are sound economic and agronomic reasons that they should (Francis et al., 1975; Trenbath, 1975; Harwood and Price, 1976; Willey and Rao, 1981).

The idea of conducting crop competition studies in a maize crop may appear at first to be an exercise in redundancy. There is a long history of yield/density studies that have been conducted to determine density or row width effects on corn yields, dating to the beginnings of experiment station research in the United States. Still, the lack of development of underlying principles or theories on the corn-density issue led veteran corn researcher W.G. Duncan to say as late as 1972: "I think most of you would agree that we have something resembling chaos" (Caldwell, 1972). Although corn yields respond to plant density in fairly predictable ways, the relationship cannot be one of cause and effect, since plant density contains the component of plant arrangement, which also influences yield. The development of a more basic approach to the quantification of competition effects on yield and yield components is needed.

It may be claimed that there is some incongruity between the subject areas addressed in this thesis: intercropping with groundnuts in the Semi-Arid Tropics and competition in a corn stand in the humid northeastern United States. Yet these studies follow a natural progression which contains at least some degree of logic. The issue of the methodology for assessing crop competition in mixed cropping arose while the author was conducting studies on corn-soybean intercrops for quality forage production in the United States (Putnam, 1983; Herbert et al., 1984; Putnam et al. 1985; Putnam et al., 1986). An elaborate proposal with the aim of segregating above- and below- ground competitive effects in a semi-arid cropping system (the original impetus for going to India) was funded by the Fulbright Foundation for 1984. Two experiments along this line were actually planted in India, but due to unforseen (non-technical) problems, these were never seen to completion, and a more applied pattern-density study was conducted. The idea of a non-competitive control was developed and tried (although the data is not extensively reported here as it was only applied in one season). It was decided that upon returning to the United States, the application of a competition approach to the (simpler) corn monoculture system would be of great interest in developing these ideas. The further development of methodology to assess competition within mixed crops remains of great interest, and it is hoped that some of the ideas contained here will be of help towards that goal.

The objectives of the groundnut intercropping studies were to explore the yield response in grounut:sorghum and groundnut:sunflower mixtures over a wide range of planting patterns and densities and to assess the competitive effects on the yield and yield components of each species in intercropping versus sole cropping.

The objectives of the corn competition study were to quantify competitive effects on maize yield and yield components utilizing the isolated plant as a model and to assess the effect of time of reduction in competition on yield and yield components.

CHAPTER II

THE NATURE OF PLANT COMPETITION

Introduction

The highly interactive and complex nature of plant competition cannot be over-emphasized. Competition has been viewed as a "purely physical process" (Clements et al., 1929), whereby if a necessary growth factor falls below the combined demands of the organisms, competition begins. This definition has been basically confirmed by Milne (1961) and Clements and Shelford (1939), Donald (1963), Odum (1975), and Trenbath (1976), whereby competition is viewed as occurring only <u>for</u> something, ie. water, light, nutrients or CO2. Justus von Liebig (1840) expressed the role of a limiting resource very well in his "Law of the minimum", whereby plant growth is limited by the essential factor which is in shortest supply. Later, researchers have added two conditions to this, ie. first that it only applies strictly to steady-state conditions, when inflow equals output, and secondly that factors tend to interact in a complex manner (Odum, 1971).

Competition for Above-Ground Resources

There are fundamental differences between the resources required for growth. If soil conditions are non-limiting, photosynthesis and growth rates are said to be near to proportional to the radiation intercepted by the plant (Baker and Meyer, 1966; Puckridge and Donald, 1967). Light is not merely another growth factor, but is the driving force for all vital processes within the plant. Sunlight is only available as a "passing stream" to be intercepted or not, unlike other growth factors which can be thought of as a "pool" to be depleted or recharged (Donald, 1963).

Plant characteristics which are thought to confer competitive ability for light are: large leaves to reduce penumbra effects (Norman et al., 1971), early rapid expansion of leaf canopy (Donald, 1963), leaves horizontal under overcast conditions (Monsi and Saeki, 1953) and vertical under sunny conditions (Brougham, 1958), leaves with low transmissivity (Saeki, 1960), leaves arranged in a mosaic (Acock et al., 1970), rapid stem extension in response to shading (Williams, 1964), and a C4 photosynthetic pathway (Black et al., 1969; Patterson et al., 1984). Adaptations to lower light intensities can occur, allowing a shaded crop to endure stress. These include lower rates of dark respiration (Kumura, 1968), a lower root/shoot ratio (Brouwer, 1966) greater leaf area/leaf weight ratio (Blackman, 1956), and greater stem elongation (Williams, 1964). Of course, shading leads to reduction of maximum photosynthetic rates (Bowes et al., 1972).

The turbulence within canopies is usually great enough so that competiiton for CO2 seems unlikely to occur (Inoue, 1974), although it is theoretically possible. Nevertheless, CO_2 has been established as a yield-limiting factor in many crops. CO_2 increases from the normal 300 ppm to 2400 ppm resulted in yield increases of 90% in rice (Yoshida, 1972). In a study of a wide range of agronomic crops, it was found that crop yield might increase by 33% with a doubling of atmospheric CO_2 concentration (Kimball, 1983). Daily fluxes of CO_2 have been recorded (Chang-Chi Chu, 1968), indicating the day-time demand. Increase in CO_2 would be expected to favor C3 plants over C4 plants, effecting the competitive balance between crops and weeds (Patterson and Flint, 1980; Patterson et al., 1984).

Competition for Soil Factors

Competition for the soil factors of water, macro- and micronutrients may vary. The uptake of water or dissolved ions or oxygen from the soil by developing plants cause concentration gradients to occur, whereby further supplies diffuse towards the root. Movement of substances by diffusion and mass flow through the soil to the root causes a zone of depletion in the vicinity of the root. The dimension of this zone will depend upon the ability of the soil to supply the nutrient, the mobility of the nutient, and the demand of the plant. Nitrate ions and water are more mobile in the soil than are potassium and phosphate (Bray, 1954) and are taken up primarily by mass flow (Renger and Strebel, 1976). The zones of depletion around active roots will be expected to increase in size fastest and overlap the soonest for these factors (Andrews and Newman, 1970). Competition only begins when there is an overlapping of depletion zones, not when individual roots come into contact. Depletion zones for water have been calculated as 25 cm from a single root (Klute and Peters, 1969) or 12 cm (Dunham and Nye, 1973) or even greater (Stone et al., 1973).

Provided uptake is not limiting, depletion zones for mobile ions such as nitrate will be as large as those for water (Barber, 1962).

Nutrients such as ammonium, calcium, potassium and phosphate which are adsorbed strongly onto the surfaces of soil particles or fixed by other mechanisms are in low concentration in the soil solution and move to the plant root primarily by diffusion (Mengel and Kirkby, 1982; Brewster and Tinker, 1970). Since this is a slow mechanism, zones of depletion will extend only a short distance from the root surface (0.7 cm phosphate depletion zone after a week, Bhat and Nye, 1973). Depletion of labled rubidium (a potassium analogue) in the zone immediately around the plant root has been demonstrated by Barber (1968). Soils with higher nutrient levels have steeper concentration gradients, allowing for higher rates of uptake. For this reason, the width of the zone of depletion may be higher in soils with high nutrient levels than in soils with low nutrient levels (Mengel and Kirkby, 1982), as demonstrated by work done on phosphate (Lewis and Quirk, 1967). Rates of diffusion and mass flow are highly dependent upon moisture content of the soil (Rowell et al., 1967). Other interactions between nutrients are known to occur. For example, Macleod (1969) found very different barley yield responses to N with differing levels of K.

The narrowness of depletion zones for non-mobile elements means that competition for these nutrients will only occur at very high root densities if at all (Andrews and Newman, 1970, Baldwin et al., 1972), although competition for more mobile elements occurs more readily.

Success in competition for soil factors has been linked with high root density (Andrews and Newman, 1970), early, fast penetration of the soil (McCown and Williams, 1968), root length (Olsen and Kemper, 1968), extensive root hairs (Barley, 1970), a high proportion of the roots actively growing (Andrews and Newman, 1970), and high uptake potentials (Nye and Tinker, 1969). Early uptake seems to be important in competition for mobile nutrients (Kawano et al., 1974).

Interactions

In general, if a plant absorbs less than its share of one growth resource due to competition, it is likely to acquire a correspondingly small share of all growth factors (Donald, 1958; Milthorpe, 1961; Trenbath, 1976). A plant with an early slow growing root system will usually display a smaller leaf area, which will in turn compete less favorably for light. A system of positive feedback occurs so that small differences in growth rates, size, leaf display, or rooting depth early in the season lead to severe dominance or suppression later in the season. The differences in competitive effects between two competing species was four times as great in a shallow soil versus a deep soil in an experiment on oats, where competition was principally for light (Trenbath and Harper, 1973).

Ingenious techniques for segregating above and below-ground competition have been devised and used (Donald, 1958; Aspinall, 1960; Shreiber, 1967; Eagles, 1971; Snaydan, 1971; Snaydan, 1979; Martin and Snaydon, 1982; Willey and Reddy, 1981). The highly interactive nature of plant competition, and the usual inclusion of unrealistic aerial and soil partitions make the interpretation of such experiments problematic. Trenbath (1976) points out that, while it is difficult to determine what type of competition occurs first, given levels of growth factors at any moment will determine the balance between above- and below-ground competitive effects. Lockart (1965) summarized a useful progression from earlier ideas: that the limiting factor is either the single growth factor or each of a set of growth factors for which an increase in concentration gives a positive response of growth rates.

A Working Definition

These considerations lead to a proposed working definition of competition:

> "Competition is a force which has the effect of changing (reducing) yield per plant, and is traceable only to the presence of neighboring plants"

Classical definitions of competition state that competition arises where two or more organisms are in need of a common resource, the supply of which is below the combined demand of those organisms (Clements et al., 1929; Donald, 1963) or a "striving" for the same growth resource (Odum, 1975). However, other interactions may occur which confound the effect of direct competition for resources as so defined. These include a) allelopathic effects, b)other biotic influences such as changes in soil microflora, N fixation and transfer, insect or animal predators, or diseases which are solely due to the presence or absence of neighboring plants, and C) changes in the physical environment or microclimate. These may be conveniently divided into primary and secondary competitive effects; primary effects being those due directly to the reduction of growth resources (light, water, and nutrients) and secondary effects being due to indirect between-plant interactions: allelopathy, biotic influences and changes in microclimate. Fuerst and Putnam (1983) made a similar distinction between direct interference and indirect interference. For example, the immobilization of nutrients by saprophytes on a plant host (Kimber, 1973) or the production of chemicals by a plant which prevents mineral uptake by another (Harper and Balke, 1981) are certainly competitive effects, but they are indirect, as the agent is not directly depleting the resource (Fuerst and Putnam, 1983). These are often difficult to separate (Dekker et al., 1983).

Competition as proposed above is used in the broad sense, and so is probably closer to the term "interference" which was preferred by Harper 1977 and Fuerst and Putnam (1983), and includes primary competition for resources and secondary interferences.

It should be pointed out that plant interactions don't always have a negative effect on plant growth and yield, especially secondary effects. For example, plants which compete moderately for water early in the season may be forced to increase rooting depth, which might give them advantages in nutrient extraction over non-competing plants if water is restored later in the season. Competition for resources within a plant may also be suboptimal in a non-competitive plant. This possible loss of efficiency is discussed by Donald (1963) and cited by

Duncan (1984) and could be viewed as a positive interaction between plants. The microclimatic effects of neighboring plants also might be beneficial, for example in decreasing wind speeds or moderating temperature or humidity. Similar examples might be hypothesized for biotic or allelopathic interactions. However, unless there are demonstratable overriding considerations, we must assume that these positive effects of neighboring plants will be small in relation to interactions which have the effect of reducing yield per plant: competition for nutrients, water, and light. The definition of competition offered above includes both positive and negative interactions.

Furthermore, since we are primarily interested in the effect of competition on plant yield (and other parameters), we must state that competition may take place for a resource, but inasmuch as the effect is non-observable, according to our working definition, competition has not taken place. There may be circumstances where a resource is in short supply because of the presence of neighboring plants, but the plant is somehow able to adjust so that yield or growth rate is not effected, and, according to our working definition, competition has not taken place. This is a broad definition and lends itself easily to empirical competitive studies.

CHAPTER III.

GROUNDNUT INTERCROPPING - LITERATURE REVIEW

Introduction

Groundnut (Arachis hypogae L.) is an erect, sparsely hairy annual herb 15-60 cm in height which is grown as an agricultural crop in latitudes 40 degrees either side of the equator. It is a warm season crop, requiring at least 45 cm of water during the growing season. There are two basic growth habits: bunch (Spanish-Valencia) and spreading-runner (Virginia).

Groundnut originated in South America and was probably domesticated in the valleys of southern Bolivia and northern Argentina. Excavated samples dated 2000-3000 B.C. have been found in coastal Peru and in Mexico about the time of Christ, but groundnut was probably domesticated much earlier. In the 16th century, the Portugese took them from Brazil to West Africa, and later to India. The Spaniards introduced groundnuts to the Pacific and the Phillipines, from where they spread to China, Japan and Malaysia (Gregory and Gregory, 1976). Peanuts were introduced into colonial America via Africa and the slave ships (Martin et al., 1967).

Groundnut is the world's second largest source of vegetable oil (the largest is soybean) and India is by far the largest producer of groundnuts, producing about 6.9 million tons on 7.2 million hectares in 1984, or about 40% of the world's crop (FAO, 1984). The importance of groundnuts to less developed countries should not be underestimated. Eighty-four percent of the vegetable oil exported by the U.S. (the U.S. is the major exporter) goes to less developed countries, much of it to India (USDA, 1984). One third of Indias' agricultural trade with the U.S. in 1983 was in edible oils (USDA, 1984). Production of groundnuts in India dates to colonial times when a large percentage of the production entered the world market. Now it is virtually all consumed in India, mostly in the manufacture of ghee (rarified butter) by hydrogenation and as an animal feed (oilseed cake). Often shortages develop and difficult political decisions are presented as to how much to import while maintaining prices at acceptable levels.

The amount of irrigated land in India has increased from 22.6 million to 58.5 million hectares between 1950-1980, and groundnut hectarage has shared substantially in this increase. The use of irrigation has increased yields, making the production of groundnut in the post-rainy season quite attractive for those farmers who have access to irrigation. Most of the groundnut grown under irrigation in India is grown as a sole crop, not as an intercrop.

Groundnut is frequently grown as an intercrop in the rainy season (kharif), where the risks due to insufficient rains or disease incidence may be greater.

Groundnut-Cereal Intercrops

Early reports have shown advantages to intercropping groundnut with cereals. An intercrop of ragi (finger millet, *Eleusine coracana*

(L.) Gaertn.) and groundnut gave significantly higher monetary returns than either cotton, groundnut, or ragi, or any other binary or three way mixture. The yield of ragi in combination with groundnut was also higher than sole crop ragi in five out of six years of experimentation suggesting a biological advantage to the intercrop (Algappan et al., 1960). Mixed cropping of groundnuts with maize in addition to sorghum or millet increased cash returns cormpared with sole crop groundnuts under varying conditions in Nigeria (Baker, 1978). Groundnut-cereal mixtures as practiced in Nigeria never produced less returns than sole crops and were considered to be more secure than sole cropping (Baker, 1974; Baker,1980).

In India, it was found that sowing sorghum in 60 cm rows with one row of groundnut planted in-between gave good monetary returns, but this was equal to a paired row system (30cm + 90cm) with two rows of groundnut in the 90 cm space (Bapat, 1976). In another study in India, yield and monetary return from sole crop sorghum in 45 cm rows was statistically similar to sorghum intercropped with groundnut or soybean in between 60 cm rows (although the sole crop tended to be higher, Bhale Rao et al., 1976). Yield advantages for intercropping were also found in sorghum:groundnut intercrops in a 2 row sorghum:8 row groundnut mixture (Bodade, 1964).

A tendency for decreased groundnut yields with increasing millet densities in a groundnut:millet intercrop in the Sahelian region of Niger was found (Cunard, 1980). Groundnut:sorghum intercrop in a ratio of 3:1 or 4:1 was reported to give the highest monetary return as compared with either sole crop (Lingagowoa et al., 1972). Yields or yield components of sorghum were similar when grown alone, in paired rows or with a groundnut intercrop (Mohammad and Upadhyay, 1977).

Land Equivalent Ratios of 1.25 were found for a groundnut:sorghum intercrop grown in Chad (Nigueux, 1959), and yield advantages of up to 44% were recorded for intercrops of finger millet:groundnut in Uganda (Osiru and Kibira, 1979). In a study of pearl millet and groundnut intercrops at ICRISAT (India) it was found that LERs were between 1.21 and 1.32 in the rainy season and from 1.25 to 1.29 in the post-rainy season under irrigation, and that water or nitrogen stress tended to increase LERs (Reddy et al., 1981). The efficiency of the system was attributed to improved efficiency of conversion of light, not to the interception of more light or to increased efficiency of the rooting system (Reddy & Willey, 1981, Reddy & Willey, 1980). In another experiment which combined several millet and groundnut genotypes in intercropping, it was concluded that the magnitude of yield advantage (25 to 30%) was mainly determined by the groundnut genotype whereas the proportion of groundnut yield to millet yield was mainly determined by the millet genotype (Willey & Rao, 1979). However, in another study in India, sorghum sole crops were found to give maximum net returns compared with sorghum:groundnut intercrops (Palaniappan and Balasubramanian, 1976).

Schilling (1965) found that when intercrops of groundnut and sorghum or groundnut:millet were compared with a rotational pattern in Senegal, groundnut yields were decreased by about 10% while those of the cereals doubled compared with sole crops. This was considered of importance as the farmers subsistance is gained from the cereal (Schilling, 1965). In a monsoon trial on the companion cropping of rice, sunflower or groundnut associated with sorghum, it was found that a sorghum:groundnut mixture produced the maximum net profit per hectare (Upadhyay & Shaik, 1976).

Groundnut-Maize Intercrops

In a study where goundnuts were intercropped with maize, planted simultaneously and on different dates, it was found that the earlier planted crop invariably gave greater yields, and the traditional practice of simultaneous planting gave intermediate results (Azab, 1968). Land Equivalent Ratios (LERs) of 1.23 to 1.29 were obtained by intercropping maize with groundnut in treatments where the maize sowing was delayed from 0 to 20 days in Malang. The greatest income was obtained from the groundnut sole crop, the least from the maize sole crop, and intercropping tended to increase profits compared with maize (Sitompul et al., 1980). Although corn grain yield was reduced by 20% and groundnut yield reduced by 31% when intercropped, the productivity was higher than the sole crop controls in a study done in the Philippines (Cruz and Cadiz, 1977). LERs as high as 1.4 without N fertilization have been reported in Australia, lower LERs were acheived with less nitrogen (Searle et al., 1981).

LERs of 1.19 were obtained in maize-groundnut intercrops grown in Africa, though Leaf Area Index, Leaf Area Ratio, Specific Leaf Weight, and Dry Matter of the groundnuts was significantly reduced in the intercrop (Edje, 1980). An increase in total grain and protein yields was recorded for a maize-groundnut intercrop as compared to maize (Gangwar & Kalua, 1978). A corn-groundnut intercrop was 30% more productive (total yields) when compared with monoculture checks, and plant density had a greater effect on productivity than did row-arrangement (Herrera et al., 1975). An increase in "yield per stand" for corn and no difference in yield per stand for groundnuts as compared with respective sole crops was recorded in Nigeria (IAR, 1968).

Many of the studies in the literature merely report monetary returns as a basis of evaluation of intercrops. Net returns were greater than either sole from a 50% corn 50% peanut mixture grown in Malang (Isgiyanto et al., 1980). Evans (1960) obtained yield advantages ranging from 9-54% from 5 different experiments conducted at two locations in Tanzania, and advantages of 6-16% were reported from wetern Cameroon (Mutsaers, 1978). However, no difference in intercrop versus sole crop yields or returns were found over 3 years of experimentation in Ghana, except when in one year damage to the groundnut from Sclerotium rolfsil was greater in sole than mixed crops (Koli, 1975). A reduction of incidence of groundnut rosette virus in a maize:groundnut intercrops was recorded in Nigeria (IITA, 1974) but Cercospora leaf spot was less severe in the sole crop than the intercrop.

Groundnut-Cotton

Intercropping groundnut with cotton has been of some interest in India, with a high demand for both of these cash crops. The practice of interplanting cotton with groundnut has received a mixed review, however. Cotton was found to completely smother the growth of groundnut at the Palur District Research Station in India at narrower row arrangements (Algappan et al. 1960), while row proportions of 8 to 1 groundnut:cotton did not effect groundnunt yields and cotton yields ranged from 260 to 380 pounds of seed cotton per acre in Guntur District, India (Anon., 1949).

Several other experiments reported from India indicate economic advantages from groundnut/ cotton mixtures (Giri and Upadhyay, 1980). Results from a two year study of pre-monsoon irrigated intercrops of groundnut and cotton in Haryana, India showed that the intercrop had a greater return over other intercrop combinations and pure cotton (Birajdar & Nankar, 1978). Birajdar et al. (1978) found that cotton as an intercrop with groundnut gave a 40% net income benefit over sole crop cotton, which was greater than any other intercrop tried (blackgram, mung, soybean or maize). LERs for a groundnut:cotton intercrop (6 feet between cotton rows, 1, 2, or 3 rows of intercropped groundnut) ranged between 1.4 and 1.66 (Joshi and Joshi, 1965). Monetary advantages to intercroping groundnut with cotton were found in Gujurat (Patel et al., 1979) and in Madras (Pillai et al., 1957). When cotton was intercropped with groundnut, yields of cotton were not reduced, and a "bonus" crop of groundnut was obtained, whereas with other intercrops, cotton yields were lower than sole crop (Varma & Kanke, 1969), although others reported reduced seed cotton yields from intercropping with groundnut (Verma et al., 1973).

In Kenya, returns were shown to be higher with cotton:groundnut intercrops "on the flat", but not when the crops were confined to 3 foot tiered ridges (Anon., 1957). In Sudan, three years of experimentation indicated that cotton interplanted with groundnuts or several other legumes would not be recommended due to quite varied results (Anthony and Willimott, 1957).

Groundnut-Legume

Three years of experimentation in both rainy and post-rainy seasons in India showed significantly more income from mixed crop of redgram (pigeonpea, Cajanus cajan) and groundnut than from a pure crop of groundnut (Appadurai and Selva Raj, 1974). However, the groundnut in a pigeonpea-groundnut intercrop in Haryana, India failed to mature apparently because of excess shading from the pigeonpea (Gupta et al., 1979). Reddy and Reddy (1980) found advantages to growing pigeonpea with greengram (Vigna radiata) and groundnut, but not with other legumes. Kaul & Sekhon (1974) reported a 21% increase in cash return when groundnut was intercropped with pigeonpea, even though pigeonpea grain yields were reduced (75 cm between pigeonpea rows). In an irrigated study in South India, groundnut yields in widely spaced intercrops of 6:1 or 8:1 row arrangements with pigeonpea were reported to be similar to those of sole crop, and a 6:1 ratio was considered to give greater returns than sole crops (Veeraswamy, 1974).

Other Groundnut Intercrops

The number of potential combinations between species is enormous, and attempts have been made to intercrop groundnuts with several other species common to the tropics which have sufficient demand for either market-sale or for on-farm use.

Intercropping sesame with groundnut increased the total oilseed production as well as economic return in India (Desai & Goyal, 1980).

Castor bean with groundnut ususally showed an overall gain in production per acre, never an overall loss (Evans and Sreedharan, 1962). Similar results were reported by Reddy et al.,(1965).

Groundnut has been sucessfully planted with tapioca (cassava, Potti and Thomas, 1978, Thomas and Nair, 1979). Mixed cropping of groundnut with cotton, castor, redgram or sorghum and other crops in the rainy season was found to be more renumerative than sole crops (John et al., 1943). A good review of intercropping with cassava can be found in Weber et al. (1979).

Yield advantages and economic advantages were found for a niger-groundnut mixture in India (Kachapur, 1977).

In the Philippines, it was concluded from four field trials that intercropping sugarcane with groundnuts does not affect sugar yields, and that this may be profitable for sugarcane labor--if they were allowed by sugarcane growers to manage the intercrops by themselves (Villarico and Ledesma, 1976). These findings were collaborated by

Wijanarko et al. (1980).

Intercropping of one row of sunflower with groundnut grown at 30 X 5 cm. gave total oil yields of 787 kg ha^{-1} compared with 638 for groundnut at the same spacings. Total protein yeilds were also greater in the mixed crop (Venkateswarlu et al., 1980). Little reduction in sunflower yield was seen when intercropped with groundnut in India (Chandrasekar and Morachan, 1979).

CHAPTER IV.

PLANTING PATTERN AND DENSITY STUDIES IN A GROUNDNUT-BASED INTERCROP

Introduction

Groundnut (Arachis hypogae, L.) is the second largest source of vegetable oil in the world (the largest is soybean). Most of the groundnut is produced in the Semi-Arid zones of the world. India, which is the worlds' largest producer, generates about 40% of the worlds' total production, yet edible oils are imported in substantial quantities (FAO, 1984).

In semi-arid regions, groundnut is frequently grown as an intercrop with cereals (sorghum, pearl millet or maize) or with longer-seasoned crops such as cotton, pigeonpea or cassava (Reddy et al., 1981). In the more humid tropics, groundnut is frequently intercropped with tree crops such as coconut or oil palm (Harwood & Price, 1976; Aiyer, 1949). It has been estimated that between 56 and 95% of the groundnut hectarage in Uganda and Nigeria respectively was grown as a mixed crop (Okigbo & Greenland, 1976; Kassam, 1976). In India, groundnut is often grown as an intercrop in the rainy season (kharif) and is grown as a sole crop on residual moisture or under irrigation in the post-rainy (rabi) or summer season (which follows rabi).

There is clear evidence of the potential for yield or monetary advantges to growing groundnuts with intercrops. Advantages have been demonstrated for intercropping groundnuts with finger millet (Aligappan et al.,1960; Schilling, 1965; Baker,1978; Osiru & Kibira, 1979; Baker,1980), sorghum (Nigueux, 1959; Bodade, 1964; Schilling, 1965; Lingagowda et al., 1972; Mohammad & Upadhyay, 1977; Reddy et al., 1981), maize (Evans, 1960; Herrera et al., 1975;, Cruz and Cadiz, 1977; Gangwar & Kalro, 1978; Mutsaers, 1978), cotton (Joshi & Joshi, 1965; Varma & Kanke, 1969; Birajdar & Namkar, 1978; Birajdar et al., 1978; Patel et al., 1979), sunflower (Singh and Singh, 1977; Chandrasekhar and Morachan, 1979; Venkateswarlu et al., 1980), and other legumes (Kaul & Sekhon, 1974; Farrell, 1976). Most of these studies were carried out under non-irrigated (rain-fed) conditions employing a limited number (one or two) of plant arrangements or densities in the intercrop treatments.

Although there are a number of studies reporting results of sorghum:groundnut trials with limited treatments, few studies have been made on groundnut:sunflower intercrops. Narwal and Malik (1985) found severe reductions in pod yield in a sunflower:groundnut intercrop in India, and indicated a yield disadvantage to the practice compared with sole crops (LER = 0.77 to 0.82) with a 1:1 row ratio treatment. However, others have indicated a potential for substantial yield advantages (Singh and Singh, 1977; Venkateswarlu et al., 1980; Mohammad, S. 1986, pers. communication, Andhra Pradesh Agric. Univ., Hyd., India). In general, the validity of employing an intercrop strategy for groundnuts in the post-rainy season in the Semi-Arid Tropics remains largely unexplored. The purpose of this study was to quantify the yield response of groudnut:sorghum and groundnut: sunflower intercrops over a wide range of planting patterns and densities under irrigation in the post-rainy rabi (Oct.-Feb.) and summer (Jan.-May.) seasons.

Materials and Methods

Groundnut (*Arachis hypogaea* L.) was grown under irrigation as an intercrop with sorghum (*Sorghum bicolor* (L.) Moench.) and sunflower (*Helianthus annus* L.) in the post-rainy season (rabi) and summer season at the Andhra Pradesh Agricultural University, Hyderabad India. The soil is predominately a sandy loam, but with 8-16% clay. The physical and chemical properties of the two experimental sites (located 1 km apart) are given in Table 1.

The experimental design was a two-way factorial systematic design with three replications adapted from the "fan" design of Nelder (1963) and later proposed designs (Mead & Stern, 1980), where the treatments are arranged in sequence rather than randomly in the field. The advantages and disadvantages of using this type of design are explored by Willey (1979b) and Mead & Riley (1981).

Six intercrop planting patterns and 7 sorghum or sunflower densities were combined to form the systematic fans (42 treatment combinations per fan) as shown in Figure 1. The planting patterns consisted of a "replacement series" (deWit, 1960) where rows of sorhgum or sunflower replaced groundnut in 1:1, 2:1, 3:1, 4:1, 5:1, 6:1 groundnut:sorghum ratios. Each systematic ray (shown in Figure 2)

Table 1. Physical and chemical characteristics of a sandy loam soil at the experimental sites in the Rabi (A) and Summer (B) seasons, Andhra Pradesh, India.

PHYSICAL PROPERTIES:

Site	Repl.	Mechanical Analysis Sand	Silt	Clay	Cation Exchange Capacity	Bulk Density	Field Capacity	Hydraulic Conductivity
		--------%--------			(me 100 g-1)	(g cc-1)	(%)	cm hr-1
A	1	49.2	38.8	12.6	18.2	1.65	54	8.50
A	2	69.8	24.2	6.0	17.5	1.62	60	7.20
A	3	49.9	41.7	8.4	23.4	1.56	62	9.65
B	1	59.8	27.4	12.8	22.6	1.59	58	7.92
B	2	42.1	40.1	15.6	18.7	1.54	60	8.25
B	3	50.5	27.3	12.1	14.6	1.71	67	9.06

CHEMICAL PROPERTIES:

Site	Repl.	pH	E.C.*	Organic Carbon	Nutrient Status N	P205	K20	Zn+	Cu+	Fe+	Mn+
		(1:2.5)	mmhos cm-1	%	------kg ha-1-----			----------ppm--------			
A	1	7.8	0.13	0.75	183.3	31.5	397.4	0.63	4.25	27.5	21.0
A	2	7.5	0.10	0.62	175.6	32.6	346.4	0.48	3.59	17.4	14.0
A	3	7.9	0.17	0.71	167.3	39.8	352.9	0.73	3.71	18.0	20.0
B	1	7.3	0.17	0.56	159.2	28.5	267.5	0.84	3.56	28.0	22.0
B	2	7.1	0.06	0.43	281.5	27.6	397.5	0.95	3.42	25.3	18.3
B	3	7.8	0.20	0.75	123.8	35.6	362.2	0.76	4.64	26.4	23.5

*Electrical Conductivity
+Micronutrients, EDTA extractable

Table 2. Intercrop and sole crop plant spacing treatments, systematic design, groundnut intercropping experiment.

Treatment No.	Sorghum Row Basis	Sorghum Area Basis*	Sunflower Row Basis	Sunflower Area Basis*
	plts. m-1	plts. m-2	plts. m-1	plts. m-2
1	7.0	23.3	3.1	10.3
2	8.3	27.7	3.6	12.0
3	9.8	32.6	4.3	14.3
4	11.5	38.3	5.1	17.0
5	13.5	45.0	5.9	19.7
6	16.1	53.6	7.0	23.3
7	18.9	63.0	8.3	27,7

*Based upon a sole crop at 30 cm row spacing

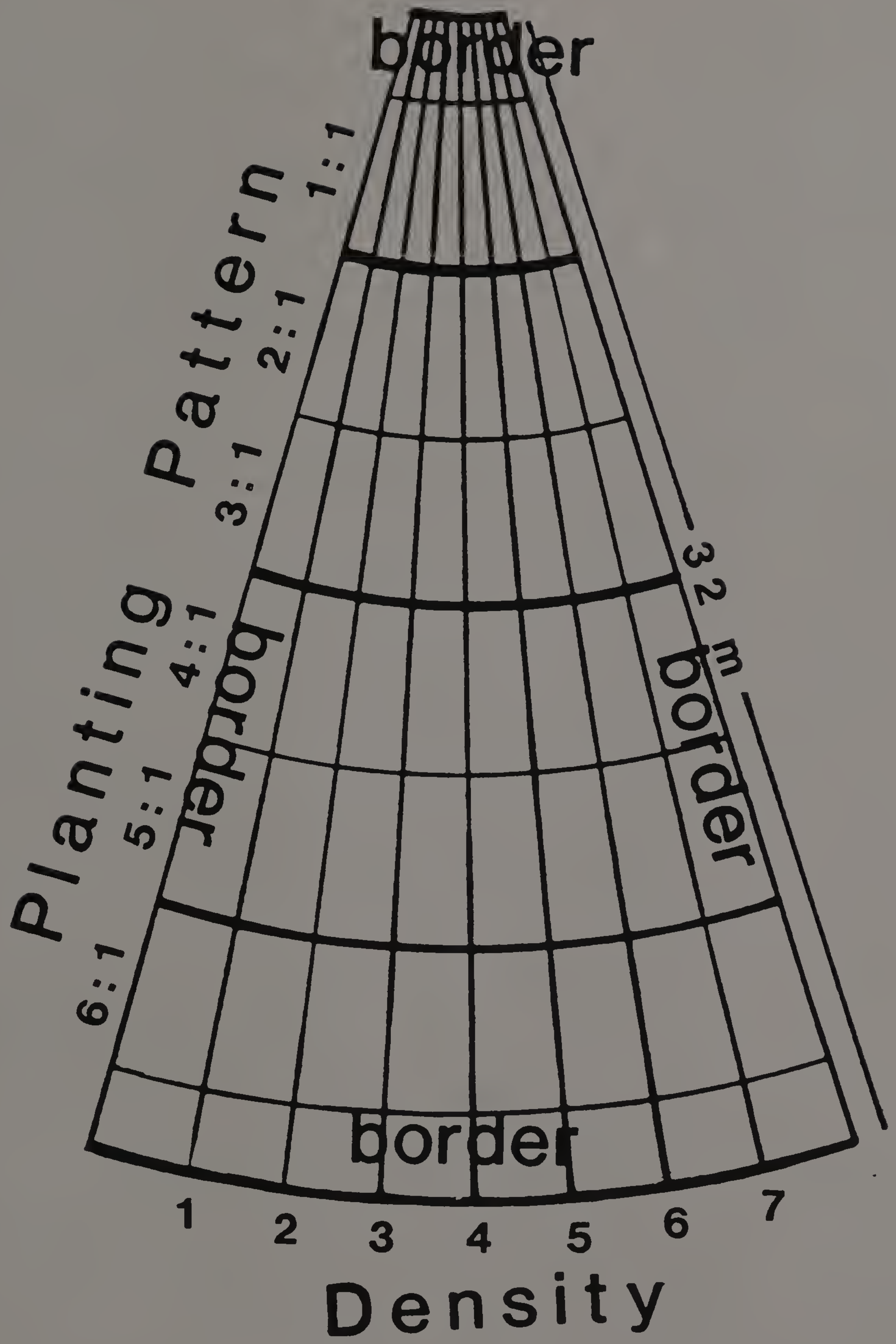

Figure 1. One replicate of a systematic fan, groundnut intercropping systematic design. Groundnut rows are not shown. Planting pattern treatments vary from origin to circumference and density varies from row to row across the fan.

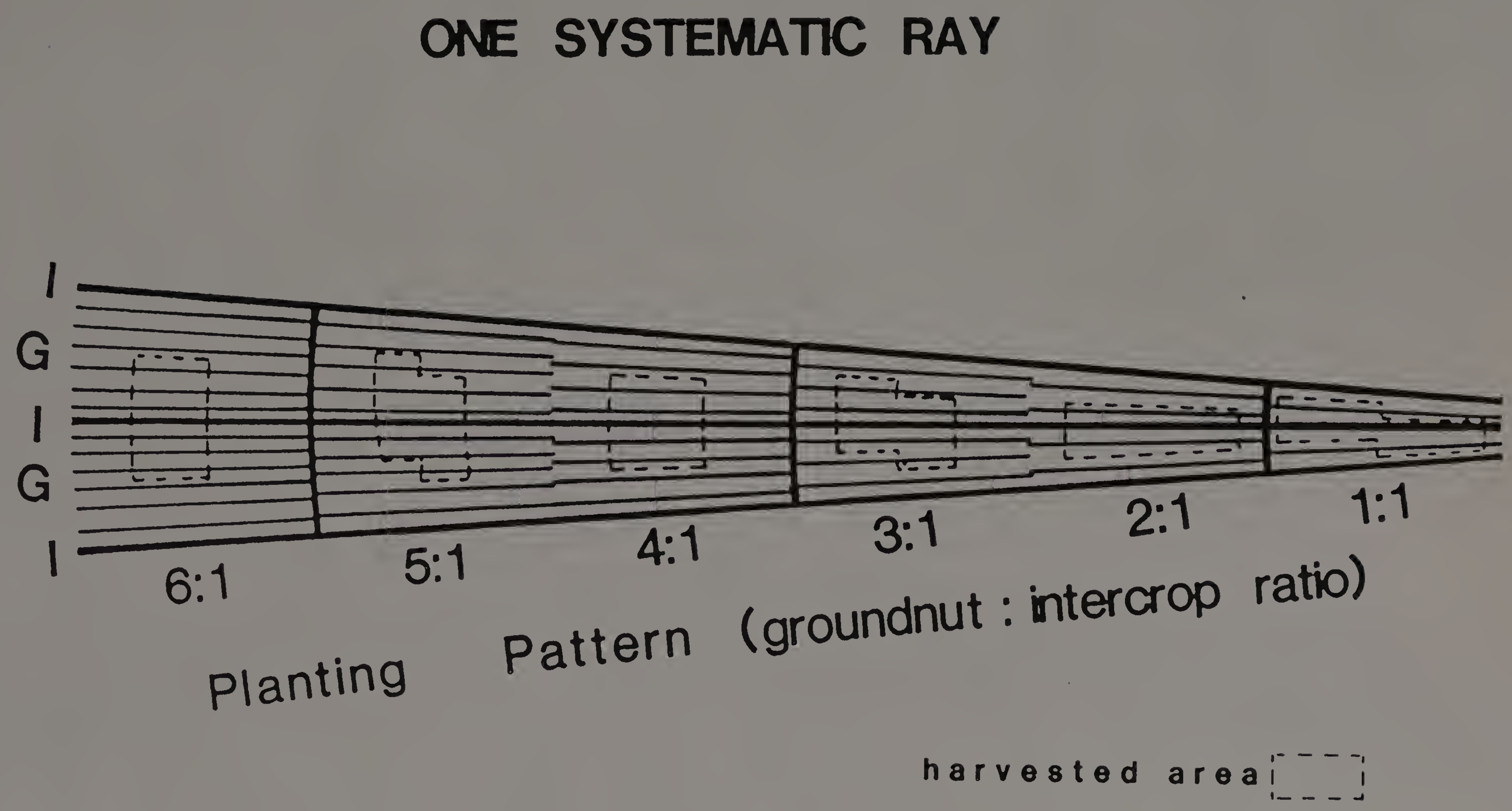

Figure 2. Enlargement of one systematic ray, groundnut intercropping systematic design. Planting pattern (row arrangement) treatments and harvested areas are shown. I represents the intercrop (sorghum or sunflower) and G represents groundnut.

thus formed a continuous variable ranging from 50% groundnut (1:1) to 86.7% groundnut (6:1) in the planted intercrop mixture.

