To the Graduate Council:

I am submitting herewith a thesis written by Julie A. Hale entitled "The Effects of Population Density and Spatial Arrangement on the Yield and Development of Broccoli." I have examined the final form of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Plant and Soil Science.

Carl E. Sams

Carl E. Sams, Major Professor

We have read this thesis
and recommend its acceptance:

David L. Coffey

Charles A. Mullins

Accepted for the Council:

CW Minkel

Vice Provost
and Dean of The Graduate School

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a Master's degree at The University of Tennessee, Knoxville, I agree that the Library shall make it available to borrowers under rules of the Library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgment of source is made.

Permission for extensive quotation from or reproduction of this thesis may be granted by my major professor, or in his absence, by the Head of Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Signature Julie Ann Hale

Date May 25, 1987

THE EFFECTS OF POPULATION DENSITY AND SPATIAL ARRANGEMENT ON THE YIELD AND DEVELOPMENT OF BROCCOLI

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Julie A. Hale

June 1987

ACKNOWLEDGMENTS

I wish to acknowledge the following individuals who have provided assistance and support during the course of my graduate program:

My parents, James and Bloma Hale, for their interest and encouragement.

My committee members, Dr. David L. Coffey and Dr. Charles Mullins, for their advice and comments.

A number of technicians and fellow graduate students, who aided me in my research work and data analysis.

In particular, my advisor, Dr. Carl E. Sams, for his guidance, suggestions and patience.

ABSTRACT

A spacing study utilizing broccoli (*Brassica oleracea* var. *italica*) was conducted at two locations in the spring and fall of 1984 and 1985. Rectangular and square spatial arrangements were evaluated using a central composite experimental design. Spacings ranged from 15 x 15 cm to 122 x 122 cm at 15 cm intervals. As spacing decreased, total yields increased, with maximum yields of 18,000 kg/ha predicted at the closest spacing tested. However, a high proportion of commercially undesirable heads (i.e., culls) were produced at the very closest spacings. Increases in spacing resulted in increased leaf number and size, sideshoot quantity and size and whole-plant size. However, leaf area index decreased as spacing distance increased. Plants grown at wide spacings also had larger heads, greater incidence of hollow-stem and a higher crude fiber content than those grown at narrow or intermediate spacings. The general conformation of plants was altered in response to changes in spacing. The narrowest spacings produced slender plants with elongated stalks, while plants grown at wide spacings were stocky and robust. No correlation was detected between plant spacing and mineral composition of leaf tissue, and no nutrient deficiencies were detected at any spacing tested. Soil moisture content was greatest at the wider spacings while leaf stomatal conductance was highest at the narrower spacings. At the wider spacings, leaf area per plant

was ten times greater than at the narrowest spacings, while head size was only three times larger, indicating a lower horticultural production efficiency of heads per unit leaf area.

TABLE OF CONTENTS

CHAPTER PAGE

PART II: THE EFFECT OF POPULATION DENSITY AND SPATIAL ARRANGEMENT ON THE MORPHOLOGICAL AND PHYSIOLOGICAL DEVELOPMENT OF BROCCOLI

LIST OF FIGURES

FIGURE PAGE

INTRODUCTION

Broccoli (Brassica oleracea var. Italica cv. Premium Crop) may be grown for fresh-market sale or for use as a processing crop. Size requirements vary according to intended use of the product. Broccoli grown for processing should possess a head diameter of approximately 15 cm. For fresh-market sale, however, smaller heads about 10 cm in diameter are most desirable. This is due to the fact that consumers generally prefer a package consisting of four to six small stalks, rather than bunches containing a few overly large stalks or great numbers of small ones (Zink and Akana, 1951).

A variety of factors may influence broccoli yield and quality. Traits such as earliness, uniformity of maturity and yield all appear to be manifestations of hybrid vigor in broccoli (Borchers, 1968). It has also been demonstrated that broccoli yield performance at a given population is somewhat dependent on the cultivar grown (Thompson and Taylor, 1970). However, certain cultural practices can be employed in order to produce a commodity of the desired size. Plant spacing has been shown to influence yield and/or product size of several vegetable species, including beet and carrot (Warne, 1948), Tabasco pepper (Sundstrom, et al., 1984) and tomato (Nichols, 1973). However, close plant spacing may cause intense competition among plants, which in turn may adversely affect yield or product quality.

A substantial decrease in individual head size has been observed in plants grown in very high-density arrangements (Bradley, et al., 1962; Bradley, et al., 1965; Thompson and Taylor, 1970; Palevitch, 1970; Cutcliffe, 1975; Chung, 1982, 1985; Salter, et al., 1984; Dufault and Waters, 1985). Furthermore, the percentage of commercially undesirable heads (i.e., culls) has been shown to increase as spacing decreases (Zink and Akana, 1951; Mack and Baggett, 1963; Cutcliffe, 1975; Thompson and Taylor, 1976). Spacing may also influence the incidence and severity of a physiological disorder known as hollow-stem. The condition, which appears as elliptical transverse gaps in the stalk tissue (Cutcliffe, 1972) has been noted to occur most frequently in broccoli plants grown at wide spacings (Zink and Akana, 1951; Zink, 1968; Cutcliffe, 1972; Hipp, 1974; Dufault and Waters, 1985).

In addition to its effects on yield and quality, spacing may affect growth and development of the whole plant. A change in the overall conformation of plants grown at various spacings has been observed (Zink and Akana, 1951; Zink, 1968). Experiments in cauliflower (Salter, 1961) have suggested that leaf area and total fresh weight of individual plants may be influenced by spacing. Another valid consideration is that of spacing effects on chemical composition and fiber content of the plant. The limited amount of research performed in this area (Massey, et al., 1962) showed no apparent differences in chemical composition between broccoli plants grown at two different spacings.

Although many spacing studies have been undertaken in broccoli, none have attempted to fully investigate the wide range of physiological and morphological characteristics which may be affected by changes in population density and spatial arrangement.

The objectives of the following study were therefore:

1. To devise a prediction model for broccoli yield and head size, based on data from varying years, seasons and climatic conditions.
2. To determine the effects of population density and spatial arrangement on the morphological growth and development of field-grown broccoli plants. These included the following:
    a. Head size
    b. Incidence and severity of hollow-stem
    c. Leaf number and size, sideshoot quantity and size, and whole-plant Leaf Area Index (LAI)
    d. Whole-plant size and conformation
    e. Mineral and fiber composition of plant tissue
    f. Stomatal behavior and transpiration rate
    g. Soil moisture differences

CHAPTER I

ORIGIN, HISTORY AND GENERAL INFORMATION

According to Gray (1982), the wild forms of Brassica oleracea were forerunners of our modern cole crops. Most varieties have been cultivated by man for so long that details regarding their exact origin are sparse. It is thought, however, that sprouting broccoli originated in the eastern Mediterranean region.

Giles (1941) presented an historical perspective of broccoli and cauliflower. He noted that the ancient Greeks and Romans were familiar with some forms of the genus Brassica. The Roman naturalist and author Pliny is said to have mentioned a number of its related forms in his writings some two thousand years ago (Giles, 1941).

Members of the genus Brassica show considerable diversity of form, and there is often confusion in the literature concerning their correct nomenclature. It has been suggested that a clear distinction between broccoli and cauliflower can be made on the basis of their comparative ontogeny upon attainment of the mature harvestable stage. This distinction also corresponds to their taxonomic classification (Gray, 1982). Therefore, the term "broccoli" as used in this paper refers to the annual green sprouting form, Brassica oleracea var. italica. It is variously referred to in other literature as calabrese, Italian broccoli, or sprouting broccoli.

Broccoli may be grown for fresh-market sale or for use as a processing crop. It is well suited for freezing, as it results in a high-quality frozen vegetable product (Massey, et al., 1962). The quality of an individual head may be judged by certain attributes, including tightly closed buds of fairly uniform size in addition to an overall compactness of the head. Absence of bracts on the upper stem is also a desirable characteristic (Thompson and Taylor, 1970).

In general, size requirements in terms of head diameter are dependent upon intended use of the product. Different countries may also vary as to their definition of a desirable head size. In the United Kingdom, small heads of broccoli as well as the axillary buds (referred to as "sideshoots") are most often used for processing. Heads for quick-freezing generally range from 2.5 to 7.0 cm in diameter and possess a stem length of approximately 15 cm (Thompson and Taylor, 1976). In the case of cauliflower grown for processing, more importance is placed on floret shape and core-to-floret ratio than on absolute size of the head (Garner, 1978).

In the United States, smaller heads about 10 cm in diameter are grown for fresh-market sale, while larger heads about 15 cm in diameter are preferred for processing. Stem diameter is reportedly used as the criterion for size in California, with 1.8 cm being the minimum acceptable limit for spear-grade broccoli (Brendler, 1971). On the basis of standards used by other countries, it has been suggested that broccoli grown for processing might ideally possess a head diameter ranging from 2.5 cm to 7.0 cm and a stem diameter of approximately 1.8 cm (Chung, 1982). In general, consumers prefer a .68 to .90 kg bunch of broccoli consisting of four to six stalks, rather than bunches containing a few overly large stalks or great numbers of small ones (Zink and Akana, 1951).

Attempts to alleviate the high labor requirement and trimming losses associated with processing traditional-size curds led to the development of "mini-cauliflowers" (Honma and Bert, 1977). By use of very high-density plantings, mature cauliflower curds only 3.8 to 8.9 cm in diameter were produced. These mini-cauliflowers were purported to be suitable for the pre-packaged market as well as for processing. Logically, it would appear that manipulation of plant density and spatial arrangement could also be used in broccoli crops to achieve a head having appropriate size in relation to intended use of the product.

Alternatively, several workers have investigated the possibility of exploiting the lateral inflorescences to obtain maximum yields, albeit a smaller product. Sizable yields of sideshoots can be obtained over an extended period after harvest of the mature terminal inflorescences. It has been reported that successive harvesting of broccoli sideshoots from plants grown at wider spacings may amend total yield by 10 to 100 percent (Thompson and Taylor, 1970). In general, however, sideshoots are more expensive per unit area to harvest, strip of leaves and handle than are center heads (Zink and Akana, 1951).

CHAPTER II

GENETIC EFFECTS ON HEAD INITIATION AND MATURITY CHARACTERISTICS OF *BRASSICA* CROPS

A fairly large component of genetic variation is present in broccoli. Traits such as uniformity of maturity, yield and earliness all appear to be manifestations of hybrid vigor in broccoli (Borchers, 1968). However, other studies have indicated that inbreeding depression, appearance of anomalies and reduced seed production due to self-incompatibility were apparent from generation to generation (Honma, 1965). The inheritance of eight economically important characteristics which are often apparent in broccoli crops have also been described (Dickson, 1968). These included the following: 1) leafiness of the head, 2) large cotyledons, 3) starring or rosetting of the center buds of the whorl, 4) earliness of flowering, 5) bud openness, and 6) plant height. All of these traits behaved as single dominant characters. The two remaining characteristics, plant blindness and puffiness of buds, were shown to behave as recessive characters. Uniform bud size (considered a desirable trait in broccoli) is subject to a large amount of variation, even in the best stocks (Thompson and Taylor, 1970). All of the above traits may affect the overall quality, yield performance and time of maturity in a given broccoli crop.

Continuity of supply is an important factor in fresh-market sales of broccoli. In commercial operations this may be best achieved by sowing several different cultivars in succession, as has been recommended for cauliflower (Salter and Williams, 1974). However, with the advent of mechanical harvesting techniques, more importance has been placed on uniformity of maturity. Crops which possess a concentrated range of maturity facilitate the use of a single destructive harvest, thus lessening the time and labor demands imposed by a succession of hand harvests. It has been suggested that those broccoli cultivars having a tendency to head prematurely and produce only a single spear per plant might be well suited for mechanical harvest (Baggett and Mack, 1970). Other workers (Honma, 1965; Borchers, 1971; Hulbert and Orton, 1984; Crisp, et al., 1985) have undertaken breeding programs designed to improve uniformity of maturity in broccoli crops. To accomplish this, existing lines are inbred for several generations. These inbreds are subsequently hybridized, with the resulting hybrids exhibiting both greater head size and increased uniformity of maturity in comparison to their parent inbreds (Honma, 1965; Borchers, 1968). In addition to their quick, early maturity, many of these hybrids possess characteristics such as long stems which minimize the number of leaves attached to the head when harvested (Brendler, 1970).

CHAPTER III

USE OF MECHANICAL HARVEST TECHNIQUES IN BROCCOLI CROPS

Appropriate timing of harvest for broccoli crops is crucial for obtaining maximum yields of high quality. Although it is difficult to define the optimum harvest stage, Thompson and Taylor (1970) have listed several guidelines. The maximum width of the largest "beads" (individual flowers) should not exceed .25 cm, and only the slightest elongation of the bud stalk should be apparent. Ideally, spears should be allowed to grow for as long as possible prior to harvest, as a 60-g spear may increase its weight by approximately 1.8 g per day during the several days it is considered harvestable. However, delaying harvest for an overly long period will result in too great a fiber content of the head, thereby sacrificing quality for yield.

Attempts to devise an easy method that would enable growers to determine the "best" harvest date for once-over mechanical harvesting have met with limited success. Because the yield and quality of a broccoli crop changes so rapidly from day to day, sampling of a field has proven to be an inaccurate predictor of harvest date. By the time that the maximum number of heads have attained sufficient size to be judged "spear" grade, the percentage of over-mature heads is unacceptably high (Brendler, 1971). In other experiments, data taken at the time of maximum total yield were compared to data taken during the period of optimum yield (i.e., the period when the highest proportion of plants was graded as marketable). Harvesting at the time of optimum yield resulted in an average yield reduction of 10 percent in comparison to that obtained at time of maximum total yield. However, the quantity of waste material attributable to over-mature plants was minimized sufficiently to compensate for the reduction in total yield. Therefore, it was concluded that once-over mechanical harvest at the time of optimum yield was most appropriate for broccoli grown as a processing crop (Chung, 1982).

Other workers devised an experimental model to optimize the policy of selective harvesting in cauliflower crops (Corrie and Boyce, 1972). The program was designed to be adapted for the particular needs of the grower, which might involve optimization of total yield, gross value of the harvested crop, or crop returns less the cost of harvesting and marketing. Although the model had not been tested over a wide range of crops, the authors believed that their basic program could be applied to similar crops in order to optimize multi-stage harvests. Consequently, additional information regarding maturation patterns of the crop in question, as well as crop response to different climatic and soil conditions, would contribute to the program's usefulness.

CHAPTER IV

SPACING STUDIES IN OTHER VEGETABLE CROPS

Spacing studies have been conducted in many other vegetable crops, the general objective being to optimize yields. Early experiments involved the use of close within-row spacings in beet and carrot crops (Warne, 1948). Both vegetables were sown in rows spaced 46 cm apart. Carrots were thinned to plant spacings of 2.5, 5.1, 10.2 and 15.2 cm. Thinning distances for beets were 5.1, 7.6, 10.2 and 15.2 cm. At the closest spacing (2.5 cm) plant growth of carrots was somewhat restricted and mean root weight decreased. However, the overall number of roots which attained an acceptable size was increased. Beets grown at the 5.1 cm spacing showed similar growth and yield responses.

Plant population studies using bush snap beans were conducted to investigate the relationship between plant density and crop yield (Stang, et al., 1979). Five cultivars were tested at 10 plant densities, which ranged from 21 to 110 plants·m^{-2}. Results indicated that optimum population density varied according to cultivar. In general, the smaller, more compact types showed the best yield performance at high population densities. However, certain other cultivars showed superior yields at all plant densities investigated.

Other vegetable spacing studies examined the effect of two different within-row spacings on the yield of sweet (bell) peppers

(Campbell and Swingle, 1965). Using standard row widths of 107 cm, it was found that plant spacings of 25 cm resulted in higher marketable yields than the yields obtained with plant spacings of 51 cm. Studies were conducted in mechanically harvested Tabasco peppers (Sundstrom, et al., 1984). Plant spacings of 10, 20, 41 and 81 cm were tested in rows spaced 1.7 m apart. Total yields were highest at the 10 and 20 cm spacings. It was also noted that close spacings resulted in a decrease in plant diameter. However, plants grown at the 10 cm spacing showed a substantial reduction in the amount of stem breakage caused by mechanical harvesting equipment. The authors suggested that closely spaced treatments allowed for adjacent plant support, thus reducing the incidence of mechanical damage during harvest.

In plant density experiments involving direct-seeded tomatoes, it was similarly noted that tomatoes planted in a high-density, low-rectangularity (i.e., square) system tended to remain more upright (Nichols, et al., 1973). High plant densities (40 to 62 plants$\cdot m^{-2}$) also resulted in increased total plant weight, total fruit weight and ripe fruit per unit area in comparison to low-density plantings.

Other studies have concerned the effects of spacing on cabbage grown for once-over harvest (Miller, 1969). At standard row widths of 1.0 m, plant spacings of 23 cm resulted in higher yields than those achieved using plant spacings of 31 or 38 cm. There also appeared to be a trend toward greater uniformity of plants grown at closer spacings. These results were reiterated by similar studies in cabbage crops (Csizinszky and Schuster, 1985). Within-row spacings of 38 cm and 23 cm were compared. Although individual head sizes were smaller at the closer spacings, total yields were higher in widely-spaced treatments.