The density treatments (Table 2) varied from row to row across the fan. In no case did density vary more than 18% from plot to plot. The assumptions made in this design were that border effects from plot to plot are minimal and that trends in soil or aerial factors which are confounding treatment effects are minimal or can be alleviated by replication. The direction of the density systematic treatments was alternated, and the orientation of the fans was changed from replication to replication to minimize possible confounding trends (Figure 3).

The sole crop control plots were planted to the side of the whole fans (figure 3). Groundnut density in the intercrop and sole crop plots was constant at 30 cm between rows and 10 cm between plants. The sorghum and sunflower sole crop plots were planted using the same systematic spacing variables as the intercrops at 45 cm and 60 cm row widths (Figure 4). In all plots, border areas were left on the outside of the systematic plots, and some borders were left between systematic plots, allowing a harvested area of 2.5 m^2 $plot^{-1}$ in the intercrops and 1.25 m^2 $plot^{-1}$ in sole crops (duplicate samples were taken in the groundnuts).

The groundnut variety used was Kadiri-3 (selection from Robut-33-1). This is a small, semi-spreading type which has been shown to yield well in intercropping (Reddy et al., 1979; Reddy et al., 1981). Sunflower variety EC68414, an exotic culture from Peredovic line was

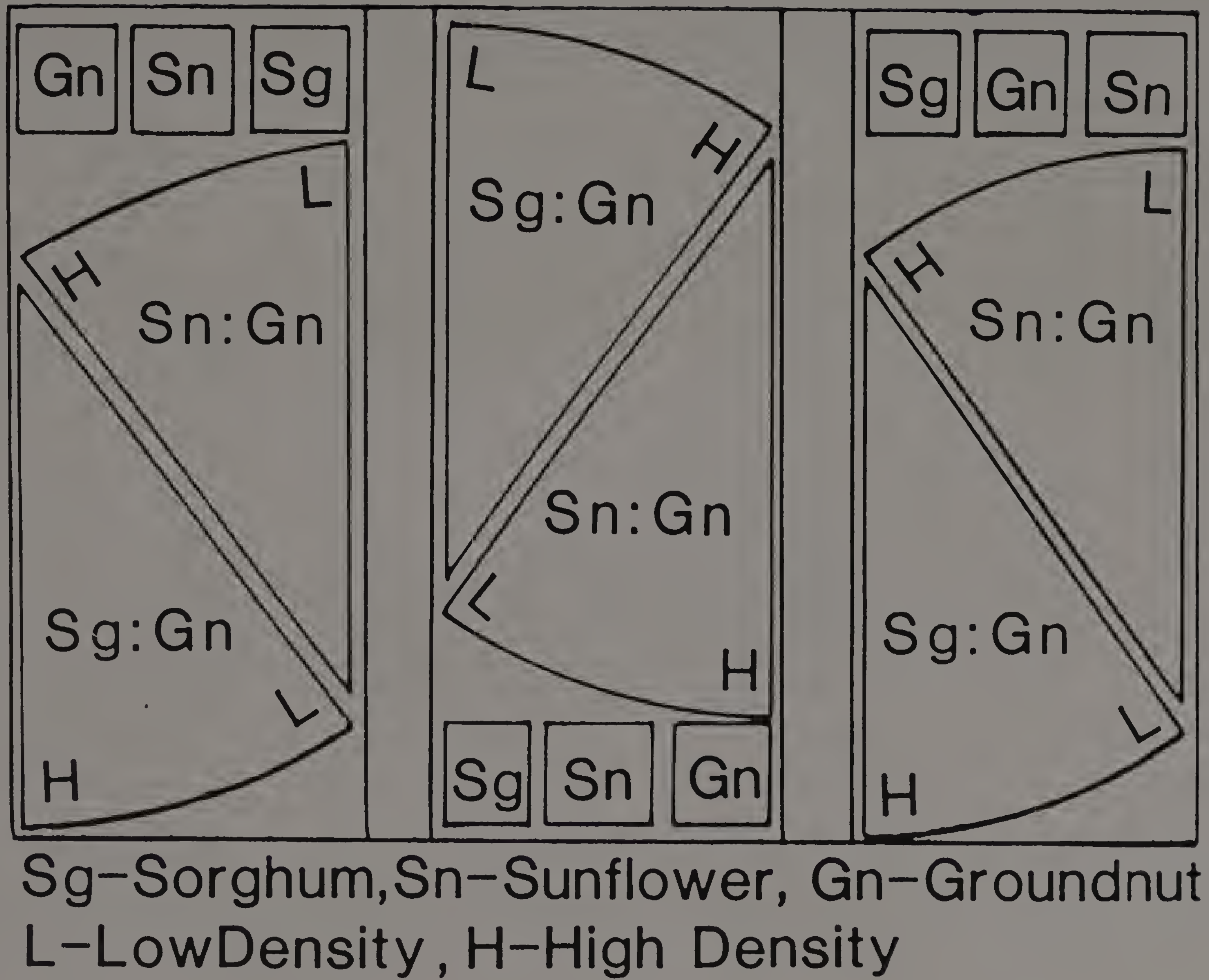

Figure 3. Field layout, Rabi season. Segments represent whole systematic intercrop plots (Figure 1), boxes represent sole crop plots. L and H represent low and high intercrop density extremes.

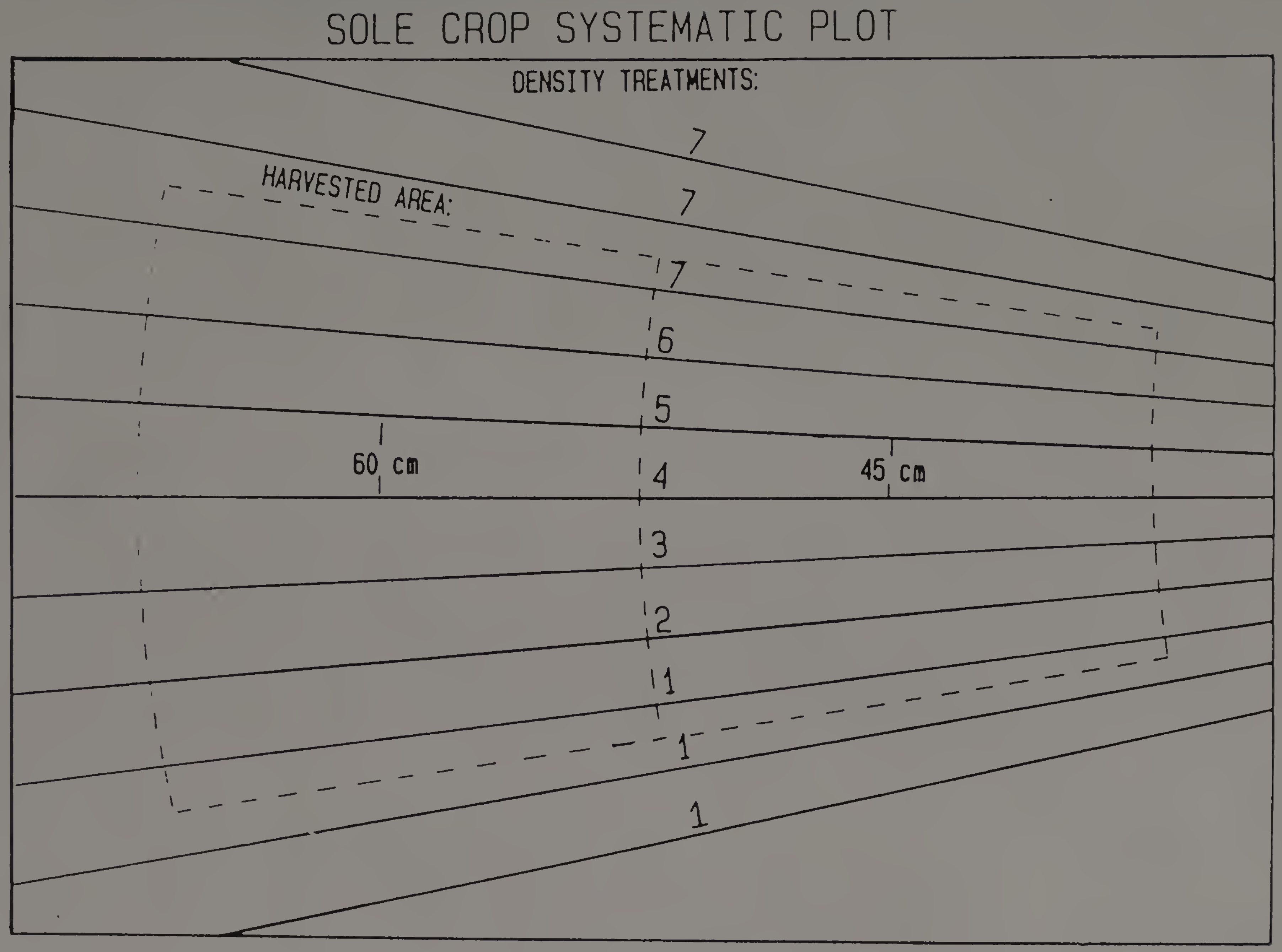

Figure 4. Sole crop systematic plots of sorghum and sunflower (groundnut spacing was constant in sole crop and intercrop). Density treatments were identical (on a within-row basis) with intercrops.

used. Sorghum hybrid CSH8R was used for the Rabi study and hybrid CSH6 was used for the summer planting (All-India-Coordinated Sorghum Project, Rajendranagar, A.P., India)

Preplant broadcast applications of 20 kg ha^{-1} N and 53 kg ha^{-1} P as diammonium phosphate and 25 kg ha^{-1} K as muriate of potash were made at both sites. Urea was applied as a sidedress to the sorghum and sunflower 30 days after planting at the rate of 80 kg N ha-1 (based upon the area planted to that species in the intercrop).

Groundnuts were hand-shelled and treated with captan and innoculated with *Rhizobium* before planting. The three crops were hand-planted simultaneously using marked twine as guides, and one replication was planted per day beginning 7 November, 1984 (College Farm location, rabi season) and January 16 (Student Farm location, summer season). Germination differences were observed in the Rabi season between replications, with the first replication exhibiting excellent groundnut germination and the third replication very poor germination, and the second replication intermediate. The third replication was replanted entirely to groundnut, and gaps were filled in the second replication 15 days after planting. There were no differences in germination of the other crops or in the Summer season with groundnuts, where germination was excellent. The poor germination in one replication was attributed to *Aspergillus flavus* infection, which may have been due to slight differences in soil moisture and soil temperature between the replications.

Sorghum seedlings at the College Farm were sprayed with monocrotophos applied at the rate of .5 l ha-1 a.i. for the control of shoot fly and at the student farm with quinolphos (Sandoz, India, Ltd.) at the rate of 1.5 l ha-1 was sprayed on sorghum and groundnut for the control of shoot fly in sorghum and leaf roller in groundnut. The catepillar *Diacrisia obliqua* Wlk. (lepidoptera), a herbivore which effects sunflower was destroyed by hand. Birdscarers were employed to prevent bird damage of groundnut and sunflower before emergence and 10 days before harvest of sunflowers and sorghum. Weeds were controlled by hand with at least 3 weedings per season.

Sunflower head diameter and sorghum head length were measured at harvest. Sunflowers were harvested 97 days after planting at physiological maturity (complete yellowing of head). Sorghum harvest was completed approximately 125 days after planting and groundnuts 140 days after planting. Samples were air-dried to a constant weight and weighed. Groundnut pods were counted from each plot and shelling percentage was determined from a 100 gram subsample. Seed weight of the intercrop was determined from a 300 seed sample from each plot.

Response surfaces for the yield and yield component observations for the three crops were calculated for each main effect (Planting Pattern and Density) using multiple regression, backward-selection techniques to determine the appropriate response (see Mead and Riley, 1981 and Mead and Stern, 1980 for a discussion of analysis fo systematic designs). No interaction was found between planting pattern and density using a full model for any of the variables, and so only the response due to main effects is presented. Dummy variables were used in the regression model to account for the sums of squares attributable to replication (Damon, R., pers. comm., Univ. of Mass., 1986).

Land Equivalent Ratios (LERs - Mead and Willey, 1980) were calculated for each component crop, and a response was estimated using a full regression model which included the independent variables of density and planting pattern and their quadratic terms. The non-significant interaction term was dropped from the model in this and other analyses. The total LER is expressed as the addition of these two predicted values. Predicted values for total LERs were also calculated using the actual total LERs, and since the differences between the two methods were small, the former method was used, so as to apply the same values for the SLER comparison below.

Staple Land Equivalency Ratios (SLER) comparisons were used because this comparison provides additional practical information (Reddy and Chetty, 1984). The predicted component LERs for groundnut and total LERs, calculated as described above, were used.

Results and Discussion

Individual Crop Response

Groundnut Component. Groundnut pod yields were reduced by more than 78-89% when alternate 30 cm rows of groundnut were replaced by rows of either sorghum or sunflower (50% groundnut, Figure 5). (A photograph illustrating the groundnut:sunflower and groundnut:sorghum systematic fans is provided in Figure 6.) An increase in pod yield

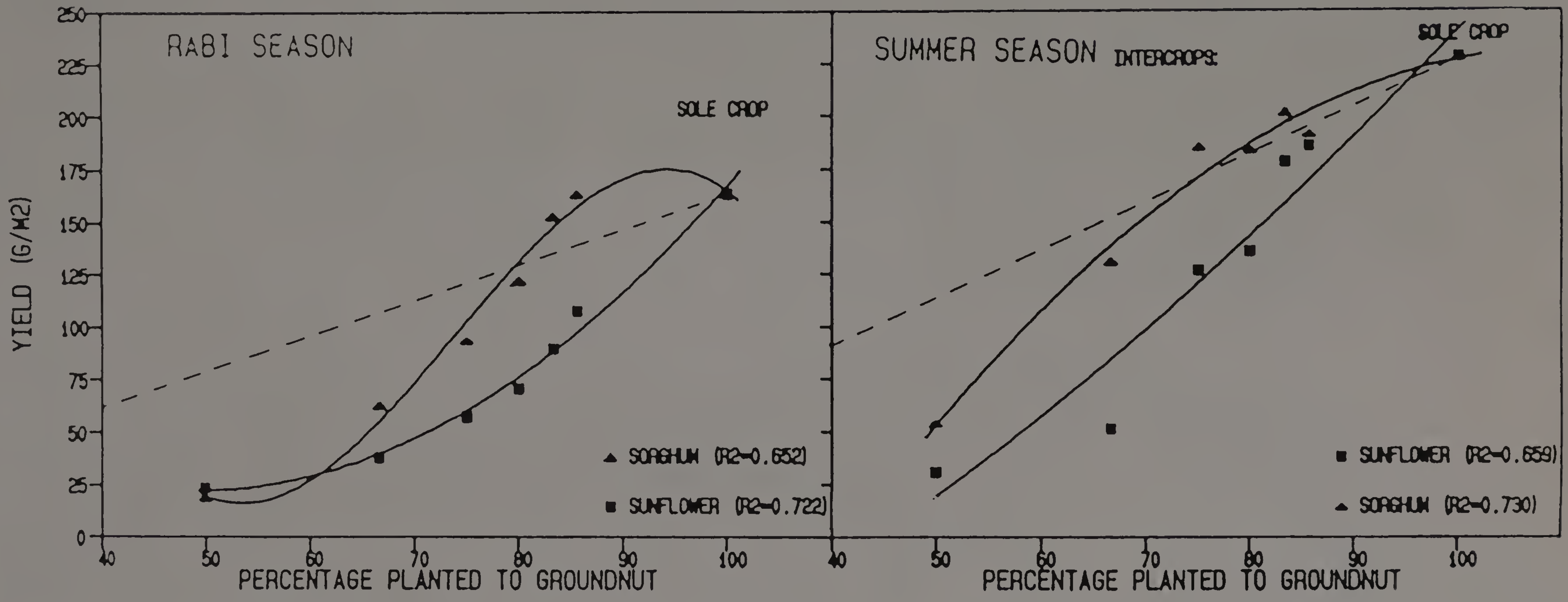

Figure 5. Planting pattern effects on groundnut pod yield, Rabi and Summer seasons. Symbols are means across densities, lines are calculated responses. Dashed line represents groundnut yields expected if intercrop competition was equal to sole crop competition.

Figure 6. Photograph of sorghum:groundnut intercrop fan (top) and sunflower:groundnut intercrop fan (bottom), Rabi season. Experiment was located at the Andhra Pradesh Agricultural University, Rajendranagar, Hyderabad, India, 1984-5.

resulted from a greater proportion of the planted area allocated to groundnut. This was a function of both the percent planted area and competitive effects of the intercrop. An estimation of the competitiveness of groundnut within the different intercrop patterns can be made by comparing the yields expected from the sole crop at given planted ratios (broken lines, Figure 5) and the fitted response estimated from the intercrop field data (solid lines, Figure 5). Groundnut yields were supressed in association with sorghum at planted ratios of less than 75-80%, but at higher groundnut:sorghum ratios (5:1 to 6:1), yields were similar to or greater than those expected from the same area planted to sole crops. Reddy and Willey (1985) found pod yields only slightly less than "expected" from sole crops at a 3:1 groundnut:pearl millet ratio (30 cm row spacing), results which agree well with this study. In both seasons, interplanted sunflower supressed grundnut yields at all planting patterns compared to the yields expected at that planted ratio (Figure 5).

Groundnut pod yields were greater when intercropped with sorghum than in the sunflower intercrop (Figure 7). The mean of the sole crop yields was greater than the mean of either intercrop. Variation in density of sorghum or sunflower had little effect on groundnut yield in either season (groundnut density was constant at 30 cm X 10 cm).

The yield trends due to planting pattern and density were similar across seasons, although the overall pod yield level in the second season was higher than in the first (Figures 5 and 7).

The reduction in groundnut yield in the intercrops was due both to

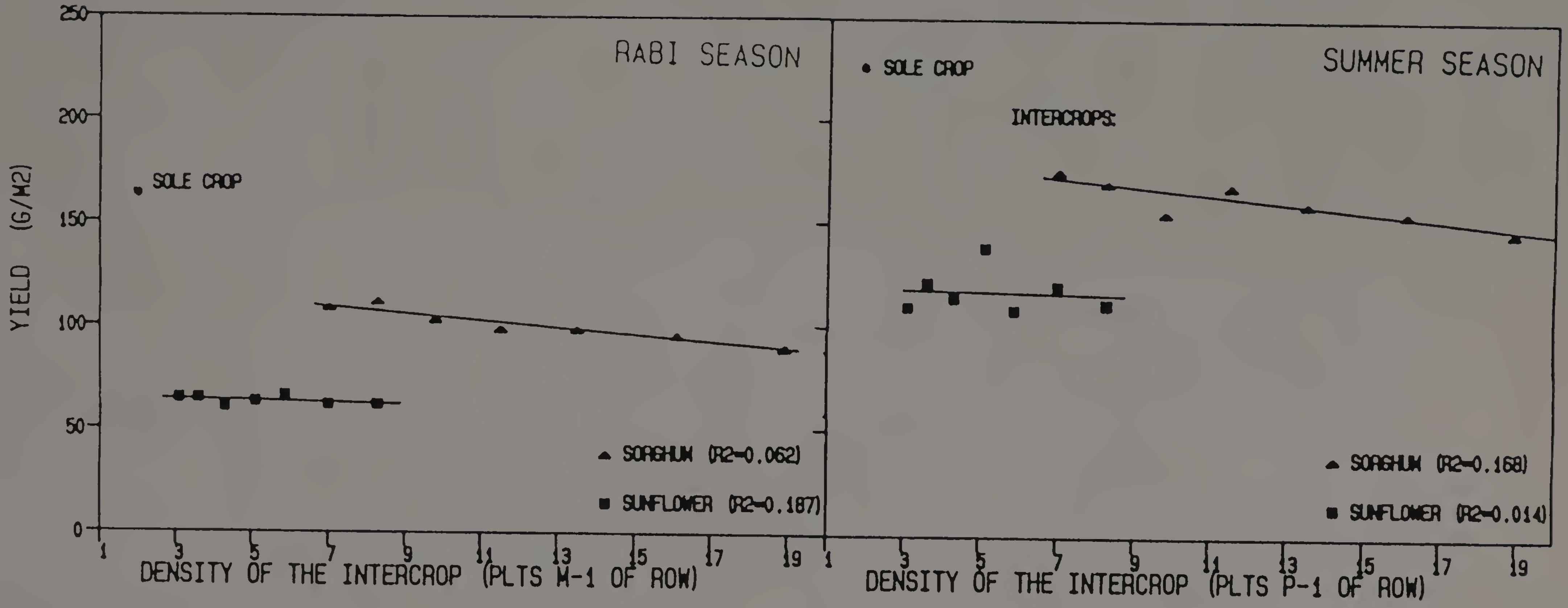

Figure 7. Density effects on groundnut pod yield, Rabi and Summer seasons. Symbols are means across planting patterns, lines are calculated responses.

a reduction in pod number and pod weight (figures 8 and 9). As the intercrop rows narrowed in the systematic design (more "intimate" patterns) to the 50:50 pattern, pod number per plant was decreased by up to 64% and 70%, sorghum and sunflower respectively (Figure 8), while pod weight was reduced by about 33% in both crops compared with the sole crop. The differences in yield trends between the sorghum and sunflower intercrop responses was primarily a result of differences in pod number, not pod weight, which can be seen by comparing responses in Figure 9. No differences were found in Pod number or weight due to changes in intercrop plant spacing (Figure 9).

Shelling percentage was reduced insignificantly when groundnut was intercropped with sorghum at any planting pattern, but reduced from 58% (sole crop) to 46% (50:50 intercrop) in the sunflower intercrop (significant linear trend) in the Rabi season (Figure 10). In the summer season, similar reductions in shelling percentage due to planting pattern were found for both crops (Figure 10), although the trend was only significant in the sunflower intercrop. There were only slight reductions in shelling percentage due to changes in intercrop sorghum density (Figure 11).

Shading of peanuts during critical periods has been shown to reduce yield. Shading at peak flowering reduced number of flowers and shading during pegging reduced total peg and pod number (An, 1979). Shading for 21 days during pod fill caused the greatest yield loss (31%--An, 1979). The greater shading in the sunflower intercrop (Figure 6) was possibly responsible for the differences between that

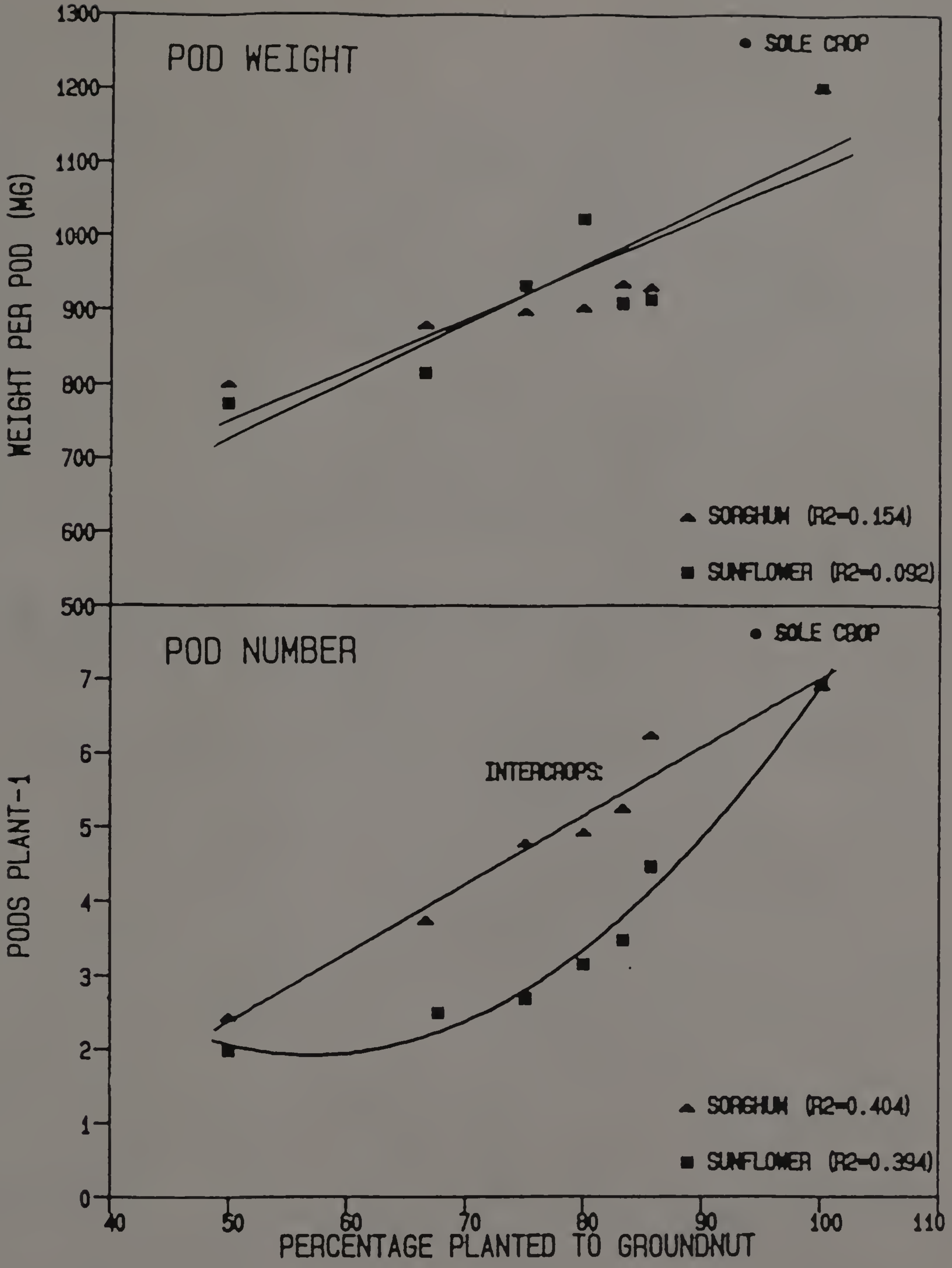

Figure 8. Planting pattern effects on pod number and pod weight, Rabi season. Symbols are means across densities and lines are calculated responses.

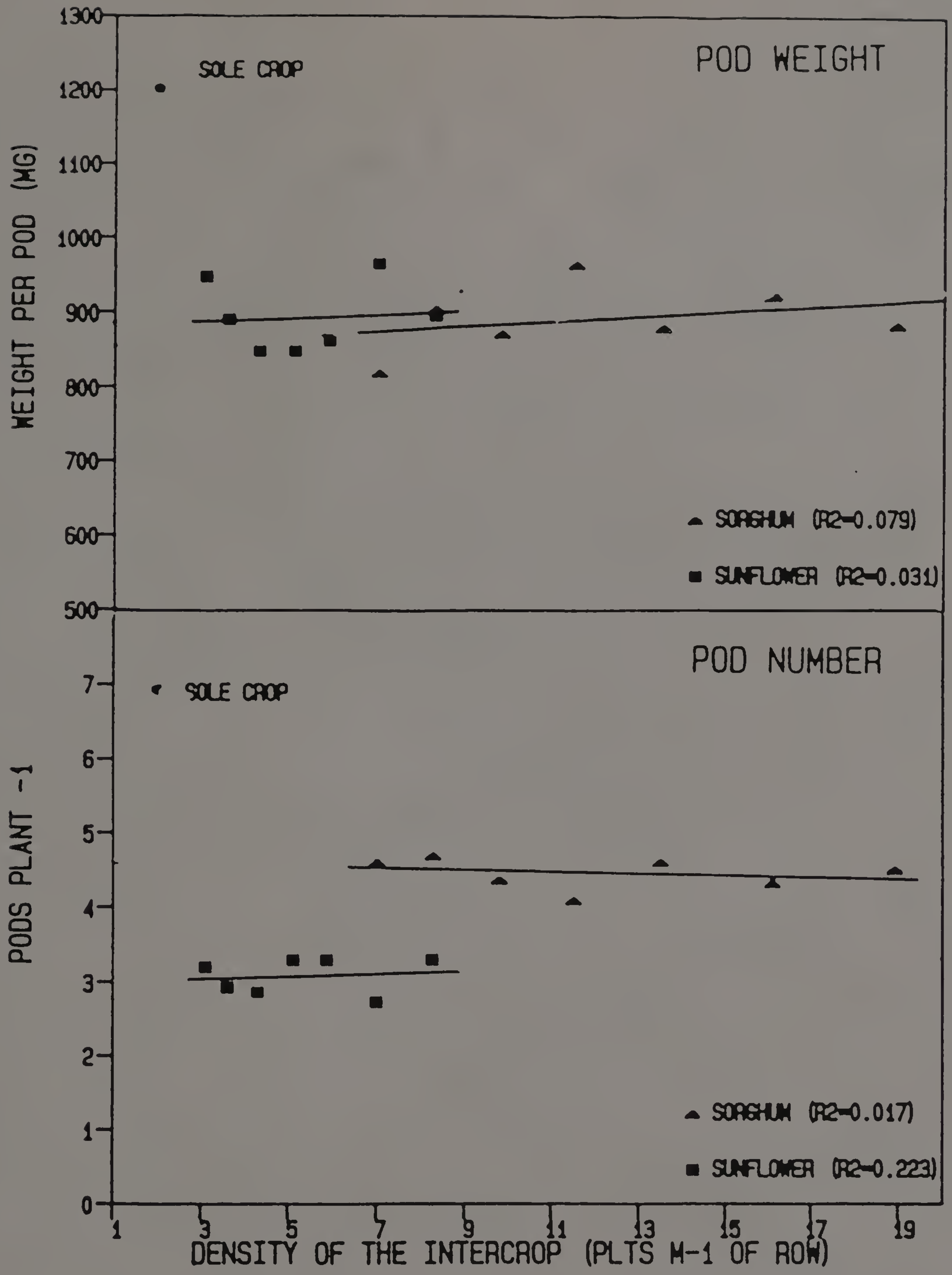

Figure 9. Density effects on pod number and pod weight, Rabi season. Symbols are means across planting patterns and lines are calculated responses.

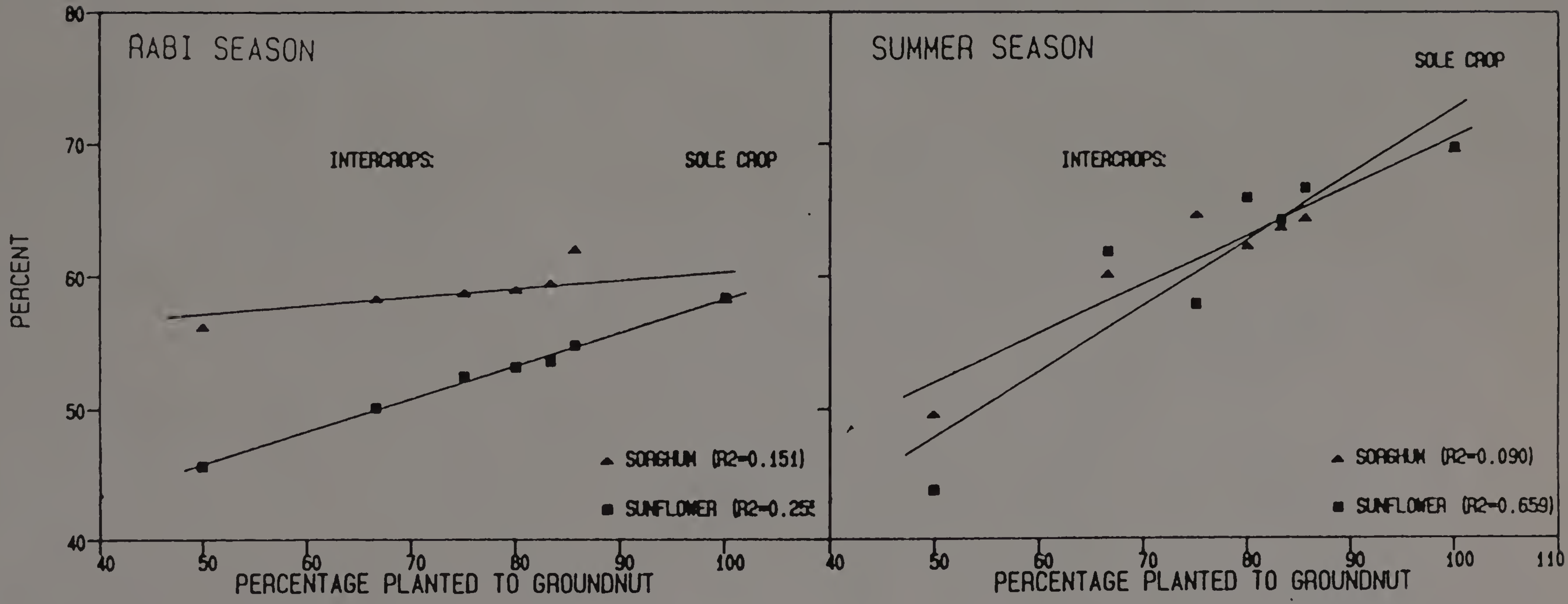

Figure 10. Planting pattern effects on groundnut shelling percentage, Rabi and Summer seasons. Symbols are means across densities and lines are calcualted responses.

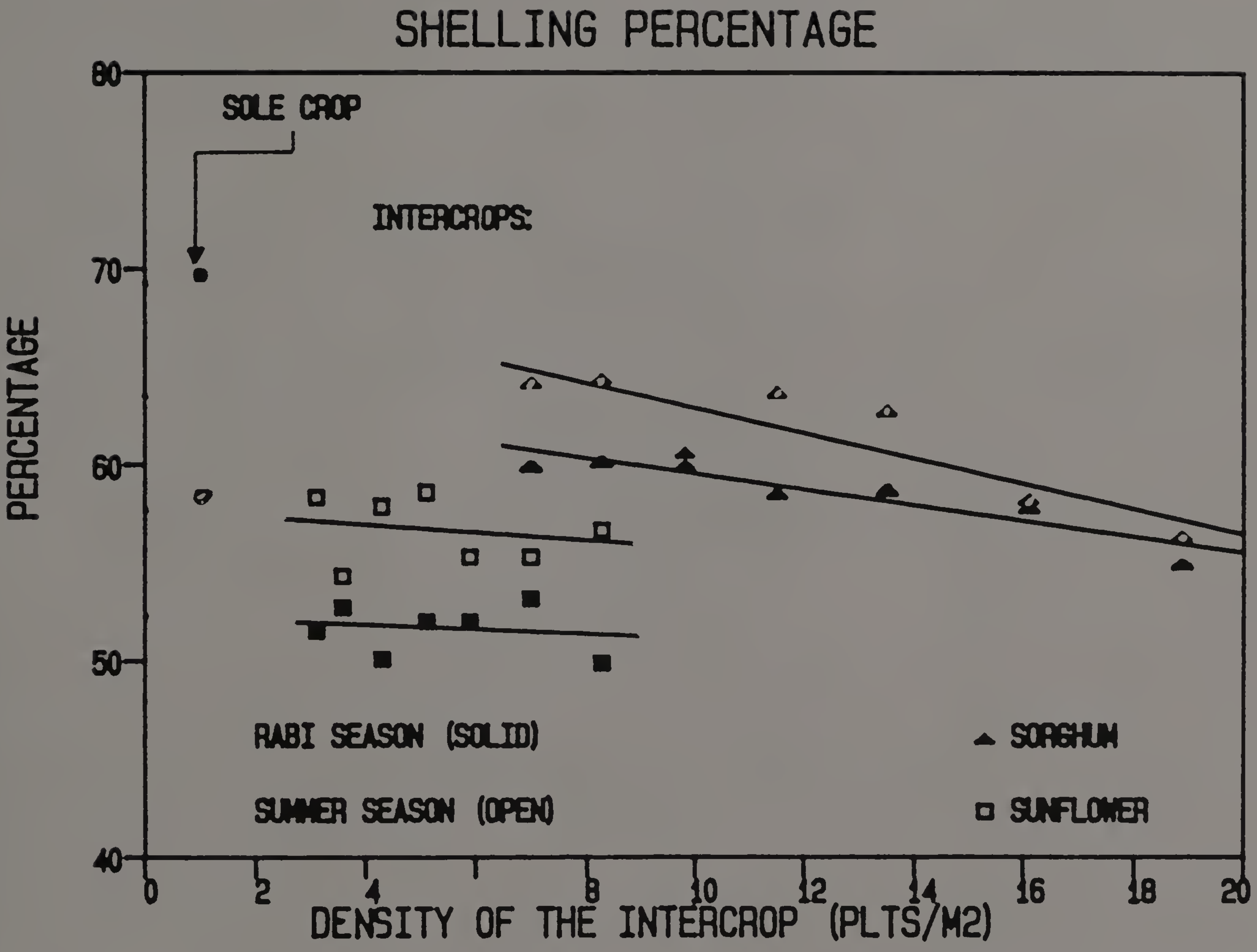

Figure 11. Density effects on groundnut shelling percentage, Rabi and Summer seasons. Symbols are means across planting patterns and lines are calcualted responses.

and the sorghum intercrop, although this should be confirmed experimentally. If intercrops could be design with greater differences in maturity between the sunflower and groundnuts (allowing a longer competition-free period for the groundnuts during pod fill), groundnut yields could be increased further.

In general, there were no significant trends in groundnut yield or yield components due to the density of the intercrop component. In all cases, the interaction term between density and planting pattern was also non-significant. (The assumptions inherent in an analysis of variance method of determining response surfaces are not satisfied with a systematic design: thereby this remains an imperfect method of determining response in a non-random design such as this).

Sunflower component. Sunflower yields were remarkably constant over a wide range of densities and intercrop and sole crop planting patterns (Figure 12). Intercrop planting patterns ranging from 1:1 to 4:1 groundnut:sunflower ratios produced sunflower yields which were similar to or greater than yields obtained from the sole crop. Yields were an average of 81-91% (Rabi season) and 79-85% (summer season) of sole crop control when sunflower occupied only 17% and 14% respectively of the intercropped land area (Figure 12). This is similar to the results of Chandrasekar and Morachan (1979) who found little reduction in sunflower yields when intercropped.

The adjustment in sunflower yield per plant (Figure 12), which made possible the maintenence of sunflower yields at very wide row

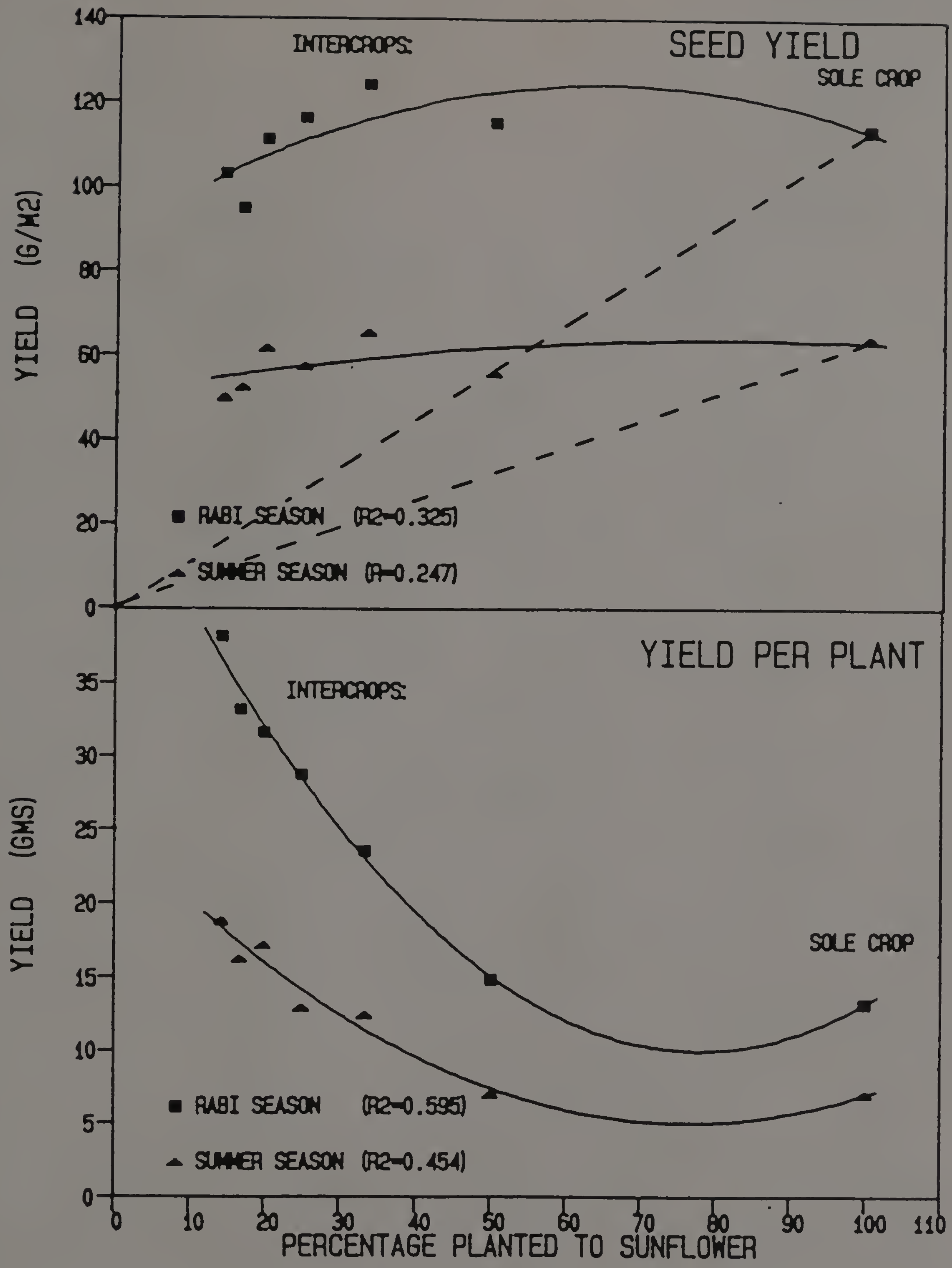

Figure 12. Planting pattern effects on sunflower seed yield, on an area and per-plant basis, Rabi and Summer seasons. Symobols are means across densities and lines are calculated responses. Dashed lines represent yields expected if intercrop competition were equal to sole crop compeitition.

spacing (with groundnuts interplanted) was due to increases in head diameter (Figure 13), seed number and seed weight (Figure 14). The data indicated that head diamter and seed number might continue to rise with even lower planted ratios of sunflower to groundnut, whearas average seed weight might remain constant at ratios greater than 1:4 (seed weight leveled off at about 4.8 gm 100 seeds-1 for the 3:1 through 6:1 patterns, while seed number and head diameter continued to increase, Figures 13 and 14).

Only slight differences in sunflower seed yield due to sunflower density were found in either the sole crops or the intercrops (Figure 15). This was due to linear reductions in yield per plant (Figure 15), head diameter (Figure 13), seed number and seed weight (Figure 16) with increased density. It should be pointed out that since the data is presented as the mean of the planting pattern treatments, the density effect in the intercrop are calculated at a mean planted percentage of about 22%

There was a small but significant linear trend for increase in yield with increased sunflower densities in the intercrop in the Rabi season, not in the summer season or with sole crops in either season (Figure 15). This was probably due to slight changes in seed weight, since differences in slope between the intercrop and sole crop responses were found for this parameter, not for seed number (Figure 16).

In addition to the treatments reported here, sunflower plants were also grown in isolation in plots adjacent to the systematic segments in

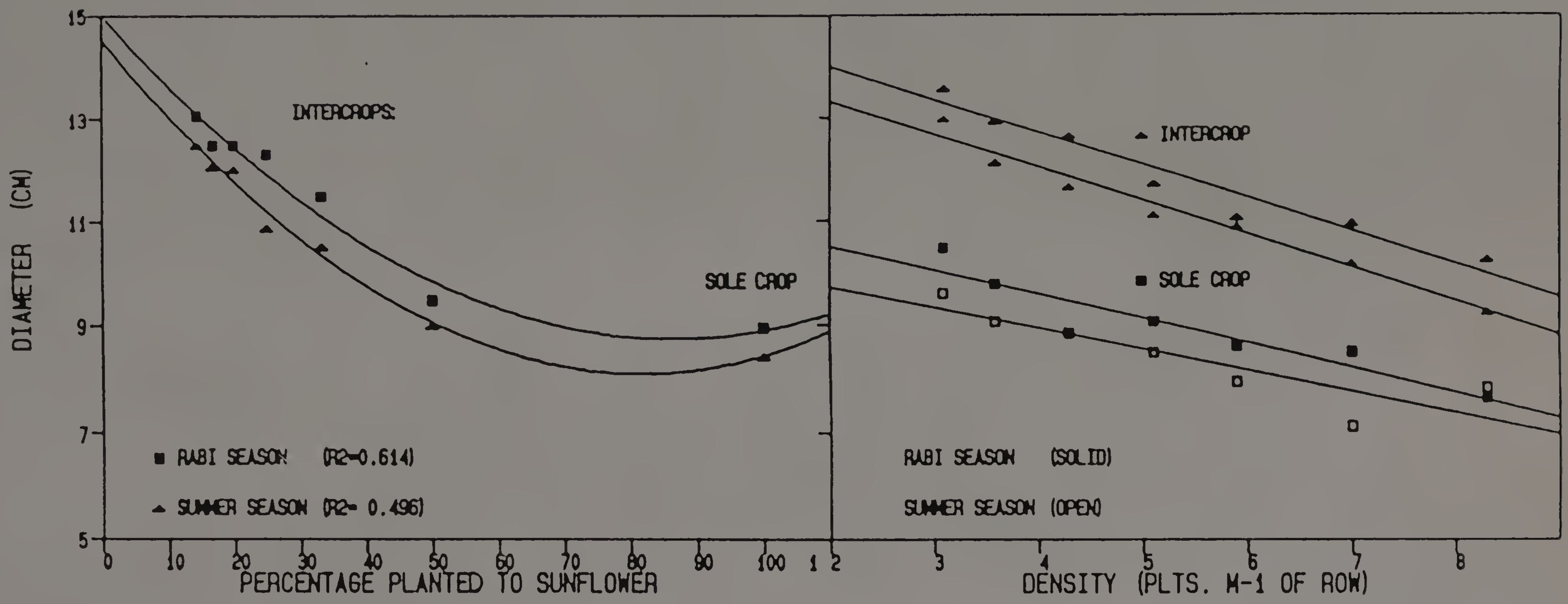

Figure 13. Density and planting pattern effects on sunflower head diameter, Rabi and Summer seasons. Symbols are means and lines are calcualted responses. R^2 values are: Rabi season intercrop (0.671), sole crop (0.523), Summer season intercrop (0.371), sole crop (0.558).

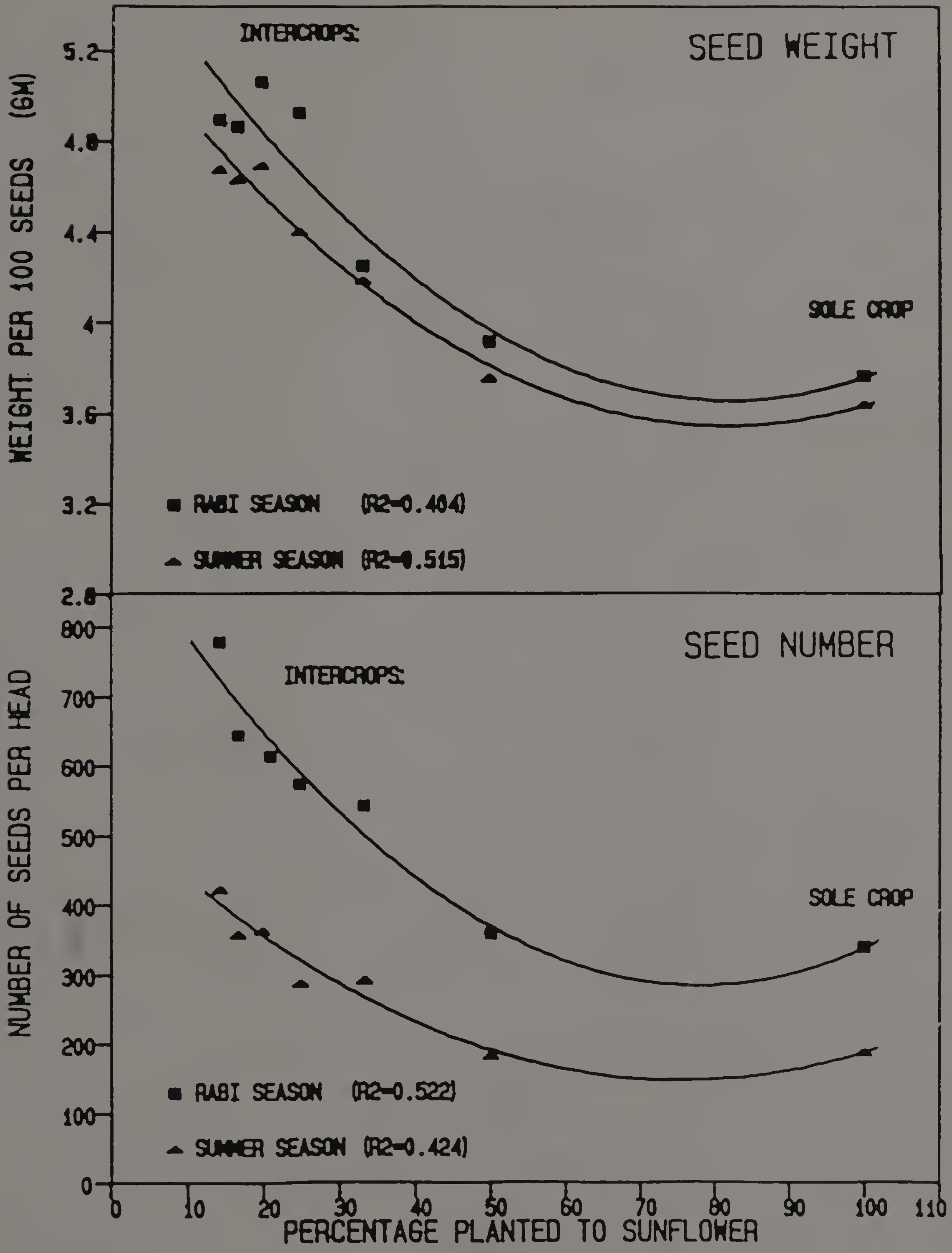

Figure 14. Planting pattern effects on sunflower seed number and seed weight, Rabi and Summer seasons. Symbols are means and lines are calculated responses.

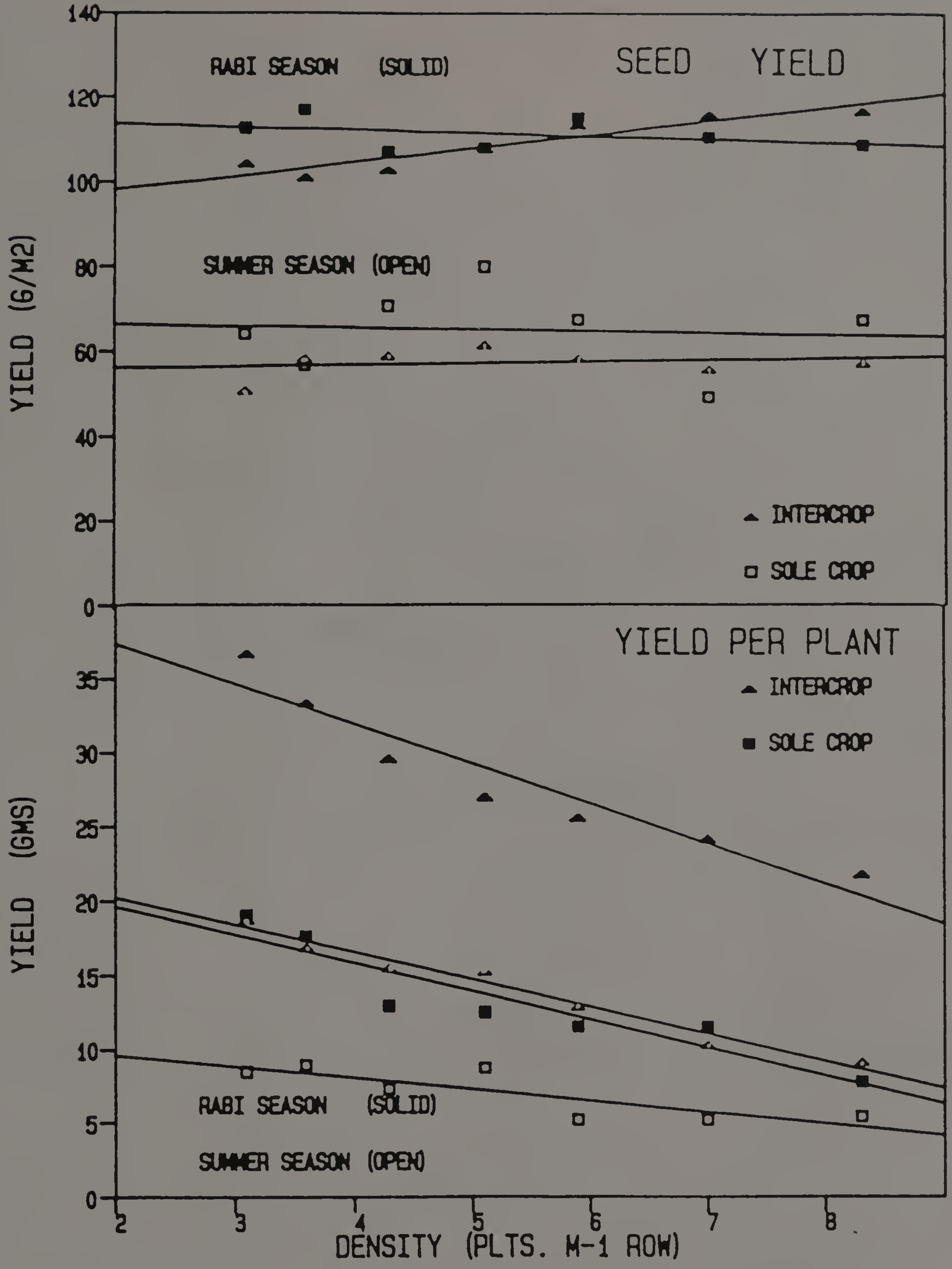

Figure 15. Density effects on sunflower seed yield on an area and per-plant basis, Rabi and Summer seasons. Symbols are means across planting patterns and lines are calculated responses.

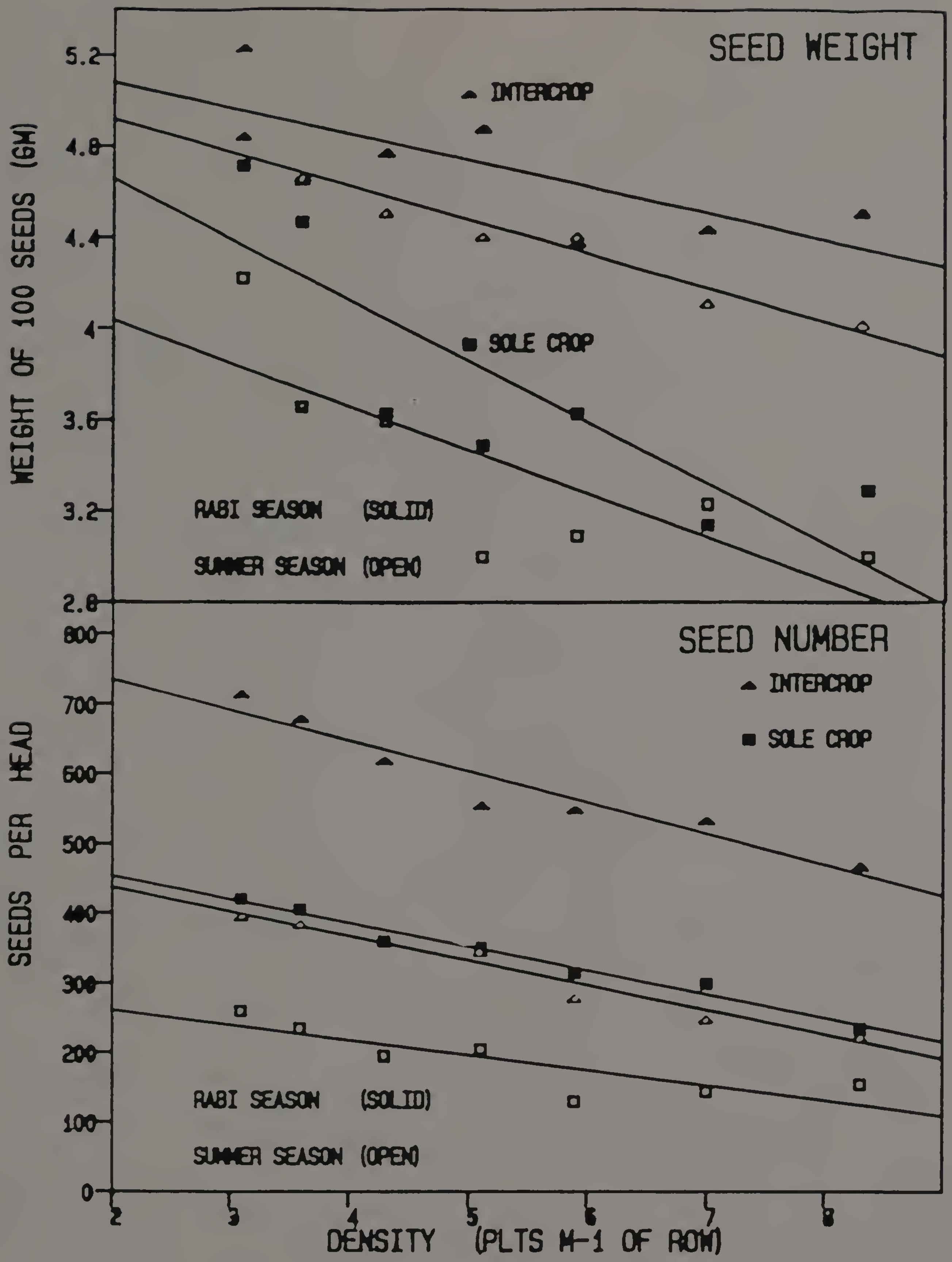

Figure 16. Density effects on sunflower seed number and seed weight, Rabi and Summer seasons. Symbols are means across planting patterns, lines are calculated responses.

the summer season. The same cultural practices were applied. This provides an estimate of the maximum genetic limit of a crop within a given environment. It is interesting that the yields per plant of sunflower plants in isolation were 90% greater than those in the best intercrop (6:1 pattern), and on the order of 4 times as great as the sole crop. Head diameter was increased by 50%, seed weight by 36% and number of seeds by 30% over the 6:1 intercrop. This gives an idea of the range of the yield parameters that can be manipulated merely by changing the degree of competition. It also illustrates the plasticity over a wider range.

The ability of sunflower to adjust yield components to maintain yield over a wide range of densities and row widths has been shown in other studies (Robinson et al., 1980; Prunty, 1983; Mathers and Stewart, 1982; Miller et al., 1984; Miller and Fick, 1982). That this plasticity in sunflower yields might be exploited to improve productivity in intercrop systems is not as well documented.

Sorghum component. Sorghum yields were reduced due to the reduction in the area planted to sorhgum (Figure 17). However, this yield reduction was not as great as the yield reduction expected from lower planted ratios of sorghum sole crop (estimated by dashed lines, Figure 17), indicating a release from competition in the intercrop sorghum as compared with sole crop. The degree of competitive advantage to sorghum when planted near the less competitive groundnuts was not greater at the lower planted ratios than higher ratios (seen by

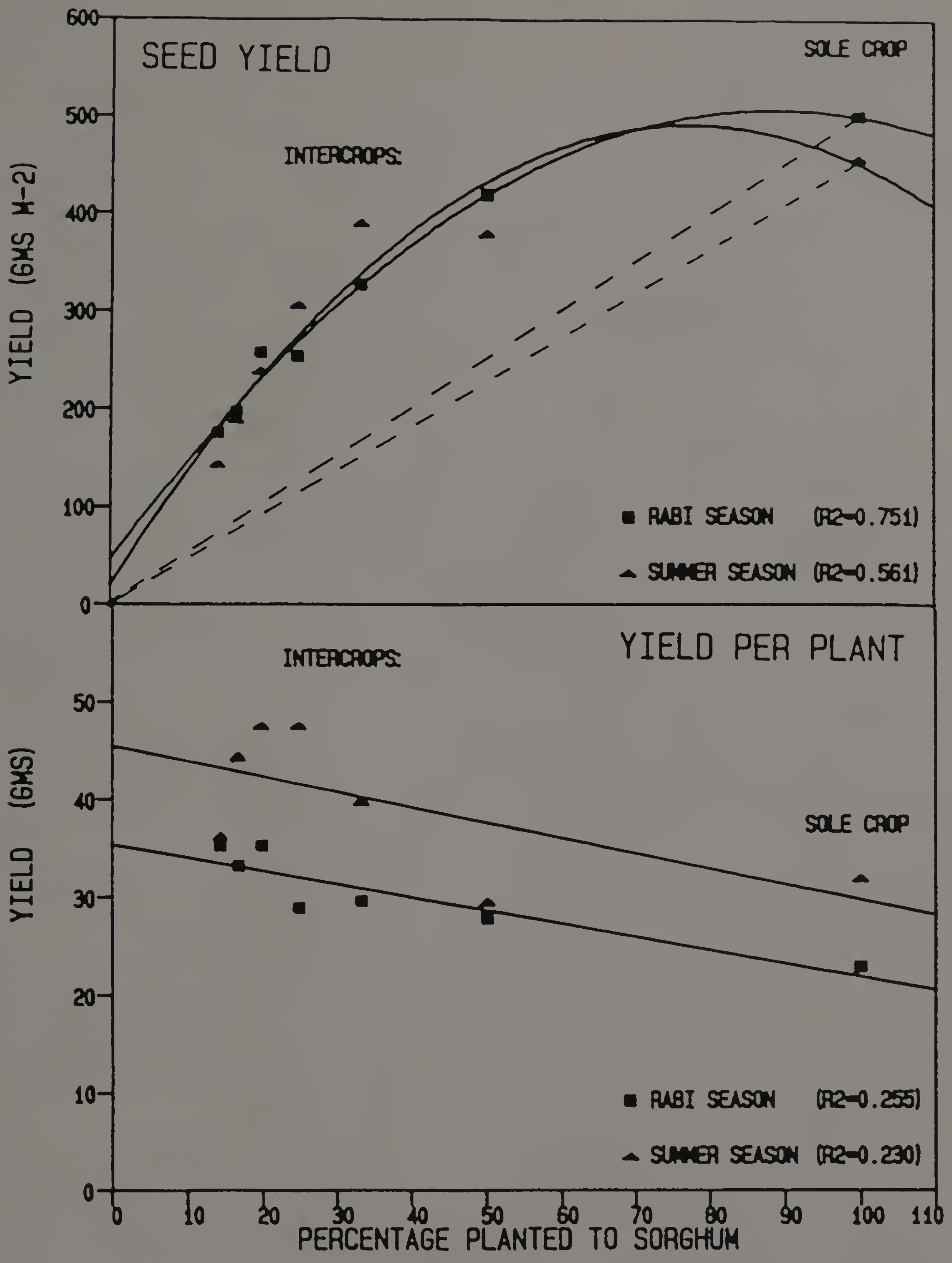

Figure 17. Planting pattern effects on sorghum seed yield, area and per-plant basis. Symbols are means across densities, lines are calculated responses. Dashed line indicates sorghum yields expected if intercrop competition were equal to sole crop competition.

comparing the dashed lines with the solid lines, Figure 17). Unlike sunflower, the competitive advantages to sorghum were apparent in the lower planted ratios (1:1 and 2:1) and did not increase at wider spacings. For example, at 50% of the area planted to sorhgum, intercrop yields were 83% of sole crop yields (33% competitive advantage), whereas at 14% of the planted area, sorghum yields were 31.5% of the sole crop yields (17% competitive advantage) in the summer season. Sorghum yields were similar between seasons.

Sorguhm yields per plant increased at lower planted ratios (Figure 17), although this was not as great as with sunflower. This was due to changes in seed number and slight changes in seed weight (Figure 18). Panicle length was only slightly effected by pattern treatments (Figure 19), but a trend was found for increased panicle head length in the intercrops vs sole crops, and especially comparing greater than 2:1 patterns with 1:1 or sole crop.

Sorghum yields in the intercrops (mean effect) were reduced by about 35% in both seasons, and there was little effect of density on yield (Figure 20). Decrease in yield per plant (Figure 21), seed number and seed weight (Figure 22) were responsible for maintaining yields at a constant level over the range of densities studied. Seed number was reduced by densities similarly in the intercrop and the sole crop, whereas seed weight was reduced in the sole crops not the intercrops (Figure 22). Panicle length was reduced at high densities in both the intercrop and the sole crop, and there was a trend for longer panicles in the intercrops compared with sole crops (Figure 19).

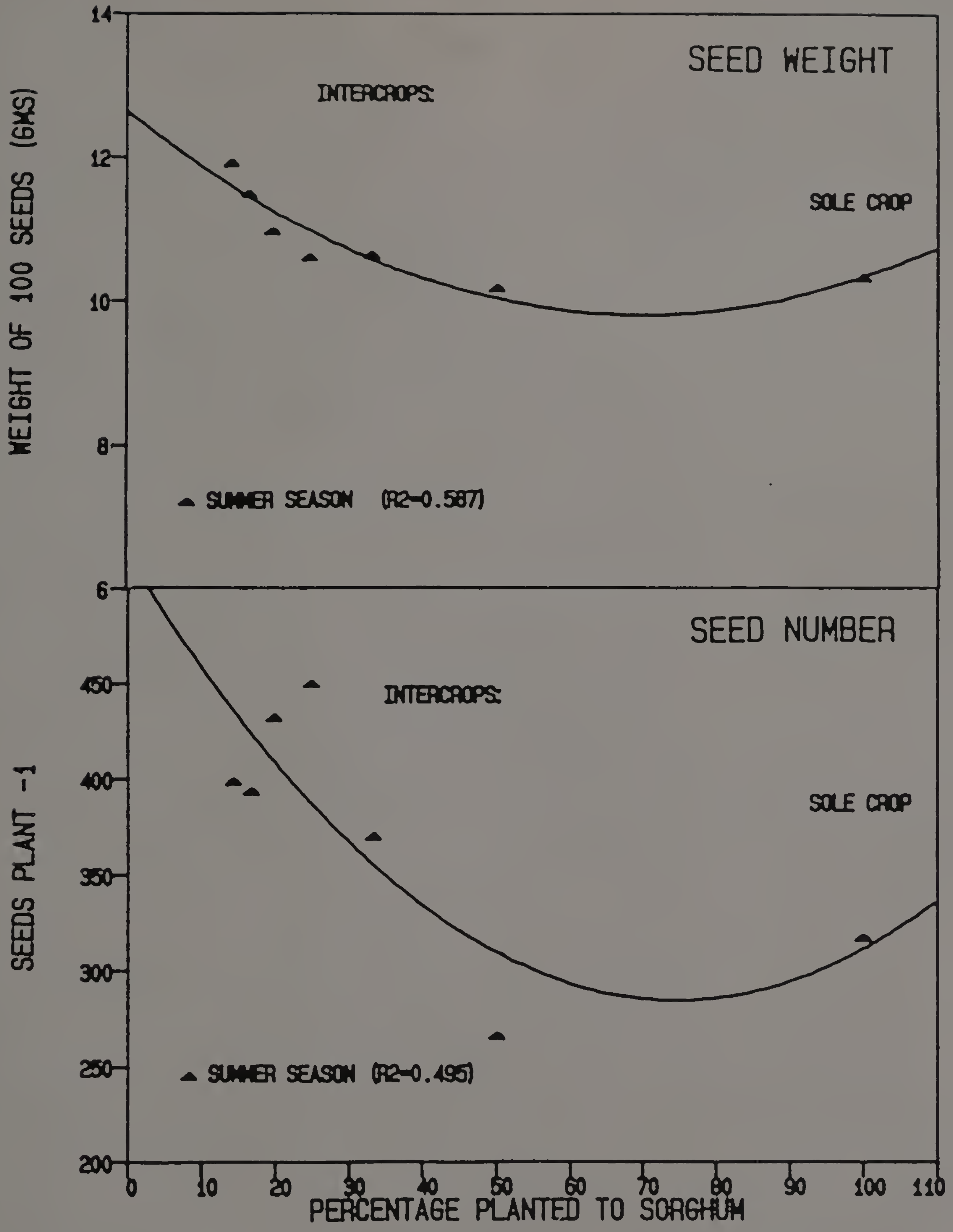

Figure 18. Planting pattern effects on sorghum seed number and seed weight, Summer season. Symbols are means across densities and lines are calculated responses.

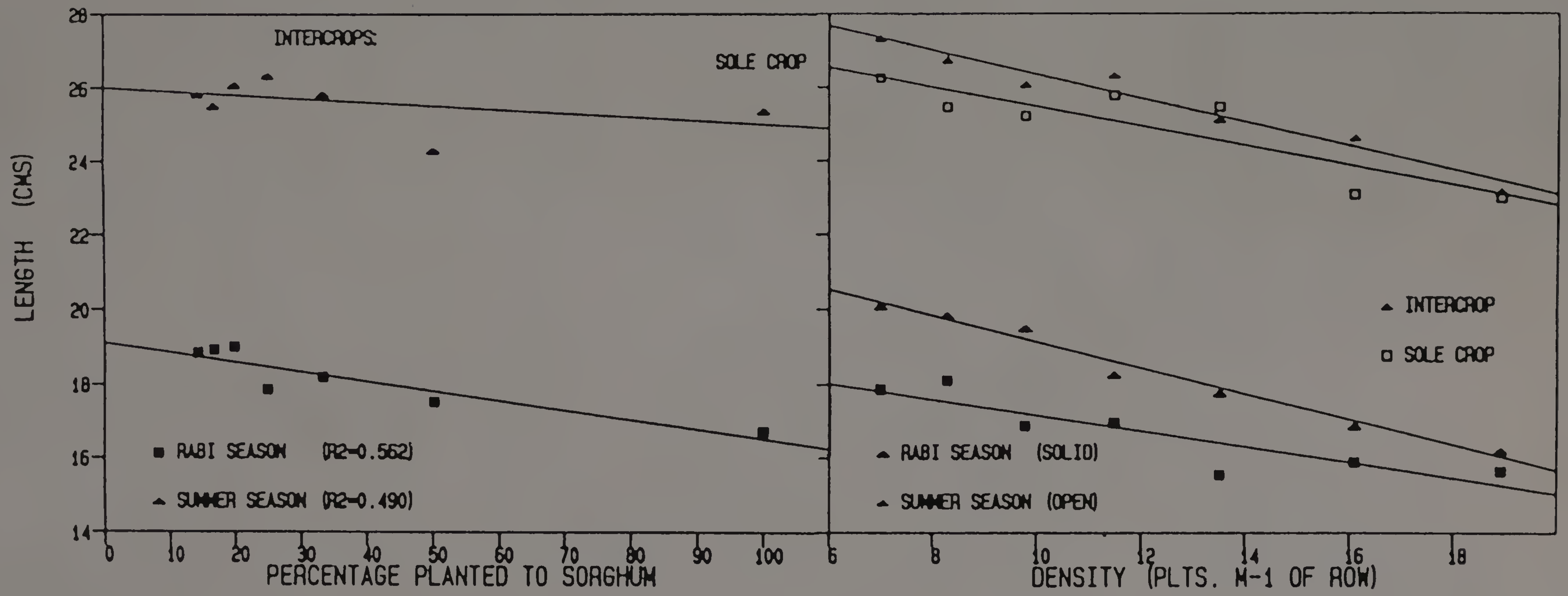

Figure 19. Planting pattern and density effects on sorghum panicle length, Rabi and Summer seasons. Symbols are means and lines are calculated linear responses. R^2 values, density effects are: Rabi season intercrop (0.571), sole crop (0.602), and summer season intercrop (0.390), sole crop (0.736).

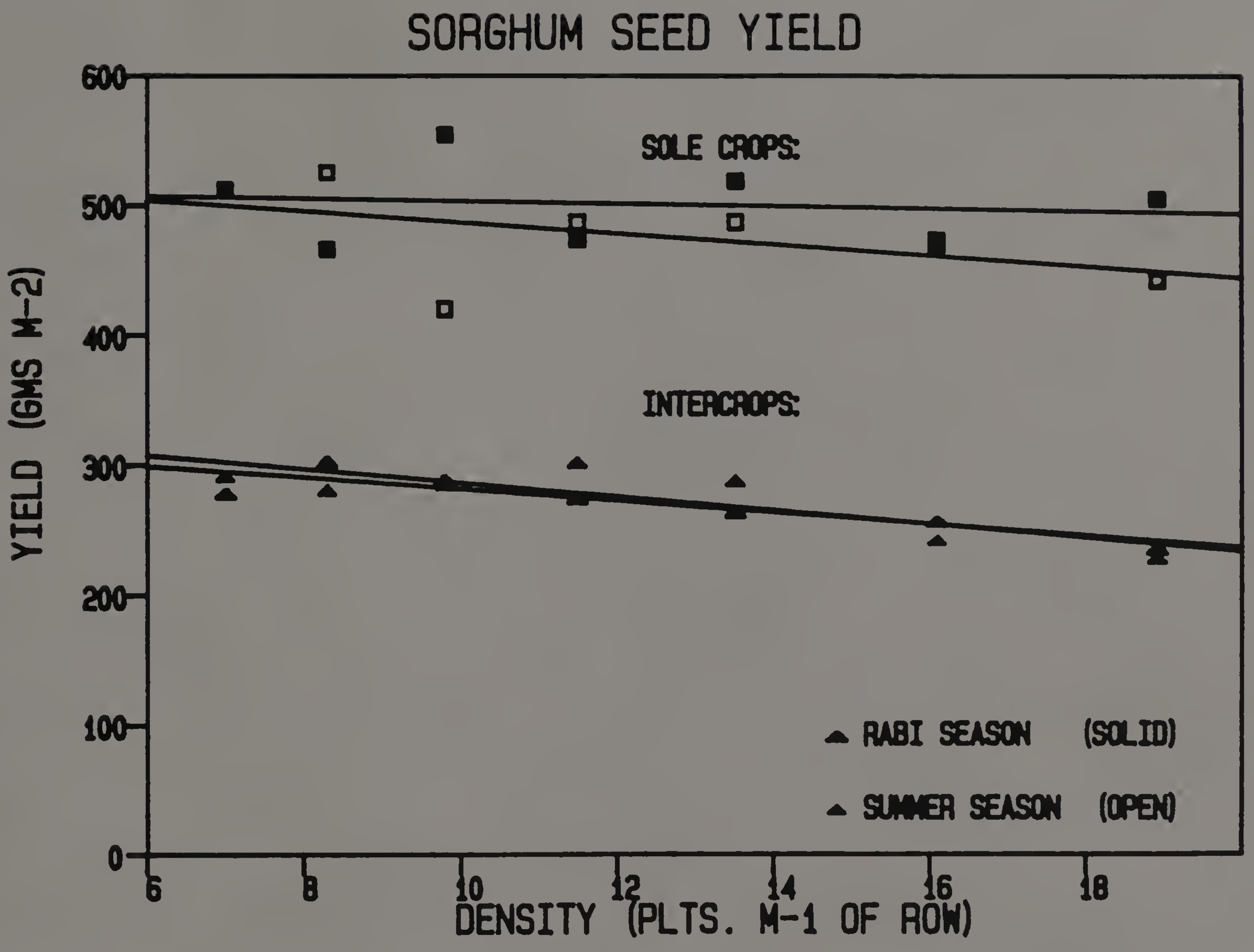

Figure 20. Density effect on sorghum yield, area basis. Symbols are means across planting patterns, and lines are calculated responses. R^2 values are: Rabi season intercrop (0.290), sole crop (0.326), Summer season intercrop (0.145), sole crop (0.140).