In another study, the crop was being grown for use as livestock fodder (Bradshaw, 1984). The objective in this case was to determine a planting distance which would give the highest yield of heads while allowing for an adequate stand, thereby eliminating the need for thinning. Results of comparisons between 13 cm and 25 cm plant spacings showed several advantages of utilizing the wider spacing. Crop establishment was satisfactory, which made later thinning unnecessary. Also, the percentage of plants which headed was much higher in plots planted at the 25-cm spacing. However, whole-plant dry matter yield per hectare was higher at the close spacing in almost all of the cultivars tested. In the case of a cabbage crop being grown for use as livestock fodder, it was concluded that appropriate plant spacings could best be chosen on the basis of their effect on overall head dry matter yield. In situations where cabbage crops are produced for human consumption, spacings which produce maximum yields of high-quality heads would be most desirable.

In general, results of these experiments support the idea that plant spacing can be manipulated in order to better achieve higher yields and to influence size of the product to some extent. However, there are a host of other considerations involved when using unconventional spacing arrangements. It may be necessary to modify certain cultural practices so as to manage the crop effectively. A knowledge of the weed flora present, and the feasibility of its control by chemical means, should prove helpful when using row spacings too narrow for cultivation (Thompson and Taylor, 1976). Insect and disease control may be a problem in high-density cauliflower crops, thereby dictating the need for preventive measures from planting until harvest (Honma and Bert, 1977). The economic feasibility of using high plant densities should be carefully examined as well. If transplants are used, the overall yield of small heads associated with close spacings must be substantial enough to justify the extra cost of the large number of transplants needed per acre (Honma and Bert, 1977).

CHAPTER V

ECOLOGICAL ASPECTS OF PLANT DENSITY AND SPATIAL ARRANGEMENT IN BRASSICA CROPS

The effects of population density and spatial arrangement in broccoli crops may be examined from an ecological perspective--that is, the interrelationship of organisms and their environment. Given that a particular crop is planted at a variety of population densities, a different level of competition will exist at each density. Rennie (1974) proposed the following definition of competition, which he derived in part from the writings of Odum (1959) and Milne (1961):

> competition is a process in which two or more organisms in proximity interact for a portion of an environmental factor which is not available in a supply sufficient to meet their combined demands.

It has been noted that the three main environmental factors are water, nutrients and light (Frappell, 1979). Since most modern agricultural production systems are able to supply crops with adequate water and mineral nutrients, Donald (1961) proposed that competition for light is the most strongly limiting factor of plant growth.

A thorough discussion of plant competition in vegetable crop communities has been presented by Frappell (1979). He noted that in most crop production systems, competition may be manifested in two forms. Intraspecific competition is that which exists between individual crop plants, while interspecific competition refers to the type which occurs between crop plants and weeds. In spite of these distinctions, however, Frappell pointed out that the mechanisms and effects of competition are similar regardless of the circumstances involved. Some studies (Thompson and Taylor, 1976) have supplied evidence that most self-thinning of broccoli plants takes place during the early stages of growth, thereby serving to reduce potential competition somewhat. These results were in accordance with previous findings (White and Harper, 1960) which supported the general assumption that the smallest plants in a population are the first to thin, thus leaving the larger ones to grow more rapidly. Thompson and Taylor (1976) noted that in very high-density plantings, however, competition may remain intense and as a result some plants will survive but will fail to produce marketable heads. Since these unproductive plants constitute a drain on available resources but do not contribute to yield, they exist as a competitive element which serves to retard the growth of productive plants. In cauliflower crops, the overall density of the stand may be influenced by the vigor of the cultivar grown (Garner, 1978). It has also been shown that broccoli yield performance at a given population is somewhat dependent on the cultivar grown (Thompson and Taylor, 1970). Certain cauliflower cultivars have been shown to be genetically more variable than others (Salter and James, 1975). As a result of this variability, differences in plant size within a population would therefore be expected to increase with time under highly competitive conditions. It has been inferred (Thompson and Taylor, 1975) that the results of most variety trials conducted at a single spacing are probably biased, since cauliflower cultivars have been shown to exhibit yield differences based on their varying sensitivity to competition.

The morphological characteristics of a particular cultivar may also render it more adaptable to a given situation. Plants having large, broad leaves are more able to exploit the extra space available at wide spacings, while compact types with smaller, shorter leaves are better suited to the greater competition pressure which exists at close spacings (Salter and James, 1975). Conversely, plant competition may impose restrictions on growth of the plant and prevent it from attaining its potential size. High crop yields can be achieved only if foliage canopies develop to the extent whereby a maximum of photosynthetically active radiation is intercepted during the reproductive stage (Frappell, 1979; Wiegand and Richardson, 1984). The same situation is noted to be true for early stages of crop growth, when light interception is usually very small. Frappell postulated that any change which resulted in increased leaf area index during early stages of crop growth could be of considerable benefit. Assuming that this is so, plant spacing might significantly affect crop production by means of its effects on leaf area index and leaf duration. When plant spacing was included as a variable in experiments involving irrigation of cauliflower, results showed that leaf area per plant was reduced progressively by closer spacing, regardless of the irrigation regime used. Total fresh weight of the plants also decreased in response to closer spacing (Salter, 1961).

Other workers have attempted to correlate leaf photosynthesis with leaf area (Bhagsari and Brown, 1986). In experiments using peanut, soybean and sweet potato, the researchers noted that leaf position on the stem tends to markedly influence leaf size as well as the extent to which other leaves are shaded. Therefore, an experimental bias may result when testing photosynthetic capability of a leaf based on its size. Larger leaves tend to occupy lower stem positions on the plant and consequently are likely to be older, more heavily shaded and lower in CO_2 Exchange Rate (CER).

Other studies involving the effects of leaf area on photosynthesis and crop yield have been undertaken in cotton (Karami and Weaver, 1972), barley (Berdahl, et al., 1972) and soybean (Mandl and Buss, 1981). These results have been fully reviewed by Bhagsari and Brown (1986) who concluded that the agronomic advantages of large vs. small leaves still remain unclear. Some authorities further maintain that it is the angle of the leaf which most strongly affects photosynthetic ability. In corn, for example, it has been suggested that a vertical or nearly vertical leaf will minimize shading of the lower leaves while maximizing light interception (Army and Greer, 1967).

In addition to reduction of photosynthetic capability, heavy shading of lower leaves may result in altered stomatal responses (Army and Greer, 1967; Berdahl, et al., 1972). Stomatal behavior may also be greatly influenced by row spacing and evaporative demand, as demonstrated by comparisons of differential stomatal action between irrigated peanut crops grown in narrow vs. wide rows. Measurements performed on adaxial surfaces of fully illuminated leaves indicated that stomata tend to close earlier in the day for plants grown in narrow row spacings, in contrast to the behavior of stomates observed at wide row spacings (Stone, et al., 1985). Furthermore, it has been demonstrated in rice (Saini and Rathore, 1984) and soybean (Brady, et al., 1975) that stomata are sensitive to gradually increasing soil water deficit.

High plant populations may also result in intense competition between plants for available nutrients. Many workers have investigated the relationship between plant growth and fertility levels in broccoli and cauliflower crops (Salter, 1961; Zink, 1968; Cutcliffe, 1968; Cutcliffe, 1971; Cutcliffe and Munro, 1976; Letey, et al., 1983; Dufault and Waters, 1985). In one such study, Salter (1961) reported that nitrogen supply became a limiting factor in cauliflower crops grown at close spacings, with nitrogen deficiency symptoms clearly visible at later stages of plant growth. Zink (1968) reported similar deficiencies in broccoli crops grown at close spacings. Dufault and Waters (1985) sought to manipulate nitrogen fertility and plant population so as to obtain maximum yield and quality in broccoli and cauliflower crops. Three population densities (24,000, 36,000 and 72,000 plants/ha) were factorially combined with a variety of nitrogen treatments (56 to 224 kg/ha N). Results showed that for all three population densities, broccoli head weight increased linearly in response to increasing nitrogen rate. Even when the highest population was combined with the highest rate of nitrogen, no leveling-off of yield increase was apparent. Therefore, highest yields were obtained at plant populations of 72,000 plants/ha using nitrogen applications of 224 kg/ha N. In addition, broccoli cull production decreased linearly with increasing rates of nitrogen. However, head weight decreased linearly when nitrogen rate was held constant and plant populations were increased. Cauliflower showed entirely different responses to nitrogen rate and plant populations. Increases in nitrogen rate resulted in nonlinear changes in curd size, and increased in plant population caused a reduction of marketable yields.

Water requirement of broccoli crops can also be affected by plant spacing. At high populations, plant leaves tend to form a dense canopy which may slow down the rate of evapotranspiration. However, competition for water will be more intense at higher populations due to the increased number of plants per unit area. Holliday (1960) stated that competition resulting from increased plant density may restrict the depth to which roots can penetrate. Consequently, the quantity of water which can be absorbed from the soil profile will be reduced. Irrigation studies in broccoli crops have yielded conflicting results. Some findings have indicated that broccoli grown on high-moisture plots was superior in quality to that produced in low-moisture plots (Massey, et al., 1962), while other workers have concluded that irrigation need only be applied in amounts sufficient to replenish water lost through evapotranspiration (Letey, et al., 1983). It was believed that such a program of water management provided for both higher yields and nitrogen use efficiency than that obtained with excessive irrigation. Still other results indicated that high yields of broccoli could be obtained with relatively low nitrogen applications, provided that irrigation was frequent and efficient (Beverly, et al., 1986). It is apparent that the yield of irrigated crops may be influenced by plant spacing, as well as soil fertility levels and other factors (Salter, 1962). Therefore, a knowledge of these factors and their interrelationships would be necessary in order to define the optimum irrigation regime for a particular crop.

Population density has been shown to affect various morphological and physiological characteristics in Brassica crops. A condition known as "hollow-stem" is often seen in broccoli crops. It is characterized by elliptical, transverse gaps in the stem tissue which enlarge as the plant grows (Cutcliffe, 1972). This disorder is considered a detriment to quality, in that the affected area is visible upon display of the produce; furthermore, the area may exhibit discoloration (Hipp, 1974). Several cultural and environmental factors have been associated with the incidence of hollow-stem, including wide plant spacings. Zink (1968) was one of the first workers to study probably causes of the disorder. Various within-row spacings, as well as nitrogen treatments, were shown to affect the incidence of hollow-stem. At any given nitrogen treatment, the number of plants affected by hollow-stem was markedly reduced at close plant spacings. Similarly, an increase in nitrogen at any given plant spacing resulted in an increased percentage of hollow-stem. Cutcliffe (1972) reported similar results and noted that individual cultivars differed in regard to the particular spacing distance at which the greatest effect on hollow-stem occurred.

An increased incidence of hollow-stem has been observed in broccoli which grew rapidly and was harvested first, in comparison to those plants which matured slowly and were harvested last (Hipp, 1974). Accelerated plant growth and development, possibly caused by high nitrogen rates or hot weather, has been mentioned by other workers as a probable contributor to the disorder (Zink and Akana, 1951; Cutcliffe, 1972; Proulx, 1981). However, at least one study found incidence of hollow-stem to be negligible and unaffected by nitrogen or population treatments (Dufault and Waters, 1985).

In general, average head weight has been shown to decrease progressively as plant density increased. This effect was especially marked when the increase in plant density was achieved by reductions of within-row spacing (Palevitch, 1970). It has also been demonstrated that close spacings resulted in a decreased percentage of heads and stems of acceptable size. However, the actual number of heads of satisfactory size was greater in closely-spaced plots than in widely spaced ones simply because of the higher populations (Zink and Akana, 1951).

Characteristics other than head size and weight may be affected as well. It has been demonstrated that both plant spacing and nitrogen fertilization may alter the general conformation of broccoli plants (Zink, 1968). Broccoli head shape has been shown to vary with plant density and sowing date (Salter, et al., 1984). Plants grown at low plant densities (less than 20 plants·m^{-2}) produced heads having a flatter shape than those grown at higher densities.

Overall quality of the crop may be affected by changes in plant spacing (Frappell, 1979). Several workers reported that cauliflower grown at high densities showed a decline in percentage of marketable curds (Thompson and Taylor, 1975; Salter, 1961). In separate experiments involving broccoli crops, however, it was observed that spear quality visibly improved as plant density increased. This improvement was attributed to several factors, including a reduction of bractiness and hollow-stem, suppression of axillary bud development and production of fewer leaves on the spear stem (Thompson and Taylor, 1976).

The effect of population density on maturity characteristics of Brassica species has been studied by many workers. Although time of maturity is a highly heritable trait (Crisp, et al., 1985), it may also be affected by cultural practices and environmental factors. Evidence has also been presented that a high degree of genotype x environment interaction exists in cauliflower (Crisp and Kesavan, 1978). One particular study examined the effects of several cultural treatments on the maturity characteristics of cauliflower (Salter and Fradgley, 1969). Results indicated that time of maturity was influenced by such factors as use of graded vs. ungraded seed; transplanting vs. direct drilling; age of transplants at planting time; selection for uniformity in young plants, and plant density and nitrogen levels during early seedling growth. Seed size has also been shown to influence broccoli maturity rate (Tompkins, 1966) as has planting date. Early plantings of broccoli showed more uniformity of maturity than late plantings (Hulbert and Orton, 1984). It has been reported that broccoli head initiation (Fontes, et al., 1967) and maturity (Hoyle, et al., 1973) may be delayed by high temperatures. Several workers have investigated the effects of cold treatments on floral initiation and maturity in Brassica crops. Fontes, et al. (1967) attempted to determine whether the variability of maturity seen in broccoli might be attributable to differences among plants in their quantitative cold requirements for floral induction. It was found that both cultivars tested underwent a "juvenile stage" when approximately 3 weeks old. If exposed to cold temperatures during this stage, no floral primordia were initiated. However, plants 5 weeks of age and older had passed this stage, and floral induction was actually hastened by exposure to cold temperatures. It was further noted that plants of the same age vary individually as to length of cold exposure needed for floral induction. Fontes, et al. (1967) concluded that this variation between broccoli plants of the same cultivar may be responsible for non-uniform floral induction under field conditions, thus resulting in lack of uniform maturity at harvest. Thompson and Taylor (1970) reported that while a well-defined cold treatment is not required for flower induction in most broccoli varieties, use of such a procedure tended to influence both head maturity and number of leaves produced by the plant. Gauss and Taylor (1969) also investigated the effects of temperature and other environmental factors on reproductive differentiation in broccoli. Their results showed that low temperature did not influence chronological time of differentiation or floral development except when plants were grown under continuous light. Gauss and Taylor (1969) noted that their study was conducted in growth chambers, and that results previously reported by Fontes, et al. (1967) may have been influenced by variations in day length, light intensity and quality. A series of experiments performed by Salter and others (Salter and Ward, 1972; Salter and James, 1974; Wheeler and Salter, 1974) demonstrated that cold-treated cauliflower transplants showed a much more uniform rate of maturity than crops grown from untreated plants. In addition, the resulting curds were superior in quality to those obtained from untreated plants.

Several studies have attempted to relate floral initiation and development of Brassica species to various environmental factors (Salter, 1960; Salter, 1969; Salter and James, 1974). Salter (1969) explored the feasibility of using plant leaf number as an indicator of curd initiation and maturity. Two cauliflower varieties were studied over a 2 year period. By using dissection techniques and a "time-scale" method involving cumulative measurements of day-degrees, it was possible to estimate the time of curd initiation for each dissected plant. Using this data, regression equations were calculated for both varieties in both years. Results indicated that within a single crop, plants which showed a progressively later time of curd initiation had also formed a progressively greater number of leaves prior to curd initiation. Furthermore, leaf counts performed at maturity indicated that plants which matured first had the lowest final leaf counts. Likewise, late-maturing plants showed a progressive increase in their final leaf number. These results demonstrated that a positive quantitative relationship existed between the time of curd maturity and the final leaf count of a plant. Similarly, the time of curd initiation and the final leaf number per plant could also be described in terms of a positive quantitative relationship. Given the leaf number of a particular plant, it was therefore possible to calculate the time required from curd initiation to maturity. Having established these relationships, Salter than proposed that there might be an association between the length of the maturity period and the length of the curd initiation period. To test this, data which involved the duration of crop maturity was plotted against data which represented the duration of curd maturity. It was apparent that a strong positive correlation existed between the lengths of the initiation and maturity periods. It was concluded that various cultural and environmental factors might exert their effects at very early stages of plant growth, thereby altering crop maturity significantly. In addition, weather conditions during the actual maturity period might produce varying responses in crop maturity (Salter, 1969).

Several other workers have investigated the association between final leaf number and time of curd maturity. Aamlid (1952) and Jensma (1957) were credited by Salter (1969) for their respective findings which demonstrated that the earliest-maturing varieties of cauliflower had fewer numbers of leaves per plant than did late-maturing types. Other reports in the literature indicate that within a crop, the leaf number of individual plants tends to show a progressive increase with later maturity (Salter, 1960; Watts, 1965).

The actual time required for a crop to mature may be directly affected by spacing. Broccoli crops grown at wider spacings often produce a higher proportion of their total yield earlier in the season, in contrast to those grown in closer spacings. This has been attributed to the fact that close spacings result in heavy shading of some plants by others, a condition which may delay maturity of the shaded heads until adjacent plants are harvested (Aldrich, et al., 1961). Zink and Akana (1951) reported similar results and noted that shaded plants frequently produced smaller heads of inferior quality. Results of another study also indicated that broccoli maturity was delayed at high plant populations (Cutcliffe, 1971). In contrast, Salter, et al. (1984) found that broccoli grown at high plant densities showed a tendency to mature several days earlier when grown at low densities. However, no significant effects of spatial arrangement (i.e., rectangular vs. square planting pattern) on maturity characteristics were apparent.