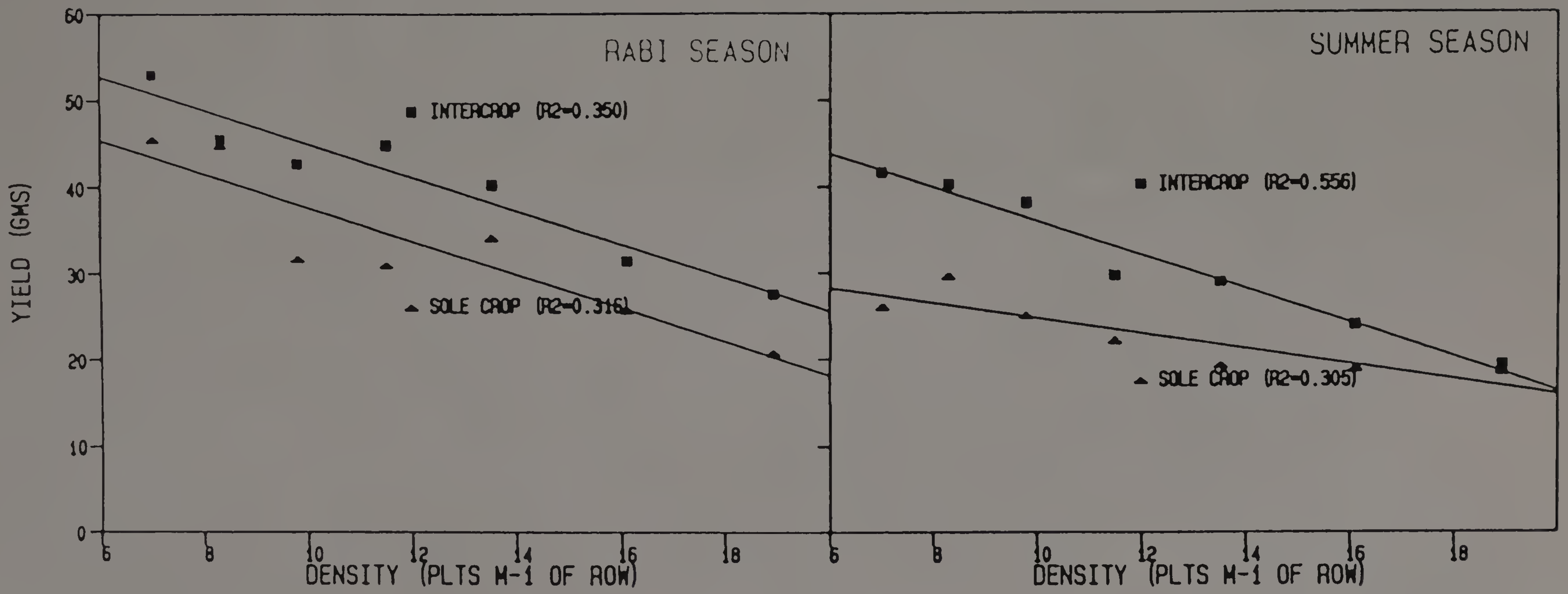

Figure 21. Density effect on sorghum yield per plant, Rabi and Summer seasons. Symbols are means across patterns and lines are calculated responses.

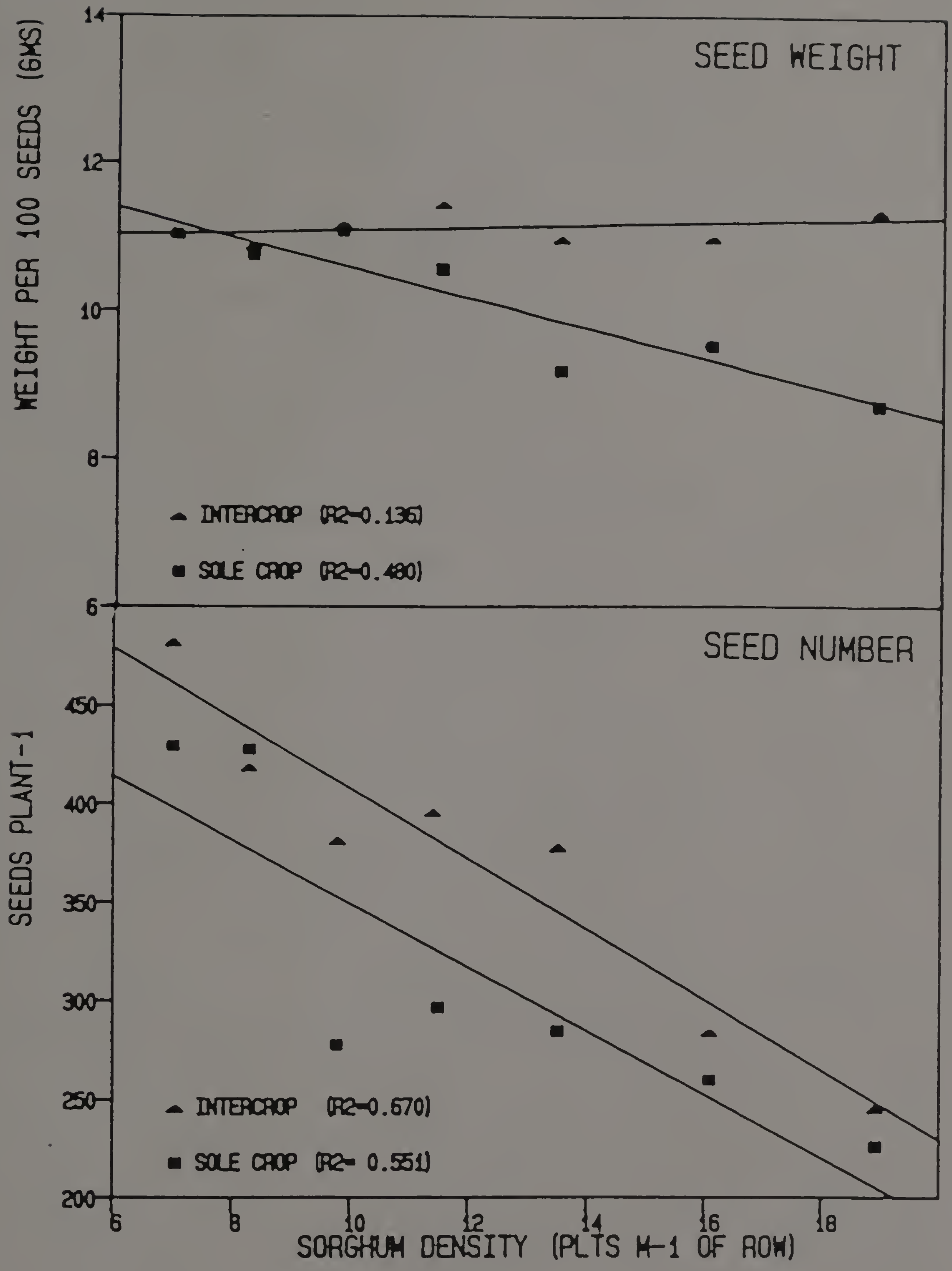

Figure 22. Density effects on sorghum seed number and weight, Summer season. Symbols are means across planting patterns and lines are calculated responses.

Total Productivity

Land Equivalent Ratio. Land Equivalent Ratio responses are given in Figures 23 through 26. The potential for LERs up to 1.46 for the sorghum:groundnut intercrop and up to 1.60 for the sunflower:groundnut intercrop were predicted by the data. In both intercrops, planting pattern effects on LER were greater than density effects.

In the sorghum:groundnut systematic plots, higher LERs resulted from wider spacings of the intercrop rows, but the shape of the response differed between seasons (Figures 23, 24). In the Rabi season, LERs increased to a maximum in the 6:1 pattern, whereas in the summer season, LERs were greater at a 3:1 pattern and levelled off or declined at higher ratios. This was due to the differences in response in the groundnut between seasons, which was not as suppressed at 2:1 and 3:1 ratios under sorhgum in the summer versus rabi seasons. Groundnut productivity overall was greater in the summer season versus the rabi season. This was attributed to a greater disease incidence in the rabi versus the summer season, possibly linked to cooler temperatures.

In the groundnut:sunflower intercrops, a similar trend for an increase in land-use efficiency with increased proportions planted to groundnut was found as in the sorghum, and this trend differed little between seasons (Figures 25 and 26). Although at a 6:1 planted ratio in the sunflower intercrop, LERs were still increasing, the differences were small, possibly indicating that a maximum was being approached

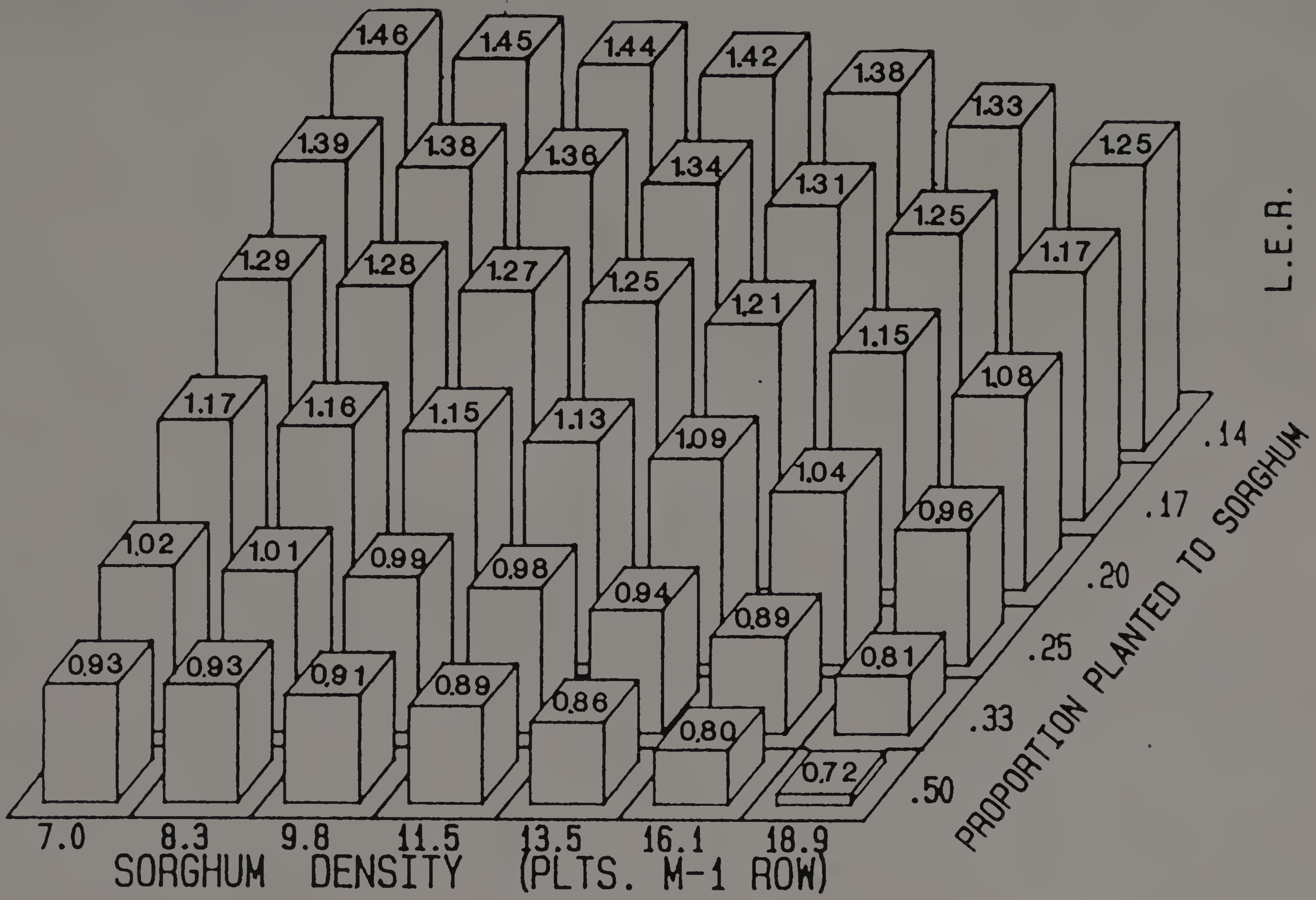

Figure 23. Density and planting pattern effects on Land Equivalent Ratio for the groundnut:sorghum intercrop, Rabi season. Values shown represent added predicted LERs for each crop. R^2 values for groundnut = 0.94, and for sorghum, 0.882.

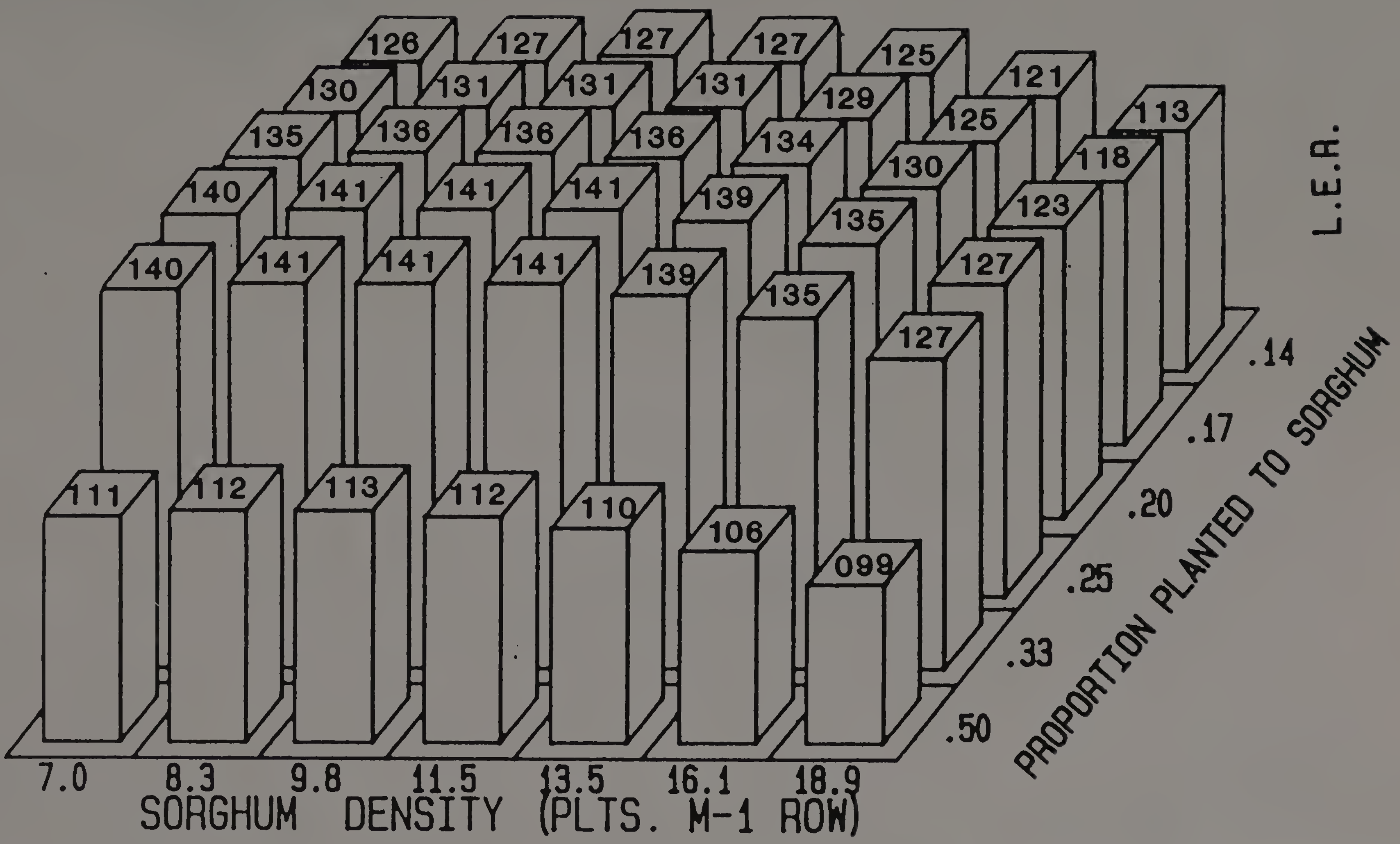

Figure 24. Density and planting pattern effects on Land Equivalent Ratio for the groundnut:sorghum intercrop, Summer season. Values shown are added predicted LERs for each crop. R^2 values for groundnut = 0.902 and for sorghum, 0.88.

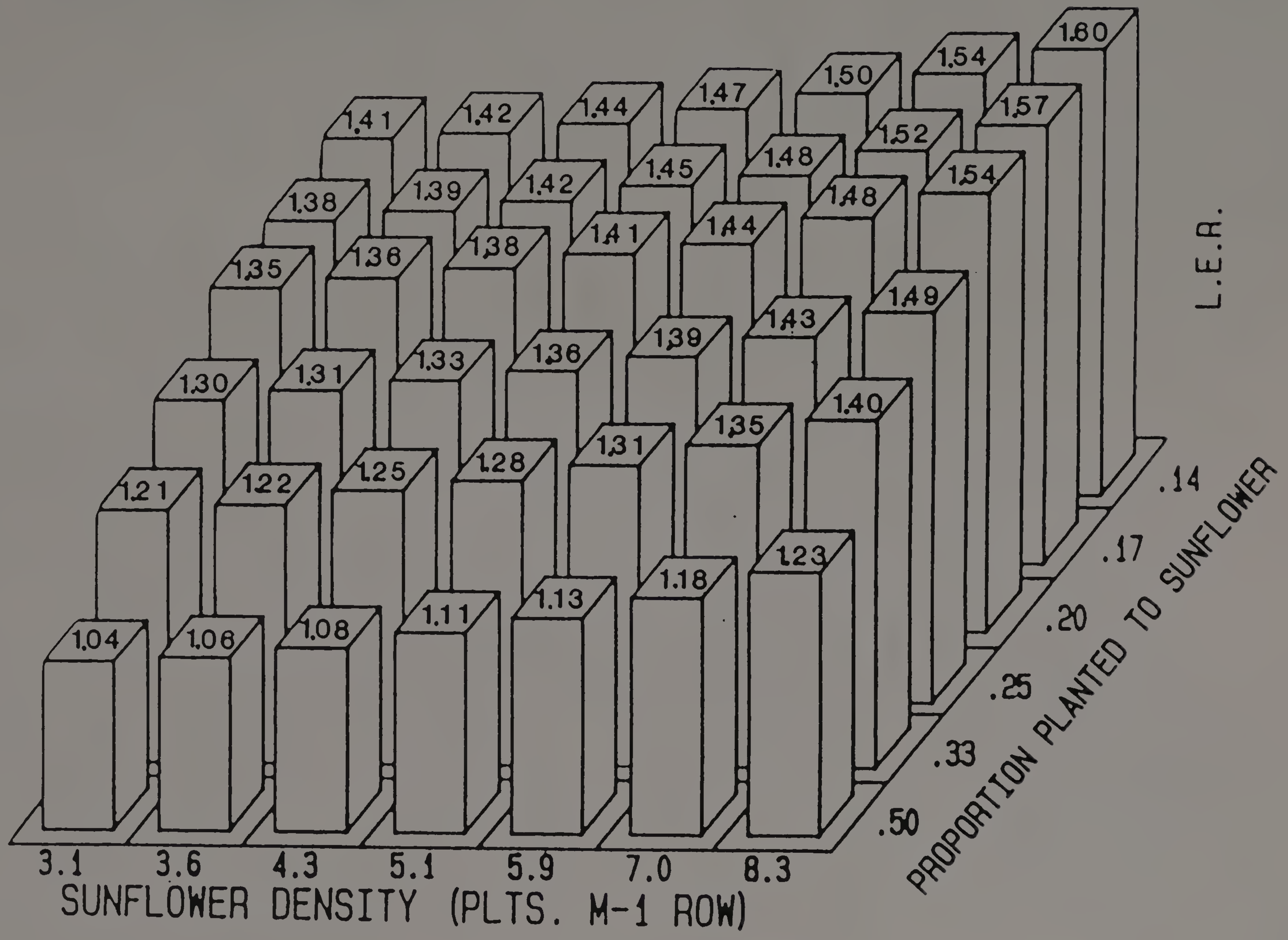

Figure 25. Density and planting pattern effects on Land Equivalent Ratio in the groundnut:sunflower intercrop, Rabi season. Values shown are added predicted LERs for each crop. R^2 values for groundnut = 0.925 and for sunflower, 0.519.

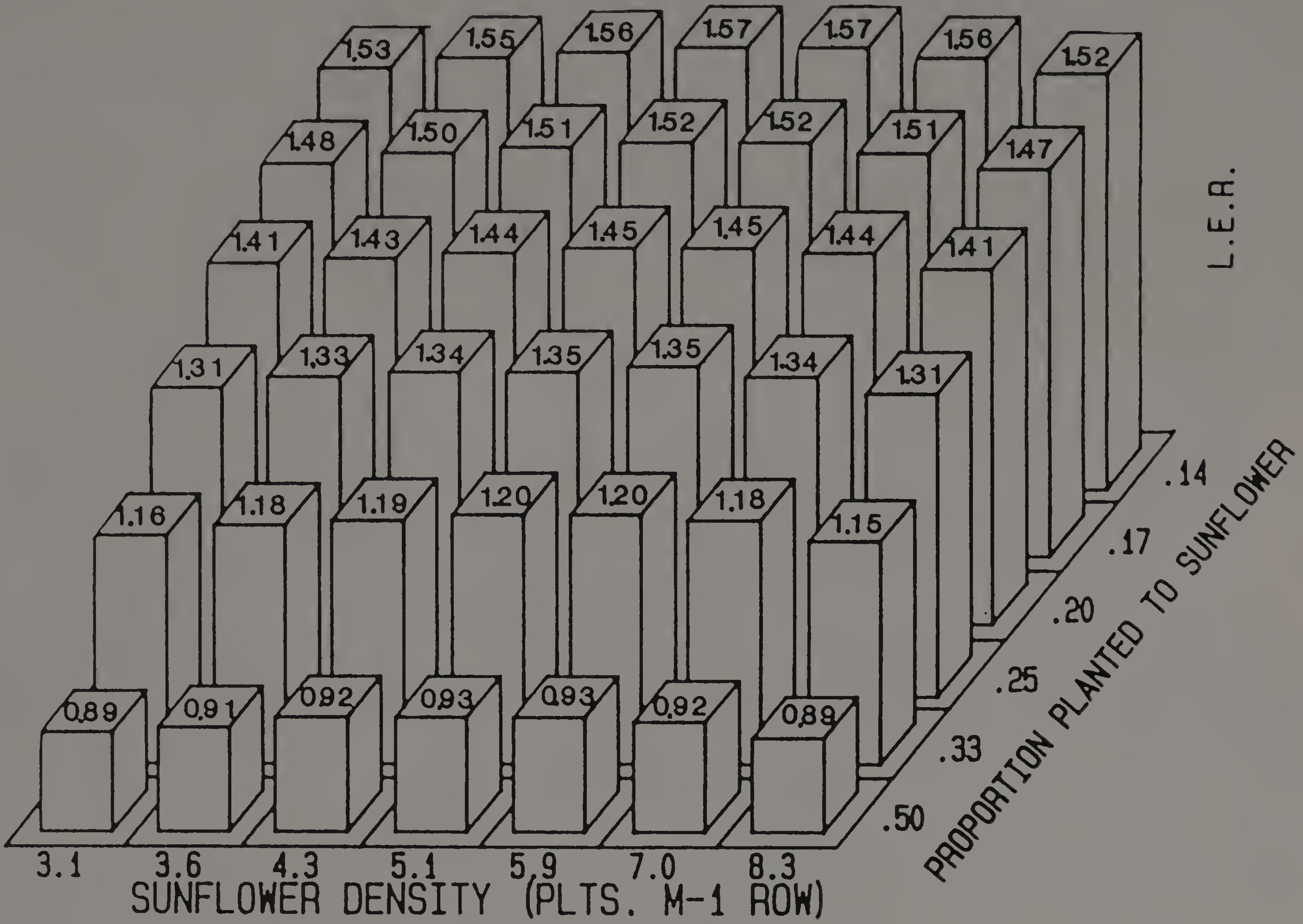

Figure 26. Density and planting pattern effect on Land Equivalent Ratio for the groundnut:sunflower intercrop, Summer season. Values shown are added predicted LERs for each crop. R^2 values for groundnut = 0.88, and for sunflower = 0.24.

(Figures 25 and 26).

The lower LERs observed at lower ratios of groundnut to sunflower are similar to the findings of Narwal and Malik (1985) who found no yield advantages to alternating 45 cm rows of sunflower and groundnut under rainfed conditions. However, others (Mohammad, S.,1986, personal communication) have found LERs of up to 1.49 with alternating row sunflower:groundnut intercrops in the summer season under irrigation, and similar responses under rainfed conditions. In this study, higher LERs were consistantly found only at higher planted ratios.

Higher sorghum densities consistently reduced total LERs in both seasons, although this effect was not as pronounced as the planting pattern effect (Figures 23 and 24). This was due to reductions in groundnut yields as well as reductions in sorghum yields at high densities, which, though insignificant individually, tended to reduce the total productivity (LER).

In contrast, density of sunflowers in the intercrop tended to increase total LER in the Rabi season (due to slight sunflower yield increases), but no effect was found in the summer season. Growth conditions for the sunflower were better in the rabi season than in the Summer season, as indicated by the higher sunflower yields (Figure 12), and small increases in intercropped sunflower yield with higher plant density were observed in that season (Figure 15).

In both crops, the potential for high LERs can be attributed to the increased yields in the intercropped species and lack of severe reductions in groundnut yields at wide spacings. The yield benefit to the sunflower due to intercropping was greater than to the sorghum, but the yield reduction in groundnut was less under sorghum. Thus the total yield advantages came primarily from the sunflower in the groundnut:sunflower intercrop and primarily from the groundnuts in the groundnut:sorghum intercrop. Lack of severe reductions in groundnut yield in a groundnut:millet intercrop (a similar system) in a 3:1 pattern were recorded by Reddy and Willey (1985), producing LERs of 1.24. Groundnuts in this intercrop intercepted 27% as much and the millet 2.1 times as much PAR as intercepted by respective sole crops. Yet dry weight doubled in the millet and groundnut yield remained constant in the intercrops versus sole crops (row basis, Marshall and Willey, 1983). The maintenance of yield in groundnut was attributed partly to the recovery from competition after the cereal harvest (Willey et al., 1983). This corraborates the results found here with a similar sorghum:groundnut system.

It is apparent that with row ratios of 3:1 or greater, sorghum: groundnut intercrops are capable of producing LERs substantially greater than unity. Whether there would be advantages to greater than 3:1 ratios for the sorghum intercrop was not determined by this study, as results were not consistant between seasons.

Land Equivalent Ratio does not express the absolute yield level, nor the relative production of each component species. Although LER expresses quite adequately the land-use advantages to intercropping as compared with sole crops, the comparison is made at a given yield ratio (it is assumed that this is the desired yield ratio). Furthermore, total yields or economic productivity may be of interest and are not addressed by this comparison.

Staple Land Equivalent Ratio. Staple Land Equivalent Ratio as defined by Reddy and Chetty, (1984) is a version of LER with the stipulation that the farmer may desire a given percentage of a base (staple) crop, and will design a cropping system that will meet that need. In the context of this experiment, groundut is considered the staple crop with sorghum or sunflower as the "bonus" crop. The percentage of sole crop yields which are considered acceptable will depend upon the cultivators' need for a food crop (ie. sorghum), market risk factors (ie. the degreee of price security of groundnut versus sunflower) or other factors (such as tennant commitments).

The mean effect of planting pattern on Staple Land Equivalent Ratio is given in Figure 27. The symbols represent the point at which required yield (expressed as a proportion of sole crop) of groundnut equals that of the intercrop pattern, and SLER=LER. The lines are sets of calculated points, and represent the probable yield advatages to be found when the farmer allocates a proportion of land to the intercrop and the rest to the sole crop which is in short supply (Reddy and Chetty, 1984). The best planting pattern to be used to obtain a given staple yield can be judged by comparing lines at various desired staple yield levels (x axis, Figure 27).

An absolute comparison between the sorhgum and sunflower intercrop systems is not automatically appropriate, given the differing yield

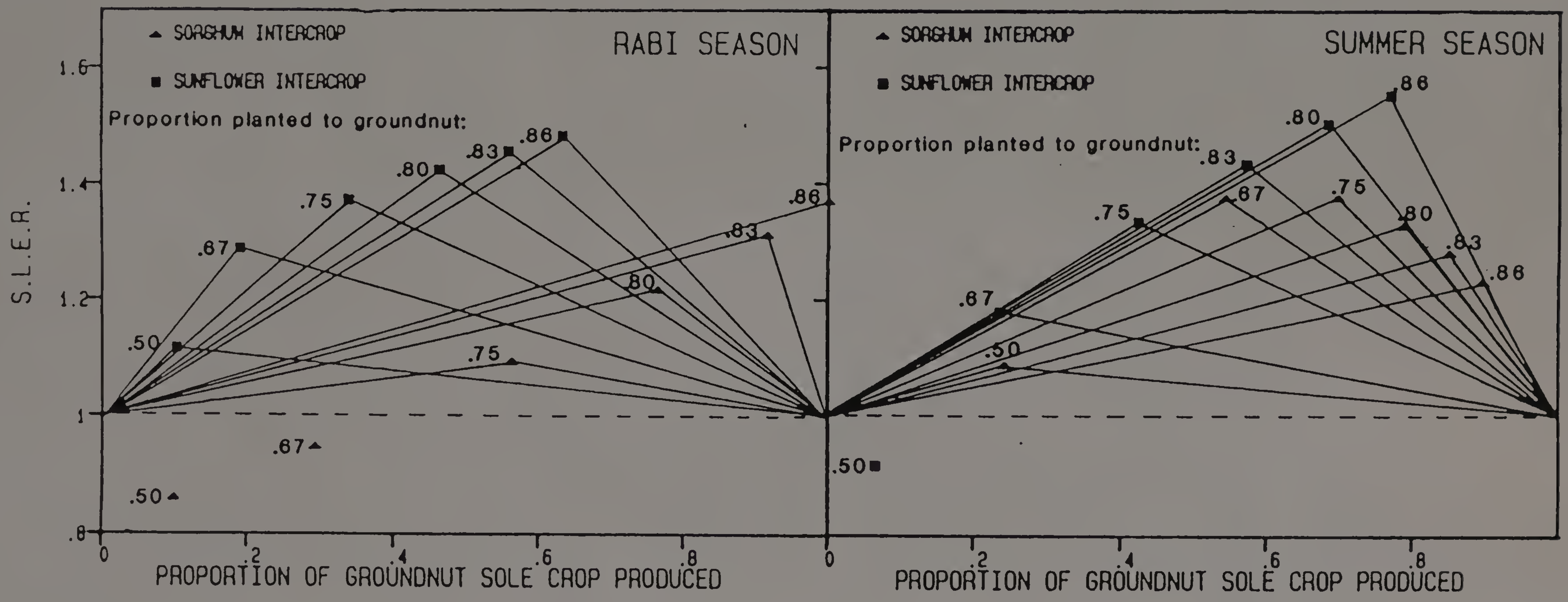

Figure 27. Planting pattern effects on Staple Land Equivalent Ratio for the Rabi and Summer seasons. Symbols are means across densities, lines represent LERs which would be acheived by planting a combination of the intercrop shown and the sole crop in short supply to achieve a given ratio. Predicted values are used for the total and partial LERs (X axis).

goals of the two systems (ie. a food:cash crop mixture and a cash:cash crop mixture). But if there are definite requirements for a groundnut yield level, this comparison would be appropriate in relative terms. In general, higher groundnut yields, expressed as a proportion of the sole crop, were found in the sorghum intercrop versus the sunflower (Figure 27). That planting pattern can be manipulated to attain various groundnut yield levels can readily be seen in Figure 27.

Although intercrop density effected total LER slightly as discussed previously, the proportion of groundnut sole crop obtained by the intercrop was not appreciably changed by the intercrop density (Figure 28).

Although trends can be discerned from this data, variation from season to season makes it difficult to predict with a great deal of precision the proportion of the staple crop to be realized with an intercrop treatment. For example, a 3:1 planted ratio of groundnut:sorghum produced SLERs of 1.37 at 70% of the groundnut sole crop in the summer season, while the same treatment produced SLERs of 1.09 yielding 56% of the groundnut sole crop in the rabi season (9 Figure 27). With sunflowers, the trends are only slightly more consistent. Nevertheless, the SLER provides considerably more information than the LER, and therefore is of help in evaluating intercrops where a given level of a base crop is desired.

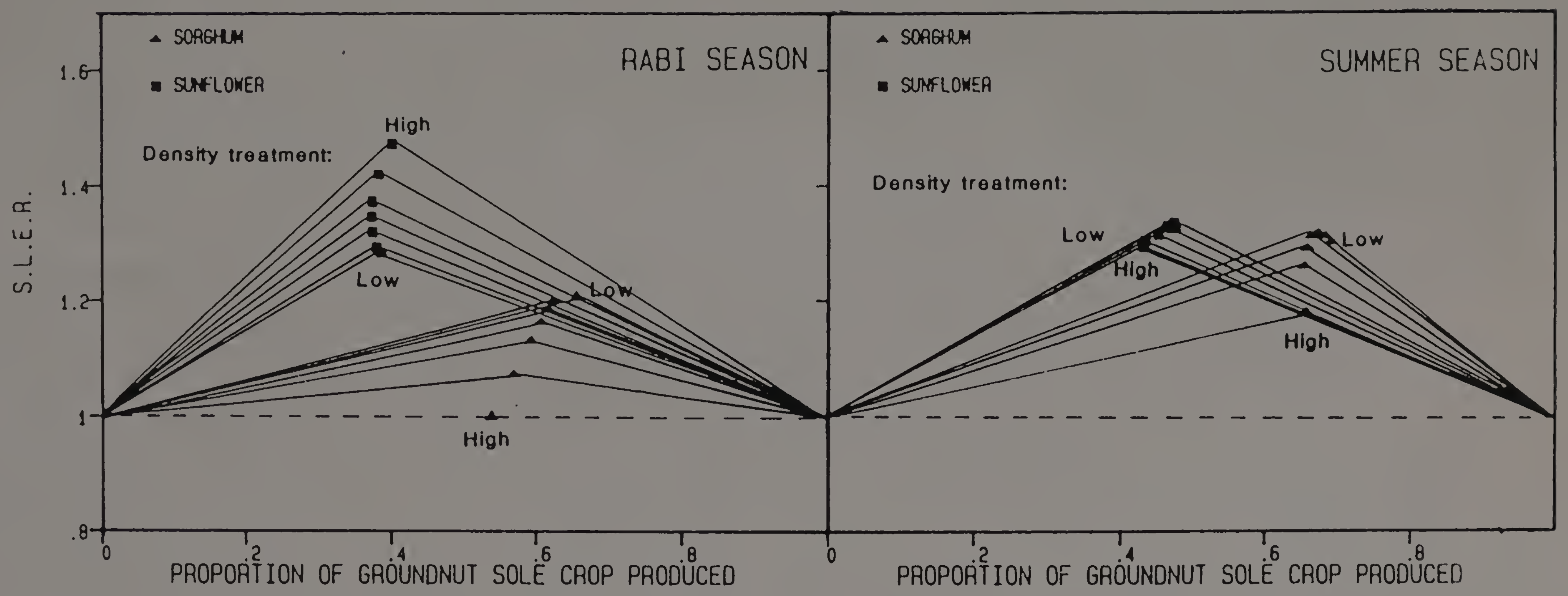

Figure 28. Density effects on Staple Land Equivalent Ratio for the Rabi and Summber seasons. Symbols are means across planting patterns. (See Figure 27 and text for explaination of lines.)

Summary

Yield response surfaces for a wide range of groundnut-sorghum and groundnut-sunflower planting patterns and densities were calculated from a two-season experiment in Hyderabad, India. The following conclusions were made:

Groundnut yields were reduced to a greater extent when intercropped under sunflower than sorghum and more at lower planted row-ratios higher planted row-ratios.

Competitive supression of groundnut yield was due both to reduced pod number and pod weight with lower planted ratios in the intercrop.

Density of either intercropped species had little or no effect on groundnut yield, intercrop species yield, LER, or SLER.

LER potentials of 1.46 and 1.60 were found for the sorghum and sunflower intercrops respectively. Land use efficiency was due primarily to the groundnuts in the sorghum:groundnut intercrop and primarily to the sunflower in the groundnut-sunflower intercrop.

Staple LERs can be manipulated by changing the planting pattern, not intercrop density.

CHAPTER V.

PLANT COMPETITION IN CORN - LITERATURE REVIEW

Introduction

In addition to the reasons for developing yield/density equations (ie. to estimate optimum density and maximum yield and to generalize a yield/density relationship), there may be reasons to more vigorously quantify the degree of plant competition within a crop community. From an agricultural viewpoint, it might be desireable to:

a) know the extent or range within which yields can be effected by manipulating competition.

b) differentiate between between-plant competition and within-plant competition (limitation of source or sink), as the means to address these two problems will differ (see Duncan, 1963 for discussion).

c) quantify the differences between cropping patterns and cropping practices in exploiting a given environment.

d) quantify differences between genotypes in tolerance to competition.

e) assess whether reductions in yield per plant are due to suboptimum resource availability or competition per se.

f) quantify differences between competitive effects on different aspects of crop growth or yield components where this occurs.

These objectives may or may not be satisfied by any one methodology. Some of the methods to quantify the yield/density relationship and competition with special reference to corn are reviewed below. Relevent studies on the source-sink relationship in corn as it relates to competition are also reviewed.

Equations Used to Quantify Plant Density Effects

Plant density has long been recognized as a major factor in manipulating the degree of between-plant competition within a corn stand. Observations that higher planting rates produce smaller ears but higher yields date to the beginnings of Experiment Station research in the United States (Latta, 1889; Anon., 1889).

Many experiments have been conducted to determine optimum plant populations and to describe changes in yield components and growth associated with increased densities (Stickler, 1964; Eik and Hanway, 1966; Rutger and Crowder, 1967; Bryant and Blaser, 1968; Nunez and Kanprath, 1969; Brown et al., 1970; Genter and Camper, 1973). Equations have been developed relating plant populations to yield of grain, usually based upon the mean yield of a single plant (Duncan, 1958; Bleasdale and Nelder, 1960; Warren, 1963; Carmer and Jackobs, 1965; Willey and Heath, 1969; Fery and Janick, 1971). The simplest reason for defining the relationship between crop competition and yield is to evaluate such characteristics as maximum yield and optimum density. In addition, comparisons can be made between density responses of differing genotypes and under different environmental conditions. It is desireable that whatever mathematical empiricisms are made, that they have some biological validity in fact, and be applicable to a range of environments.

The Yield/Density Relationship

Holiday (1960b) was perhaps the first to generalize yield/ density relationships into two possible responses: an asymptotic response, where yield rises to a maximum and is then constant with increasing densities, and a parabolic response, where yield per unit area rises to a maximum with increased densities and then declines. These responses are illustrated in Figure 29. Although exceptions occur, an asymptotic relationship tends to apply to total crop (above-ground) yields, and to crops in which the whole plant is harvested, such as fodder rape (Holliday, 1960a), subterranean clover (Donald, 1951), and long beet (Warne, 1951). The parabolic relationship between density and yield has been suggested as a basic biological relationship for reproductive yield (seed yield), and has been demonstrated to have applicability to crops such as corn (Lange et al., 1956; Holt and Timmons, 1968; Fery and Janick, 1971), barley (Willey and Heath, 1969) and wheat (Holliday, 1960a).

Although some have argued that these two basic forms may be different portions of the same relationship, it is clear that two distinct types of resposnes can be observed, and must be treated differently mathematically.

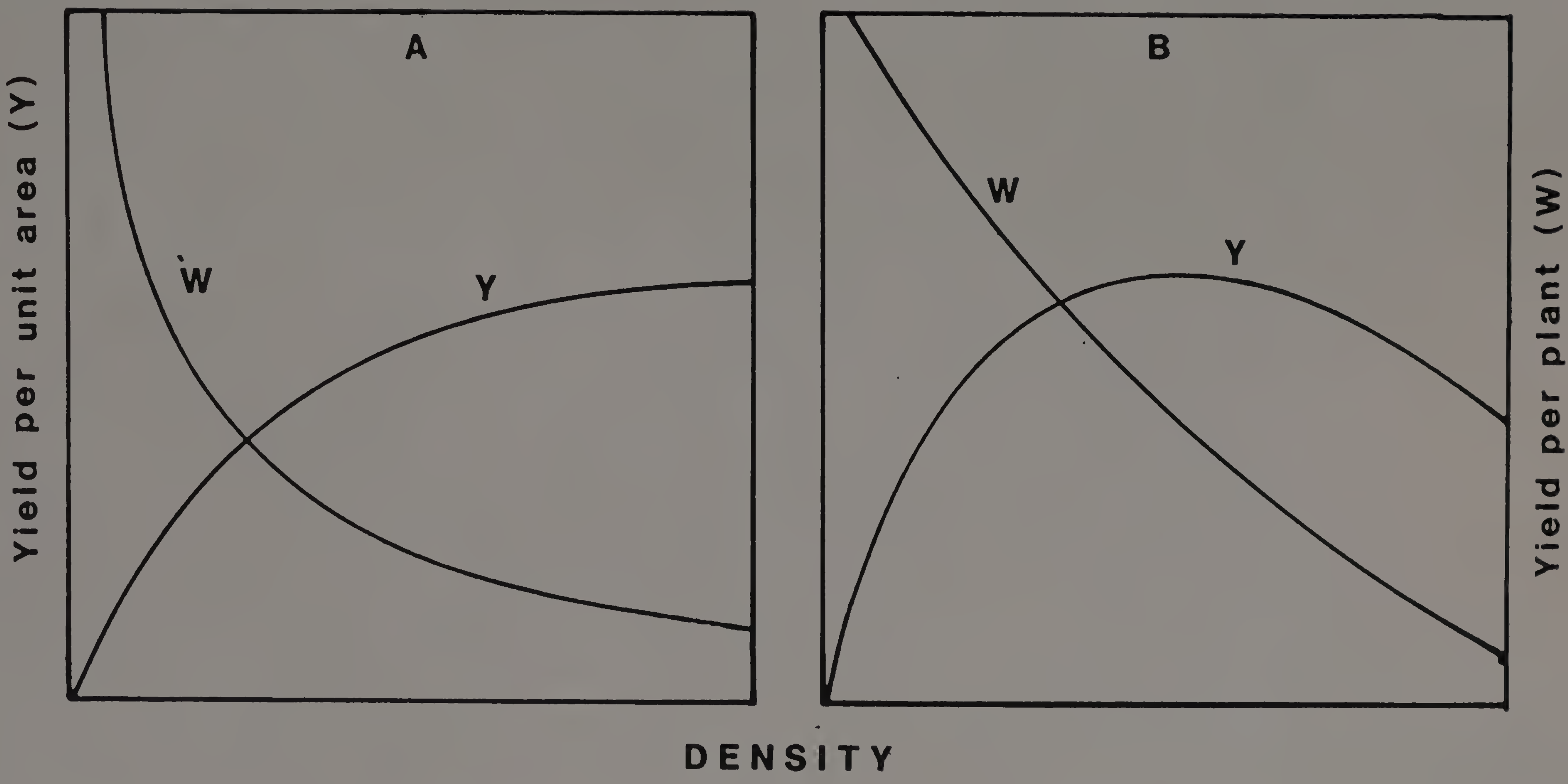

Figure 29. Illustration of the asymptotic (A) and parabolic (B) density/yield relationships, idealized data from Holiday, 1960a (graph A, giant rape), and Lange et al., 1956 (graph B, corn grain).

Equations Describing a Parabolic Response

Hudson (1941) and Pickett (1944) used the quadratic expression:

$$Y = a + bd + cd^2$$

where Y is the yield per unit area and a, b, and c are constants and d is plant density, to describe the relationship between yield and density. This curve, which is symetrical around a maximum value of yield, offers little flexibility in fitting , as at a very high density, yield must drop to zero, and at zero densities, the yield is equal to a, which in practice may be positive or negative. Attempts to make this curve less symetrical were made by Sharpe and Dent (1968):

$$Y = a + bd + cd^{.5}$$

This curve is less symetrical than the quadratic expression described above, but holds the same unrealistic implications at very high or low densities, and in turn must be questioned on biological grounds, certainly making extrapolations difficult (Willey and Heath, 1969). This equation is more appropriately used for curve-smoothing and simple response surface estimation, without extrapolation out of the experimental range.

Exponential Models

Duncan (1958) reveiwed data from several corn belt states and derived a linear relationship between the logrithm of grain yield per plant and population density or:

$$\log W = \log K + bd$$

$$\text{or} \quad Y = dK10^{bd}$$

where K is a constant, b is the slope of the regression line, Y is the yield per unit area, W is the yield per plant and d is plant density. Duncan proposed this as a general relationship between plant population and corn grain yield and suggested that since the relationship was linear, only two densities would be needed to determine maximum yield and the whole yield-density curve. He demonstrated correlations ranging from r = 0.98 to 0.99 for this equation based upon a large amount of data over many years. Others (Carmer and Jackobs, 1965; Willey and Heath, 1969) emphasised that it would be safer in practice to include a third intermediate density so that the calculated maximum would be close to an actual data point.

Carmer and Jackobs (1965) proposed a similar model for the relationship between corn population and yield:

$$Y = dAK^{d}$$

where A and K are constants. The product AK represents the yield when there is only one plant per unit area (ie. d = 1) and it denotes the maximum yield per plant under the particular set of genetic-environmental conditions under study. K is a proportionality constant (a positive value less than one) and indicative of the plants competitive abilities. The value of K would be greater for varieties or treatments showing less rapid decreases in yield per plant than for those showing the largest decreases with increases in plant density.

Exponential equations such as these exhibit greater flexibility than quadratic equations, and have been demonstrated to fit data from parabolic yield-density curves quite well (Lange et al., 1956; Duncan, 1958; Carmer and Jackobs 1965), but do not give a practical fit to asymptotic relationships (Willey and Heath, 1969).

Warren (1963) used a non-logrithmic, linear equation to describe a relationship between yield per plant and density to analyse data for maximum yields of sweet corn in New York State:

$$W = a + bd$$

He also examined data of Colville and McGill (1962) for field corn and Vittum et al. (1959) for processing sweet corn and suggeted that this simpler equation might have broader empirical applications, since highly significant correlations between yield per plant and plant population were found. No other uses of this model have been reported, however.

A reciprocal equation derived from Richards (1959) was proposed by Bleasdale and Nelder (1960):

$$W^{-z} = a + bd^{O}$$

where a,b, z and 0 are constants for any particular set of data. The authors point out that if z exceeded 0, then the equation would describe a parabolic situation and argued that, given changes in the constants, the equation would describe both parabolic as well as asymptotic yield/density curves. The equation was later modified, for practical reasons to set 0 to unity, since the <u>ratio</u> of the two estimated parameters was more important than the absolute values (Bleasdale and Thomson, 1966). This then became:

$$W^{-z} = a + bd$$

Gillis and Ratkowsky (1978) criticized this model due to intrinsic biases and correlations between the constants. However, Mead (1979) found the biological advantages to this model to override these considerations and recommended it, along with other reciprocal equations to provide a good framework to investigate the practical aspects of the yield/density relationship.

Farazdaghi and Harris (1968) derived a yield/density equation from a logistic growth curve to yield:

$$W^{-1} = a + bd^{z}$$

where a, b and z are constants. This can describe either an asymptotic or parabolic yield/density situation, depending upon the value of z (for asymptotic curves, z=1, for parabolic curves, z is greater than 1).

Equations Describing an Asymptotic Response

A "law of physiological relations" was formulated by Mitscherlich (1919) in which the supply of an essential growth factor was related to yield per plant. This was subsequently applied generally to the relationship between "space" and plant growth and so serve as a yield/density equation:

$$W = W'(1 - e^{-Ks})$$

where W = yield per plant, W' = maximum yield attainable by a plant and s is the space available to a plant and K is a general space constant or factor. This equation describes an asymtotic situation not a parabolic one. An examination of the consistancy of K values across densities was made by Kira et al. (1954) who found that, based upon a single value for W' for subterranean clover, K values changed by over 10 fold across densities and could not be regarded as constant. The apparent change in competitive ability with decreasing space per plant throws doubt upon the biological basis of the constant. Despite the questionable value of the equation for practical application over a range of densities, the asymptotic response is of interest, especially at low densities, and other equations are often unable to produce such a description at low densities (Willey and Heath, 1969). Nelder (1963) found the Mitscherlich equation to give as good a fit to some lucerne data as other equations, although the same was not found by Donald (1951) for subterranean clover. The application of the Mitscherlich equation to a corn growth competition study was done by Caldwell (1984). He found that the model fit the data in two of three years, where an asymptotic yield/density curve (total dry matter) was found, but the fit was poor in a third droughty year where an parabolic relationship was found (Caldwell, 1984).

"Power Equations"

"Power" or geometric equations were put forth by Warne (1951), assuming a linear relationship between log of yield (using the yield of root crops) and the log of density:

$$\log W = \log A + b(\log S)$$

or

$$Y = A(d)1-b$$

A similar relationship was proposed by Kira et al. (1953):

$$\log K = \log W + a(\log d)$$

or $K = Wd^a$

Under competition, total dry matter per unit area approaches an asymptote with increasing populations, but at a decreasing rate, something they called their "Law of Final Constant Yield" (Kira et al., 1953), expressed as:

$$Y = K = Wd$$

where the yield/density curve becomes a straight line, with value K, at high densities. Thus, with these equations, yield must be increasing (at decreasing rates) with all increases in plant density, fitting only asymptotic density relationships, and those not entirely too well (Willey and Heath, 1969).

The agronomic interpretation of the constants in the power equations (b for the Warne equation and a for the Kira et al. equation) was stressed by the authors; ie. the higher the constant, the greater the degree of competitive stress, or the more the plant was dependent upon the space available to it. The failure of these equations, as well as all of the other equations reviewed to describe the levelling of per-plant yields at low densities (where competition does not substantially occur) has been noted (Sinozaki and Kira, 1956, Willey and Heath, 1969). The log-log equation was found to be inadequate in describing the response of corn grain or top yield to population pressure over a wide population range (Fery and Jannick, 1971), as the data did not follow an "asymptotic" relationship.

Reciprocal Equations

Shinozaki and Kira (1956) later termed the power equation only a "crude approximation" of a reciprocal equation derived from a simple logistic growth curve and the law of constant final yield:

$$W^{-1} = a + bd$$

assuming a linear relationship between the reciprocal of yield per plant and density. This was proposed as a better approximation of asymptotic yield/density situations, because it describes both the horizontal and inclined portions of the curve. This equation was tested and seen to hold true for the asymptotic yield/density curve (Shinozaki and Kira, 1956), but not for parabolic relationships. Holliday (1960a) later arrived at the same equation in studying the yield density relationships of rape, kale, potatoes and perennial ryegrass, largely deriving his equations empirically. Dewit and Ennik (1958) derived a similar equation which described a linear relationship between the reciprical of yield per unit area and row width (distance was constant). Willey and Heath (1969) as well as Mead (1979) have emphasized the importance of reciprocal equations in fitting a wide range of yield/density curves, and the biological validity of the constants.

Several workers have pointed out the inability of this and other equations to describe density relationships at very low densities and some have termed the calculated intercepts (a) values as "apparent maximum" yields, rather than those yields which would actually occur at very low densities. Holliday (1960a) modified his equation to describe the intercept as the density at which competition first starts (ie.

identifying the density at which W does not change with lower densities). The independent variable (density) is then reduced by this amount. The reciprical of this new "intercept" (a') would then be the true maximum yield per plant. Shinozaki and Kira (1956) suggested a way of allowing for competition-free low densities by adding a factor to the density (d) value, a term which would be negligible at high densities and of major importance at low densities. However this has been criticized as having little biological meaning and difficult to determine in practice. Holliday then proposed the addition of a quadratic term:

$$W^{-1} = a + bd + cd^2$$

which gave a greatly imporved fit over a linear equation for parabolic types of yield density curves. This provided a curve that is not symetrical about its maximum and flattens out realistically at higher densities (Holliday, 1960b).

DeWit (1960) proposed a modification of the linear reciprical equation to consider the area available per plant. This can be written:

$$W^{-1} = (PQ)^{-1} + (d)P^{-1}$$

(where P and Q are constants, P is the asymptote of yield per unit area). This is a somewhat different approach as it considers the space available to a plant and the ability of that plant to take up that space. This equation was derived from studies of mixtures of two species and describes an asymptotic relationship and is similar in form to the other reciprocal equations, but no modifications have been offered to describe parabolic relationships (Willey and Heath, 1969).

For asymptotic curves, the reciprocal equations of Shinozaki and Kira (1956), Holliday (1960a), Bleasdale and Nelder (1960) and Farzdaghi and Harris (1968) can be generalized as follows (Willey and Heath, 1969):

$$W^{-1} = a + bd$$

$$\text{or} \quad Y = d(a + bd)^{-1}$$

As density tends to zero, the value of yield per plant tends to a^{-1} and this would be the theoretical yield per plant at zero competition. However, as discussed previously, little competition occurs at lower densities, and therefore this 'constant' is not realistic and only represents the "apparent" maximum at 0 density (Holliday, 1960a).

Biological Meaning of the Constants

Willey and Heath (1969) have pointed out that the usefulness of an equation in generalizing a yield/density curve is directly related to the biological meaning which can be inferred from the constants.

The validity of the constant b (slope of the line in the linear reciprocal equations) was examined by Shinozaki and Kira (1956), Holliday (1960), Bleasdale (1966b), Bleasdale and Thompson (1966), Jones (1968), and Willey and Heath, (1969). It was proposed that, if b is a meaningful factor indicative of environmental potential, that with plant growth it would fall at first rapidly, and then more slowly as the season progressed to a more constant b. This is the point where: b^{-1} is the asymptote of yield per unit area or the potential of a given environment (from the law of final constant yield). With a few exceptions, this was found to be the case and the meaning of b was thought to agree with the proposed biological significance (Willey and Heath, 1969).

Bleasdale (1960) suggested that a might be dependent upon the variety (genetic potential) and that b might be dependent upon soil fertility or other environmental factors, a hypothesis that was borne out by Bleasdale and Thompson (1966) for parsnips and supported by Willey and Heath (1969) for wheat.

Holliday's reciprocal equation (Holliday, 1960a) was evaluated by defining $A = a^{-1}$ as the "apparent" maximum yield per plant and thereby:

$$(1 + Abd)^{-1}$$

is the manner in which A is reduced by increasing competition at high densities, a "competition function". The yield per unit area is then:

$$Y = Ad(1 + Abd)^{-1}$$

for an asymptotic curve and

$$Y = Ad(1 + Abd + Acd^2)^{-1}$$

for a parabolic curve. The competition function for this latter case would be:

$$(1 + Abd + Acd^2)^{-1}$$

The flexibility of reciprocal equations and the ability of these functions to satisfactorily describe both asymptotic and parabolic curves makes the use of them more attractive (Willey and Heath, 1969). Mead (1979) affirmed the validity of Holliday's (1960), Bleasdale and

Nelder's (1960) and Nelder's (1960) reciprical equations which were seen as a satisfactory framework within which to investigate practical yield-density relationships. Willey and Heath (1969), in discussing the biological validity of the constants, however warned that the interactions of (at the most) two constants may not be adequate to describe what is in reality a very complex situation, and recommend a more thorough examination of these equations in order to elicit a more meaningful biological relationship between density and yield.

The Influence of Pattern

Duncan (1984) remarked that regardless of the precision of correlation between density and yield, it cannot be a relationship of cause and effect, because population includes the component of planting pattern or plant arrangement within a crop community. For example, one would expect that the yield per plant would vary at a constant population if the rows were 30 cm. apart versus 300 cm apart. The confounding effects of population and arrangement in many density studies was also pointed out by Willey and Heath (1969). These authors as well as Holliday (1960b) also mentioned the difficulties in deciding the population unit (ie. plants, or tillers or stems) and the yield unit of interest (ie. yield per unit area, mean yield per plant or variation in yield per plant), the latter problem was also noted by Goodall, 1960.

Attempts to quantify the effect of rectangularity on the yield of a crop have been made. Plant rectangularity (an index of uneveness) may 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). Several researchers have noted the reduction in yield as rectangularity increases for peas (Vincent, 1958), pigeonpea (Manjhi et al., 1973), lupins (Sims, 1976), cowpea (Haizel, 1972), soybean (Wiggans, 1939) and corn (Pendleton and Seif, 1961). At high densities, uniform spacing seems to be more important (Weber et al., 1966).

A model was offered by Goodall (1960) to cover a range of row widths and densities in soybean:

$$W = as_1^b s_2^c$$

$$\text{or} \quad \log W = \log a + b\log s_1 + c\log s_2$$

where s_1 is the intrarow spacing and s_2 is the interrow spacing, and $s_1 s_2$ is the space available per plant. This has been criticized by Donald (1963) who pointed out that if b is greater than c, then optimum spacing at any given density would be that which in one direction is as wide as possible and in the other as narrow as possible. Berry (1967) also criticized the equation for lack of fit of logW versus $\log s_1$, and because s_1 and s_2 did not overlap, different values for b and c were guaranteed. He proposed the equation:

$$W^{-0} = a + b(s_1 + s_2)^{-1} + c(s_1 s_2)^{-1}$$

to account for rectangularity. This is a modified version of the equation of Bleasdale and Nelder (1960). For this model, W is greatest when $s_1 = s_2$ which makes sense on theoretical grounds. This model was used by Hearn (1972) who examined a wide range of cotton spacings and densities.

Competition Models

A different approach which takes into account the objections to using only plant density as the independent variable in evaluating competitive effects in a corn stand was taken by Duncan (1984). He reasoned that the amount of yield reduction for a given environment and pattern was dependent only on how near and how numerous the neighboring plants were. He proposed the value "C" or crowding, which is an expression of all forms (causes) of interplant competition lumped together and is defined as:

$$C = \sum_{p=1}^{p=n} SFalpha$$

where SF = [(DMAX - Separation)/(DMAX)], DMAX is the distance at which plants are essentially "isolated", p=1 to n is all plants within the circle with radius DMAX, and alpha ia a constant. In theory, DMAX is the smallest radius of a circle of plants which would not reduce the yield of a plant at its center. In practice, however, DMAX could be approximated without much relative or absolute error, as long as it was large enough to include plants which have an effect on the yield at the center (the target plant, Duncan, 1984).

The relationship between C, SF and distance can be easily seen in Figure 2. Duncan reasoned that as two widely spaced plants were moved closer together, Crowding increases at an increasing rate to a maximum

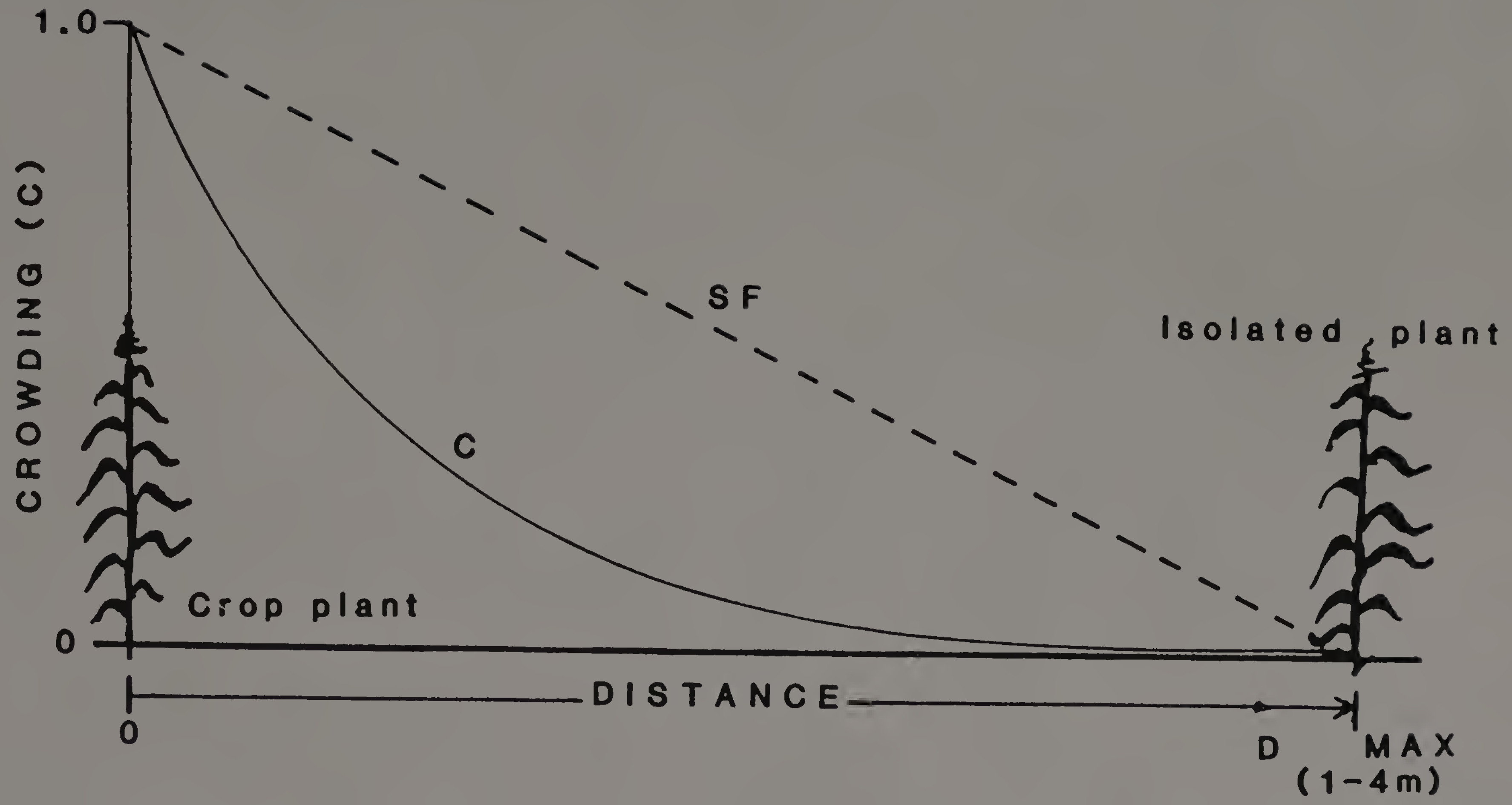

Figure 30. Relationship between Crowding (C), Separation Fraction (SF), and Distance according to the model of Duncan, 1984. As two widely separated plants are brought closer together, Crowding increases at an increasing rate. Crowding value for a cropping pattern is the summation of all C values for plants within the radius DMAX (defined in text).

(defined as = 1) when the plants are in contact (the two plant hill).

The value of alpha is calculated from suitable experimental data, where in some treatments alpha is known or ascertainable. Duncan calculated alpha values of 3.06 (at DMAX = 2.5), which differed little from alpha of 4.0 (at DMAX = 3.0 m) in its precision in predicting yields from a data set of Kohnke and Miles (1951). The equation proposed to relate C with yield (and used to test alpha values) begins with the assumption that the effect of crowding is to change yield per plant a fixed fraction for every change in crowding:

$$EW = dW/dC$$

where W is the yield per plant, E is a constant fraction of yield reduction, the effect, and C is crowding. Thereby:

$$\ln W = \ln W_o + EC$$

$$W = W_o e^{EC}$$

which is akin to the logistic function developed by Duncan (1958) for yield/density relationships. The proposed value of C can be used to more precisely calculate the effect of planting pattern and row width on yield per plant, as well as to obtain more basic information about the nature of the parabolic yield/density curve for corn (ie. that corn yield per unit area tends to a maximum at finite populations and then declines). Duncan found that his model for the effect of crowding on corn grain yield explained the parabolic nature of this curve without any assumptions about barren plants (Duncan, 1984). Applications and theoretical aspects of this model are discussed in following sections.

Use of the Isolated Plant as a Model

The idea of comparing plants under low crowding or non-competitive plants with plants in a crop community is not new. Bleasdale (1960) proposed comparing the weight of a plant at a given plant arrangement to a plant grown in isolation as an index of competition enabling "competition to be defined and studied in quantitative terms". Black (1957) grew widely spaced (1 plant m^{-2}) plants of subterranean clover of differing seed size and compared the growth of these plants with a crop stand of 625 plants m^{-2}. He found that the seed size differential was maintained in the yield of the widely spaced plants but not the plants under competition. Donald (1963) contrasted "isolated" or widely spaced plants with competing plants when reviewing competitive effects over a range of crops. He pointed out the differences in morphology between "isolated" and crop plants, but noted that not all plant characteristics were effected equally with increased density.

In many of the equations cited in this review the idea of the non-competitive or low density plant is contained implicity. The difficulty of many of these equations to adequately describe the yield density curve at low densities has been cited (Willey and Heath, 1969). In some cases, extraneous terms have been added to equations to improve the degree of fit at low densities (Shinozaki and Kira, 1957) or other modifications have been made (Holliday, 1960a). In the model of Duncan, Y_o serves as the idealized maximum yield per plant under zero crowding (isolated plant). The principle of a maximum genetic limit, acheived at very low densities (Donald, 1963), is considered important, but the empirical estimation of this limit is not often discussed or reported.

Other models are of relevance. Mack and Harper (1977) proposed a "neighborhood" model for dune annuals that predicts the biomass of individual plants based purely upon the size, distance and spatial arrangement of its neighbors. Later, Weiner (1982) proposed the equation:

$$R = Rmax/1 + W$$

where R = reproductive output of an individual plant and Rmax = the reproductive output without competition and W = a measure of competitive effect of neighboring individuals. Here, Rmax represents the reproductive output of an isolated plant. A neighborhood model such as this overcomes some of the limitations in dealing with various ages, densities, proportions and spatial arrangements which are implicit in other models (Radosevich et al., 1986). This applies the reciprocal yield law (Spitters and van den Berg, 1982) on an individual basis (Radosevich et al., 1986).

A neighborhood model was developed by Wagner (1982) to estimate the competitive status of a conifer seedling and uses an index based upon height, cover, and distance of surrounding plants to estimate Competitive Influence (CI), defined as:

$$CI = HC/100[1/(r_1 - r_2)]$$

where CI = index value representing the competitive influence of a single plant species surrounding a sample tree, H = average height of plant, C = % cover of the plant and r_1 = distance of closest plant and

r_2 = distance of farthest plant. The total Competitive Influence is the summation of CIs for every species within a defined radius. When tested in a four year old Douglas fir plantation in Oregon, a significant negative relationship between TCI and tree stem volume was found but less than 20% of the variation was accounted for by the model (this was attributed to factors such as soil compaction and deer damage). It is interesting that this model employs the notion of DMAX also proposed by Duncan (1984) and recognizes the primacy of distance from a target plant for estimating competition. This model includes the additional factors of height and canopy cover.

An interesting model postulated by Caldwell (1984) defines the intensity of competition per plant (ICPP) in corn as the difference between the growth rate of a plant grown in isolation and that of a plant under various row width and density treatments. He uses the asymptotic equation of Mitscherlich (1919) and critical densities and row widths, (points at which competition begins), were defined for growth parameters. Competition was modelled directly in relation to a plant in isolation, and the effect of time, density and row width quantified (Caldwell, 1984).

Competition in Corn-Source:Sink Relationships

Several researchers have studied the relationship between the ability of the sink (kernels or ears) to utilize photosynthate and the ability of the source (leaves, stem) to supply photosynthate. Different portions of the source-sink and translocation process may be under varying degrees of environmental and genetic control. A better understanding of the degree to which different constraints on the system could be altered environmentally or genetically might be helpful in designing improved cropping practices or genotypes. The subject of source-sink relations is of relevance to competition studies because of the importance of timing of competition on eventual yield formation.

Source sink relationships in corn were reviewed by Tollenar (1977), who concluded that sink capacity (ability to remobilize all nutrients stored in stalk during early grainfill) is commonly limiting to yields south of the northern perephery of the corn belt. Others have indicated that assimilate supply may be limiting to yields (Yoshida, 1972; Duncan, 1974).

Increases in yields have been demonstrated from light enrichment due to the use of reflectors (Pendleton et al., 1967; Schoper et al., 1982) and thinning treatments (Schoper et al., 1982; Baenziger and Glover, 1980). Shading has been demonstrated to reduce yields and shade tolerance varies with hybrid (Stinson and Moss, 1960). Shading even for short times during the reproductive phase has been found to be more detrimental than shading during vegetative or maturation phases (Early et al., 1967). Baenziger and Glover (1980) demonstrated that thinning treatments effected grain yield and yield components from 30 days after emergence to 20 days after midsilk. Kernel number was effected more than kernel weight, and competition after pollination had a greater effect on grain weight per ear than competition during vegetative stages (Baenziger and Glover, 1980). Hanway (1969) found that defoliation reduced number of kernels and yield, especially when applied around silk emergence. Hawkins and Cooper (1981) determined that the number of grains per plant was related to the growth rate during the pre-flowering period. Schmidt and Colville (1967) applied thinning and leaf removal treatments and shaded the lower canopy in medium density corn stands. They found that leaf removal above the ear reduced yields the most and 100% shade below the ear leaf reduced yields only 14%. Similarly, Pinter (1980) found that leaf removal effected the number of seeds, not weight. Egharevba et al. (1976) found no difference in yield reduction between removing leaves above the ear versus below the ear.

A series of shading treatments applied to corn before, during and after the reproductive period led researchers to conclude that there was a critical period after pollination which caused reduction in kernel number, possibly due to limited endosperm cell number of some tip kernels. These kernels would not fill even if stress was relieved (Kiniry and Richie, 1985). Source-sink manipulations (ear tip removal, defoliation) performed on corn in Minnesota led researchers to similar conclusions (Jones and Simmons, 1983). Frey (1981) and Tollenaar and Daynard (1978a) also concluded that corn alters the number of kernels per ear in response to assimilate supply during a critical period 2 the three weeks after 50% silking. Rates of kernel dry matter accumulation were similar for kernels from basal and middle regions of the ear, but tip kernels filled at slower rates (Frey, 1981). Egharevba et al. (1976) found similar effects of defoliation shortly after mid-silking on kernel number, but later defoliation effected kernel weight to a greater degree. Kernel weight is also effected by photosynthate interruption (Jones and Simmons, 1983; Egharevba et al., 1976), but to a lesser degree than kernel number.

This critical period for carbohydrate translocation and grain formation should not be understated. Labelling studies have shown that less than 10% of grain yield is attributable to assimilates formed before silking (Simmons and Jones, 1985; Swank et al., 1982). However, nitrogen remobilized from sources which had assimilated carbohydrate before mid-silk is quite important for yield formation (Swank et al., 1982) and may establish sink capacity (Tsai et al., 1978) and thus be quite important to the final yield (Simmons and Jones, 1985). Stress may increase the contribution of pre-silking assimilates to yield (Allison and Watson, 1966).

CHAPTER VI.

ESTIMATION OF COMPETITIVE EFFECTS IN A CORN STAND

Introduction

Competition for the growth factors of light, CO2, water, nutrients is said to occur when a single growth resource falls below the combined demands of a crop community (Clements, 1939). However, the complex interactions which occur between plants make quantification of competition difficult. The effect of compeitition may be quantified, however, by measuring the reduction of yields per plant which is caused by increased densities or reduced resource availability.

There is ample evidence that increased densities have the effect of reducing corn yields per plant (Woods & Rossman, 1956; Duncan, 1958; Brown etal., 1970; Remison & Lucas, 1982). This reduction in yield may be the result of lower number of first or second ears (Stickler, 1964; Remison & Lucas, 1982), rows per ear (Remison & Lucas, 1982), fewer kernels (Poneleit and Egli, 1979; Shoper etal., 1985; Karlen & Camp, 1985), or lower kernel weight (Genter & Camper, 1973; Shoper etal., 1985; Karlen & Camp, 1985), or combinations of these factors.

Many studies have described the relationship between corn population and yield, and several equations have been developed to model this relationship. The relationship between corn population and kernel yield per unit area has been described as a parabolic one, where yield increases with increased densities to a maximum and then declines

(Carmer and Jackobs, 1963). While some studies have looked at the effects of increased densities on yield components of corn, few have tried to analyse the differential effect that competition may have on the different yield components.

The timing of competitive stress may also be important. Several researchers have identified a critical period just after midsilk for determination of number of kernels (Tollenaar and Daynard, 1978a; Baenziger and Glover, 1980; Frey, 1981; Jones and Simmons, 1983; Kiniry and Richie, 1985). Photosynthate supply interruption during this time leads to reduction in tip kernel number (Frey, 1981), as well as to reduced kernel weight (Egharevba etal., 1976; Jones and Simmons, 1983).

The purposes of this study were to:

1.Quantify intraspecific competitive effects on maize yield and yield components using the isolated plant as a model.

2. Assess the effect of time of reduction in competition by plant removal on maize yield and yield components.

3. Apply two methods of assessing competition within a corn stand.

Materials and Methods

'Cornell 281' corn was planted June 7, 1985 at the Massachusetts Agricultural Experiment Station in two experiments to examine theoretical aspects of plant competition in the field. The soil type is a Hadley Fine Sandy loam (Typic Udifluvent, coarse-silty, mixed, nonacid, mesic). The experimental site received a basal application of 49 kg N, 93 kg P, and 125 kg K ha-1 after planting and before secondary tillage in the spring. Nitrogen was also sidressed at the rate of 200 kg ha^{-1} as ammonium nitrate four weeks after planting in the Randomized Block Design (RBD). Weeds were controlled by the use of preemergence application of alachlor (2-chloro-2', 6' -dicthyl -N- (Methoxymethyl) acetanilide) at 1.7 kg a.i. ha and linuron (3- (3,4 -dichlorophenyl) - 1- methor -1- methylurea) at 0.85 kg ha^{-1}.

Two experimental designs were used. In the Randomized Block Design (RBD), three plant densities (3.4, 6.7 and 10 plants m^{-2}) were combined factorially with three thinning treatments where alternate plants were removed (cut at the soil surface) at different times during the growing season. These were: no removal control (full season, 101 day competition), removal at 50% tasselling (46 days of full competition), removal at end of silking, beginning grain fill (70 days of full competition). All plots were hand thinned initially to the desired densities two weeks after planting. One plot per replication was allocated to widely spaced or "isolated" plants, which were separated by approximately 2 m between plants (0.25 plants m^{-2}).

The second experimental design was a central composite design (CCD, Cochran and Cox, 1957), where the variables of plant density, plant removal and nitrogen were combined. These treatments are described on Table 3. In this design, the zero levels of each variable are completely replicated and provide n-1 degrees of freedom for estimation of error at and around the central points. The 1 and -1 levels are combined to form a complete factorial (2^3 = 8 plots) replicated once, while the extremes (-1.63 and 1.63) are combined once with the central values (6 plots). The lack of replication especially for the extremes provides less confidence for these values, but the advantage of this design (20 plots) over a complete factorial (125 plots with one replication) in saving space for response surface estimation has been noted (Cochran and Cox, 1957).

Table 3. Central Composite Design (CCD) design parameters and treatment levels. Numbers in parentheses indicate number of times the level appears in combination with other treatment factors.

FACTOR	TREATMENT LEVEL -1.633	-1	0	1	1.633
			plants m^2		
DENSITY	1.2	3.4	6.7	10.0	12.2
			days of full competition[1]		
REMOVAL	38	46	58	70	78
			kg ha^{-1}		
NITROGEN[2]	21	56	112	166	203
NUMBER OF TIMES APPEARING	(1)	(4)	(10)	(4)	(1)

1. Removal of alternate plants X days after emergence.
2. Nitrogen applied as a sidedress 4 weeks after planting.

Leaf area and dry weight were determined at the two times of plant removal. One meter of row was chosen randomly and leaf area was estimated using a Licor-3100 area meter (Licor Instrumentation, Lincoln, NB). Height was measured from soil to tip of tassel. Yield samples were taken September 20, 105 days after sowing at physiological maturity from four meters of row. First ears and second ears and stover were separated and weighed in the field. First ears were considered above second ears if two were on main stalk. Second ears came from both the main stem and tillers. Percent tillers and number of barren plants were calculated from a 15 plant count at harvest. Dry weight for stover was determined using a two plant subsample. The entire first and second ear samples were dried at 70° C to a constant weight and weighed. A ten ear subsample was selected randomly from the 1st ear sample for determination of shelled grain yield, ear length, number of rows, number of seeds and weight per seed. The entire second ear sample was shelled, counted and weighed.

Analysis of variance with appropriate single degree of freedom breakdown of the treatment sums of squares was performed. In addition, parameters for each dependent variable were indexed; dividing observations by the mean for the isolated plants. This then is the proportion (ratio) of the maximum yield or yield component obtained by the competing plant (see literature review). An estimation of the change in these proportions with changes in density was made by applying a linear regression model of the indexed yield component versus density.

The values for Crowding (for Duncan's model) were calculated using a fortran program provided by the author (W. G. Duncan, Univ. of Fla., pers. comm.). Distances (from a target plant) were calculated by using the within- and between-row spacing variables to calculate the hypotenus for every plant located within the circle with radius DMAX (in this case 3 meters, a value suggested by the author). The values for E and Y_o were calculated using linear regression of the natural log of yield per plant versus Crowding (see Chapter V and Discussion section, this chapter for a further examination of the model).

Results

Yield Per Unit Area

Total kernel and dry matter yields per unit area are given in Table 4. Yields were at a maximum at the highest density in the control (no plant removal) plots, and were reduced significantly with lower densities or with thinning The significance of the treatment effects and results of the single degree of freedom comparisons are shown for this and all dependent variables in Table 5. Grain yield per unit area increased with each increase in density in this experiment and so no 'yield plateau' was described. This data conforms to neither a parabolic nor an assymtotic yield /density relationship, as discussed in the literature review, but probably to the portion of the curve which is at less than the maximum yield.

Since alternate plants were removed in the removal treatments, one half of the control yields would be expected from the thinned plots if competition after thinning was the same as without thinning. The percent increase in yield per unit area due to reduction in competition by thinning is shown on Table 4. In other words, plants were able to recover between 23 and 85% of the yield reduction expected when the stand was thinned by one half. This compensation tended to be greater when plants were thinned earlier than later (though the yield differences between the means of the removal treatments were non-significant, Table 5). There seemed to be no trends in compensation due to density considering total dry matter, but kernel yield was adjusted more in medium and low densities than at high density.