Dufault and Waters (1985) found broccoli maturity to be unaffected by plant density. These conflicting results may be attributable to differences between broccoli types, as it has been shown that broccoli cultivars differ in their response to plant density (Cutcliffe, 1975). Studies in cauliflower have also yielded variable results. Findings of one study (Honma and Bert, 1977) indicated that an increase in uniformity of maturity was associated with close spacings, while in another (Garner, 1978) planting density had very little effect on time of maturity in winter-hardy cauliflower crops.

CHAPTER VI

A MODEL TO PREDICT YIELD AND HEAD SIZE OF BROCCOLI GROWN AT DIFFERENT POPULATION DENSITIES AND SPATIAL ARRANGEMENTS

Pant (1979) stated that density-dependent effects on yield are attributable to the competition for necessary natural resources which occurs among adjacent plants. A number of attempts have been made to relate crop yield to stand density by means of a mathematical equation or model. Holliday (1960) proposed an equation which could be used in many cases to describe the yield/density relationship in crop plants. The equation, reduced to its simplest form by Bleasdale and Nelder (1960), is as follows:

$$1/w = \alpha\rho + \beta \qquad (1)$$

where w is the yield per plant, ρ is the number of plants per unit area and α and β are constants. Holliday acknowledged that the equation was applicable in situations where yield was the result of vegetative growth, i.e., where an asymptotic relationship existed.

In cases where yield was the result of reproductive growth, however, the equation was incapable of accounting for the parabolic relationship which existed. Bleasdale and Nelder (1960) raised the question of whether yields resulting from vegetative and reproductive growth could accurately be defined as asymptotic and parabolic relationships, respectively. They proposed a modification, one which would compensate for the inadequacies of Holliday's equation by allowing for both asymptotic and parabolic relationships. This equation may be written as:

$$1/w^{-\theta} = \alpha + \beta\rho\phi \qquad (2)$$

which introduces another parameter, ϕ, and where $0 < \theta \leq 1$. In an asymptotic relationship, $\theta = 1$. Frappell (1979) stated that the equation most commonly used for the analysis of plant density experiments is one proposed by Bleasdale (1966):

$$1/w^{-\theta} = \alpha + \beta\rho \qquad (3)$$

which is actually a simplified version of equation (2). Berry (1967) pointed out that the usefulness of these equations is limited by the fact that they do not allow for different plant arrangements. Therefore, when different arrangements as well as different densities are being considered, it becomes necessary to fit the appropriate equation separately for each arrangement. Berry proposed a model which extended the relationship in order to include different plant arrangements. Again, this model had limitations in that its applications were restricted to regularly spaced crops where spacing is constant both within and between rows. Berry noted, however, that the model could apply to cases where spacing irregularities have previously been observed to have either little effect, or an equal effect, on all arrangements. The model was thus:

$$w^{-\theta} = a + b\left(\frac{1}{x_1} + \frac{1}{x_1}\right) + \frac{c}{x_1\, x_2} \qquad (4)$$

and the symbols are defined as:

x_1 = intra-row spacing

x_2 = inter-row spacing

w = yield per plant or biologically definable part of plant,

and where a, b and c are positive constants and $0 < \theta \leq 1$.

An extension of the relationship was also proposed in order to allow for row-orientation effects. Willey and Heath (1969) presented an inclusive review of these and several other mathematical functions, and concluded that reciprocal equations allow for the best fit of both asymptotic and parabolic equations. The basis for these equations is a linear relationship between the reciprocal of the weight per plant and density (Frappell, 1979). Gillis and Ratkowsky (1978) also compared the suitability of equation (3) to equation (1) when fitting a model with three parameters. Still another reciprocal equation was proposed by Farazdaghi and Harris (1968):

$$1/w = \alpha + \beta\rho^{\varepsilon} \qquad (5)$$

where ε becomes the third parameter of the model. Asymptotic relationships are described by $\varepsilon = 1$, while for parabolic relationships $\varepsilon > 1$. Frappell (1979) stated that in the case of asymptotic relationships, a simple biological interpretation may be assigned to parameters α and β. As density approaches zero, the value associated with weight per plant tends to $1/\alpha$. This value represents a measure of the genetic potential of a crop in a given environment. Conversely, as density tends toward infinity, yield per unit area approaches $1/\beta$ in an asymptotic fashion. This value serves as a measure of the potential of the environment. In the case of parabolic relationships, it is more difficult to interpret the parameters α and β in biological terms.

Mead (1966) noted that the majority of plant spacing studies were concerned with the effect of spacing on mean yield of the total population. Consequently, little attention had been directed toward the effects of spacing on the variation of individual plant yield within a population. For example, direct-drilling of a crop such as carrots was observed to result in bands of irregularly spaced plants. It was believed that part of the variation in individual plant yield could be attributed to this irregularity of spacing within the bands. Mead presented a method for describing plant arrangement in irregularly spaced row crops based on allocation of a polygonal area of ground to each plant. Each polygon was defined by three parameters. These parameters designated polygon size, shape and also the position of the plant within the polygon in relation to the polygon's center. Mead defined the parameters as follows:

1. Area = area of the polygon.
2. Eccircularity = a measurement which is always >1. It defines how elliptical, rather than circular, the shape of the polygon is. In the case of a regular n-sided polygon, tends to 1 as the polygon assumes a more circular shape.
3. Abcentricity = describes the position of the plant relative to the center of the polygon. By definition, this value is zero when a plant is at the centroid (center of gravity) of its polygon. Likewise, as a plant approaches a vertex of the polygon the value tends to unity.

Mead applied this method in describing the relationship between plant arrangement of carrots. His results indicated that polygon variation (i.e., spacing irregularities) accounted for no more than 20 percent of the variation in individual plant sizes. Nelder (1962) developed a series of systematic spacing designs which have subsequently been used in a number of plant spacing experiments involving vegetable crops (Bleasdale and Thompson, 1966; Mead, 1966; Nichols, 1974; Stang, et al., 1979; Salter, et al., 1984). The designs were based on grids which could be defined by the intersections of sets of parallel or concurrent straight lines, as well as the arcs of concentric circles. They are frequently referred to as "systematic fan designs" because of their appearance. Nelder noted that when typical randomized designs are employed for use in spacing experiments, a number of complications may arise. If a constant number of plants is used for each plant density being tested, the resulting treatments will vary greatly in size and may prove awkward to fit together in a block. Likewise, attempts to keep all treatments the same size will result in the use of tremendous numbers of guard plants. Nelder's system was designed so that plant density changed gradually within the confines of each individual block. Also, the design necessitated the use of guard plants only on the outermost row of each block.

Based on some of the ideas proposed by Nelder (1962), Bleasdale (1967) proposed two types of systematic spacing designs. In both cases, only the number of plants per unit area was varied; the pattern of plant arrangement was held constant. It was possible, however, to have the plants arranged so as to achieve any desired ratio of between-row to within-row spacing, i.e., rectangularity.

Bleasdale (1967) also pointed out that systematic spacing designs are a valuable tool for experimental work on crop spacing, particularly in situations where quality and/or size of the product are important considerations. This is due in part to the difficulty of using a single mathematical model to link density, mean size and size distribution.

BIBLIOGRAPHY

BIBLIOGRAPHY

Bradley, G. A., Doyle Smittle, and H. H. Vose. 1965. Broccoli production practices. Ark. Farm Res. 14:5.

Bradshaw, J. E. 1984. The effects of sowing date, plant spacing and nitrogen top-dressing on the dry-matter yield and concentration of cabbage cultivars (Brassica oleracea var. Capitata L.) grown for fodder. Crop Res. 24:97-104.

Brady, R. A., S. M. Goltz, and E. T. Kanemasu. 1975. Relation of soil water potential to stomatal resistance of soybean. Agron. J. 67:97-99.

Brendler, R. A. 1970. Time of harvest for machine-harvested broccoli. Calif. Agric. 24:6-7.

Brendler, R. A. 1971. Once-over harvesting of broccoli for freezing. Calif. Agric. 25:12-13.

Campbell, G. M. and H. D. Swingle. 1965. Fertility level and plant spacing influence yield of ripe, sweet pepper. J. Amer. Soc. Hort. Sci. 109:642-645.

Chung, B. 1982. Effects of plant density on the maturity and once-over harvest yields of broccoli. J. Hort. Sci. 57:365-372.

Chung, B. 1985. The effects of sowing time and plant density on the once-over harvest yields of broccoli. J. Hort. Sci. 60: 57-64.

Corrie, W. J. and D. S. Boyce. 1972. A dynamic programming method to optimize policies for the multistage harvest of crops with an extended maturity period. J. Agric. Engr. Res. 17:348-354.

Crisp, P. and V. Kesavan. 1978. Genotypic and environmental effects on curd weight of autumn-maturing cauliflowers. J. Agric. Sci. 90:11-17.

Crisp, P. 1984. Factors causing small curds in cauliflower crops. J. Agric. Sci. 102:405-413.

Crisp, P., A. R. Gray, H. James, S. J. Ives, and S. M. Angell. 1985. Improving purple sprouting broccoli by breeding. J. Hort. Sci. 60:325-333.

Cutcliffe, J. A., D. C. Munro, and D. C. McKay. 1968. Effect of nitrogen, phosphorus, potassium and manure on terminal, lateral, and total yields and maturity of broccoli. Can. J. Plant Sci. 48:439-446.

Cutcliffe, J. A. 1971. Effects of plant population, nitrogen and harvest date on yield and maturity of single-harvested broccoli. Hortscience 6:482-484.

Cutcliffe, J. A. 1972. Effects of plant spacing and nitrogen on incidence of hollow-stem in broccoli. Can. J. Plant Sci. 52:833-834.

Cutcliffe, J. A. 1975. Effect of plant spacing on single-harvest yields of several broccoli cultivars. Hortscience 10: 417-419.

Cutcliffe, J. A. and D. C. Munro. 1976. Effects of nitrogen, phosphorus and potassium on yield and maturity of cauliflower. Can. J. Plant Sci. 56:127-131.

Csizinszky, A. A. and D. J. Schuster. 1985. Response of cabbage to insecticide schedule, plant spacing, and fertilizer rates. J. Amer. Soc. Hort. Sci. 110:888-893.

Dickson, M. H. 1968. Eight newly described genes in broccoli. Proc. Amer. Soc. Hort. Sci. 93:356-361.

Donald, C. M. 1961. Competition for light in crops and pasture. Symp. Soc. Expl. Biol. XV:282-313.

Dufault, Robert J. and Luther Waters, Jr. 1985. Interaction of nitrogen fertility and plant populations on transplanted broccoli and cauliflower yields. Hortscience 20:127-128.

Farazdaghi, H. and P. M. Harris. 1968. Plant competition and crop yield. Nature 217:289-290.

Fontes, M. R., J. L. Ozbun, and Sidki Sadek. 1967. Influence of temperature on initiation of floral primordia in green sprouting broccoli. J. Amer. Soc. Hort. Sci. 91:315-320.

Frappell, B. D. 1979. Competition in vegetable crop communities. J. Austr. Inst. Agric. Sci. 45:211-217.

Garner, J. R. 1978. Planting density of winter-hardy cauliflower and its effect on yield and curd size. Expl. Hort. 30:15-22.

Gauss, James F. and George A. Taylor. 1969. Environmental factors influencing reproductive differentiation and the subsequent formation of the inflorescence of Brassica oleracea var. italica, Plenck, cv. 'Coastal'. J. Amer. Soc. Hort. Sci. 94:275-180.

Giles, W. F. 1941. Cauliflower and broccoli--What they are and where they come from. J. Royal Hort. Soc. 66:265-278.

Giles, P. R. and D. A. Ratkowsky. 1978. The behaviour of estimators of the parameters of various yield-density relationships. Biometrics 34:191-198.

Gray, A. R. 1982. Taxonomy and evolution of broccoli (Brassica oleracea var. italica). Econ. Bot. 36:396-409.

Hipp, Billy W. 1974. Influence of nitrogen and maturity rate on hollow-stem in broccoli. Hortscience 9:68-69.

Holliday, R. 1960. Plant population and crop yield. Nature 86: 22-24.

Honma, Shigemi. 1965. Development and maintenance of uniformity in broccoli. Proc. Amer. Soc. Hort. Sci. 87:295-298.

Honma, Shigemi and John Bert. 1977. Growing high-density cauliflower. Amer. Veg. Grower 25:40.

Hoyle, Burton J., Kent Tyler, Bill Fischer, Don May, and Lyndon Brown. 1973. Broccoli--For the San Joaquin Valley west side. Calif. Agric. 27:12-13.

Hulbert, S. H. and T. J. Orton. 1984. Genetic and environmental effects on mean maturity date and uniformity in broccoli. J. Amer. Soc. Hort. Soc. 109:487-490.

Karami, E. and J. B. Weaver, Jr. 1972. Growth analysis of American upland cotton, Gossypium hirsutum L., with different leaf shapes and colors. Crop Sci. 12:317-320.

Letey, J., W. M. Jarrell, N. Valoras, and R. Beverly. 1983. Fertilizer application and irrigation management of broccoli production and fertilizer use efficiency. Agron. J. 75: 502-507.

Mack, H. J. and J. R. Baggett. 1963. Row spacing affects broccoli yields. Oregon Vegetable Digest 12:1-3.

Mandl, F. A. and G. R. Buss. 1981. Comparison of narrow and broad isolines of soybean. Crop Sci. 21:25-27.

Massey, P. H., Jr., James F. Eheart, R. W. Young, and G. E. Mattus. 1962. The effect of soil moisture, plant spacing, and leaf pruning on the yield and quality of broccoli. Proc. Amer. Soc. Hort. Sci. 81:316-323.

Mead, R. 1966. A relationship between individual plant-spacing and yield. Ann. Bot. 30:301-309.

Miller, C. H., W. E. Splinter, and F. S. Wright. 1969. The effect of cultural practices on the suitability of cabbage for once-over harvest. J. Amer. Soc. Hort. Sci. 94:67-69.

Milne, A. 1962. Definition of competition among animals. Symp. Soc. Expl. Biol. XV:40-61.

Nelder, J. A. 1962. New kinds of systematic designs for spacing experiments. Biometrics September:283-307.

Nichols, M. A. 1972. Letters to the editors. Can. J. Plant Sci. 52:415-416.

Nichols, M. A., I. L. Nonnecke, and S. C. Phatak. 1973. Plant density studies with direct seeded tomatoes in Ontario, Canada. Sci. Hort. 1:309-320.

Nichols, M. A. 1974. A plant spacing study with sweet corn. N. Zea. J. Expl. Agric. 2:377-379.

Nichols, M. A. and I. L. Nonnecke. 1974. Plant spacing studies with processing peas in Ontario, Canada. Sci. Hort. 2:113-122.

Odum, E. P. 1959. Fundamentals of Ecology, 2nd ed. W. B. Saunders Co., Philadelphia.

Palevitch, Dan. 1970. Effects of plant population and pattern on yield of broccoli in single harvest. Hortscience 5:230-231.

Pant, M. M. 1979. Dependence of plant yield on density and planting pattern. Ann. Bot. 44:513-516.

Proulx, E. A. 1981. Broccoli: The immigrant that came to dinner. Horticulture March:25-28.

Rennie, J. C. 1974. Some effects of competition and density of plants on dry weight produced. Ann. Bot. 38:1003-1012.

Saini, B. C. and T. R. Rathore. 1984. Diffusive conductance of rice leaves during gradually induced water stress. Ann. App. Biol. 104:537-542.

Salter, P. J. 1960. The growth and development of early summer cauliflower in relation to environmental factors. J. Hort. Sci. 35:21-33.

Salter, P. J. 1961. The irrigation of early summer cauliflower in relation to stage of growth, plant spacing and nitrogen level. J. Hort. Sci. 36:241-253.

Salter, P. J. 1969. Studies in crop maturity in cauliflower: I. Relationship between the times of curd initiation and curd maturity of plants within a cauliflower crop. J. Hort. Sci. 44:129-140.

Salter, P. J. and Joyce R. Fradgley. 1969. Studies on crop maturity in cauliflower: II. Effects of cultural factors on the maturity characteristics of a cauliflower crop. J. Hort. Sci. 44:141-154.

Salter, P. J. 1971. Mini-cauliflowers. Agriculture, London 78: 231-235.

Salter, P. J. and R. Jane Ward. 1972. Studies on crop maturity in cauliflower: III. Effects of cold treatment and certain growth regulators on crop maturity characteristics and yield. J. Hort. Sci. 47:57-68.

Salter, P. J. and Audrey M. Williams. 1974. Studies on methods of obtaining continuity of production of summer and autumn cauliflowers. Expl. Hort. 26:106-119.

Salter, P. J. and Janet M. James. 1974. Further studies on the effects of cold treatment of transplants on crop maturity characteristics of cauliflower. J. Hort. Sci. 49:329-342.

Salter, P. J. and Janet M. James. 1975. The effect of plant density on the initiation, growth and maturity of curds of two cauliflower varieties. J. Hort. Sci. 50:239-248.

Salter, P. J., D. J. Andrews, and Jayne M. Akehurst. 1984. The effects of plant density, spatial arrangement and sowing date on yield and head characteristics of a new form of broccoli. J. Hort. Sci. 59:79-85.

Stang, J. R., H. J. Mack, and K. E. Rowe. 1979. Quantitative relation of bush snap bean (Phaseolus vulgaris L.) to plant population density. J. Amer. Soc. Hort. Sci. 104:873-875.

Stone, J. F., P. I. Erickson, and A. S. Abdul-Jabbar. 1985. Stomatal closure behavior induced by row spacing and evaporative demand in irrigated peanuts. Agron. J. 77:197-202.