Table 4. Density and plant removal effects on kernel and total dry matter yields per unit area, RBD. Percent increase (in parentheses) in yield per unit area due to reduction in competition from plant removal[2] is shown.

	Kernel Yield			Total Dry Matter		
	DAYS OF FULL COMPETITION					
DENSITY	101	70	46	101	70	46
	g m^{-2}					
Low	524	370(41%)[2]	342(31%)	1275	788(24%)	771(21%)
Medium	593	413(39%)	549(85%)	1321	915(38%)	1185(79%)
High	714	440(23%)	480(34%)	1663	1015(22%)	1038(25%)
$LSD_{0.05}$		[143.5]			[255.9]	

1. 101, 70 and 46 indicate no plant removal, and alternate plants removed 70 and 46 days after emergence respectively.
2. Percentages are indexes of yield recovery, compensating for stand reduction due to plant removal at different times. Calculated: % = [(Yt - (.5Yc))/(.5Yc)] x 100, where Yt = yield in thinned plots and Yc = yield in control (unthinned) plots.

Total yields from the CCD are not presented because treatment effects are completely confounded, and these treatments do not lend themselves to yield/unit area analysis. These experiments were designed purely to study plant competition. Since competition has an

Table 5. Analysis of variance table showing significance of main effects and single degree of freedom comparisons for final yields and yield components in the Randomized Block Design.

		Yield/Area											First Ears							Second Ears		Yield/Area	
		Kern.	TDM	Dry wt./Plant			Kernel Yld./Plant			Ear No./Plant			Kern.	Kern.	Row	Ear	Barren	Tiller	E/S	Kernel	Kernel	Kern.	TDM
SOURCE	DF	Yld.	Yld.	Tot.	Stov.	Ear	Tot.	1st	2nd	Tot.	1st	2nd	Wt.	No.	No.	length	Plants	No.	Ratio	Wt.	No.	Yld.	Yld.
REP.	2	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
TRT.	9	**	**	**	**	**	**	**	**	**	n.s.	**	**	**	n.s.	**	n.s.	*	n.s.	*	**	**	**
SDF Comparisons:																							
1.Isol. vs. rest	1	**	**	**	**	**	**	*	**	**	n.s.	**	n.s.	**	n.s.	**	*	**	n.s.	*	n.s.	**	**
2.Dens. linear	1	**	**	**	**	**	**	**	**	*	n.s.	**	**	**	n.s.	**	*	**	n.s.	n.s.	**	**	**
3.Dens. quadratic	1	n.s.	n.s.	n.s	n.s	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	*	n.s.	n.s.	**	n.s.	n.s.
4.Cont. vs. Rem.	1	**	**	*	n.s.	**	**	**	n.s.	n.s.	n.s.	n.s.	**	**	n.s.	**	n.s.	n.s.	**	n.s.	**	**	**
5.40 d. vs.70 d.	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.
6.2 X 4	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	**	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.
7.2 X 5	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	n.s.	n.s.
8.3 X 4	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
9.3 X 5	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.
		—g m-2—		gms plant-1						no.			mg	no.	no.	cm.	%	%		mg.	no.	—g m-2—	
ERROR MS	29	6995	22255	2547	512	978	694	264	437	.138	.005	.123	0.1	3	0.4	0.5	23	6	.022	23	2048	6995	22255

*,** indicates significance of F test at P=0.01 and P=0.05 probability levels resprectively.

effect on an individual corn plant (and thereby the whole corn stand), yield per plant is the unit of interest. Therefore, the rest of the results are presented on a per-plant basis.

Yield Per Plant

The total dry matter production and ear/stover ratio per plant for the RBD is shown in Table 6 and for the CCD in Figure 31. Dry matter was reduced in a linear fashion due to density in the RBD and a quadratic response was found over a wider density range in the CCD. Removing alternate plants had the effect of increasing total dry weight per plant, although timing of removal made no statistical difference (Tables 6, 5, Figure 31).

Table 6. Density and plant removal effect on total dry matter production (per plant basis) and ear-stover ratio for the RBD.

	Total Dry Matter			Ear/Stover Ratio		
	DAYS OF FULL COMPETITION					
DENSITY	103	70	46	103	70	46
	-------g plant^{-1}--------					
ISOLATED	547.9			1.29		
LOW	383.8	400.7	378.5	1.27	1.54	1.34
MEDIUM	202.6	273.3	318.7	1.26	1.29	1.50
HIGH	163.0	218.4	214.5	1.19	1.26	1.34
$LSD_{0.05}$		53.6			0.08	

1. 103, 70 and 46 indicates no plant removal, alternate plants removed 70 days and 46 days after emergence respectively.

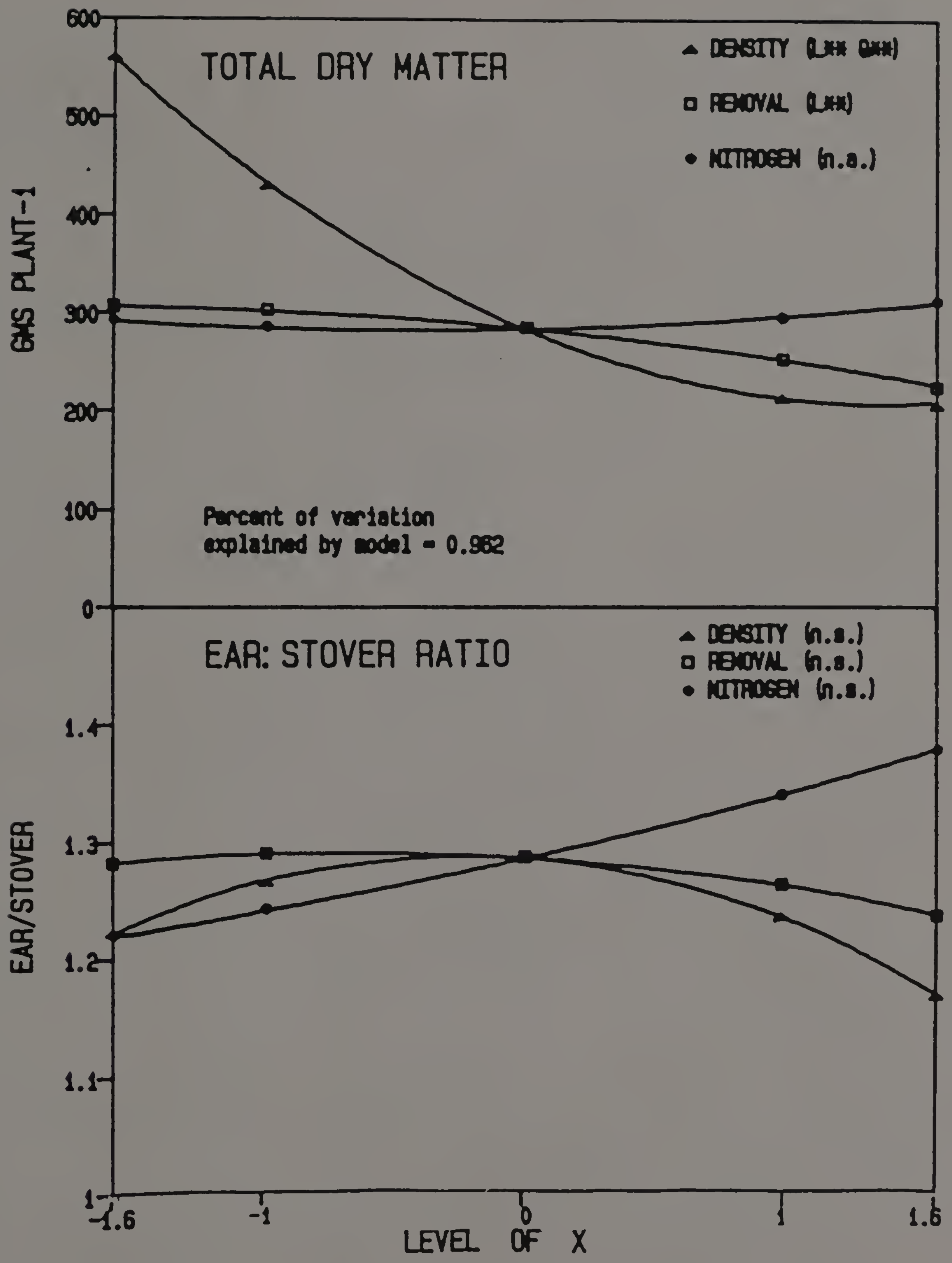

Figure 31. Density, plant removal, and nitrogen rate effects on total dry matter production and ear/stover ratio response in the CCD.

There was little overall change in ear:stover ratio due to treatments, but some interesting trends can be discerned. When alternate plants were removed at either time, ear/stover ratio increased significantly and ear/stover ratio declined with higher densities (Tables 6, 5). The isolated plants (RBD) or low density plants (CCD) tended towards a lower ear/stover ratio in both experiments (Table 6, Figure 31), with higher ratios appearing in the removal treatments. When plants were removed earlier at higher densities, higher ear/stover ratios resulted than when plants were removed later, possibly indicating a 'superior' balance between source and sink in these treatments. These trends were non-significant in the CCD.

Total kernel yield was affected in a similar fashion as total dry matter (Table 7, Figure 32). In the RBD, there were highly significant differences in grain yields due to density and removal, but no differences between the removal times or interactions in the trends were found (Table 5). In the CCD, there was a linear effect on total kernel yield due to time of removal, but this was small in relation to the effect of density (Figure 32).

The first ear kernel yields responded similarly in the RBD except that density became less important in determining first ear kernel yield per plant when alternate plants were removed at 46 days versus 70 days (significant interaction, P = 0.05, Table 5). There was a linear effect of plant removal time on first ear and total ear yield in the CCD (Figure 32), trends similar to the RBD.

Table 7. Density and plant removal effects on first ear, second ear, and total kernel yield per plant, for the Randomized Block Design (RBD).

	DAYS OF FULL COMPETITION[1]		
DENSITY	101	70	46
		g $plant^{-1}$	
First ear contribution:			
ISOLATED	134.3		
LOW	123.3	140.3	113.8
MEDIUM	91.7	124.4	139.6
HIGH	66.3	88.3	100.7
$LSD_{0.05}$		(27.9)	
Second ear contribution:			
ISOLATED	107.3		
LOW	32.8	50.2	56.3
MEDIUM	0.2	0.9	9.9
HIGH	4.0	6.4	0.1
$LSD_{0.05}$		(35.9)	
Total:			
ISOLATED	241.6		
LOW	156.1	190.4	170.1
MEDIUM	91.9	125.4	149.1
HIGH	70.4	94.7	100.9
$LSD_{0.05}$		(45.2)	

1. 101, 70 and 46 represent full season competition, alternate plants removed at 70 and 46 days after emergence respectively.

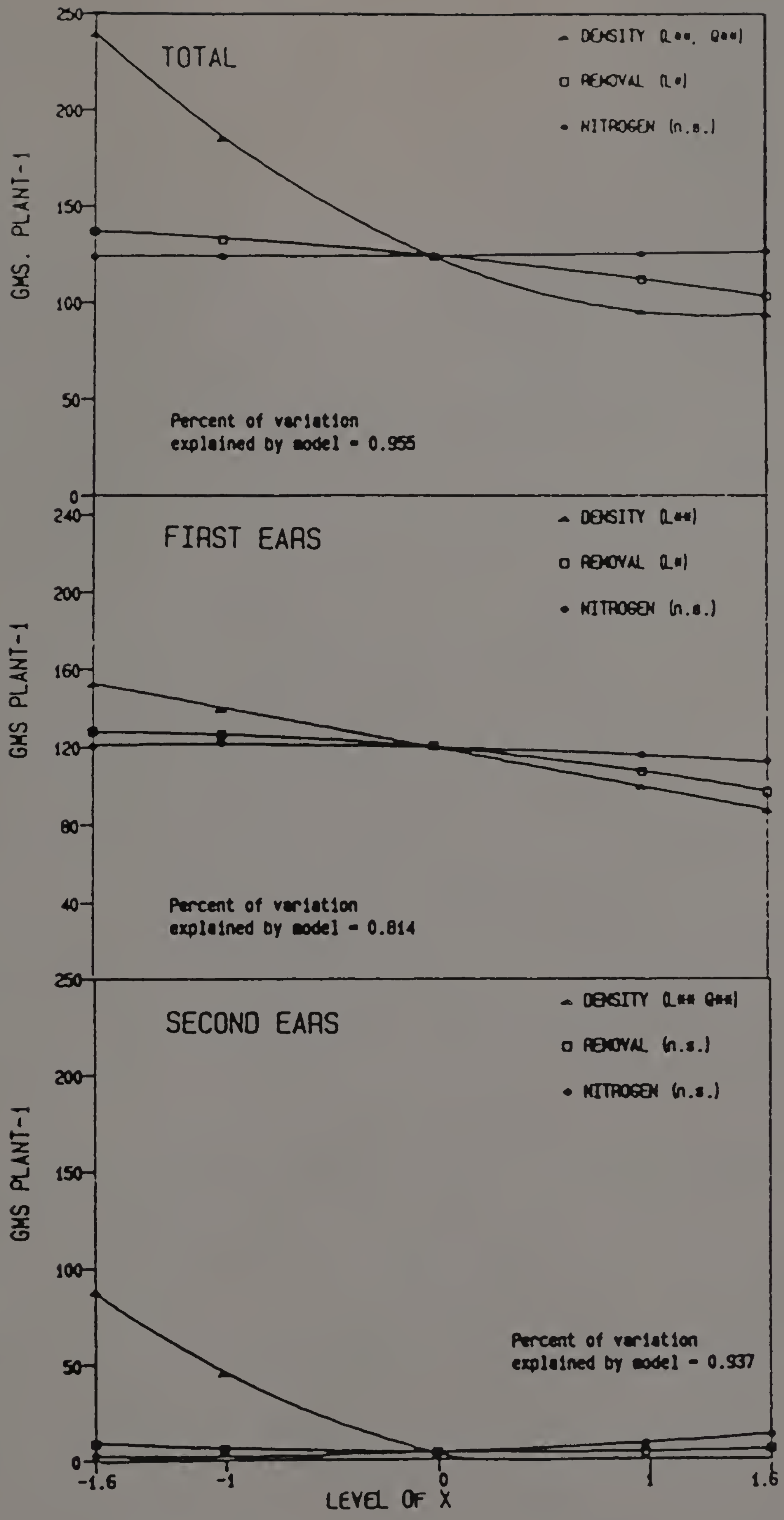

Figure 32. Density, plant removal and nitrogen rate effects on total, first ear and second ear kernel yield response in the CCD.

Second ear seed yield was reduced severely between low and middle densities in both designs (Table 7, Figure 32). Second ear contributiton to total grain yield was 44% in the isolated plants. At low density, second ear contribution was 21%, which increased to 33% and 26% when alternate plants were removed at 46 and 70 days respectively (second ear yield differences between removal times were non-significant in either design). At the middle and high densities the contribution of second ears ranged from 0 to 7%, with no discernable trends due to density or removal. This indicated that in both experimental designs there were descrete levels of competition at which second ears became unimportant, between 3.4 and 6.7 plants m^{-2}.

Ear number

The number of first ears (Table 8) was only slightly reduced with increased density (trend non-significant in RBD, Table 5, linear trend significant at p=0.05 in CCD), and unaffected by plant removal (Table 8, Figure 33). However, the number of second ears was significantly effected by density (Table 5, Figure 33), leading to large differences in total ear number due to density. Plant removal did not effect total or second ear number in either design.

First Ear Yield Components

Yield from the first ears of corn can be divided into kernel weight, number of kernels per row, number of rows per ear, and ears per plant (Table 9, Figure 34). Both the weight per kernel and number of

Table 8. Density and plant removal effects on total, first, and second ear number, RBD.

DENSITY	DAYS OF FULL COMPETITION		
	101	70	46
	ear plant^{-1}		
First ear:			
ISOLATED	1.0		
LOW	0.95	1.00	0.86
MEDIUM	0.94	0.97	0.93
HIGH	0.87	0.85	0.94
LSD$_{0.05}$		(n.s.)	
Second ear:			
ISOLATED	3.12		
LOW	1.21	0.99	1.33
MEDIUM	0.11	0.14	0.66
HIGH	0.11	0.19	0.19
LSD$_{0.05}$		(0.60)	
Total:			
ISOLATED	4.12		
LOW	2.16	1.99	2.19
MEDIUM	1.06	1.11	1.59
HIGH	0.98	1.04	1.13
LSD$_{0.05}$		(0.20)	

1. 101, 70 and 46 represent full season competition, and removal of plants at 70 and 46 days after emergence respectively.

Table 9. Density and plant removal effect on first ear kernel weight, number of kernels per row, and number of rows per ear for the RBD.

DENSITY	DAYS OF FULL COMPETITION 101	 70	 50
Kernel weight:	------------mg kernel-1----------		
ISOLATED	235.4		
LOW	233.3	252.1	248.2
MEDIUM	210.2	233.7	233.7
HIGH	208.4	214.5	228.
$LSD_{0.05}$		(20.1)	
Kernel Number:	---------- kernels row-1 --------		
ISOLATED	37.5		
LOW	36.9	38.0	36.0
MEDIUM	32.6	37.3	37.7
HIGH	23.9	32.6	31.7
$LSD_{0.05}$		(2.9)	
Row Number:	-------------rows ear^{-1}----------		
ISOLATED	15.2		
LOW	15.3	14.6	14.7
MEDIUM	15.1	15.5	14.5
HIGH	15.5	15.1	15.1
$LSD_{0.05}$		(n.s.)	

---

1. 101, 70, and 46 represent no removal (full season competition), alternate plants removed at 70 and 46 days after emergence respectively.

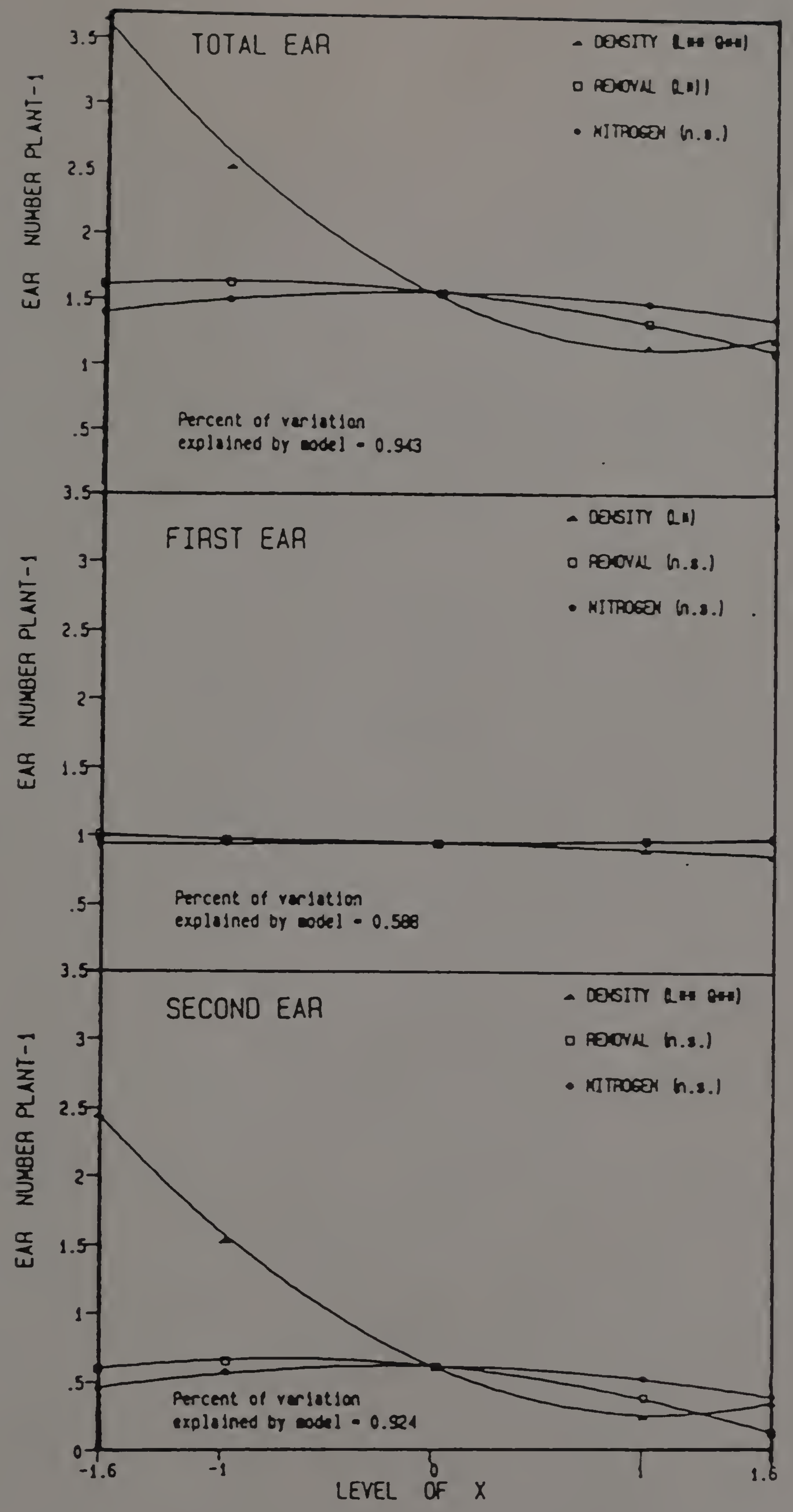

Figure 33. Density, plant removal and nitrogen rate effects on total, first ear and second ear number in the CCD.

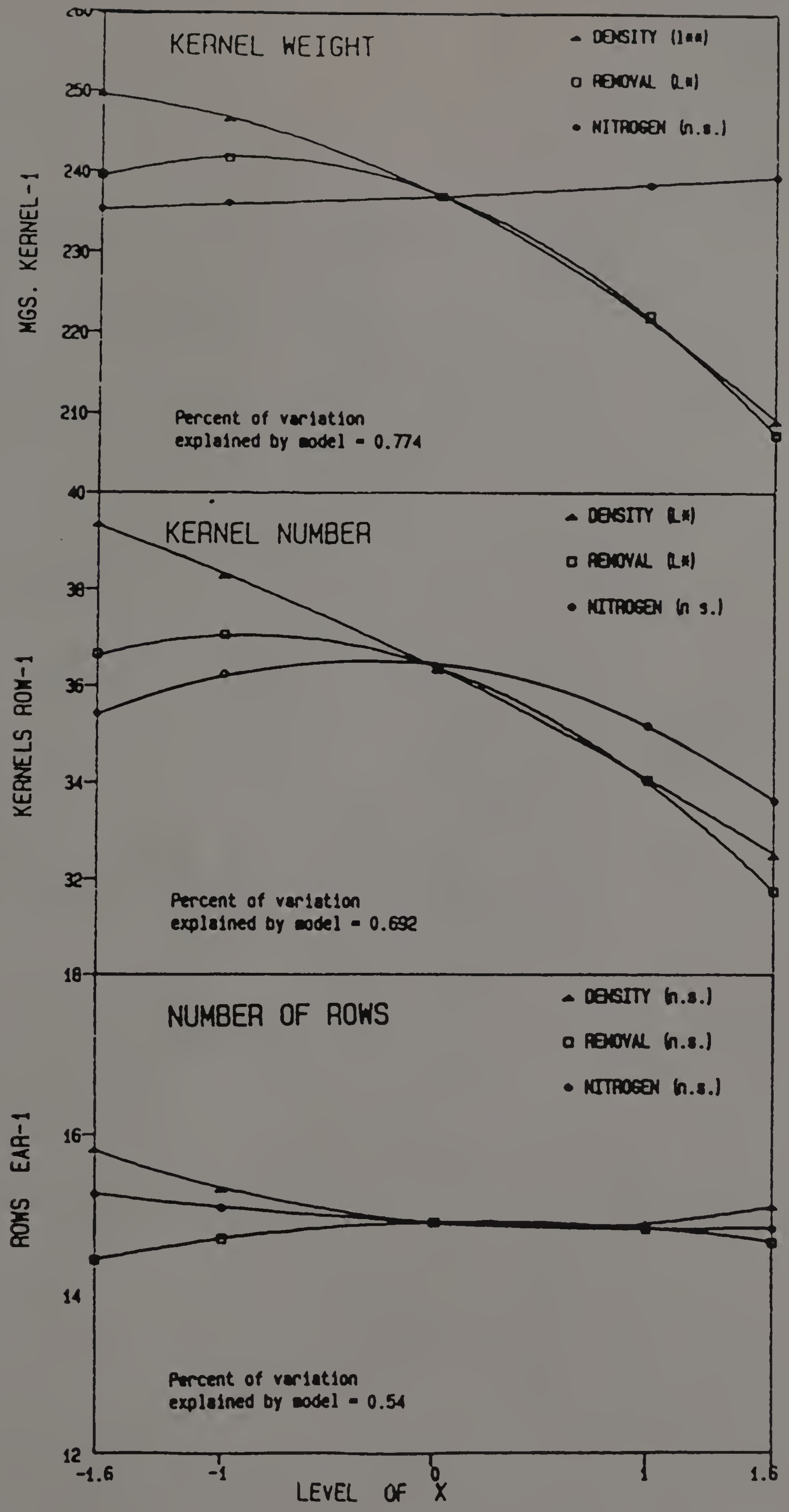

Figure 34. Density, plant removal and nitrogen rate effects on the kernel weight, kernel number, and number of rows of kernels of the first ears, CCD.

kernels per row were reduced (linear effect in both designs) with increased densities (Tables 9, 5, Figure 34). Plant removal increased kernel weight and number at all densities (Table 9) and there were significant linear trends due to time of removal in the CCD (Figure 34). However, there were no differences between the removal times for these parameters in the RBD (Table 5). The number of rows per ear was unaffected by any of the treatments in either design.

Density and removal significantly effected the length of first ears (Table 10) and there were differences in density responses in the controls versus the removal treatments (Table 5). The CCD produced similar results (Figure 35). Illustrations of treatment effects on ear size are provided in Figures 36 and 37.

Table 10. Density and plant removal effects on first ear length, RBD.

	DAYS OF FULL COMPETITION		
DENSITY	101	70	46
	---------------- cm ----------------		
ISOLATED	18.6		
LOW	18.2	18.6	17.9
MEDIUM	15.6	17.9	18.1
HIGH	13.4	15.9	15.7

1. 101, 70 and 46 represent no removal (full season competition), and removal of alternate plants at 70 ad 46 days after emergence respectively.

Second Ear Yield Components

Second ear yield components were considered to be kernel weight,

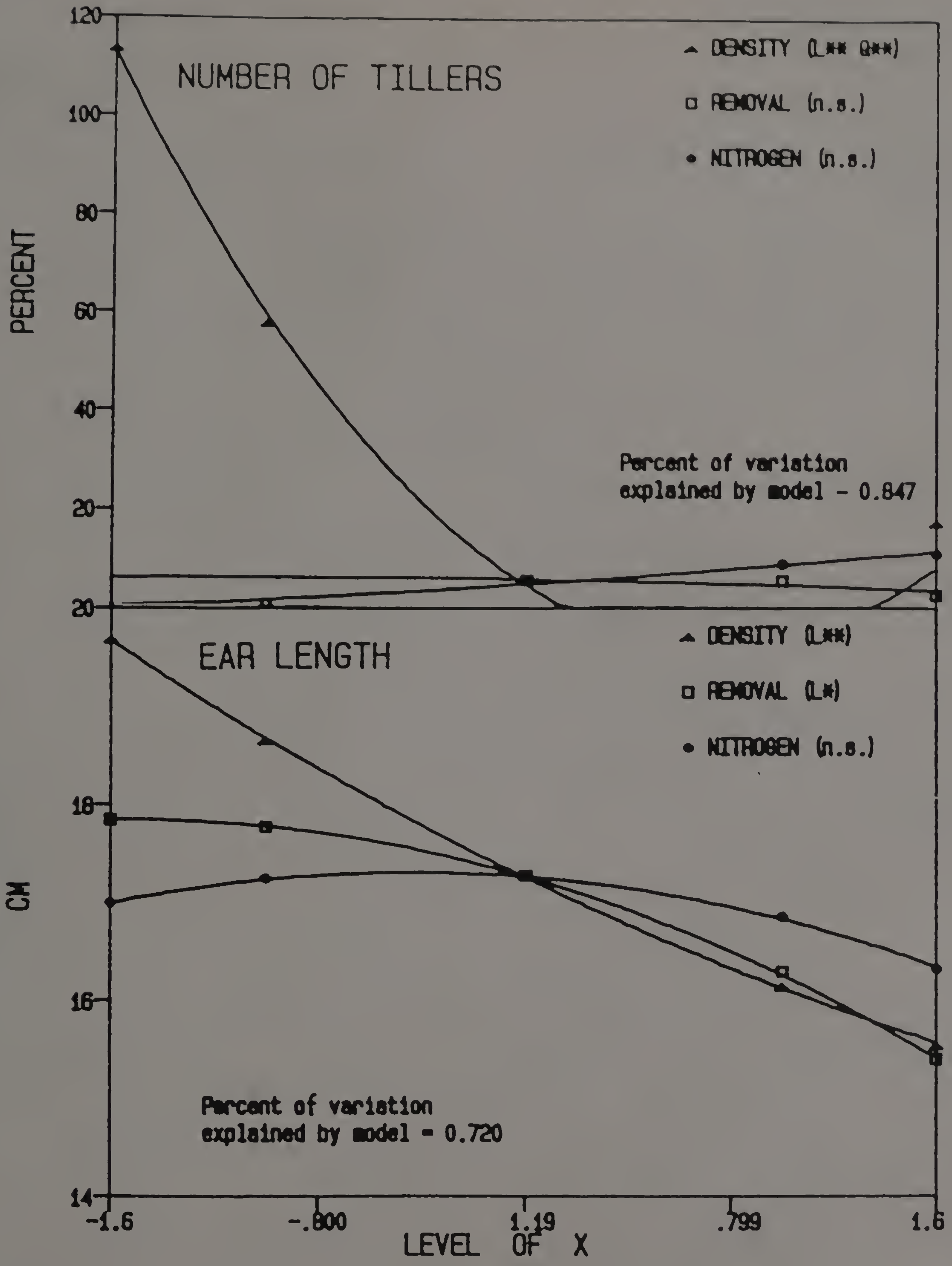

Figure 35. Density, plant removal and nitrogen rate effects on tillering and first ear length, CCD.

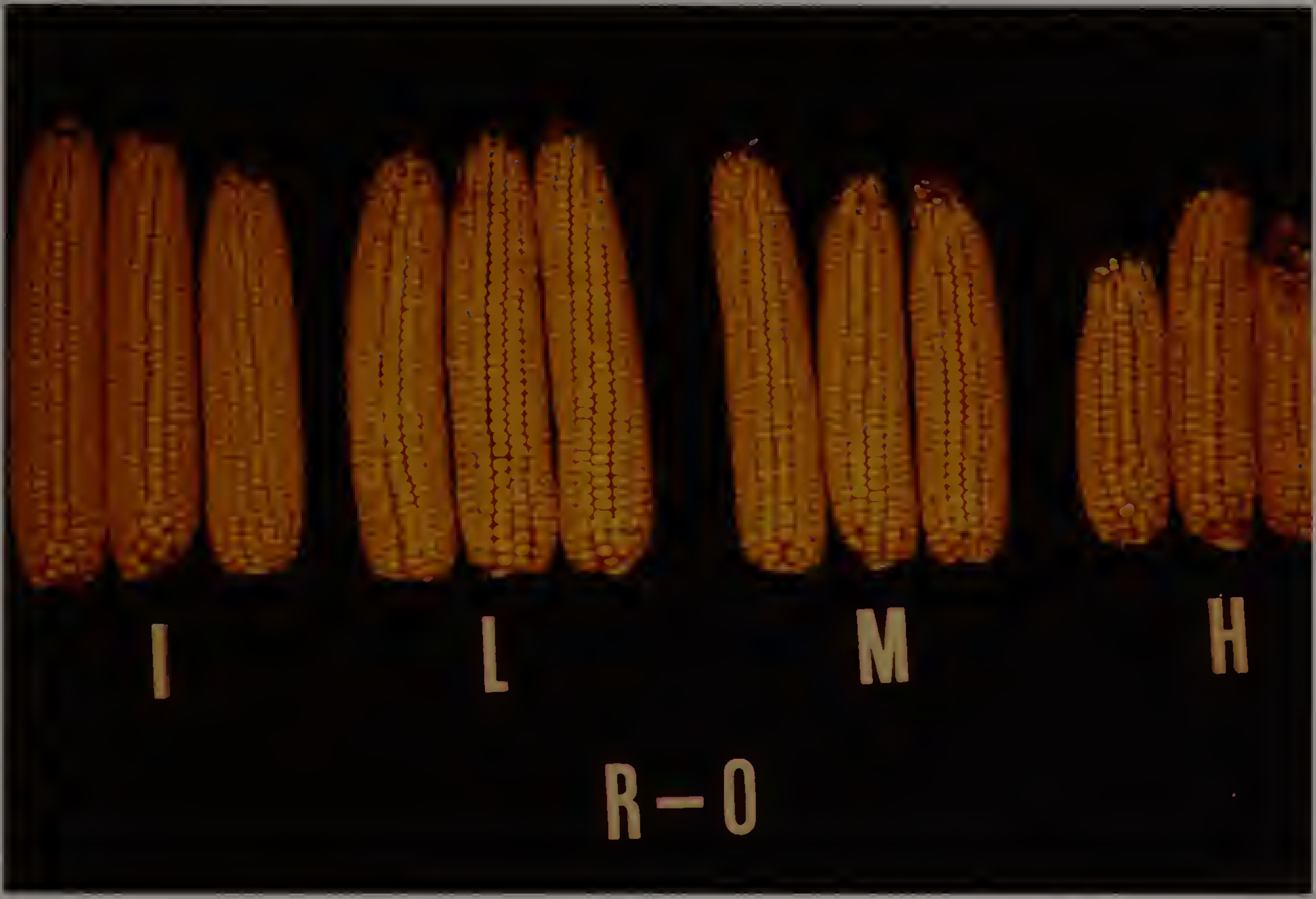

Figure 36. Photographs illustrating density effects on first ear size in the control (no plant removal) treatment, RBD. Isolated (I), Low (L), Medium (M) and High (H) densities are shown. R-0 represents no removal.

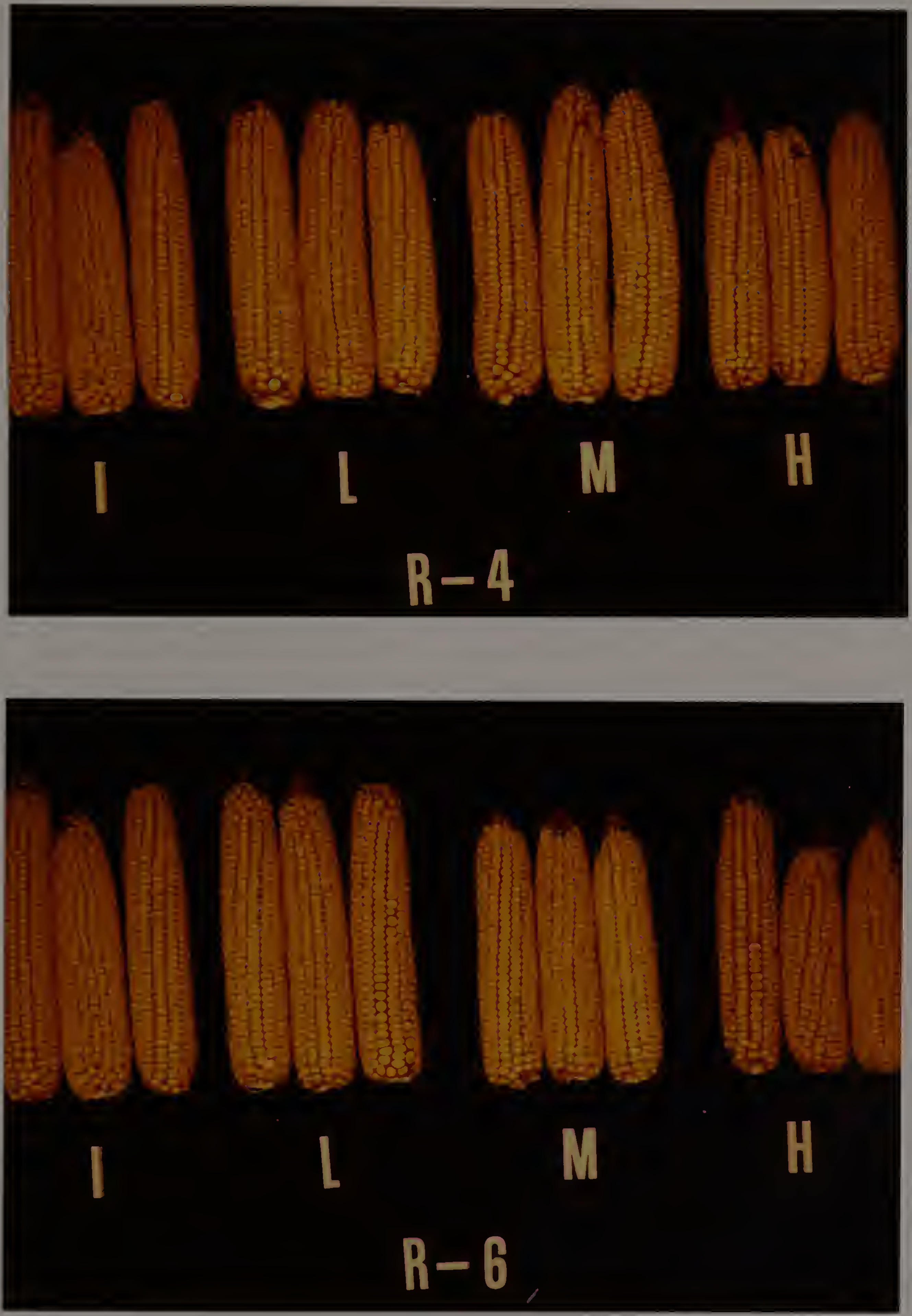

Figure 37. Illustration of density and removal effects on first ear size in the plant removal treatments, RBD. Isolated (I), Low (L), Medium (M), and High (H) densities are shown. R-4 and R-6 represent alternate plant removal at 46 days and 70 days after emergence.

number of kernels per ear, and number of ears per plant. Kernel weight and number (Table 11) showed a much higher degree of variation than for first ears (C.V. = 31.3% and 53.6% for second ear and 4.3% and 5.0% for first ear kernel weight and number respectively). Isolated plants differed from the mean of the crop plants in kernel weight but there were no trends due to density or removal (Table 5). However, there were differences in kernel number due to density and removal, generally increasing at low density versus high, and with removal of plants. Kernel number increased with removal at low densities, not high.

The number of second ears produced (Table 8) was also quite variable (C.V. = 0.44). Linear (RBD) and quadratic (CCD, Figure 33) rends in second ear number were significant, but it appears as if the changes in second ear development were not necessarily continuous. There was a three fold difference in second ear number between isolated plants and low density plants, but a 10 fold difference between low and medium densities and second ear number was not further reduced at high densities (Table 8). It was clear that second ear number was the primary determinant of second ear yield. The reduction in second ear development was alleviated to some degree by thinning at 46 days but not at 70 days (Table 8).

Number of Tillers and Barren Plants

Tiller number responded to the density and removal treatments in a fashion similar to that of second ear development (Table 12). Large differences in tiller number were found between isolated and low

Table 11. Density and plant removal effects on second ear kernel weight and kernel number per ear for the Randomized Block Design.

	DAYS OF FULL COMPETITION		
DENSITY	101	70	46
		mg/kernel	
Weight per Kernel:			
ISOLATED	273		
LOW	199	210	221
MEDIUM	128	172	191
HIGH	184	241	189
LSD$_{0.05}$		(82.1)	
		No.	
Kernel Number per Ear:			
ISOLATED	134		
MEDIUM	98	233	186
MEDIUM	16	40	68
HIGH	59	41	6
LSD$_{0.05}$		(77.6)	

---

1. 101, 70 and 46 represent full season competition, and removal of alternate plants at 70 and 46 days after emergence respectively.

Table 12. Density and plant removal effects on tiller number and barren plants, expressed as a percentage of 15 plant counts.

	DAYS OF FULL COMPETITION		
DENSITY	101	70	4
		%	
Tillers:			
ISOLATED	150.0		
LOW	17.8	48.9	53.3
MEDIUM	2.2	4.4	6.7
HIGH	0.0	0.0	2.2
$LSD_{0.05}$		(4.29)	
Barren plants:			
ISOLATED	0.0		
LOW	4.4	0.0	3.0
MEDIUM	5.7	2.8	7.0
HIGH	12.7	14.3	5.9
$LSD_{0.05}$		(11.7)	

---

1. 101, 70, and 46 represent full season competition, and removal of alternate plans 70 and 46 days after emergence respectively.

density and again between low and medium densities, with negligible differences between medium and high densities (Table 12). The effect of removal at either time was not significant (p=0.07), except at low densities (Table 12). Similarly, a quadratic trend in tiller number due to density was found in the CCD and no effect of removal or nitrogen (Figure 35). Number of barren plants increased to over 12% at high densities and was close to zero at low and isolated densities. Removal of plants had little effect on the number of barren plants (Tables 12, 5, Figure 35).

Effect of Nitrogen

There were no significant trends due to added nitrogen fertilizer in the CCD (N rates were constant in the RBD) for any of the parameters, indicating that N was not limiting in this growth environment. Fertility studies (S. J. Herbert, pers. communication) have indicated that more than three years have been required to obtain a nitrogen yield response on this soil because of a long history of fertilization.

Growth Data

Density had an effect on the dry weight of the individual corn plants and plant components after the time of the first thinning (sample taken 52 days after emergence), but there was not a significant difference between isolated plants and the mean of crop plants at this time (Figure 38, Table 13). At the time of the second removal

Table 13. Analysis of variance table showing significance of main effects and single degree of freedom comparisons for dry matter production and leaf area (per plant) and specific leaf area, 52 and 75 days after emergence samples, Randomized Block Design.

		52 Day Sample					75 Day Sample						
		Dry wt./Plant			Leaf	Sp.Leaf	Dry wt./Plant				Leaf	Sp.Leaf	Plant
SOURCE	DF	Tot.	Stem	Leaf	Area	Area	Tot.	Stem	Leaf	Ear	Area	Area	
REP.	2	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
TRT.	9	*	**	*	n.s.	n.s.	**	**	**	**	**	*	**
SDF Comparisons:													
1.Isol. vs. rest	1	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	**	**	**	*	**
2.Dens. linear	1	**	**	**	**	n.s.	**	**	**	**	**	**	**
3.Dens. quadratic	1	n.s	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
4.Cont. vs. Rem.	1	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	**	*	n.s.	n.s.	n.s.
5.40 d. vs.70 d. Rem.	1	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	**	*	n.s.	n.s.	**
6.2 X 4	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
7.2 X 5	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
8.3 X 4	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
9.3 X 5	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		gms plant^{-1}			cm^2	cm^2/gm	gms plant^{-1}				cm^2	cm^2/gm	cm.
ERROR MS	29	243	115	26	1005714	264	437	.138	.005	.123	0.1	346	153

*,** indicates significance of F test at P=0.01 and P=0.05 probabilitylevels resprectively.

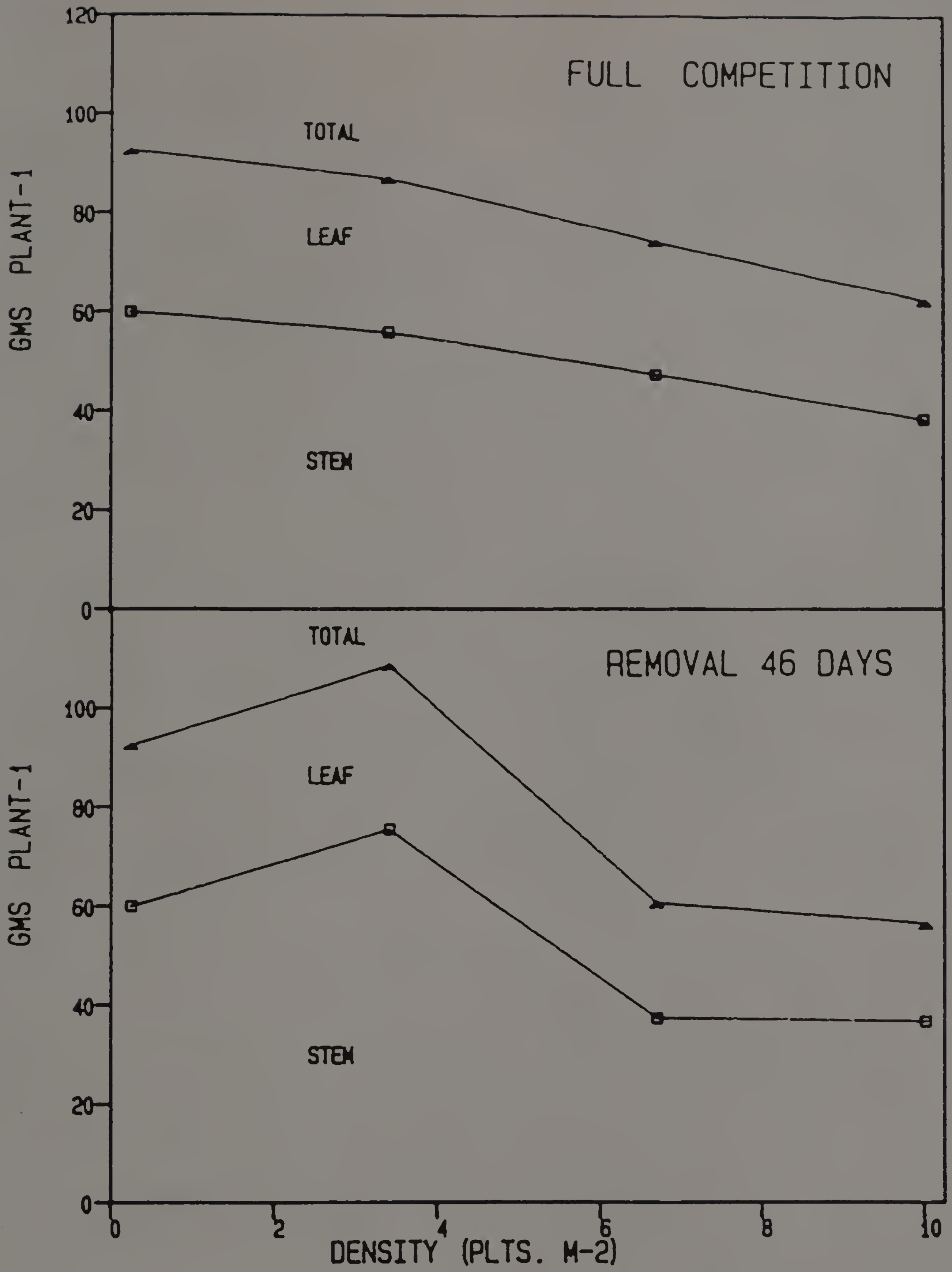

Figure 38. Density and plant removal effects on dry matter accumulation (per- plant basis) 52 days after emergence, RBD.

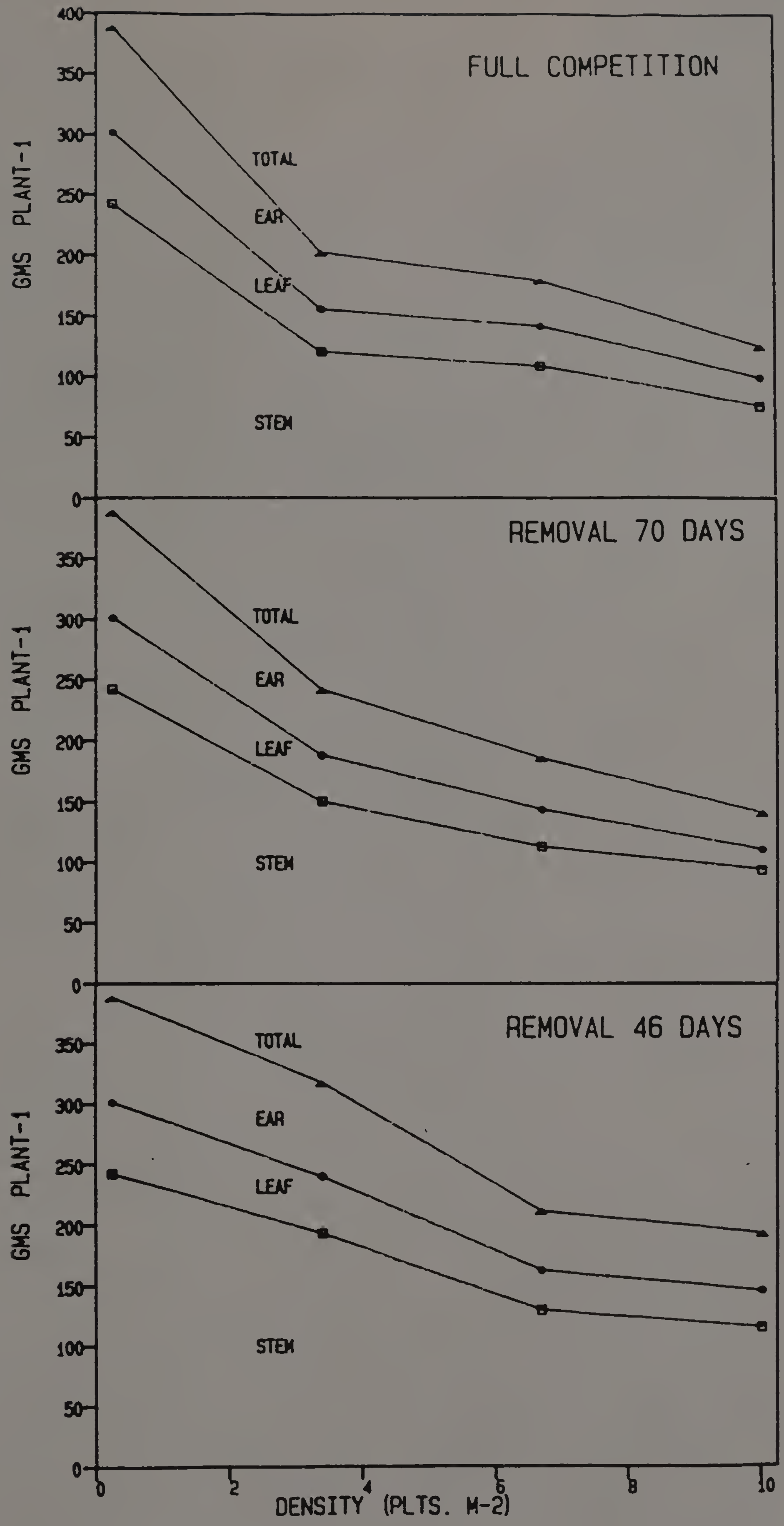

Figure 39. Density and plant removal effects on dry matter accumulation (per-plant basis) 75 days after emergence, RBD.

treatment, density reduced the dry weight of plant parts and differences between the two removal times could be detected (Figure 39, Table 13). Leaf area per plant was significantly affected by density at both harvests, but leaf area did not change due to removal treatment at any time, although there was an upward trend at the low and middle densities (Figure 40, Table 13). The isolated plants had a lower specific leaf area (ratio of leaf area to leaf weight) than crop plants and there was an increase in SLA due to density at 75 days after emergence (Tables 13, 14). No differences in SLA were found 52 days after planting. Height at 75 days after emergence was increased by increases in plant density and decreased to some degree by removal of plants at 46 days (a significant interaction between density and removal was found, Tables 13,14).

Table 14. Density and plant removal effect on specific leaf area, sampled at 52 and 75 days after emergence.

	SAMPLED 52 DAYS		SAMPLED 75 DAYS		
	DAYS OF FULL COMPETITION				
DENSITY	None	46 Days	None	70 Days	46 Days
	-----cm^2 gm^{-1}-----				
ISOLATED	170.2		144.6		
LOW	171.2	169.4	166.5	149/6	149.6
MEDIUM	143.4	172.8	155.8	163.9	166.1
HIGH	149.5	194.9	206.5	188.8	168.3
$LSD_{0.05}$	57.1			31.9	

Table 15. Density and plant removal effects on plant height measured from soil to tassel, 75 days after emergence.

DENSITY	DAYS OF FULL COMPETITION[1]		
	101	70	46
	cm.		
ISOLATED	265.1		
LOW	262.1	300.5	280.3
MEDIUM	304.1	299.3	272.2
HIGH	314.4	312.3	291.1
$LSD_{0.05}$		(21.2)	

1. 101, 70 and 46 represent full season competititon, and removal of alternate plants 70 and 46 days after emergence respectively.

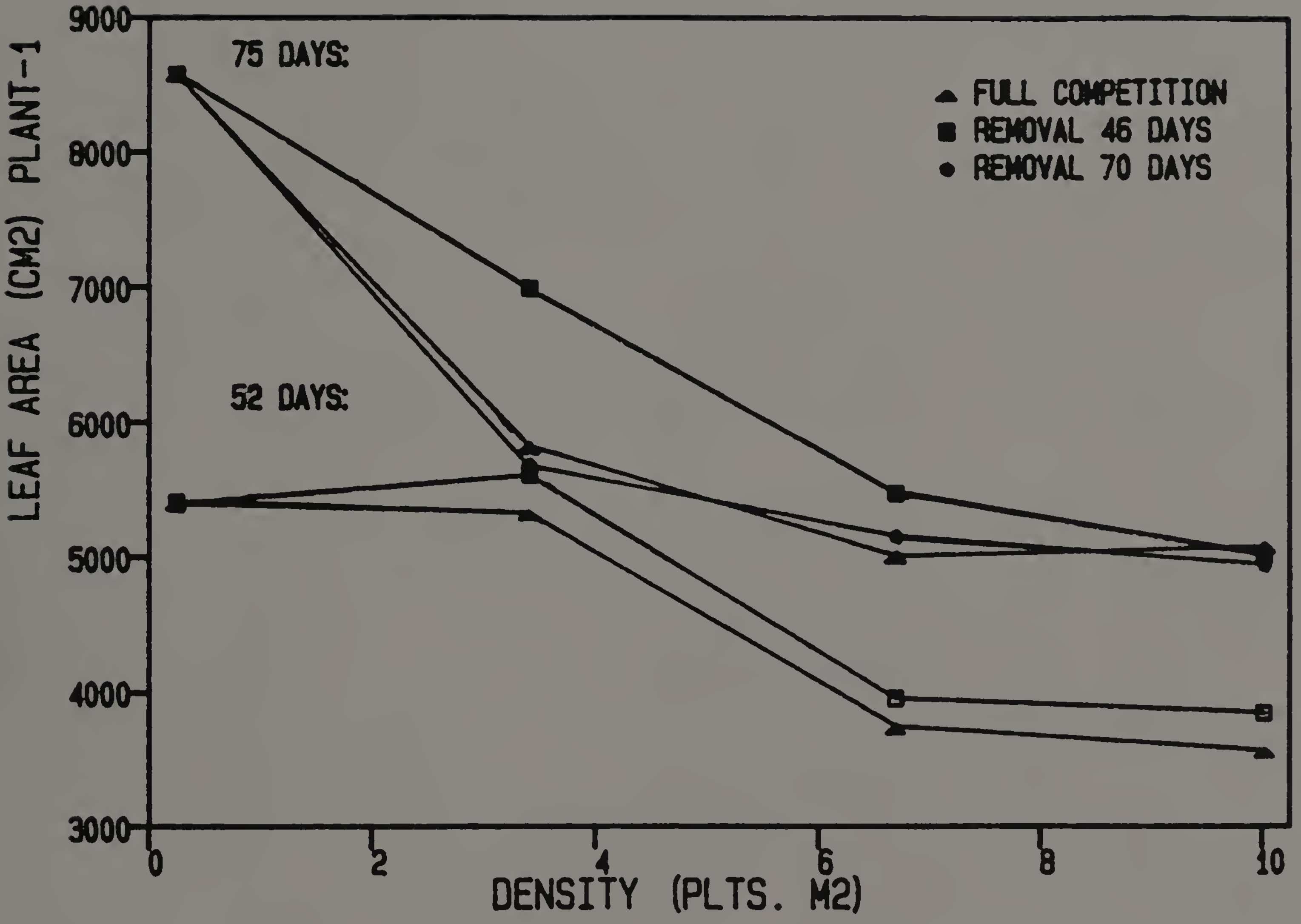

Figure 40. Density and plant removal effects on leaf area development, 52 and 75 days after emergence, RBD

Discussion-Analysis of Competition

Although much information about density effects on yield and yield components can be obtained by making inferences from the means presented in the preceeding section, there are further questions which may need to be addressed. How much competition is actually taking place, and are there differences between competitive effects on yield components due to increases in plant density? These questions may be addressed by 1. conducting competition analysis using isolated plants as models and 2. the application of a competition model to the data.

Indexing Yield Using Isolated Plants.

The yield of a plant in isolation represents the observed full yield potential of a particular genotype given a certain set of environmental constraints. The yield of the crop plant divided by the yield of the isolated plant is the proportion of the full yield potential which was obtained by the crop plant under competition, since neighboring plants are the only variable changing. This is:

$$YPc = Yc/Yi$$

where YPc is the yield proportion of the isolated plant obtained by the crop plant, Yc is the yield of the crop plant and Yi is the observed (mean) yield of an isolated plant. This method can also be applied to components of yield and other variables such as leaf area. This provides a quantitative estimate of the extent of competition taking place on any measured variable in the crop community.

place on any measured variable in the crop community.

Competitive effect of density. To estimate the effect of density on the proportion of yield potential obtained by the crop plant, a linear model is applied to each indexed variable so that the level of yield reduction and slope (competitive effect of density) can be easily compared for different variables, since the units are the same.

The competitive effect of density on the indexed yield components for first and second ears for the control (no removal) treatments are shown in Figure 41 and the intercept, slope, and r2 values for this and other variables are given in Table 16. First ear kernel yield per plant was suppressed by competition at high density, very little at low density (height of line compared with unity). Competitive effects of density (slope of line) were greatest on kernel number/row (36% reduced from isolated plants at high densities) compared with the other yield components (Figure 41). Number of first ears per plant and kernel weight were reduced about 12% at high densities versus the non-competitive control and there was no density or competition effect on number of rows per ear. The importance of the competitive effect on each yield component can be made by comparing the slopes of the regression lines (b values) and the degree of linear correlation (r^2) between the indexed variable and density (Table 16).

All second ear yield components were reduced to a greater degree than first ear components (Figure 41). The primary component of second ear yield to be effected by density was number of ears per plant. Of those ears produced (some high density plots had no second ears),

Table 16. Intercept, slope, and r^2 values for regression analysis of indexed competition variables, RBD. Observed values for each variable were divided by the mean of the observed isolated plant value, and the model $Y = a + bx$ (where Y = indexed variable, x = density and a and b are constants) was applied.

	DAYS OF FULL COMPETITION								
	101			70			46		
VARIABLE:	a	b	r^2	a	b	r^2	a	b	r^2
DRY MATTER:									
Total	0.865	-.0611*	.615	0.881	-.0504**	.836	0.859	-.0454**	.775
Stover	0.944	-.0685*	.615	0.775	-.0385**	.722	0.837	-.0457**	.672
Ear	0.803	-.0550*	.582	0.963	-.0597**	.869	0.875	-.0451**	.869
KERNEL YIELD:									
Total	0.799	-.0538*	.561	0.969	-.0600**	.913	0.870	-.0434**	.722
First	1.129	-.0642**	.771	1.269	-.0587**	.705	0.978	-.0147ns	.061
Second	0.388	-.0407*	.204	0.592	-.0617*	.514	0.736	-.0793**	.730
FIRST EAR COMPONENTS:									
Wt./Ker	1.031	-.0160*	.565	1.154	-.0242**	.685	1.108	-.0130*	.461
Ker/Row	1.182	-.0525**	.907	1.106	-.0218**	.633	1.055	-.0176ns	.361
Rws/Ear	0.990	-.0020ns	.016	0.958	+.0050ns	.105	0.948	+.0036ns	.082
Ears/Plt	1.008	-.0125ns	.208	1.089	-.0217*	.525	0.832	+.0118ns	.225
SECOND EAR COMPONENTS:									
Wt/Ker	0.720	-.0129ns	.079	0.711	+.0055ns	,016	0.873	-.0220ns	.362
Ker/Ear	0.802	-.5250ns	.072	1.511	-.0771*	.351	2.085	-.2195**	.873
Ears/Plt	0.432	-.0466*	.398	0.531	-.0563**	.690	0.653	-.0622**	.753
GROWTH SAMPLE (52 DAYS):									
Total DM	1.0611	-.0389*	.576				1.357	-.0824*	.497
Stem	1.0582	-.0413*	.544				1.453	-.0944*	.512
Leaf	1.066	-.0346*	.630				1.181	-.0602*	.434
Lf Area	0.095	-.0477	.406				1.143	-.0478ns	.031
SLA	1.032	-.0187ns	.067				1.914	+.0211ns	.160
GROWTH SAMPLE (75 DAYS):									
Total DM	0.640	-.0307**	.866	0.756	-.0398**	.793	0.947	-.0485**	.661
Stem	0.610	-.0287**	.816	0.756	-.0412**	.823	0.928	-.0482**	.697
Leaf	0.697	-.0267**	.831	0.720	-.0275**	.755	0.916	-.0458**	.774
Ear	0.684	-.0391*	.583	0.778	-.0442*	.606	1.011	-.0523**	.452
Lf. Area	0.704	-.0130ns	.179	0.699	-.0129ns	.372	0.913	-.0349**	.712
SLA	0.939	+.0419ns	.277	0.921	+.0368**	.801	0.984	+.0196ns	.269

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1. *, ** indicate level of significance of linear coefficient at P = 0.05 % and 0.01 % respectively.

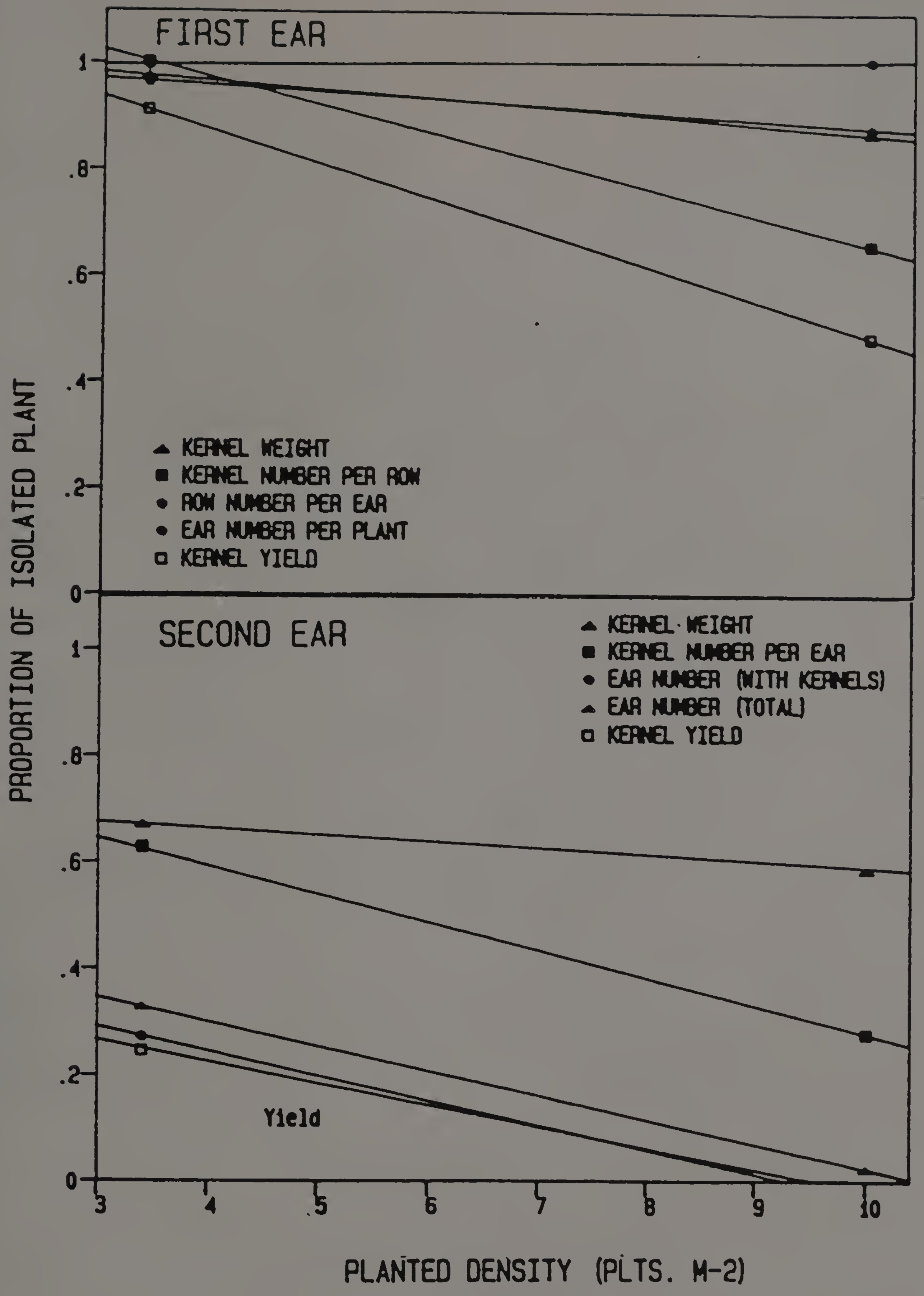

Figure 41. Competitive effect of density on first and second ear yield components, control treatments, no plant removal treatment, RBD. Lines are calculated linear respones of indexed variables versus density.

kernel number was also significantly reduced by density, but kernel weight remained relatively constant.

The significance of second ear development in maize is not clear. Anderson et al. (1980) found increases in yield with increasd nitrogen to be closely associated with an increase in the number of two eared plants.

Effect of Plant Removal. Reductions in competition by removal of alternate plants 70 days after emergence caused yield and all yield components of first ears to be adjusted upwards compared with the non-removal control (Figure 42). Seed weight and number relationship to density was significant, but there was no longer differences in the competitive effect of density (slope) for the different yield components. It is interesting that in both removal treatments at low densities, kernel weights were from 5-8% higher than isolated plants, and reduced only slightly at high density (Figures 42, 43). Plant removal at an earlier time (46 days after emergence) caused the relationship between density and yield and yield components to be non-significant (Table 16). The differences in first ear yield from plant removal were due primarily to adjustments in seed number not weight at either removal time (Figures 42, 43).

Analysis of second ear components indicated that release from competition had little effect on kernel weight but a marked effect on the number of kernels per second ear. Ear number was relatively little effected by removal treatment, though there was an increase in barren

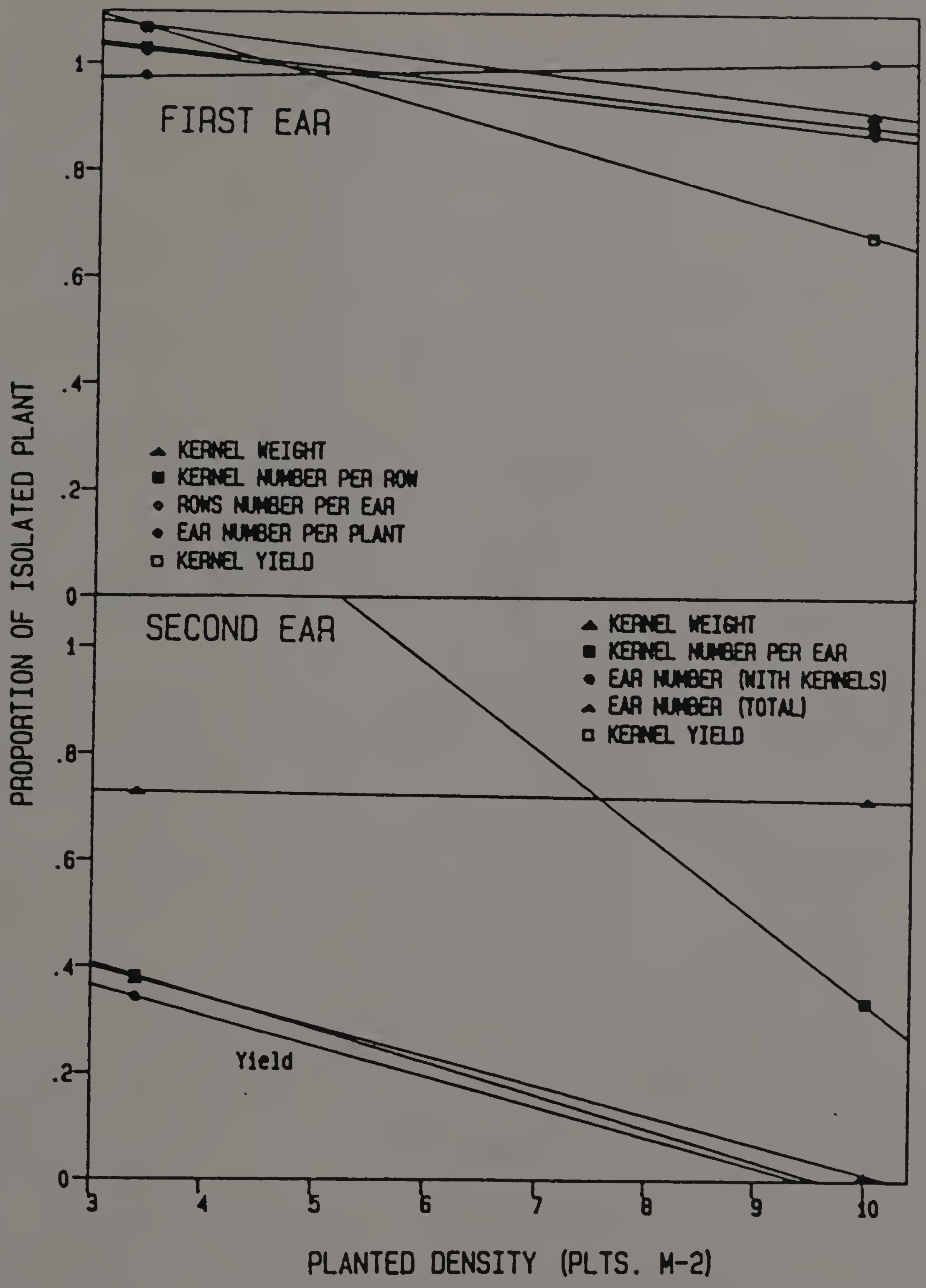

Figure 42. Competitive effect of density on first and second ear yield components in the 70 day removal treatment, RBD. Lines are calculated linear responses of indexed variables versus density.

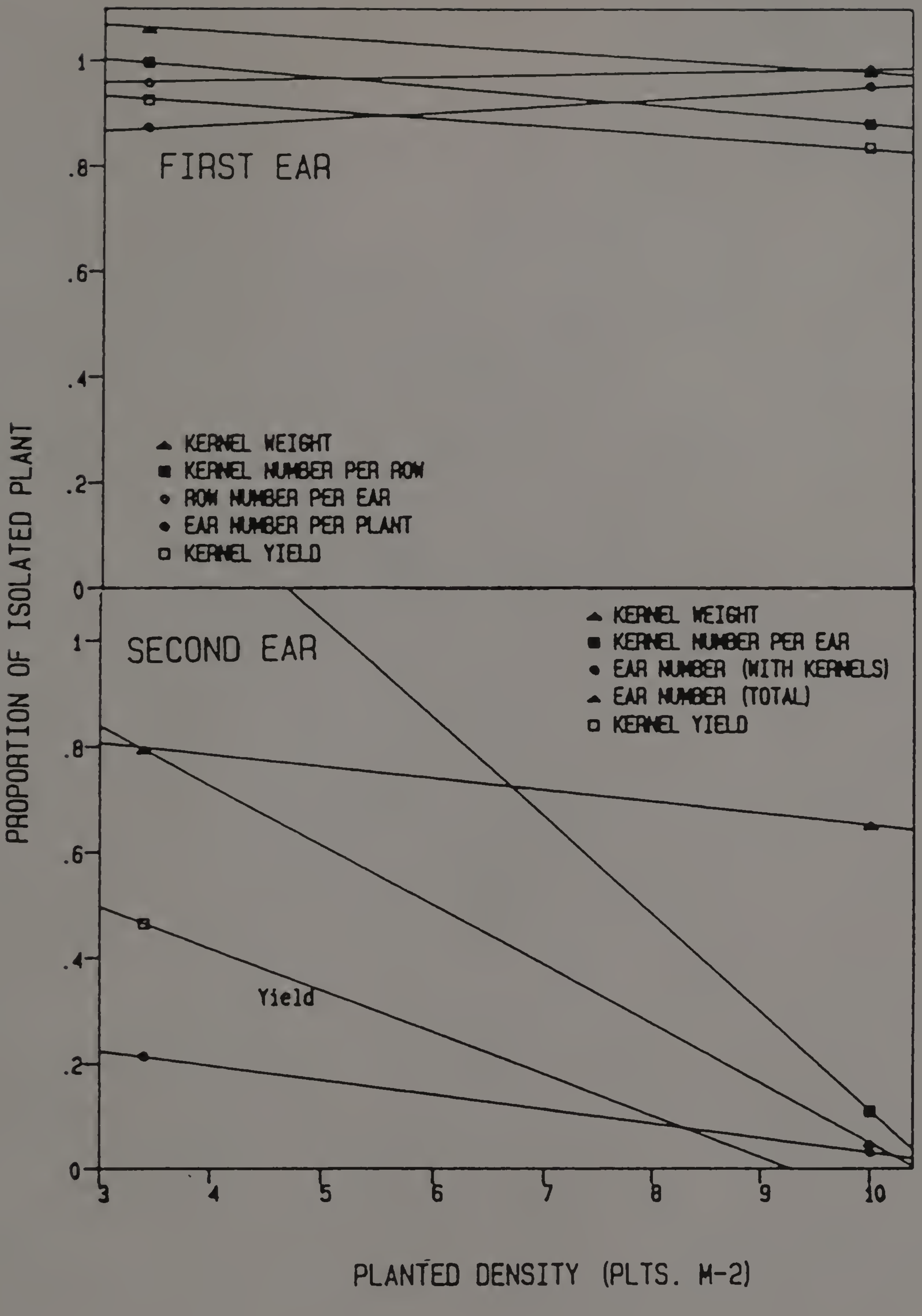

Figure 43. Competitive effect of density and on first and second ear yield components in the 46 day removal treatment, RBD. Lines are calculated linear responses of indexed variables versus density.

second ears at low densities when plants were removed at 46 days. The primary relationship between ear number and density observed in the controls was maintained in the removal treatments. The high degree of variation in this data indicate that second ear data should be view ith somewhat more skepticism. In a similar study, Fenwick (1978) found no effect of time of thinning on yield in two years of study in Indiana, though second ears were not reported. It is clear, however, that the primary determinates of second ear ear yield are number of ears and kernel number, and these respond differently to adjustments in competitive force at different times during the season.

Effect on dry matter production and leaf area during the season. Selected growth parameters were examined in the same way to see if there were differences in competition effects on plant parts or leaf area during the season. Figure 44 indicates that the differences in response of plant parts to competition (level of yield proportion) or plant density (slope) were small. However, there was a tendency at both harvest dates for leaf weight and leaf area to be supressed less by competition or density than the other observed variables. Specific leaf area was greater than control, and increased with increased densities (Figure 44).