Sundstrom, F. J., C. H. Thomas, R. L. Edwards, and G. R. Baskin. 1984. Influence of N and plant spacing on mechanically harvested Tabasco pepper. J. Amer. Soc. Hort. Sci. 642-645.

Tompkins, D. R. 1966. Broccoli maturity and production as influenced by seed size. Proc. Amer. Soc. Hort. Sci. 88:400-405.

Thompson, R. and H. Taylor. 1970. Calabrese--for fresh market and processing. Scottish Agriculture 49:166-171.

Thompson, R. and H. Taylor. 1974. Effects of spatial arrangement on the yield and size grades of Brussels sprouts cultivar 'Peer Gynt'. J. Hort. Sci. 49:171-181.

Thompson, R. and H. Taylor. 1975. Some effects of population density and row spacing on the yield and quality of two cauliflower cultivars. Hort. Res. 14:97-101.

Thompson, R. and H. Taylor. 1976. Plant competition and its implications for cultural methods in calabrese. J. Hort. Sci. 51:147-157.

Warne, L. G. G. 1948. Spacing experiments on vegetables. I. The effect of the thinning distance on earliness in globe beet and carrots in Cheshire, 1948. J. Hort. Sci. 26:79-83.

Watts, L. E. 1965. The inheritance of curding periods in early summer and autumn cauliflower. Euphytica 14:83-90.

Wheeler, J. A. and P. J. Salter. 1974. Effects of shortening the maturity period on harvesting costs of autumn cauliflowers. Sci. Hort. 2:83-92.

Whitman, C. E., J. L. Hatfield, and R. J. Reginato. 1985. Effect of slope position on the microclimate, growth, and yield of barley. Agron. J. 77:663-669.

White, J. and J. L. Harper. 1960. Correlated changes in plant size and number in plant populations. Nature 188:467-485.

Wiegand, C. L. and A. J. Richardson. 1984. Leaf area, light interception and yield estimates from spectral components analysis. Agron. J. 76:543-548.

Willey, R. W. and S. B. Heath. 1969. The quantitative relationships between plant population and crop yield. Adv. Agron. 21: 281-289.

Wong, S. C., J. R. Cowan, and G. D. Farquahar. 1979. Stomatal conductance capacity correlates with photosynthetic capacity. Nature 282:242-246.

Zink, F. W. and D. A. Akana. 1951. The effect of spacing on the growth of sprouting broccoli. Proc. Amer. Soc. Hort. Sci. 58:160-164.

Zink, F. W. 1968. Hollow stem in broccoli. Calif. Agric. 22:8-9.

PART I

THE EFFECT OF POPULATION DENSITY AND SPATIAL ARRANGEMENT ON THE YIELD AND QUALITY OF BROCCOLI

ABSTRACT

A field study utilizing broccoli (*Brassica oleracea* var. *italica* L.) was conducted at two locations in the spring and fall of 1984 and 1985. Rectangular and square spatial arrangements with spacings ranging from 15 x 15 cm to 122 x 122 cm at 15 cm intervals were evaluated utilizing a central composite experimental design. The relationship between either of the dependent variables (yield or head size) and the independent variables (within-row and between-row spacing) was best described by a second-order polynomial equation. Highest total yield (18,000 kg/ha) was predicted at the closest spacing; however, at this spacing there was a considerable reduction in quality. Commercially desirable head sizes could be obtained over a broad range of spacings. Heads 10 to 15 cm in diameter were achieved at spacings of 15 x 40 cm and 15 x 90 cm while still maintaining 90 and 65 percent of maximum total yield, respectively. No substantial yield or quality differences were found between square and rectangular spatial arrangements.

INTRODUCTION

Commercial production of broccoli in Tennessee and in surrounding areas has increased markedly over the past several years. Potential market outlets for broccoli include processing operations as well as fresh-market sales, with each industry having particular requirements in regard to size of the product. Broccoli grown for processing should possess a head diameter of approximately 15 cm, while slightly smaller heads (about 10 cm in diameter) are preferred for the fresh market. A major objective of commercial growers is to produce heads of a particular size while maintaining satisfactory yield and quality.

In general, product size is somewhat dependent on the cultivar grown and on environmental conditions which prevail. However, certain cultural practices can be employed in order to achieve a commodity of the desired size. Plant spacing is one such practice which has been shown to influence yield and/or product size of several vegetable species, including cabbage (Csizinszky and Schuster, 1985), beet and carrot (Warne, 1948), Tabasco pepper (Sundstrom, et al., 1984) and tomato (Nichols, et al., 1973). In broccoli crops, it has been demonstrated that total yields tend to increase as plant spacing decreases (Zink and Akana, 1951; Palevitch, 1970; Cutcliffe, 1971). However, competition stresses imposed by the high population densities associated with close spacings may be manifested in the form of reduced product quality. A substantial decrease in individual head size has often been observed when plants are grown in very high-density arrangements (Bradley, et al., 1962; Bradley, et al., 1965; Thompson and Taylor, 1970; Palevitch, 1970; Cutcliffe, 1975; Chung, 1982; Salter, et al., 1984; Chung, 1985; Dufault and Waters, 1985). In addition, the percentage of commercially unacceptable heads (culls) has been shown to increase as spacing decreases (Zink and Akana, 1951; Mack and Baggett, 1963; Cutcliffe, 1975; Thompson and Taylor, 1976).

Nichols (1972) noted that plant spacing actually involves two components, plant density and plant arrangement. Density is defined as the number of plants per unit area, while arrangement concerns the planting pattern, whether rectangular or square. According to Thompson and Taylor (1974) it is generally recognized that for a given population, greater competition stress exists in a rectangular arrangement than in a square one. This implies that for a given population, yields would tend to decline as rectangularity increases. Results of spacing experiments in brussels sprouts (Thompson and Taylor, 1974), broccoli (Palevitch, 1970; Salter, et al., 1984), cauliflower (Thompson and Taylor, 1974) and green beans (Frappell, 1979) have indicated that the optimum pattern of arrangement is one in which rectangularity is minimized. However, spacing studies involving sweet corn (Nichols, 1974) and peas (Nichols and Nonnecke, 1974) showed no apparent effects of rectangularity. The objectives of this study were to determine the effects of spacing, both within-row and between-row, on the yield and quality of broccoli. In addition, we wished to compare the efficiency of various spatial arrangements at a given population density so as to discern possible differences in their effects on crop yield and quality.

CHAPTER I

MATERIALS AND METHODS

General Transplant Production Methods

Broccoli seed (cv. Premium Crop) was sown in 2.54 cm Speedling® flats containing Pro-Mix BX soil media. Following germination, seedlings remained in the greenhouse for 7 to 10 days, after which time they were moved outside to a coldframe. Fenvalerate or a mixture of carbaryl plus organophosphate was routinely applied for control of insects. Seedlings were fertilized once with a mixture of Peters' 20-20-20. Plants were transferred to the field when approximately 4 weeks old (4 to 5 true leaf stage).

Plot Site and Field Production

Experiments were conducted in the spring and fall of 1984 and 1985 at the Plant Sciences Field Laboratory, Knoxville, TN and at the Plateau Experiment Station, Crossville, TN. The soil type at the Knoxville Location was an Etowah silt loam (Typic Paleudult: fine-loamy, siliceous, mesic); at the Crossville location, the experimental area was a Lily loam (Typic Hapludult: fine-loamy, siliceous, mesic). Results of soil tests previously conducted at both locations indicated medium levels of natural fertility. Broadcast applications of N, P, and K were made as necessary in order to ensure that a high level of fertility was maintained. Additional nitrogen was supplied throughout the growing season by applying 3 nitrogen sidedressings, each 5.4 kg/ha N, at 2 week intervals. Fenvalerate was applied as needed for insect control. Weeds were controlled by means of manual and mechanical cultivation. Overhead sprinkler irrigation was provided at regular intervals throughout the growing season in order to achieve a minimum of 2.5 cm of precipitation per week.

Statistical Design and Analysis

Response surface techniques were employed to allow for investigation of a wide range of spacing combinations while minimizing the actual number of experimental treatments required. Spacings used in this study ranged from 15 x 15 cm to 122 x 122 cm at 15 cm intervals. Each treatment consisted of 8 rows, with each row containing 8 plants for a total of 64 plants per treatment. The 2 outermost rows in each treatment were designated as border rows and served only to prevent any possible border effects. Individual treatments were aranged within a 27 x 37 m plot to form a central composite design. The overall treatment design has been described by Armitage, et al. (1981).

Data were analyzed using the General Linear Models procedure (GLM) within Statistical Analysis Systems (SAS). The relationship between either of the dependent variables (yield or head size) and the independent variables (within-row or between-row spacing) was best described by a second-order polynomial equation having the general form

$$Y = b_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2$$

where Y = dependent variable (yield or head size)

x_1 = between-row spacing in cm

x_2 = within-row spacing in cm

Cubic terms were tested but showed no significance, and therefore were not included in the model. Results of individual experiments were similar, and thus data from all experiments were combined in the form of an overall model. Results presented in this paper represent the overall average of 2 years' data, collected for spring and fall crops at two locations.

Harvest and Data Collection

Plants were hand-harvested when judged to be mature, in accordance with established criteria (Thompson and Taylor, 1970). Heads were cut to a uniform length of 15 cm, measured from the tip of the largest floret to the base of the stalk. Individual head weights and diameters were recorded. For the purposes of this study, yield refers specifically to head weight, expressed in kg/ha. However, quality involves subjective assessments of head shape and uniformity, in addition to measurements of head diameter, expressed in centimeters.

CHAPTER II

RESULTS AND DISCUSSION

Yield

Both within-row and between-row spacing significantly influenced yield response of broccoli. The means of the experimental values of all spacing combinations and their associated yields are given in Table 1. A response surface plot for yield (Figure 1) indicates the range of spacings at which a particular yield may be obtained. Slight skewness of the contour intervals is apparent in the overall model. This was attributed to the results obtained from an individual experiment, in which the experimental area was located on slightly sloping terrain. Consequently the soil type, soil drainage capability or the incident angle of sunlight may have varied considerably within the overall plot. It has been demonstrated in barley crops that slope position may influence crop growth and yield (Whitman, et al., 1985).

As shown in Table 1, total yields increased in response to increases in spacing. The effect became less pronounced at very high populations (108,900 to 435,600 plants/ha). These results would indicate a possible asymptotic relationship. Such a relationship has previously been reported for other experiments in which broccoli was grown at high population densities (Chung, 1982; Salter, 1984).

Table 1. Population Density, Area Per Plant, and Average Yield of Broccoli for Treatment Combinations of Within-Row and Between-Row Spacing.

Within-Row Spacing (cm)	Between-Row Spacing (cm)	Population Density ($plts \cdot ha^{-1}$)	Area Per Plant (m^2)	Yield ($kg \cdot ha^{-1}$)
15	15	435600	.02	17642
15	61	108900	.09	11761
15	91	72600	.13	10128
15	122	54450	.18	12251
30	30	108900	.09	10781
30	61	54450	.18	8221
30	91	36300	.27	10822
30	122	27225	.37	9801
38	38	69696	.14	11918
38	61	43650	.23	10193
38	91	29040	.35	9148
38	122	21780	.46	7743
46	46	48400	.21	13721
46	61	36300	.28	9964
46	91	24200	.42	10019
46	122	18150	.56	6289
61	61	27225	.37	8698
61	91	18150	.56	7923
61	122	13613	.74	7412
91	91	12100	.83	7405
91	122	9075	1.12	4696
122	122	6806	1.49	4257

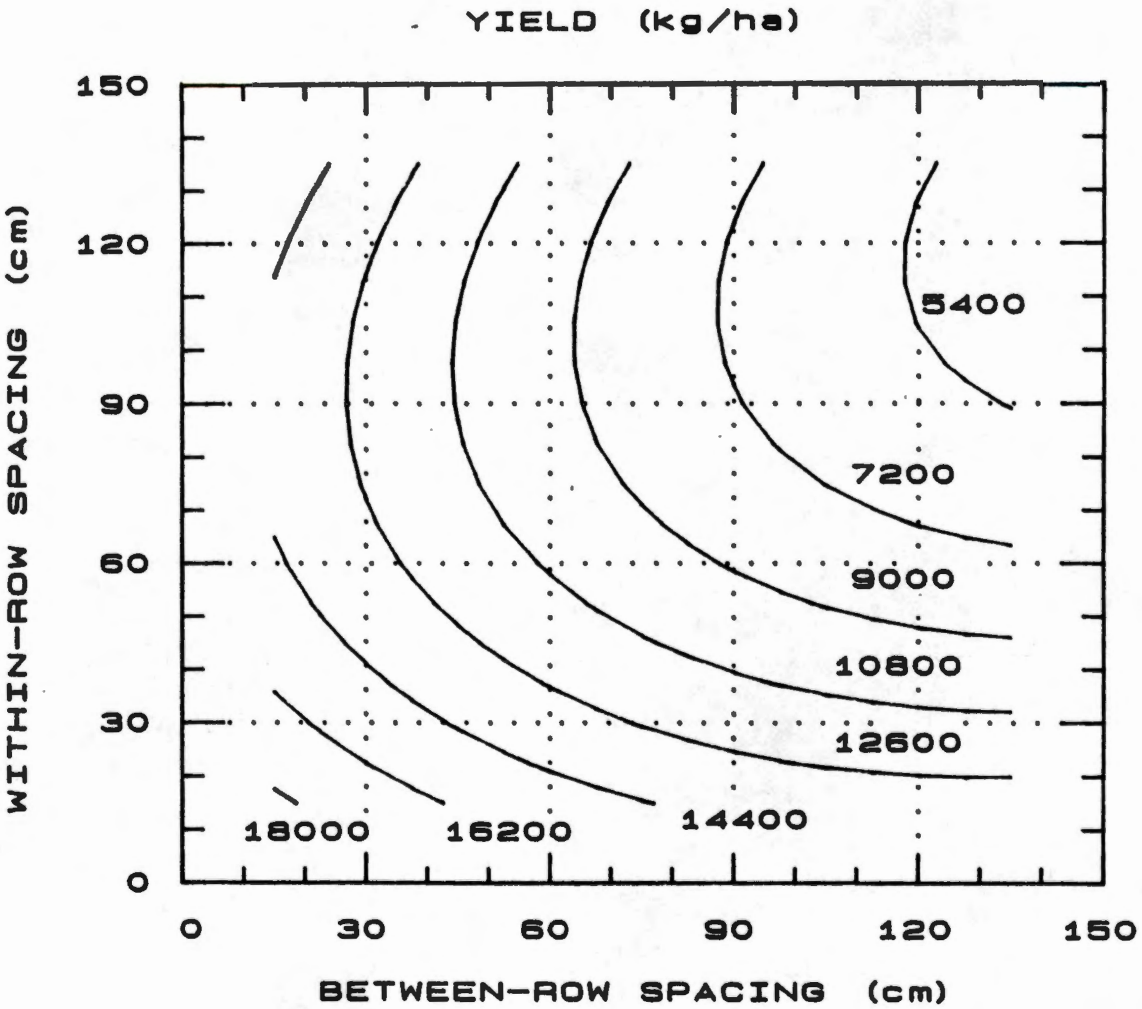

Figure 1. Effect of between-row and within-row spacing on yield of broccoli, expressed in kg/ha. Contour intervals are plotted in increments of 1/10 of maximum total yield. R^2=0.792499. Y=21533.09398 - (91.80137548 x x_1) - (135.523795 x x_2) + (0.3805981 x x_1^2) + (0.79319811 x x_2^2) - (0.40756464 x $b_1^2 b_2^2$) where Y = Yield (kg/ha), x_1 = between-row spacing (cm) and x_2 = within-row spacing (cm).

Absolute highest total yields (18,000 kg/ha) were attained at the closest spacing tested, 15 x 15 cm. The population density at this spacing equated to 435,600 plants/ha. Absolute lowest total yields (6,000 kg/ha) were obtained at a spacing of 122 x 122 cm, the widest spacing tested. The population density associated with this spacing was 6,806 plants/ha.

Results of the prediction model for yield suggest that there exists one square arrangement and a wide variety of rectangular arrangements which may be utilized to obtain any given yield. For example, a yield of 10,800 kg/ha may be obtained using a square arrangement of 60 x 60 cm; alternatively, rectangular arrangements of 40 x 90 cm or 120 x 50 cm would produce the same yield.

It has been reported that increasing rectangularity will result in plant competition being initiated at earlier stages of growth, in comparison to that which occurs in square arrangements (Frappell, 1979). Therefore, yields will theoretically be lower in rectangular arrangements, with the effect being especially significant at higher populations. Several other workers have found this to be true in broccoli crops (Palevitch, 1970; Salter, et al., 1984). Results of the present study, however, did not support these postulates. Table 2 shows results of yield comparisons between square and rectangular arrangements having the same area. No substantial differences were detected between the two arrangements, even at relatively high population densities (175,645 plants/ha).

Yields in the median range (10,800 to 12,600 kg/ha) allowed for greatest flexibility in spacing. As yields approached minimum

Table 2. Relative Efficiency of Various Spatial Arrangements.[a]

Spacing (cm)	Area Per Plant (cm)	Population Density (plts·ha^{-1})	Predicted Yield (kg·ha^{-1})	Predicted Head Diameter (cm)
24 x 24	576	175,645	16,518	10.5
18 x 32	576	175,645	16,518	10.4
16 x 36	576	175,645	16,076	10.6
40 x 40	1600	63,204	13,666	15.4
32 x 50	1600	63,204	13,718	15.2
20 x 80	1600	63,204	13,432	15.9

[a]Comparisons represent square and rectangular arrangements having equivalent areas and their effects on production of broccoli heads of a particular size. Spacings having an area of 576 cm^2 permit production of heads 10 cm in diameter, ±1 cm. Spacings having an area of 1600 cm^2 permit production of head 15 cm in diameter, ±1 cm.

or maximum values, the range of spacings which would allow for those yields tended to decrease. For example, maximum yields of 18,000 kg/ha could be achieved only at spacings ranging from 15 x 15 cm to 18 x 18 cm, and minimum yields of 5,400 kg/ha were obtained only at spacings which fell within the range of 105 x 120 to 120 x 118 cm.

Quality

Spacing effects on head size were similar to those observed for yield. A response surface plot for head size is represented by Figure 2. Head diameter consistently increased in response to decreases in spacing. As evidenced by the contour intervals, smallest heads (8 cm in diameter) were obtained over a very limited range of spacings, from approximately 15 x 20 cm to 19 x 15 cm. Conversely, large heads measuring 22 cm or more in diameter were obtained over a relatively broad range of spacings, varying from 120 x 30 cm to 60 x 120 cm. Contour intervals also indicate that each particular head size could be achieved over a certain range of spacings which included one square arrangement as well as numerous rectangular arrangements.

Response surface analysis indicated only slight differences in head size of plants grown in square vs. rectangular arrangements (Table 2). In comparisons between different spatial arrangements having the same area, it can be seen that the actual differences in head diameter were less than 1 cm. Furthermore, head size did not show a consistent response to plant arrangement. For some

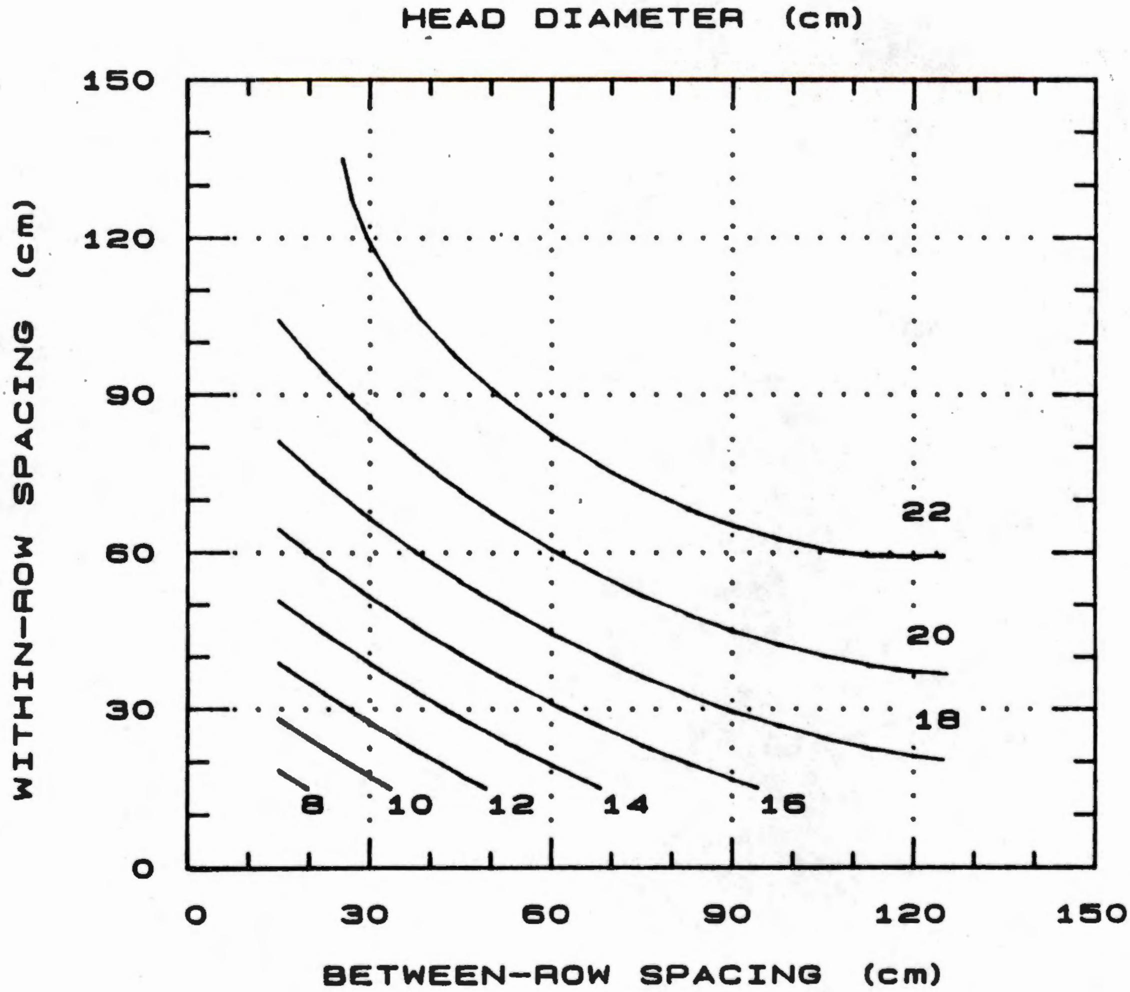

Figure 2. Effect of between-row and within-row spacing on head diameter of broccoli, expressed in cm. Contour intervals are plotted in increments of 2 cm. R^2=0.870190, $Y=1.12877559 + (0.18841274 \times x_1) + (0.25419154 \times x_2) - (0.00062391 \times x_1^2) - (0.00085063 \times x_2^2) - (0.00067698 \times x_1^2 x_2^2)$ where Y = head diameter (cm), x_1 = between-row spacing (cm), x_2 = within-row spacing (cm).

rectangular arrangements head size increased slightly, while for other rectangular arrangements head size tended to decrease.

From a practical standpoint, it is important to determine the range of spacings which will produce heads of a given size. Desirable head sizes vary according to the intended use of the product. Fresh-market sales generally utilize small heads about 10 cm in diameter. These are sold bunched together, forming individual packages consisting of 4 to 6 small heads. Conversely, broccoli grown for processing is generally somewhat larger in size, with heads approximately 15 cm in diameter representing the standard desired by the industry. Shaded areas of Figure 3 represent the range of spacings which may be used to obtain 10 and 15 cm heads (+ or - 1 cm). For the range of spacings tested in this study, there appeared to be much more flexibility in the number of spacings which produced a 15 cm head in comparison to those required to achieve the 10 cm head.

Quality factors other than head size were also affected by spacing. At very close spacings, a high proportion of commercially undesirable heads (i.e., culls) were produced. These culls were characterized by unacceptably small size (<5 cm in diameter) and/or a misshapen appearance (data not shown). This lack of uniformity was attributed to extreme competition stresses which resulted from the high population densities associated with close spacings.

Yield/Quality Interactions

Although the effects of spacing on yield (in kg/ha) and head size (diameter in cm) have been considered independently, it is

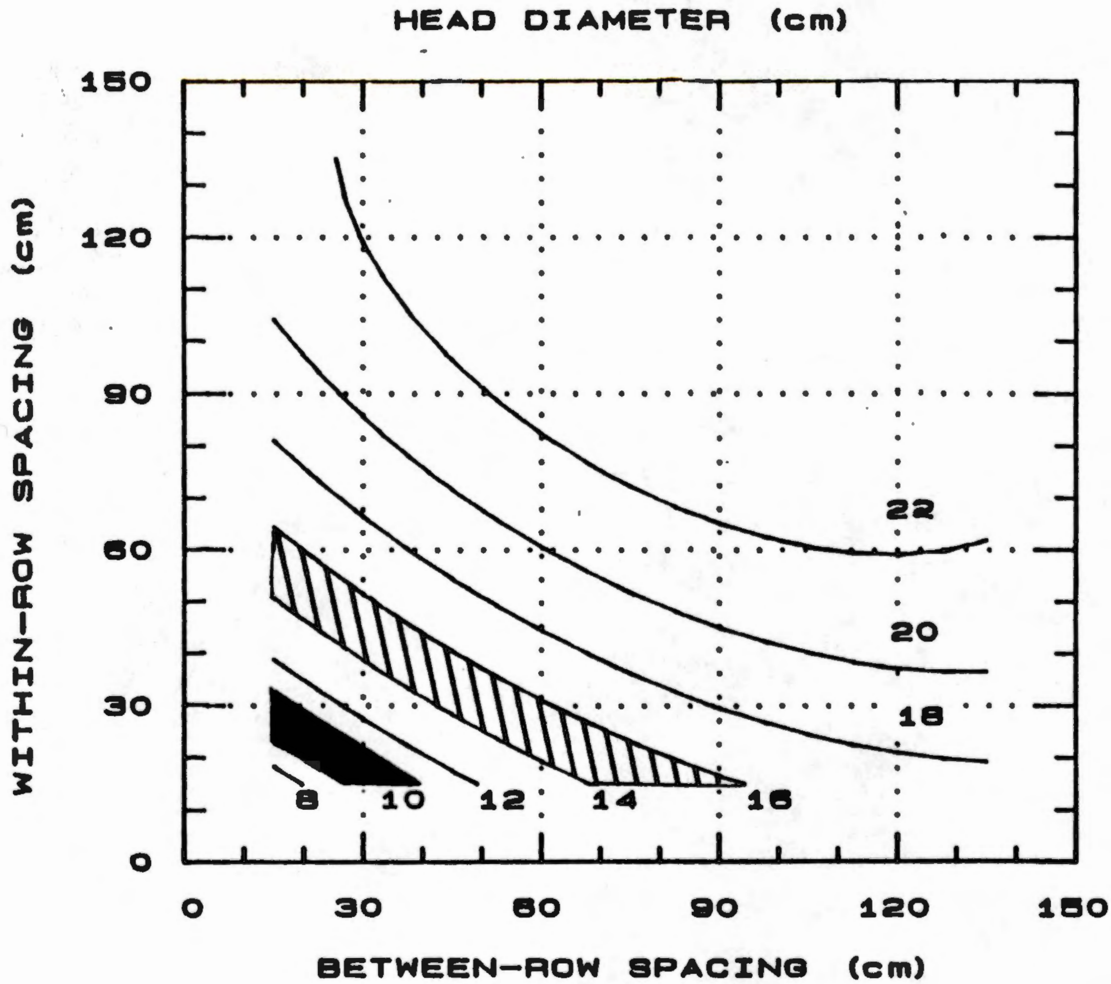

Figure 3. Range of spacings which permit production of broccoli heads of a given size. Solid shaded area represents predicted spacings which will produce heads 10 cm in diameter, ±1 cm. Striped area represents predicted spacings which will produce heads 15 cm in diameter, ±1 cm. Contour intervals are plotted in increments of 1/10 of maximum total yield. R^2=0.870190, Y=1.12877559 + (0.18841274 x x_1) + (0.25419154 x x_2) - (0.00062391 x x_1^2) - (0.00085063 x x_2^2) - (0.00067698 x $x_1^2 x_2^2$) where Y = head diameter (cm), x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

important to establish the relationship between the two factors. Figure 4 illustrates the strong linear relationship which exists between head weight and head size. Therefore, the graph suggests that for any given head size, a corresponding head weight can be reliably predicted. Because of this relationship, the spacing combinations which produce the highest yields may not result in a product which meets commercial size specifications. Figure 5 further illustrates how spacing affects the relationship between yield and head size. Spacings which allow for an increase in individual head size will also result in a reduction of total yield. The shaded areas of Figure 5 show the range of spacings which will produce a 10 or 15 cm head (+ or - 1 cm) superimposed on a graph showing projected yields for all spacings tested. As illustrated by the solid shaded area of Figure 4, spacings which produce heads approximately 10 cm in diameter will result in total yields of 17,000 kg/ha (+ or - 1,800 kg/ha). Thus, maximum attainable yields may be reduced by up to 10 percent in order to produce 10 cm heads suitable for fresh-market sale.

In similar fashion, spacings which permit for the production of increasingly larger head sizes will result in progressive yield reductions. The striped portion of Figure 5 shows spacings which will allow for production of 15 cm heads used for processing. Yields will consequently average 14,400 kg/ha, which represents a 25 percent reduction in maximum attainable yield.

In conclusion, results of this study indicated that decreases in spacing were accompanied by increases in total yield. Other

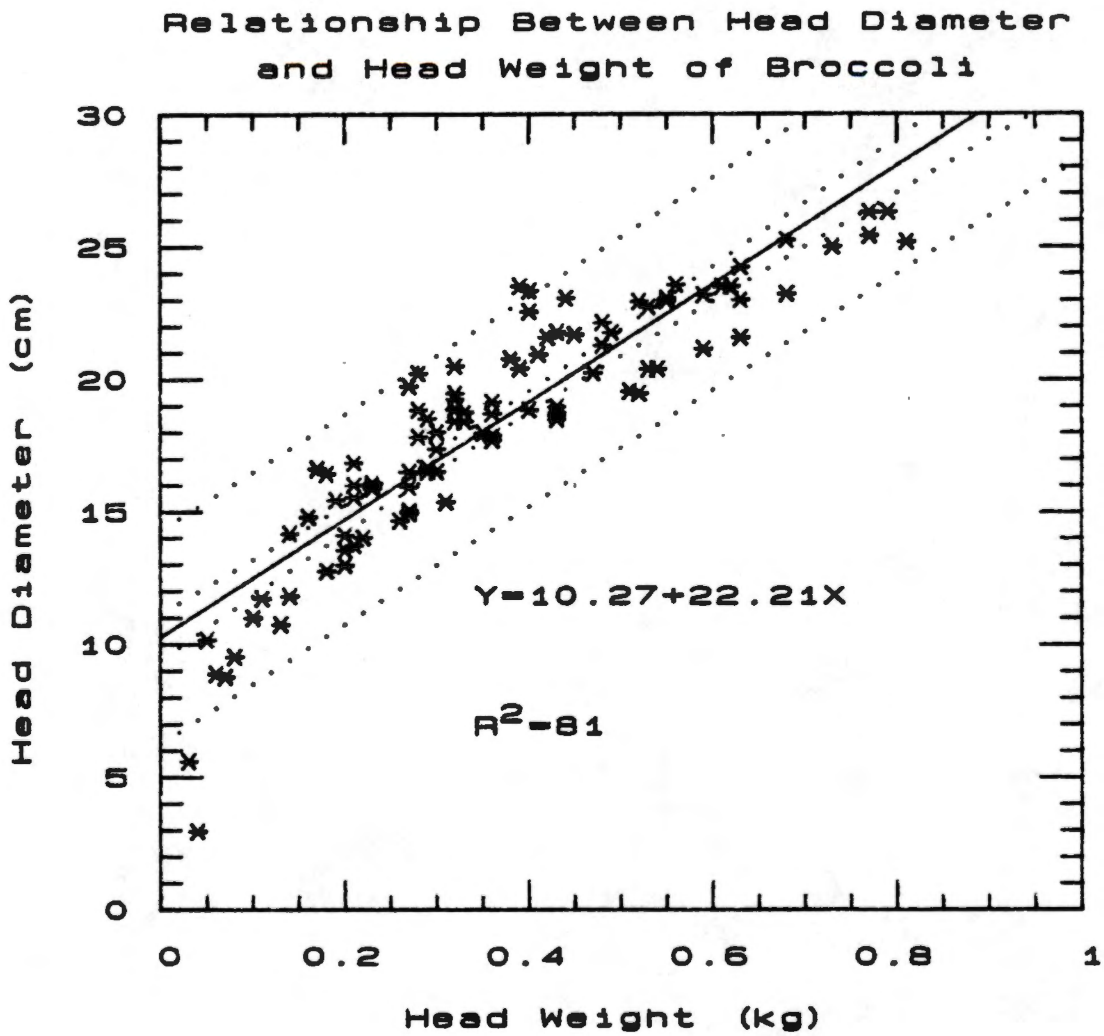

Figure 4. Relationship between head diameter and head weight of broccoli. Solid line represents the best-fit linear regression line and broken lines represent the 95 percent confidence limits.