Use of a Competition Model

Duncan (1958) had proposed a geometrical relationship between density and corn yield:

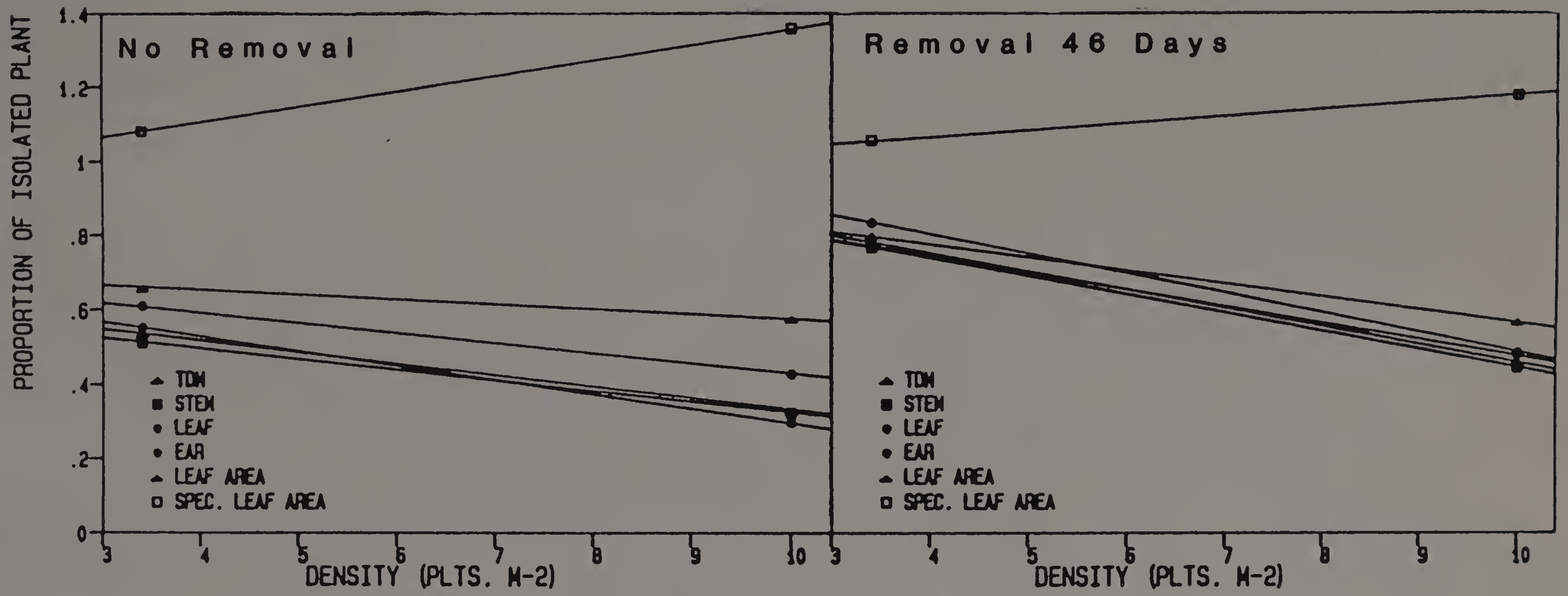

Figure 44. Competitive effect of density and removal on dry matter production, sampled 75 days after emergence.

$$\log Y = \log K + bd$$

where K and b are constants, Y is yield per plant, and d is the population in plants/unit area. Later, Duncan (1984) proposed a theory to explain this model which involved the use of the concept of "Crowding" (C) and the "Effect" of Crowding (E) as postulated components of competition in a corn field. These are related to grain yield by the equation:

$$Y = Y_o e^{EC}$$

$$\text{or:} \quad \ln Y = \ln Y_o + EC$$

where C is constant for any given density and planting pattern which will increase with increased densities or sub-optimal plant arrangements. Y_o and E are assumed to be constant within given environments and genotypes. Y_o is the theoretical maximum yield per plant at zero Crowding and Y is the yield per plant of the crop plant under competition, E is the effect of competition. Y_o and E may be estimated empirically for any given genotype-environment from the above equation.

Application to the Data. The C values were calculated for this experiment using values for DMAX and alpha postulated by the author (the method for calculating C is given in the literature review). C values, actual total and predicted total grain yields for this competition experiment (RBD) are shown in Table 17. The value for crowding is exactly correlated with plant density and gives the same precision of fit to the yield data ($R^2 = 0.708$, $n = 9$). (The theoretical nature of this model will be discussed in a subsequent section.) The predicted value for plants at zero crowding (isolated plants) was 201 grams, considerably below the 242 grams observed in plants grown two meters apart (the model assumes a DMAX, or radius of no competition of 3 meters). The effect of crowding (E) was estimated at -0.0591 for this study as compared with -0.044 estimated for other studies (Duncan, 1984).

Table 17. Actual yields (from the zero removal treatments), values calculated for Crowding (C), and predicted yields from the corn competition study (RBD) using Duncan's (1984) model. DMAX = 300 cm and alpha=4.0 were values suggested by the author used to calculate C.

		TOTAL		FIRST EAR	
DENSITY	Crowding (C)	Actual Yield	Pred. Yield	Actual Yield	Pred. Yield
--Plts m^{-2}--		---------------g	$plant^{-1}$	-----------	
0.25[1] (Isol)	0.751	241.6	201(Y_o)	134.3	162(Y_o)
3.4	5.689	156.1	144	123.3	123
6.7	12.076	91.9	99	91.7	90
10.0	18.477	70.4	67	66.3	66

1. Crowding value calculated for the isolated plants in the RBD assuming population of 0.25 plants m^{-2}. Isol. plant observed yields were not used in the regression used to calculated predicted yields or to estimate E or Y_o. Predicted value for isolated plants using Duncan's model assumes 3 m as DMAX, whereas isolated plants in this experiment were grown 2 meters apart.

No mention is made by the author describing the relative role of first ears and second ears in determining the shape of the yield/competition curve (Duncan, 1984). It is interesting to note that when only first ears are considered, the relationship between C and yield is linear ($R^2 = 0.766$) and the model predicts yields considerably better than when total yields are considered (Table 17). In addition, the predicted value for plants at zero crowding is underestimated when considering total yields and overestimated when considering first ear yields (Table 17). Duncan's description of Yo (predicted) is that this is the potential yield per plant, since sink limitations may reduce the actual yield. His model seems to apply to estimation of first ear yields not to total yield in this experiment since low density and isolated plants adjusted sink size by adding second ears and tillers. The addition of second ear contribution to yield at low densities makes the relationship between yield and density and yield and C more non-linear (Figure 32). Perhaps the small amount of data in these treatments (n=9) is the cause for the lack of precise fit of model as given. However, this model seems to fit changes in yields when considering densities high enough so that second ears and tillering become insignificant.

Row width effects. One proposed use of this model is to evaluate the effect of row width on crop yield. For the competitive effects found in this experiment yields are predicted over a range of row widths in Table 18. Potential benefits of theoretically more optimum row widths (ie. where rectangularity approaches one compared with the row width used in the study seem to be minimal. The maximum yield reductions versus a square pattern were 14% for high density plantings at 150 cm row width. The benefits to square plantings as compared with row widths common to New England (100 cm or less) seem to be on the order of 0-4% for the amount of competition found with this genotype in this environment. Similar estimations made by Duncan (1984) indicate maximum reductions due to suboptimal row widths (at the highest rectangularity, 125 cm rows) of 7.2%, with most yield reductions predicted at less than 5%.

Table 18. Row width effects on predicted yields using the model of Duncan (1984), for the competitive effects estimated from the RBD.

	Row Spacing or Arrangement					
DENSITY	Square Pattern	60cm	91cm[1]	100cm	120cm	150cm
plts. m^{-2}	gms. plant^{-1}					
3.4	145	145	144	143	142	138
6.7	100	100	99	98	96	91
10.0	70	69	67	67	65	60

1. Row width used in this study and to predict yields for other row widths.

This estimation may be tested with the appropriate data. Bryant and Blaser (1968) grew two corn hybrids at 4 densities and 4 row widths in Virginia. The per plant yields (mean of 3 replications and two years) and values predicted by Duncans model are shown in Table 18. The effect of competition (E) and the maximum yield per plant (Y_o) were

Table 19. Row width effects on predicted yields and actual yields (in parentheses) from a two year corn density study of Bryant and Blaser, 1960.

DENSITY (Plts M-2)	Square Pattern	ROW ARRANGEMENT OR SPACING					
		36cm	53cm	71cm	89cm	120cm	150cm
			g plant-1				
Early Variety:							
3.95	155	155(183)	155(149)	155(156)	154(160)	151	146
4.94	137	137(159)	137(129)	136(150)	135(134)	132	127
6.67	110	110(102)	110(105)	110(112)	108(102)	105	99
9.88	74	74 (75)	74 (64)	73 (70)	72 (74)	68	63
Late Variety:							
3.95	136	135(127)	136(153)	135(177)	134(134)	132	128
4.95	120	120(121)	120(107)	119(131)	118(120)	115	111
6.67	96	96 (94)	96 (83)	95(108)	94 (93)	91	86
9.88	64	64 (60)	64 (65)	63 (75)	62 (62)	59	54

1. Row width used to estimate values for E and Y_o (in this study E = −0.0664, Y_o = 240.1 g and E = −0.0675, Y_o = 211.7 g for the early and late hybrids respectively.

estimated at a single row width (89 cm) and used to predict yields for the other row widths. A maximum of about 3% advantage to square plantings was predicted for high density treatments versus the wide row width. The lack of change in predicted yields with theoretically more optimal row widths is born out by the actual data, where no significant effect of row width was found (Bryant and Blaser, 1960).

More benefit would be expected using narrow rows at higher versus lower densities (Table 18,19). The model does not take into account traumatic effects such as lodging, barren ears or dropped ears which may result from greater within-row densities at high row spacing.

The model is generally corraborated in the published literature. Nunez and Kamprath (1969) found no differences in yield due to row width except under drought conditions where 106cm rows yielded 85% as much as 53cm rows. Similarly, Rutger and Crowder (1967) have found little differences due to row spacing or interactions with hybrid or density. However, Karlen and Camp (1985) have found advantages to paired rows versus single rows, and Brown et al (1970) found large advantages to narrow rows, but these were confounded with density treatments, and so the advantages may be due primarily to density. Yield differences of 6% were found when 40 inch rows were decreased to 20 inch rows, and the differences were attributed primarily to more second ears and fewer barren plants (Stickler, 1984). Others have also reported advantages to narrow rows, but these advantages are often small (Hoff and Mederski, 1960; Colville and Burnside, 1963).

In a corn competition study, Caldwell (1984) studied the Intensity of Competition Per Plant (ICPP, defined as the isolated plant growth rate minus growth rate of the crop plant) at various row widths and densities over the whole season. He found that the ICPP for each of the row widths converged over the last half of the season for all row widths, though differences were found earlier in the season. Thus, corn was able to compensate for the effect of suboptimal row widths as the season progressed, but the same was not true for density, where differences in ICPP due to density remained constant throughout the season.

In practice, the effect of row width in many environments may be too small to observe. However, the differences predicted by Duncan's model seem to agree fairly closely with the differences that have been reported in the literature. It is interesting that the model does not take into account barreness or lodging, but barren plants have been cited at least once to account for yield differences between wide and narrow rows (Stickler, 1964). This exercise underscores the importance of numbers of plants per unit area and ascribes a minor role to arrangement or pattern in determining yield, and indicates a degree of plasticity for maize within patterns of agronomic importance. Deviations from usual row widths or patterns would be expected to cause greater reductions in yield.

Estimation of Crowding within removal treatments. In the experiment reported here, since thinning of alternate plants occurred at various times during the season in some treatments, estimation of C from plant densities becomes impossible. Two densities are involved, established density and final density, and the value for crowding would be expected to fall somewhere in between. The value of C can be estimated, however, from the observed yields using the prediction equation proposed by Duncan and the values of E and Yo estimated from the controls (these are assumed to be constants for any given environment and genotypes). The expected (predicted) value for C would be:

$$C = (\ln Y - \ln Y_0)/E$$

where $\ln Y_0$ and E are constants calculated from the control (non-thinned treatments), lnY is the natural log of the yield observed in the removal treatments, and C is the predicted value for C in these treatments.

The calculated values for C for before and after thinning (planted and final densities) and the predicted values of C from the yields of the removal treatments (and calculated similarly for the controls) are shown in Table 20. Deviation in the data was found in the low density,70 days removal treatment, where yields were high enough to produce a very low predicted C value. This reflects the greater degree of variation found at low densities, lesser influence of removal on yield as well as the inability of the model to predict yields adequately at low densities.

Thinning of plants at a given time during the season might seem to be reducing the competition by one half, since the population is reduced by that amount. However, this is not exactly true as seen by the computed C values (Table 20). Crowding (C) is reduced by more than one half by 50% reduction in numbers, because the thinnned density presents a theoretically more ideal plant arrangement (lesser rectangualtity), a property intrinsic to the model.

Table 20. Effect of time of thinning treatment on the estimated value of C using the model of Duncan (1984). Values in parenthesies are estimates of the percentage of crowding accounted for by the plants which were removed.

	CROWDING				
			Days of Full Competition		
PLANTED DENSITY	Planted[1]	Final[1]	46	70	101
plts./m^{-2}	----Computed C----		---------Predicted C--------		
3.4	5.69	2.45	2.84(14%)	0.93(0%)	4.29
6.7	12.08	5.59	5.06(0%)	8.01(32%)	13.25
10.0	18.48	8.87	11.67(31%)	12.74(41%)	17.76

1. C values calculated for the initial (control) densities and for the final harvested densities (thinning treatments).
2. Days after emergence when removal of alternate plants occurred.
3. Percentages calculated: % = (Pred. C - Final C)/(Pltd. C - Final C)

Some interesting interpretations can be made from these predicted values. The difference between the planted (control) and final C values for the thinning treatments is the reduction in crowding expected from thinning, if thinning was done at day 1. The difference from the predicted C values and the final computed C values indicate the approximate amount of Crowding accounted for by the time before thinning actually occurred (expressed as a percentage of the reduction in Crowding expected from thinning). These percentages are shown on Table 20. Removal of plants at either time in the low density produced yields which indicate C values which are less than or approximately equal to final C values. At medium densities, 46 days of early competition did not effect Crowding but 70 days did. At high density, competition during either 46 or 70 days of growth had an effect on Crowding and yield, and 70 days was greater than 46 days.

Estimations for the predicted C values shown on this table contain the errors of the yield estimation as well as the errors in the model itself and the estimation of the parameters. Therefore, some skepticism should be maintained, yet some generalizations can be made:

1) In the removal treatments, the first 70 days and 46 days of Crowding were irrelevant in determining yield for the low and medium densities respectively.

2) Sixty percent of the Crowding at high densities can be attributed to interactions after 70 days after planting. Greater percentages of Crowding can be attributed to the time after 70 days for lower densities, though Crowding itself was much less.

Theoretical considerations—discussion of the model. There are a few theoretical and practical considerations involved with the estimation of the value for Crowding. A schematic diagram of the model proposed by Duncan, method of calculating C and method of estimating parameters and predicting results is shown in Figure 45.

This model has several intrinsic qualities which are illustrated

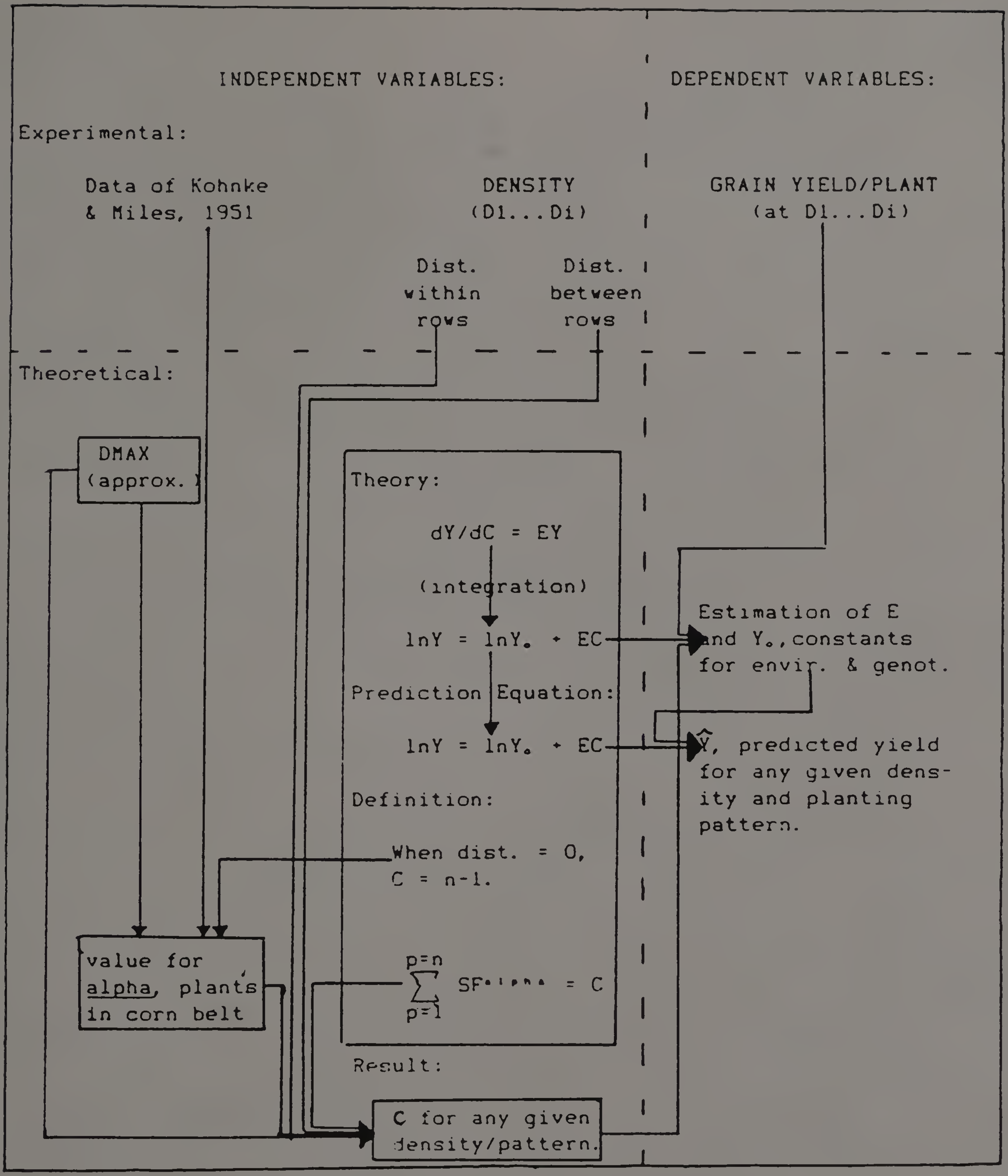

Figure 45. Schematic diagram of the model proposed by Duncan (1984). Flow chart indicates derivation of the theory of competition, methods of calculating constants and predicted values. Y=yield per plant, C=Crowding, Y_0 and E are constants estimated for any environment/genotype and alpha is a constant (proposed by Duncan).

in Figures 46 through 49. These are: 1) C increases at an increasing rate as plants get closer (Figure 46), which is really the same exact relationship as distance to density (Figure 46), and thereby, 2) C is linearly related to density and gives the same precision of fit to yield data (Figure 47). 3) For any given density, C is at a minimum at equidistant spacings and rises with wider row widths (Figure 48). At higher densities, widening row widths cause bigger changes in C, and there are critical distances at which competition increases rapidly. For most common agronomic row widths, little change in C takes place due to row width; the primary determinant of C is plant number/unit area (Figure 48). Crowding increases with increases in plant rectanguarity (Figure 49).

Critique. As a way of critiquing this model, the following are some points of interest.

There may be some doubt as to whether C would be truly independent of genotype and environment. The value for C contains a component which is purely a function of plant density (the separation fraction) and the assumed value of DMAX, and an experimentally estimated component, alpha. Duncan, using the data of Kohnke and Miles (1951) estimated alpha for planting patterns with known C values (patterns with hills of 3 plants, C=2 by definition), and generalizes the values for DMAX and alpha for all plants of the type encountered in the corn belt. Since SF has a constant relationship to distance and DMAX is a constant chosen for the type of plant under consideration (see Figure 30), it is

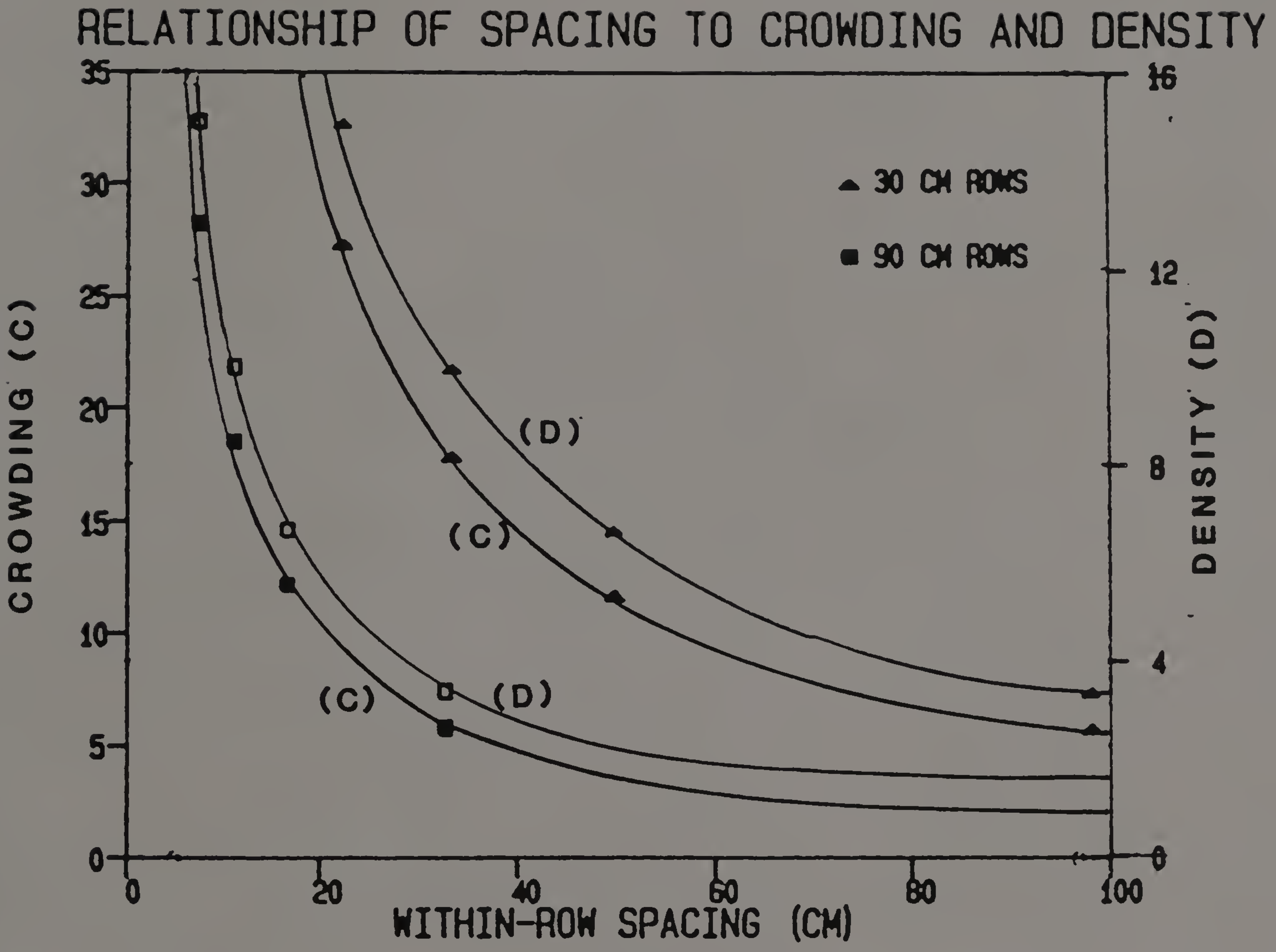

Figure 46. Relationship of within-row and between-row spacing to density (plants m-2) and crowding according the the model of Duncan (1984).

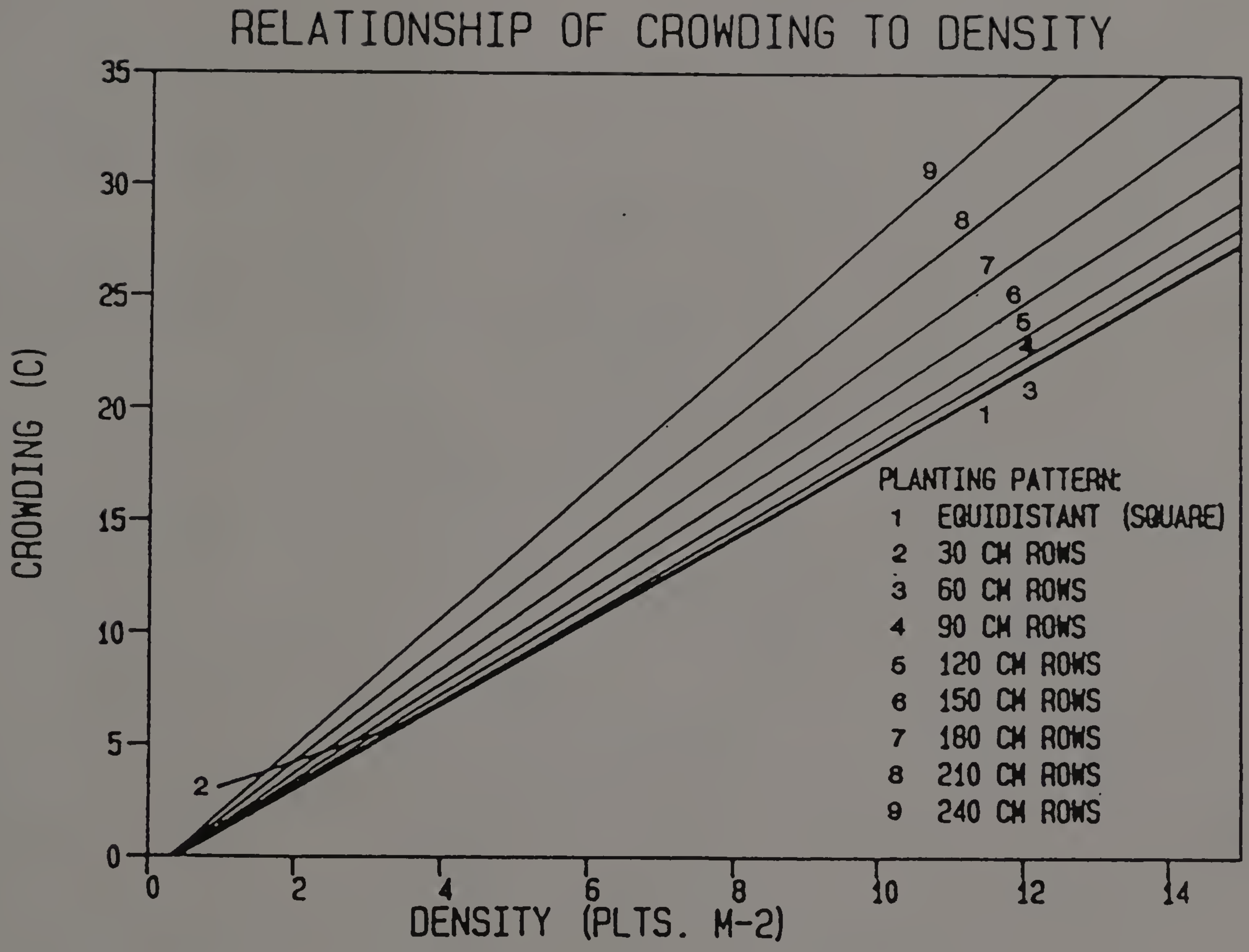

Figure 47. Relationship of density to Crowding at various row widths, according to the model of Duncan (1984). Anomoly is low density at 30 cm. row spacing, where within-row spacing greatly exceeds between-row spacing.

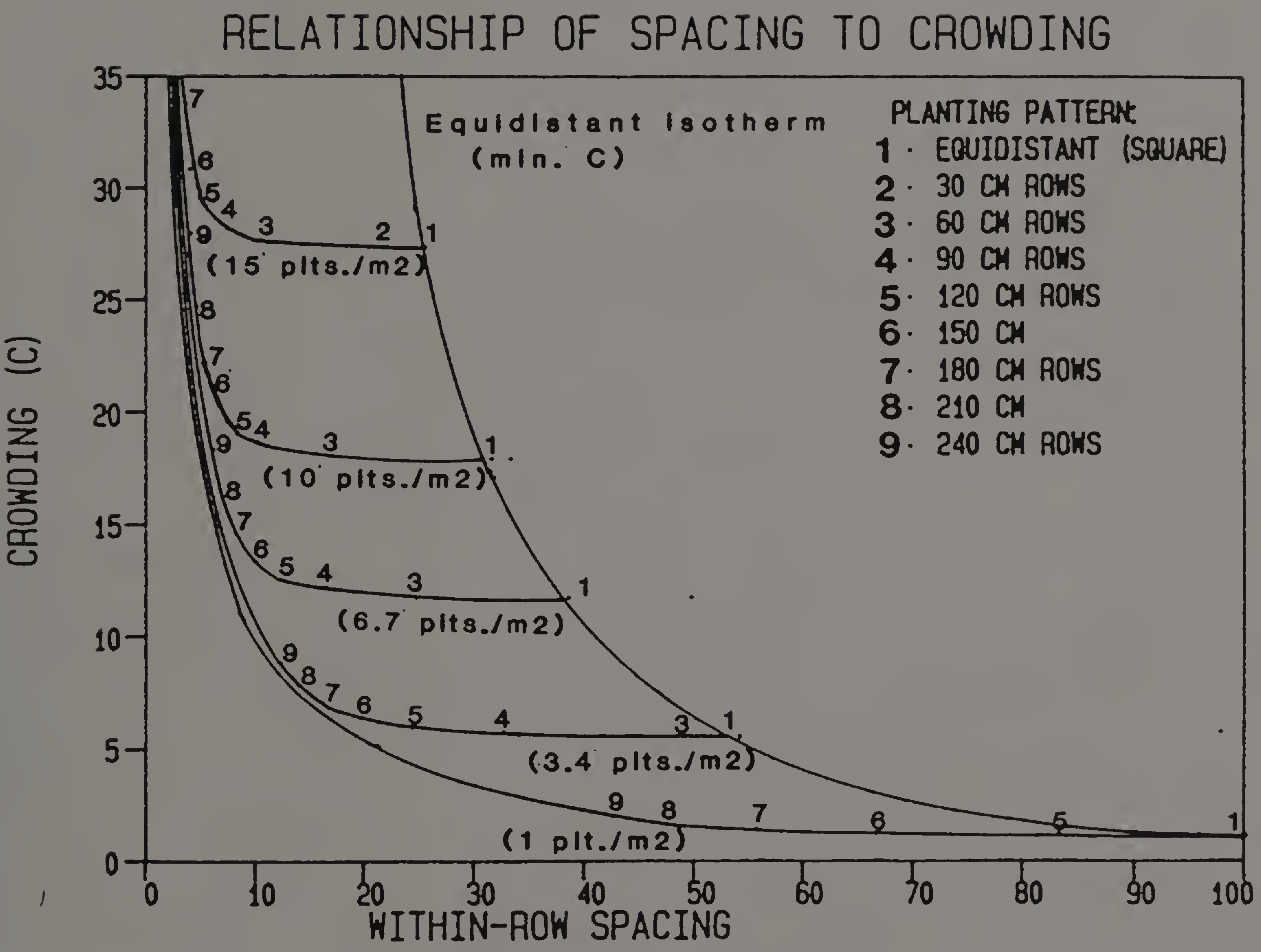

Figure 48. Relationship of plant arrangement (between- and within-row spacing), density and Crowding, according to the model of Duncan (1984).

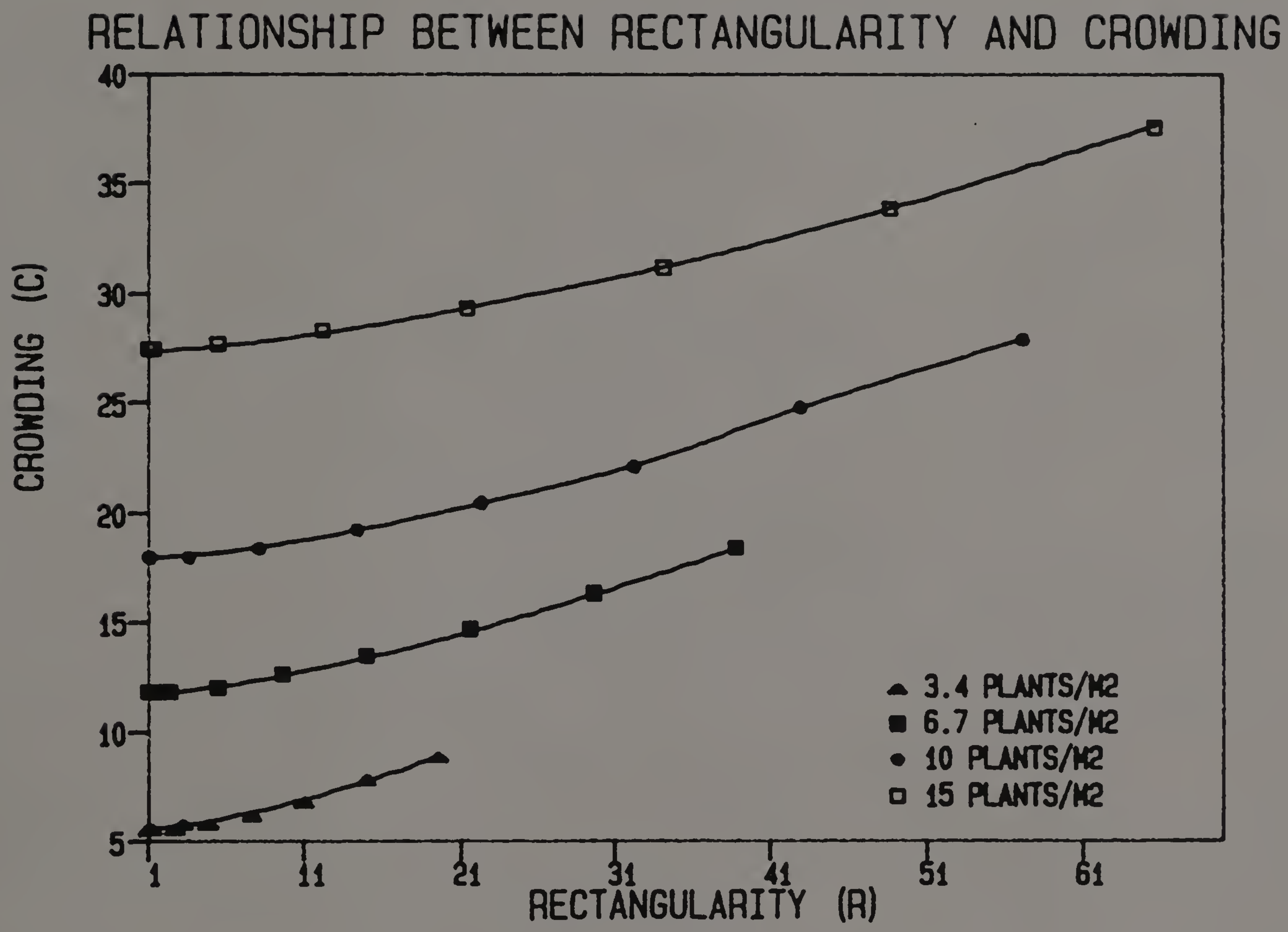

Figure 49. Relationship of rectangularity to Crowding, according to the model of Duncan (1984). Rectangularity is defined as the between-row spacing/within-row spacing.

alpha which describes the crux of the relationship between distance and Crowding for the model; that of C increasing at an increasing rate as separated plants become close. It is meant as a generalized approximation of the myriad of causes of competition, all lumped together.

In principle, as two plants are moved closer together, it is expected that the relationship between distance and Crowding (Figures 30, 46) might contain an intrinsic component (as suggested by the model), but also depend upon the level of resource or the genotype in a given season. As resource level goes down, a given level of crowding would occur at greater distances from the target plant. Mathematically, these should be encompassed by the experimental estimation of "E" and Y_o, if crowding is a universal parameter, insensitive to environomental factors. It is not clear whether this is the case.

Another consideration is that the relationship between number of plants and the distance between plants is largely unknown. It is possible that they may exert separate and interacting influences upon the target plant, but in denisty studies are usually confounded. The addition of n plants at d distance may or may not deliver $n(SF^{alpha})$ times as much Crowding as one plant, as stated by the model. This is illustrated by the fact that a value for DMAX estimated by 2 widely spaced plants will be smaller than by a ring of plants surrounding a target plant (as proposed by Duncan as a theoretical basis for DMAX). The distance at which two plants will begin interacting is possibly different than the distance at which 200 plants begin interacting.

Also, it is possible that the shape of the relationship between distance and competition is not exponetial as proposed. This objection is illustrated using the concept of "zones of depletion" as discussed in the Literature Review. As two plants are moved closer together from the distance DMAX (at which they do not compete), zones of depletion for water and mobil elements overlap first, causing competition (yield loss due to competition) to occur. As distance becomes closer, overlap of these zones would be expected to increase at an increasing rate, which would agree well with the model. However, there are discrete distances where the zones of depletion for immobile nutrients and light are likely to occur. As mentioned previously, zones of depletion for immobile elements occur only at very high densities and two plants may not acheive this even at very close spacings. This is probably more a function of number of roots (plants) arather than simply distance per se and certainly dependent upon environment.

Competition for light begins at distances related to the "drip line" of the leaves. It is possible that this represents a quantitative leap in the degree to which plants compete which occurs at discrete, not continuous distances. It is also probable that once a degree of shading between two plants occurs, further decreases in the between-plant spacing would only negligibly increase the competition for light and additional competition would come from additional plants at close spacings. Given the opposite positioning of corn leaves, the process by which two plants compete for light has a random component, dependent upon the orientation of the two competing plants.

Furthermore, there may be discrete distances at which light quality changes, possibly affecting plant morphology and yield. A sigmoidal relationship might be suggested by these considerations. It is difficult to visualize how the true relationship for maize might be arrived at, but it is sufficient to state that there are alternative shapes to the proposed relationship between spacing and crowding which have plausible biological meaning, and that numbers and distance may exert separate but interrelated effects on crop growth.

The model seems to be somewhat rigid in the estimation of competitive effects due to changes in plant arrangement or arrangement. For example, when the E value for the data of Bryant and Blazer (Table 16) were doubled, predicted yield per plant was reduced by more than half, and the effect of density was greater, but the effect of row spacing remained unchanged. When the presence of neighboring plants causes a more severe effect on yield (more negative E), one would expect that optimal plant arrangement would become more important, but the role of plant arrangement is determined soley by distance and alpha (determinants of C). Again, doubts are raised about the inclusion of an environmentally-sensitive compoent of C, as a generalisation of the cause of compenstation.

Validity of the argument. However, these are largely speculative objections. The model essentially redefines density purely in terms of distance, thereby including plant arrangement. The values of E and Y_o are estimated constants with plausible biological meaning. This offers a powerful new tool for the estimation of competition effects due to density and plant arrangement, and defines a useful framework for the study of the complex nature of crop competition. The fact that Crowding is correlated highly with density is at first disturbing, since one would expect a new technique to give a better fit to experimental data than an old method. That the number of organisms should be the primary determinate of Crowding (vs. arrangement) seems reasonable, however, given the excellent fit of density equations when arrangement was held constant or ignored. This model provides a theoretical basis for this relationship and may have many applications.

Summary

Corn plants were grown in isolation and at three plant densities, and alternate plants were removed in some treatments to study theoretical aspects of competition in the field. Several methods to quantify competition were applied. The following conclusions were made:

Yield components were effected differently by competition--kernel number was more sensitive to competition than was kernel weight or ear number. Kernel row number was unaffected by competition.

Leaf area was less effected by competition than was weight of plant parts. Leaf, stem, and ear weight were effected equally.

Row width changes would have little effect on yield in this environment, and likely many environments in the corn belt.

In this experiment, most of the crowding could be accounted for by the time after the beginning of grain fill.

The usefullness of two methods used to describe and quantify competitive effects in a corn stand have been illustrated here. The development of a theoretical basis for the observed changes in yield with density remains a worthy goal. A major point of interest is in extending a model to fit more unusual situations, such as mixed cropping, where the need to estimate competitive effects is even greater. There is a need to discover and describe underlying principles which can then be applied in many practical ways. The model proposed by Duncan and the isolated plant method are certainly steps in the right direction.

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