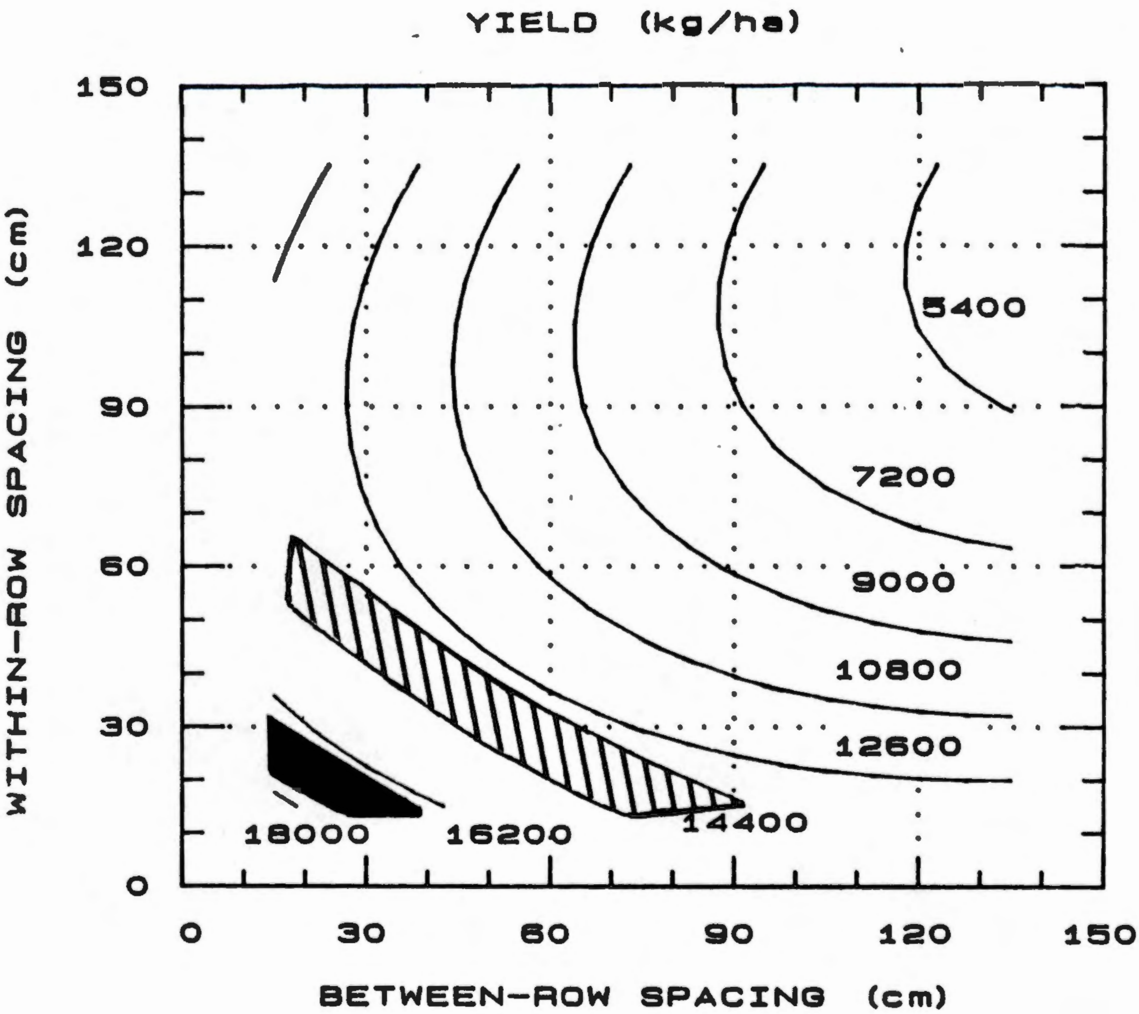

Figure 5. Ranges of spacings which permit production of heads of a given size, and the yields associated with those head sizes. Solid shaded area represents predicted spacings which will produce heads 10 cm in diameter, ±1 cm. Striped area represents predicted spacings which will produce heads 15 cm in diameter, ±1 cm. Contour intervals at plotted increments of 1/10 of maximum total yield. R^2= 0.792499, Y=21533.09398 - (91.80137548 x x_1) - (135.523795 x x_2) + (0.3805981 x x_1^2) + (0.79319811 x x_2^2) - 0.40756464 x $x_1^2 x_2^2$) where Y = Yield (kg/ha), x_1 between-row spacing (cm), and x_2 = within-row spacing (cm).

spacing studies in broccoli have reported similar findings (Aldrich, et al., 1961; Mack and Baggett, 1963; Cutcliffe, 1975). Although individual head size also decreased in response to decreases in spacing, higher yields were achieved because the actual number of heads produced per hectare was increased. These findings are in accordance with results obtained in other spacing experiments for broccoli crops (Cutcliffe, 1975; Dufault and Waters, 1985). These results also demonstrate how manipulations in spacing may be used to produce a commodity having an appropriate size in relation to its intended use.

Changes in quality may occur as a response to high plant densities. Product appearance and uniformity were adversely affected dat the closest spacing tested (15 x 15 cm). No substantial differences in yield or head size were detected in comparisons between plants grown in square vs. rectangular arrangements having equal areas.

Since the data presented here are composed of results from both spring and fall crops collected over a 2 year period in two separate locations, a wide range of climatic and geographic conditions is represented by the overall models. These models should prove useful in assessing the degree to which broccoli yield and quality are influenced by changes in spacing, when grown under conditions similar to those represented by the model.

LITERATURE CITED

LITERATURE CITED

Aldrich, Thomas M., Marvin J. Snyder, and Thomas M. Little. 1961. Plant spacing in broccoli--affects yield, head size, earliness. Calif. Agric. 15:10-11.

Armitage, A. M., W. H. Carlson, and C. E. Cress. 1981. Determination of flowering time and vegetative habit of Tagetes patula through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

Bradley, G. A., Doyle Smittle, and H. H. Vose. 1962. Broccoli as a processing crop in Arkansas. Ark. Farm Res. 11:10.

Bradley, G. A., Doyle Smittle, and H. H. Vose. 1965. Broccoli production practices. Ark. Farm Res. 14:5.

Chung, B. 1982. Effects of plant density on the maturity and once-over harvest yields of broccoli. J. Hort. Sci. 57:365-372.

Chung, B. 1985. The effects of sowing time and plant density on the once-over harvest yields of broccoli. J. Hort. Sci. 60:57-64.

Cutcliffe, J. A. 1971. Effects of plant population, nitrogen, and harvest date on yield and maturity of single-harvested broccoli. Hortscience 6:482-484.

Cutcliffe, J. A. 1975. Effect of plant spacing on single-harvest yields of several broccoli cultivars. Hortscience 10:417-419.

Dufault, Robert J. and Luther Waters, Jr. 1985. Interaction of nitrogen fertility and plant populations on transplanted broccoli and cauliflower yields. Hortscience 20:127-128.

Frappell, B. D. 1979. Competition in vegetable crop communities. J. Aust. Inst. Agric. Sci. 45:211-217.

Mack, H. J. and J. R. Baggett. 1963. Row spacing affects broccoli yields. Oregon Veg. Digest 12:1-3.

Nichols, M. A., I. L. Nonnecke, and S. C. Phatak. 1973. Plant density studies with direct-seeded tomatoes in Ontario, Canada. Sci. Hort. 1:309-320.

Nichols, M. A. 1974. A plant spacing study with sweet corn. N. Zea. J. Expl. Agric. 2:377-379.

Nichols, M. A. and I. L. Nonnecke. 1974. Plant spacing studies with processing peas in Ontario, Canada. Sci. Hort. 2: 113-122.

Palevitch, Dan. 1970. Effects of plant population and pattern on yield of broccoli in single harvest. Hortscience 5:230-231.

Salter, P. J., D. J. Andrews, and Jayne M. Akehurst. 1984. The effects of plant density, spatial arrangement and sowing date on yield and head characteristics of a new form of broccoli. J. Hort. Sci. 59:79-85.

Sundstrom, F. J., C. H. Thomas, R. L. Edwards, and G. R. Baskin. 1984. Influence of N and plant spacing on mechanically harvested Tabasco pepper. J. Amer. Soc. Hort. Sci. 109: 642-645.

Thompson, R. and H. Taylor. 1970. Calabrese--for fresh market and processing. Scottish Agriculture 49:166-171.

Thompson, R. and H. Taylor. 1974. Effects of spatial arrangement on the yield and size grades of Brussels sprouts cultivar 'Peer Gynt'. J. Hort. Sci. 49:171-181.

Warne, L. G. G. 1948. Spacing experiments on vegetables. I. The effect of the thinning distance on earliness in globe beet and carrots in Cheshire, 1948. J. Hort. Sci. 26:79-83.

Whitman, C. E., J. L. Hatfield, and R. J. Reginato. 1985. Effect of slope position on the microclimate, growth and yield of barley. Agron. J. 77:663-669.

Zink, F. W. and D. A. Akana. 1951. The effect of spacing on the growth of sprouting broccoli. Proc. Amer. Soc. Hort. Sci. 58:16.

PART II

THE EFFECT OF POPULATION DENSITY AND SPATIAL ARRANGEMENT ON THE MORPHOLOGICAL AND PHYSIOLOGICAL DEVELOPMENT OF BROCCOLI

ABSTRACT

A two year spacing study utilizing broccoli (Brassica oleracea var. italica L.) was conducted at two locations in the spring and fall growing seasons. Both rectangular and square spatial arrangements were used. Spacings ranging from 15 x 15 cm to 122 x 122 cm at 15 cm intervals were evaluated utilizing a central composite experimental design. Increases in spacing resulted in increased leaf number and size, sideshoot quantity and size, and whole plant size. However, leaf area index decreased as spacing distance increased. The narrowest spacings produced slender plants with elongated stalks, while the widest spacings produced stocky and robust plants. No correlation was detected between plant spacing and mineral composition of leaf tissue, and no nutrient deficiencies were detected at any spacing tested. Plants grown at wider spacings had larger heads with a greater incidence of hollow-stem, and a higher crude fiber content than those grown at narrow or intermediate spacings. Soil moisture content was greater at the wider spacings and leaf stomatal conductance was highest at the narrower spacings. At the wider spacings, leaf area per plant was ten times greater than at the narrowest spacings, while head size was only three times larger, indicating a lower horticultural production efficiency of heads per unit leaf area.

INTRODUCTION

Plant spacing is of major importance in the production of many crop species in that it influences a myriad of growth, development and reproductive processes. It has been suggested that plant spacing actually involves two distinct components, plant density and plant arrangement. Density is defined as the number of plants per unit area, while arrangement concerns the planting pattern, whether rectangular or square (Nichols, 1972). The majority of spacing studies in Brassica crops have addressed the subject from an agronomic perspective, with primary consideration being given to the effects of spacing on total yield and individual product size.

From an ecological standpoint, however, plant spacing may affect a number of morphological and physiological characteristics in broccoli. Several workers have investigated the effects of spacing on crop maturity and postharvest quality factors. Spacing effects on crop maturity have been particularly well documented. In most cases, high population densities resulted in delayed maturity (Zink and Akana, 1951; Aldrich, et al., 1961; Cutcliffe, 1971; Cutcliffe, 1975). However, time of maturity was reportedly hastened at high plant populations in another study (Salter, et al., 1984).

An increase in the incidence and severity of hollow-stem has been observed in plants grown at progressively wider spacings (Zink and Akana, 1951; Zink, 1968; Cutcliffe, 1972; Hipp, 1974; Dufault and Waters, 1985). Less information is available in regard to spacing effects on nutrient composition and fiber content of broccoli. In comparisons of broccoli grown at two different plant spacings, Massey, et al. (1962) reported that chemical composition of broccoli plants was unaffected by spacing. Changes in head shape and plant conformation may occur as a result of the competition stresses present at high population densities. In one study, plants grown at densities below 20 plants$\cdot m^{-2}$ produced heads having a flatter shape than those grown at higher densities (Salter, et al., 1984). Other experiments have examined the effects of spacing on the general conformation of the entire plant. Plants grown at wider spacings of approximately 51 x 102 cm were short, stocky and had thick stalks. In contrast, plants grown at narrower spacings of approximately 20 x 102 cm and 30 x 102 cm were taller and had small stalk diameters (Zink and Akana, 1951; Zink, 1968). Experiments in cauliflower crops demonstrated that leaf area and total fresh weight of individual plants decreased in response to decreases in spacing (Salter, 1961). However, it was noted that nitrogen deficiencies were apparent at close spacings, a condition which may have influenced the results of that study.

A number of researchers have attempted to correlate leaf photosynthesis with leaf area. Experiments involving peanut, soybean and sweet potato indicated that the position of a leaf on the stem tends to markedly influence that leaf's size, as well as the extent to which other leaves are shaded (Bhagsari and Brown, 1986). Larger leaves generally occupy lower positions on plant stems. Consequently, these larger leaves are usually older, more heavily shaded and lower in CO_2 Exchange Rate (CER) than leaves situated higher on the stem. As a possible result of these variations, negative correlations between CER and leaf area were observed in all three crops tested.

Other studies involving the effects of leaf area and photosynthesis and crop yield have been undertaken in cotton (Karami and Weaver, 1972), barley (Berdahl, et al., 1972) and soybean (Mandl and Buss, 1981). These results were extensively reviewed by Bhagsari and Brown, who concluded that the agronomic advantages of large vs. small leaves remain somewhat ambiguous. It has been suggested that leaf orientation affects photosynthetic ability most strongly, with a vertical or nearly vertical angle being the optimum (Army and Greer, 1971).

Heavy shading of lower leaves may also result in altered stomatal responses (Army and Greer, 1967; Berdahl, et al., 1972). Moreover, stomatal behavior may also be influenced by row spacing and evaporative demand. Studies in irrigated peanut crops demonstrated that stomates of plants grown in narrow rows closed earlier in the day than did stomates of plants grown in wide rows (Stone, et al., 1985). There is also evidence that stomatal aperture is determined, at least in part, by the photosynthetic capacity of plant leaves (Wong, et al., 1979). It was suggested that stomata might behave in response to a photosynthetic metabolite (ATP, RuBP, or NADPH, for example) present in the mesophyll tissue. Concentrations of these metabolites depend on many interrelated factors, including temperature (Wong, et al., 1979).

In the present study, we wished to examine in detail the ways in which population density and spatial arrangement affect certain physiological and morphological characteristics of field-grown broccoli crops.

CHAPTER I

MATERIALS AND METHODS

General Transplant Production Procedures

Broccoli seed (cv. Premium Crop) was sown in 2.54 cm Speedling® flats containing Pro-Mix BX soil media. Seedlings were kept in the greenhouse for 7 to 10 days after germination, then moved outside to a coldframe. Insects were controlled by routine applications of fenvalerate or carbaryl plus organophosphate. Seedlings were fertilized once when approximately 3 weeks old, using a mixture of Peters' 20-20-20. Seedlings were transplanted to the field at the 4 to 5 true leaf stage (about 4 weeks old).

Plot Site and Field Production

Experiments were conducted during the spring and fall growing seasons of 1984 and 1985 in two separate locations. These included the Plant Sciences Field Laboratory, Knoxville, TN and the Plateau Experiment Station, Crossville, TN. At the Knoxville location, the experimental area was an Etowah silt loam (Typic Paleudult: fine-loamy, siliceous, mesic), while the Crossville location was a Lily silt loam (Typic Hapludult: fine-loamy, siliceous, mesic). Soil tests had previously been conducted at both locations, and results had indicated medium levels of natural fertility. In order to maintain high levels of fertility, broadcast applications of N, P, and K were applied in accordance with recommended procedures for the crop. Three nitrogen sidedressings, each 5.4 kg/ha N, were applied at 2-week intervals throughout the growing season. Weed control was accomplished by means of manual and mechanical cultivation. The crop was sprayed with fenvalerate as necessary to control insects. Irrigation was supplied through an overhead sprinkler system in order to maintain 2.5 cm of precipitation per week.

Statistical Design and Analysis

Response surface techniques were utilized for the experimental investigations. This allowed for the examination of a wide range of spacing combinations, while minimizing the actual number of experimental treatments required. Spacings ranged from 15 x 15 cm to 122 x 122 cm in 15 cm increments. Each treatment contained a total of 64 plants, arranged in 8 rows with 8 plants per row. The two outermost rows in each treatment were designated as border rows; data were not collected from border rows. Individual treatments were arranged within a 27 x 37 m plot to form a central composite design. The overall treatment design has been described by Armitage, et al. (1981).

The General Linear Models procedure (GLM) within Statistical Analysis Systems (SAS) was utilized to analyze the data. The relationship between the dependent variable (for example, leaf number or fiber content) and the independent variables (within-row and between-row spacing) was best described by a second-order polynomial equation. The general form of the equation is as follows:

$$Y = b_1 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2$$

where Y = dependent variable (leaf number, fiber content, etc.)

x_1 = between-row spacing in cm

x_2 = within-row spacing in cm

Cubic terms were tested but showed no significance, and for this reason were not included in the model. Results of individual experiments were similar, and thus data from all experiments were combined to create an overall model. Except where noted, results presented in this paper represent the overall average of 2 years' data, collected for spring and fall crops in two locations.

Sampling Techniques, Chamical Analyses and Physical Measurements

Leaf Number, Leaf Area and Leaf Area Index

Leaf number and area. Immediately prior to harvest, the circular area beneath each plant was measured in order to determine ground area per plant. These data were used in the calculation of Leaf Area Index (LAI) for individual plants. The dimensions of individual treatment plots were used to calculate LAI per treatment.

Four to six whole plants were selected at random and collected from each treatment when the central inflorescence of each was judged to be mature. All leaves attached to the plant at the time of harvest, including those undergoing senescence, were removed, counted and placed in labeled plastic sampling bags. Any vegetative growth having 3 or more leaves with an area of >30 cm^2 each, and being located in the axils of primary leaves or at the base of the plant, was classified as a sideshoot. All sideshoots were likewise removed and placed in individual bags, with counts being taken of the number of sideshoots per plant (if any) as well as the number of leaves per sideshoot. Bags were then sealed and stored at -30° C. Freezer storage was utilized in order to preserve leaves until leaf area measurements could be performed. Leaves were partially thawed and leaf area of primary leaves and sideshoots was then measured separately, using a LiCor LI-3000 Portable Leaf Area Meter. Total leaf area of each individual plant was obtained by adding primary leaf area and sideshoot leaf area. Calculations for LAI per plant were performed by dividing the total leaf area of each individual plant by its ground area. Values for LAI of each treatment were calculated by dividing the average total leaf area per treatment by the ground area of the treatment.

Stalk Circumference and Hollow-Stem

Stalk circumference. Circumference of the stalk was measured at a point 15 cm below the tip of the inflorescence.

Hollow-stem. The entire stalk was cut longitudinally, beginning at a point 2.5 cm above the roots and ending at the tip of the inflorescence. Measurements of hollow-stem length and width were performed on all plants which exhibited measurable symptoms of the disorder. Using these data, the formula for determining the volume of a cylinder was employed to calculate the total volume of each stalk and the volume of hollow-stem. Percent stalk damage was obtained by dividing the volume of hollow-stem by the total stalk volume and multiplying the result by 100. Within each treatment, plants were classified into two groups according to whether or not they showed visible symptoms of the disorder. These values are expressed as the percentage of plants per treatment affected by hollow-stem. Measurements of hollow-stem represent the results of 1 year's data.

Plant Tissue Samples for Mineral and Fiber Analyses

Mineral analyses. Mineral analyses were conducted for one experiment. Four plants were selected at random from each treatment at the time of harvest. Whole leaves, including the petiole, were collected from three separate positions on the plant in order to include newly-emerged leaves as well as those representing intermediate and senescent stages of growth. All samples were placed in labeled paper sampling bags and dried in a forced-air oven (72° C) for 48 hours. The dry material was ground in a Wiley mill to pass a 30-mesh screen. Ground tissue was stored in airtight polyvinyl bags until laboratory analyses were conducted.

Samples were prepared for nitrogen analysis by digestion in 18 mol/L H_2SO_4 and 11.9 mol/L H_2O_2, using the indophenol colorimetric method (Thomas, et al., 1967; Van Slyke and Hiller, 1933). Total amino-N nitrogen concentration of leaf and petiole tissue was determined using a Technicon Auto-Analyzer.

Samples used for determination of calcium, magnesium and potassium were first dry-ashed at 450° C for 6 hours in a muffle furnace. Following digestion with HNO_3 (1 N) and HCl (1 N), samples were filtered through #42 filter paper and diluted with deionized water to an appropriate concentration for analysis. Elemental concentrations were estimated by atomic absorption spectrophotometry on a Perkin-Elmer 5000 Atomic Absorption Spectrophotometer.

Fiber analyses. Tissue samples for crude fiber determination were obtained from 4 plants per treatment. A 5-cm section of stem was cut from the base of heads which had previously been trimmed to 15 cm in length. Fiber content of the stalk was determined by hot water insoluble fiber analysis. A 10-gram sample of tissue was weighed out and thoroughly homogenized in water. This mixture was boiled for 1 hour, then placed in a 30-mesh filter and rinsed continuously for 8 minutes. Samples were dried on tared filter paper and weighed. Fiber content was expressed as milligrams of dried fiber per gram of fresh tissue.

Soil Moisture and Stomatal Conductance Measurements

Stomatal data. A steady-state porometer (LiCor LI-1600) was used to measure stomatal conductance and transpiration rate of 4 data plants per treatment. Measurements were performed on the eighth fully expanded leaf of each plant, as leaves occupying this position on the stem were neither senescent nor heavily shaded. Data were collected within 2 hours of solar noon on clear days.

Soil moisture data. Soil samples for moisture determination were collected on the same days that stomatal conductance readings were performed. A soil probe was used to remove 5-cm long soil cores from a depth of 10.2 to 15.2 cm. Four soil cores per treatment were removed from the center of rows containing data plants (soil was not collected from border rows). The 4 soil cores were then combined in a previously tared sampling tin, weighed and placed in a forced-air oven at 65° C for 56 hours until constant weight was achieved. Tins were reweighed, with the difference in moisture content being recorded as a percentage (grams of moisture per gram of soil).

CHAPTER II

RESULTS AND DISCUSSION

Spacing Effects on Leaf Number, Leaf Area and Leaf Area Index

Primary Leaves

Increases in spacing were accompanied by increases in leaf number per plant. Figure 6 shows the range of spacings at which an individual plant is predicted to attain a given number of leaves. Plants which had attained 18 to 22 primary leaves at maturity were produced at the widest spacing tested, 122 x 122 cm. Conversely, decreases in spacing resulted in a lower number of primary leaves per plant. Plants grown at the closest spacing tested (15 x 15 cm) had the fewest number of primary leaves, ranging from a minimum of 8 to a maximum of 12. Spacings of intermediate width, for example 24 x 120 cm, 120 x 64 cm, or 60 x 60 cm, generally produced plants having 14 to 16 primary leaves. Area of primary leaves also showed a progressive increase with increases in spacing (Figure 7).

Total Leaf Area

Total leaf area per plant also increased in response to increases in spacing and decreased with decreases in spacing (Figure 8). Total leaf area per plant reached a maximum (15,696 cm^2) at the widest spacing tested, 122 x 122 cm. Lowest total leaf area

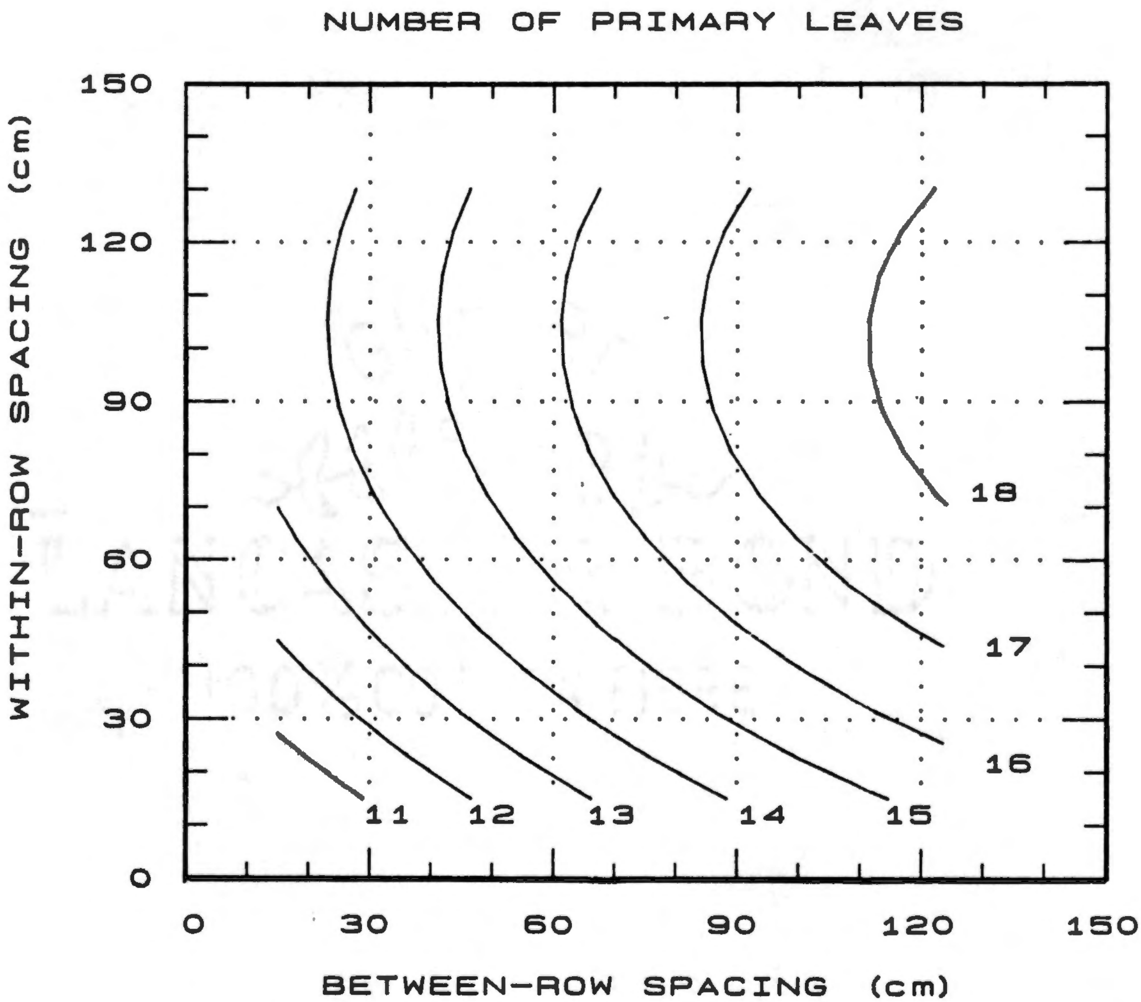

Figure 6. Effects of between-row and within-row spacing on the number of primary leaves per plant. R^2=0.581890, Y= 7.96335077 + (0.06765195 x x_1) + (0.08748087 x x_2) - (0.00014339 x x_1^2) - (0.00041349 x x_2^2) - (0.0000295 x $x_1^2 x_2^2$) where Y = number of primary leaves per plant, x_1 = between-row spacing (cm) and x_2 = within-row spacing (cm).

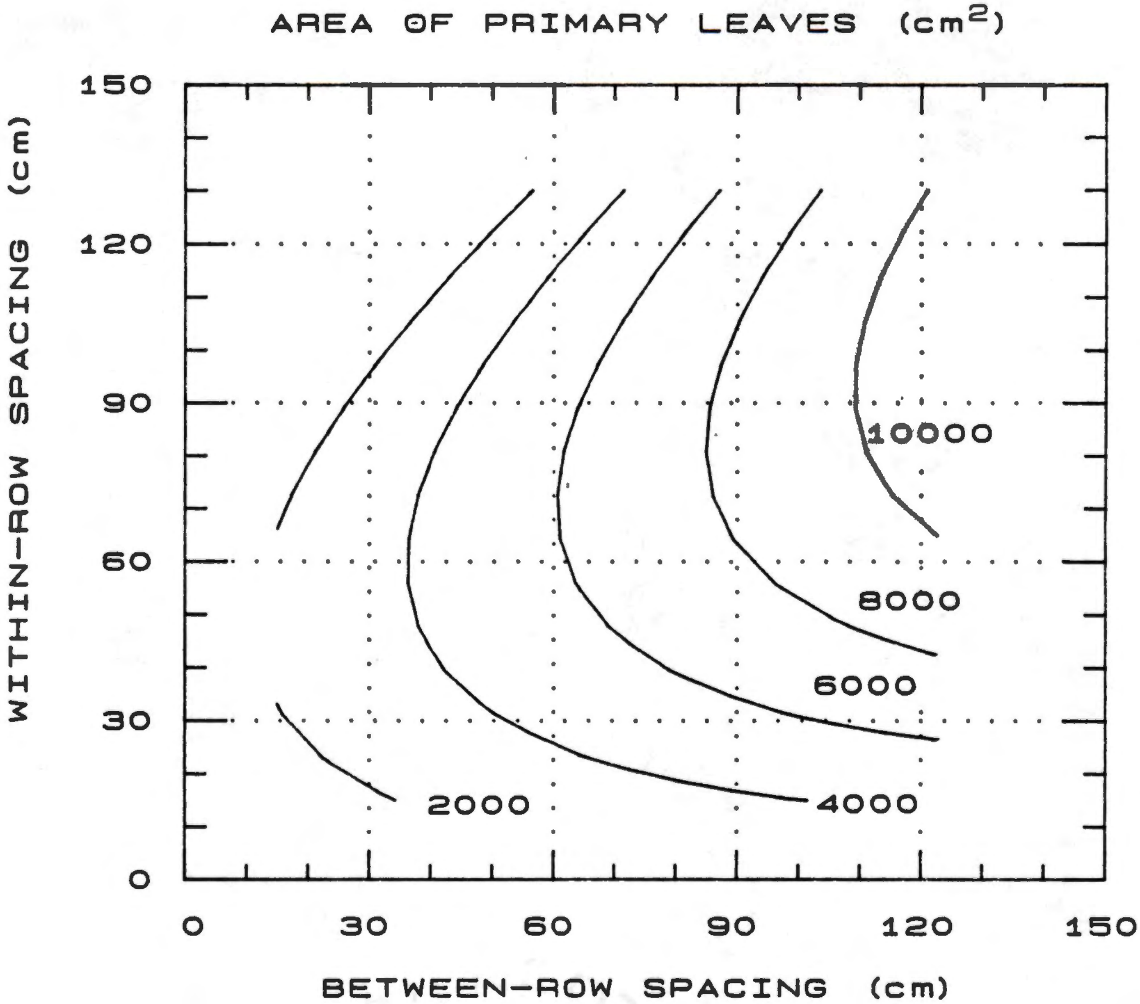

Figure 7. Effects of between-row and within-row spacing on the primary leaf area per plant. R^2=0.822097, Y=-725.4612272 + (42.7709675 x x_1) + (83.50095778 x x_2) - (0.19407119 x x_1^2) - (0.9743542 x x_2^2) + (0.8902814 x $x_1^2x_2^2$) where Y = primary leaf area per plant, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

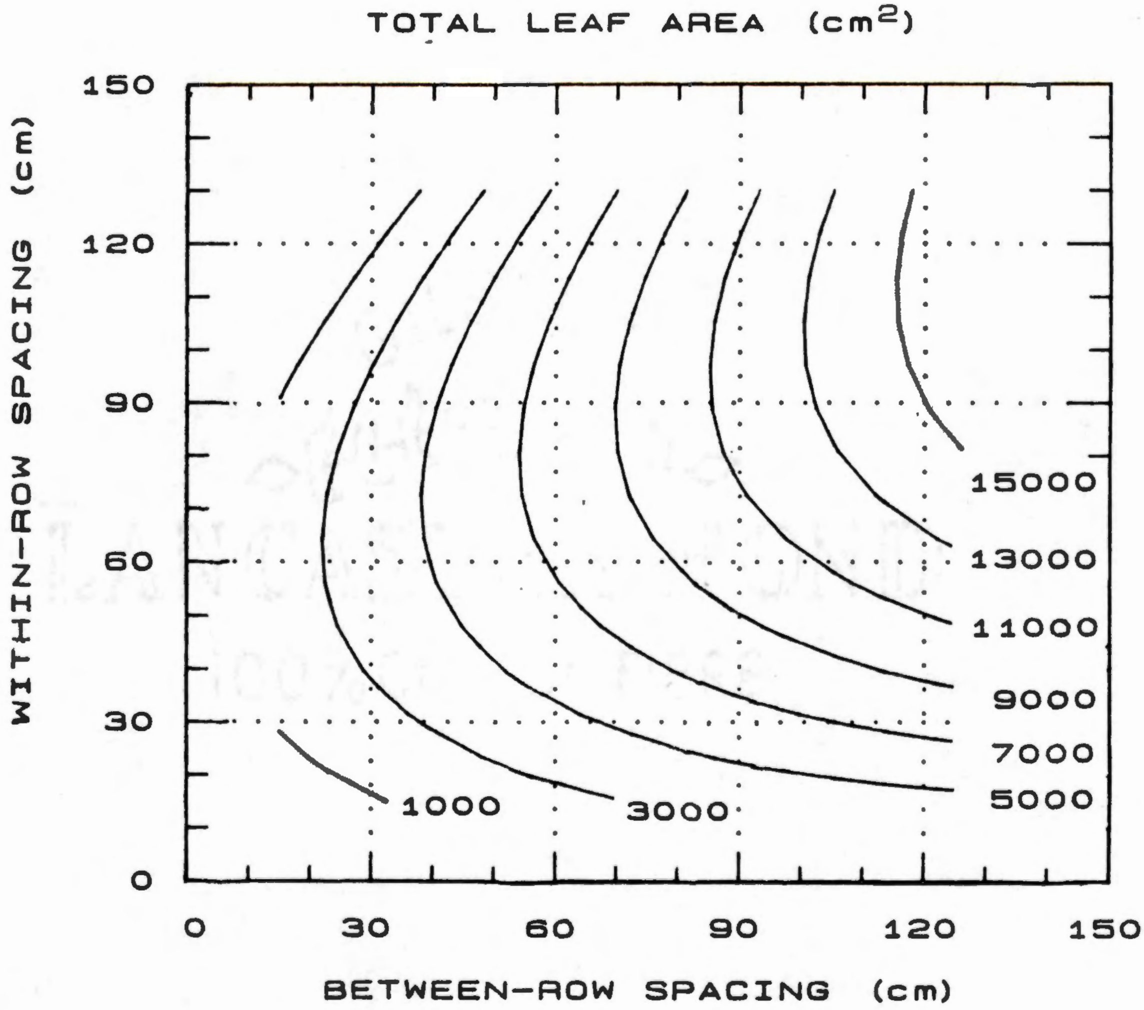

Figure 8. Effects of between-row and within-row spacing on the total leaf area per plant. R^2=0.845445, $Y=-2761.886748 + (58.53883279 \times x_1) + (119.680608 \times x_2) - (0.24338472 \times x_1^2) - (1.15409965 \times x_2^2) + (1.18647188 \times x_1^2 x_2^2)$ where Y = total leaf area per plant, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

values were associated with the closest spacing treatments. At spacings of 15 x 15 cm, total leaf area per plant averaged 1,168 cm^2. These results are comparable to findings reported by Salter (1961), who found that the average leaf area of cauliflower plants was progressively reduced in response to closer spacing. However, nitrogen deficiencies at very close spacings may have influenced results of that study. Chemical analyses of plant material collected during the present study showed no evidence of nutrient deficiencies at any spacing tested.

Leaf Area Index (LAI)

Calculations of leaf area in relation to ground area of individual plants were performed. The resulting values were arbitrarily referred to as "leaf area index per plant." These values increased with progressive increases in spacing (Figure 9). Values for leaf area index per plant reached a maximum (2.2) at the widest spacing tested, 122 x 122. Plants grown at the closest spacing tested (15 x 15 cm) had the lowest values for leaf area index per plant, which averaged 0.6. However, when LAI was calculated for each individual treatment, the reverse was shown to be true. Figure 10 shows average LAI values per treatment. LAI values were lowest at the wider spacings, and reached a minimum value of 0.5 at spacings of 122 x 122 cm. Conversely, LAI per treatment was highest at the narrowest spacings tested. Maximum values of 3.5 were obtained at spacings of 15 x 15 cm.

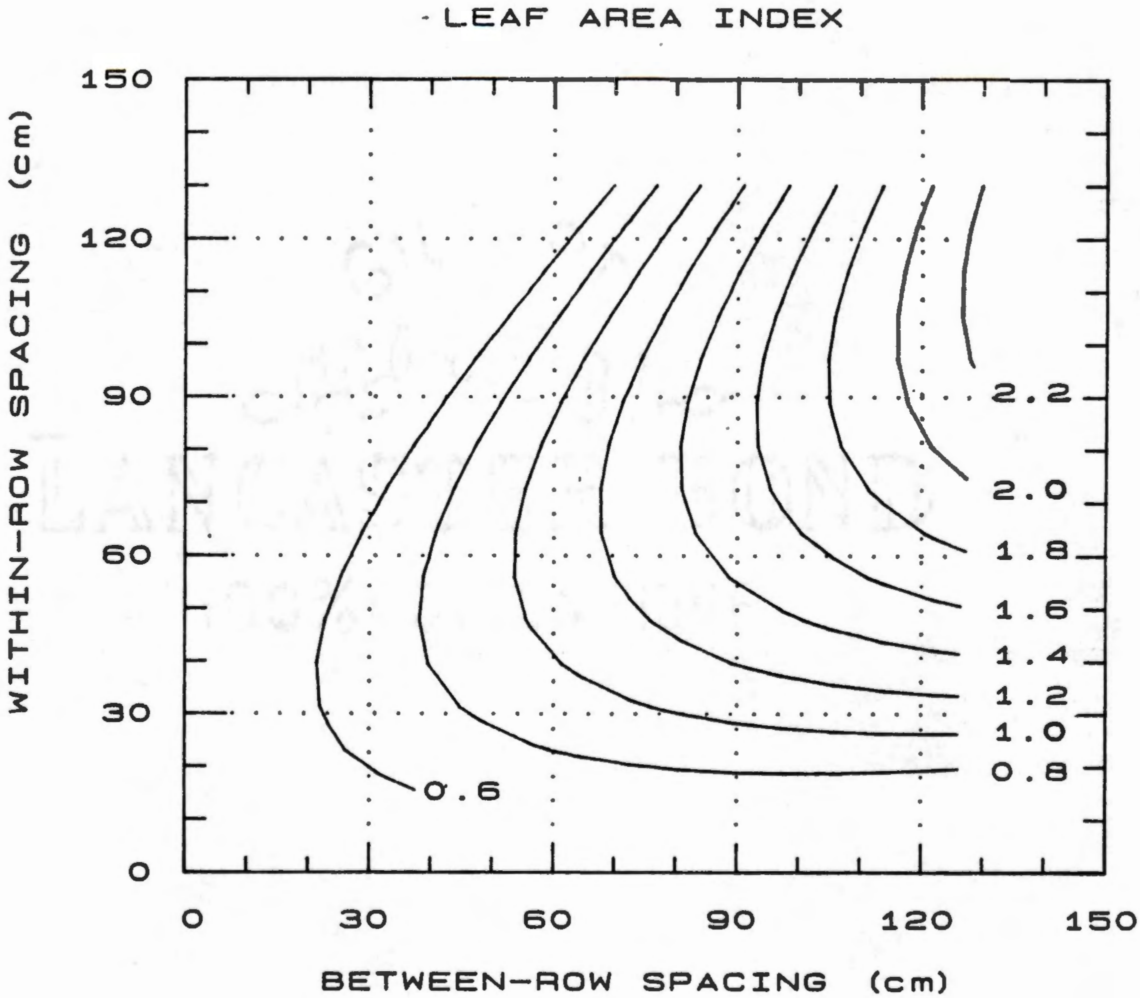

Figure 9. Effects of between-row and within-row spacing on leaf area index of individual plants. R^2=0.721997, $Y = 0.286335905 + (0.00412933 \times x_1) + (0.00807521 \times x_2) - (0.0000433 \times x_1^2) - (0.0001768 \times x_2^2) + (0.00023978 \times x_1^2 x_2^2)$ where Y = leaf area index of individual plants, x_1 = between-row spacing (cm), and x_2 = within-row spacing.

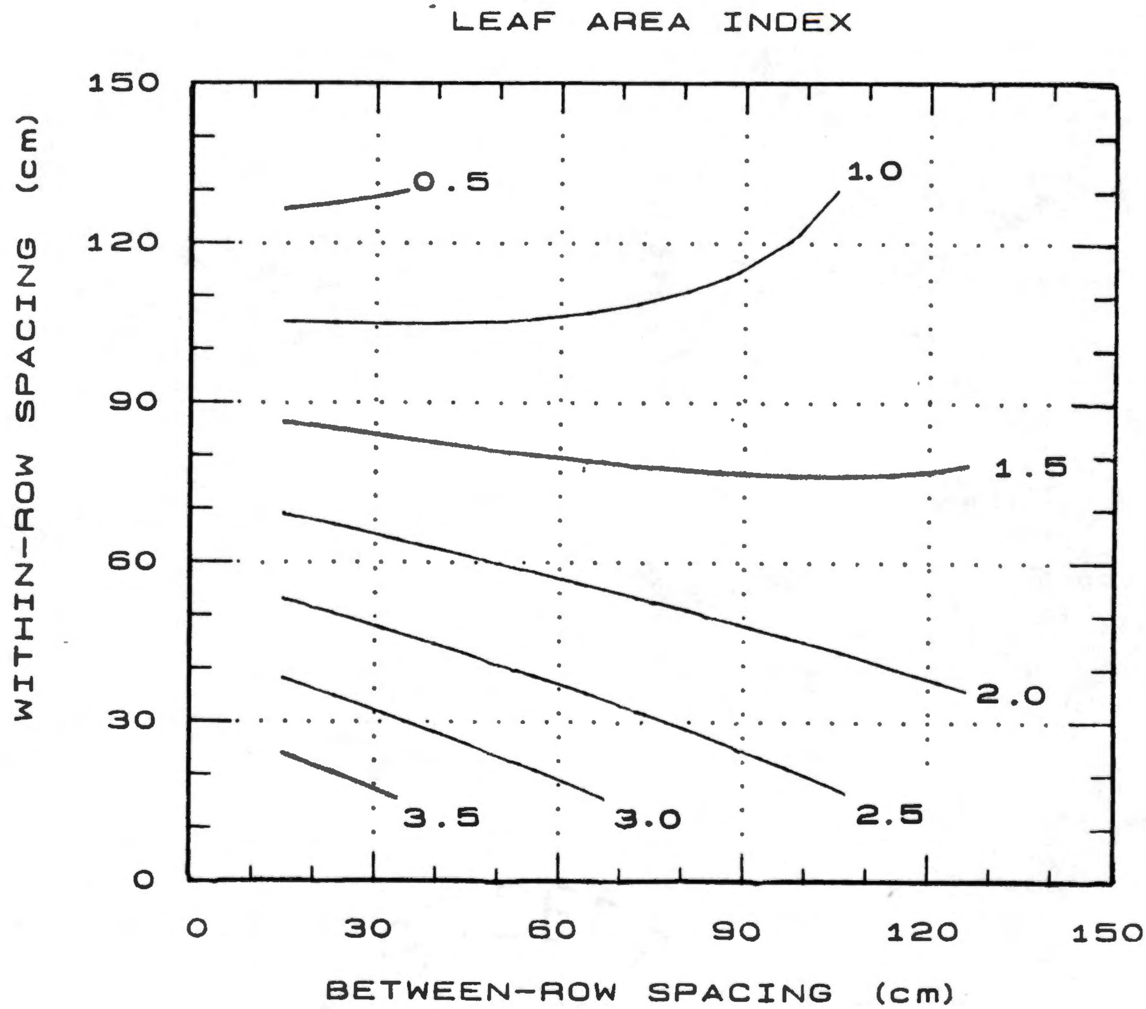

Figure 10. Effects of between-row and within-row spacing on the leaf area index per treatment. R^2=0.845445, Y=-2761.886748 + (58.53883279 x x_1) + (119.68060806 x x_2) - (0.24338472 x x_1^2) - (1.15409965 x x_2^2) + (1.18647188 x $x_1^2 x_2^2$) where Y = leaf area index, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

Sideshoots

The number of sideshoots per plant, as well as their individual number and size, was markedly influenced by spacing (Figures 11, 12 and 13). Spacing effects were similar to those observed for primary leaves. As spacing increased, the quantity, leaf number and leaf area of sideshoots also increased. Likewise, decreases in spacing resulted in reduction of sideshoot quantity, leaf number and leaf area.

Sideshoots contributed substantially to the total leaf area of an individual plant. Primary leaf number of a plant grown at an intermediate spacing of 31 x 91 cm averaged 5,040 cm^2, while side-shoot leaf area of a plant grown at the same spacing averaged 601 cm^2. Therefore, sideshoot area comprised 10 percent of the total (6,016 cm^2) average leaf area per plant. The contribution of sideshoot area to total leaf area also increased in response to increases in spacing. At the widest spacings of 122 x 122 cm, primary leaf area per plant averaged 10,241 cm^2 and sideshoot leaf area averaged 5,455 cm^2. Sideshoot leaf area thus amounted to 35 percent of the total (15,696 cm^2) average leaf area.

Spacing effects on primary leaf number, leaf area, and LAI are potentially important in terms of their influence on productivity and yield. As previously shown, maximum values for leaf number and leaf area were associated with the two widest spacings tested, 91 x 122 cm and 122 x 122 cm. Largest individual head weights of 0.6 kg or greater were also obtained at these wide spacings (Figure 14).

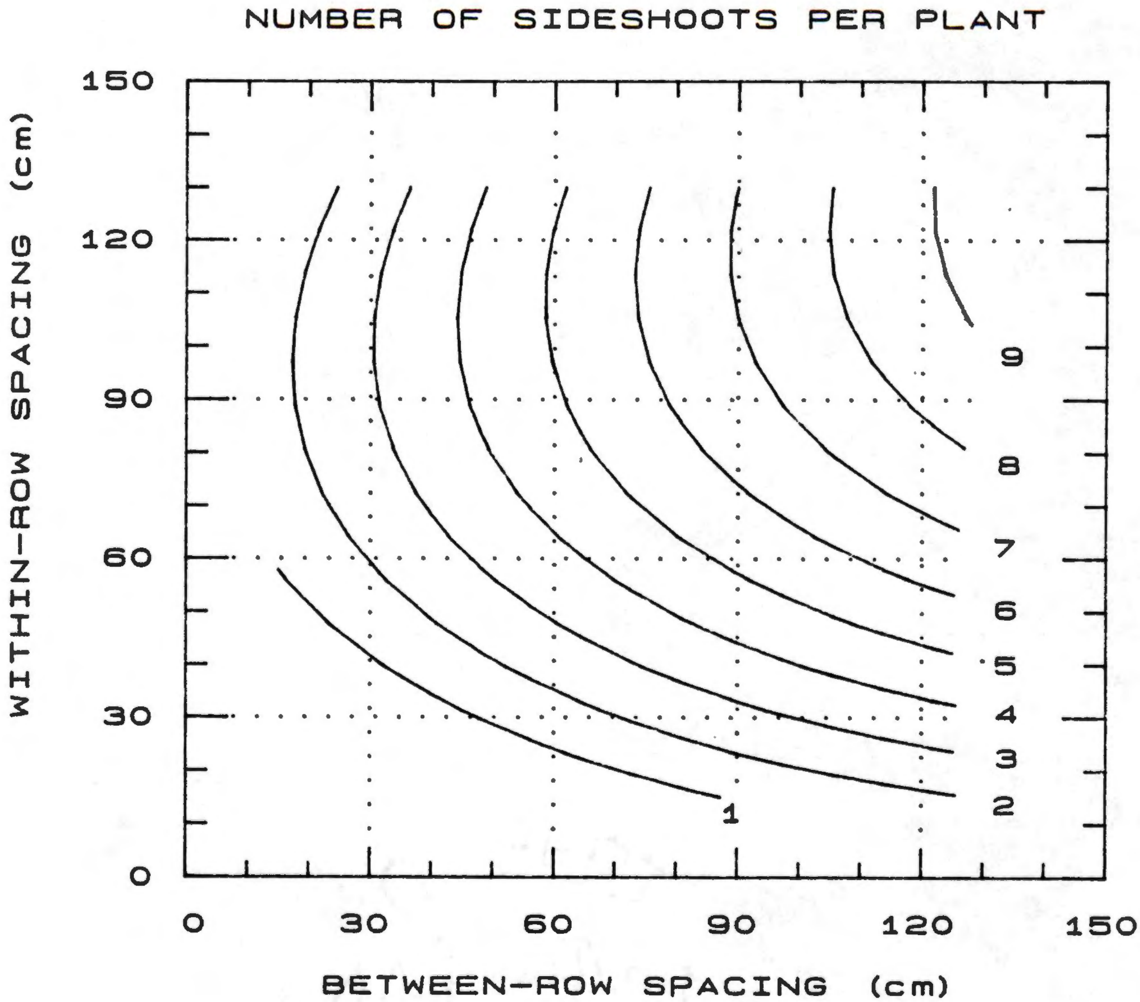

Figure 11. Effects of between-row and within-row spacing on the number of sideshoots per plant. $R^2=0.530908$, $Y=-4.10992439 + (0.0495375 \times x_1) + (0.10408364 \times x_2) - (0.00014129 \times x_1^2) - (0.00056820 \times x_2^2) + (0.00033110 \times x_1^2 x_2^2)$ where Y = number of sideshoots per plant, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

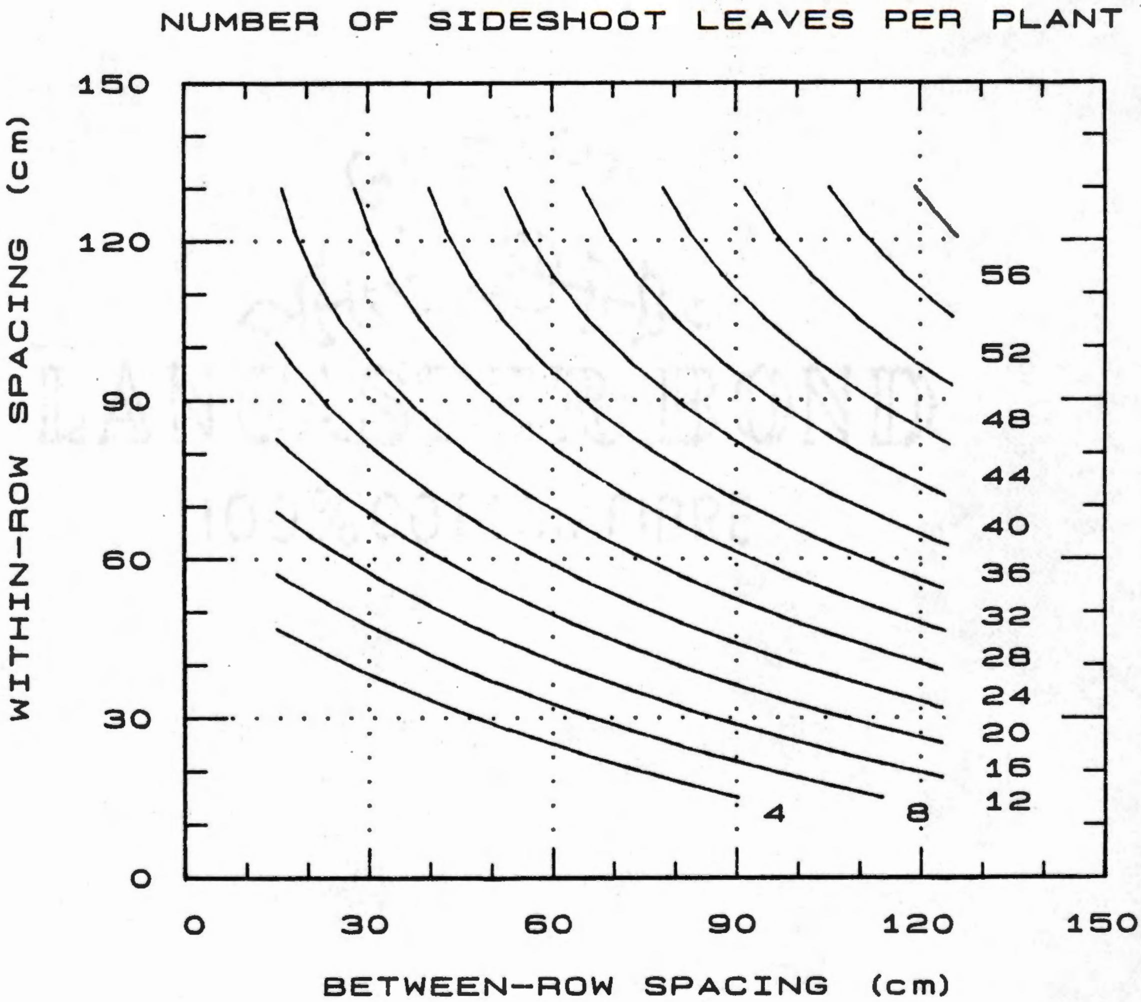

Figure 12. Effects of between-row and within-row spacing on the number of sideshoot leaves per plant. R^2=0.642485, Y=-22.5749158 + (0.21291077 x x_1) + (0.58197871 x x_2) - (0.00028379 x x_1^2) - (0.0020436 x x_2^2) + (0.00103845 x $x_1^2 x_2^2$) where Y = number of sideshoot leaves per plant, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

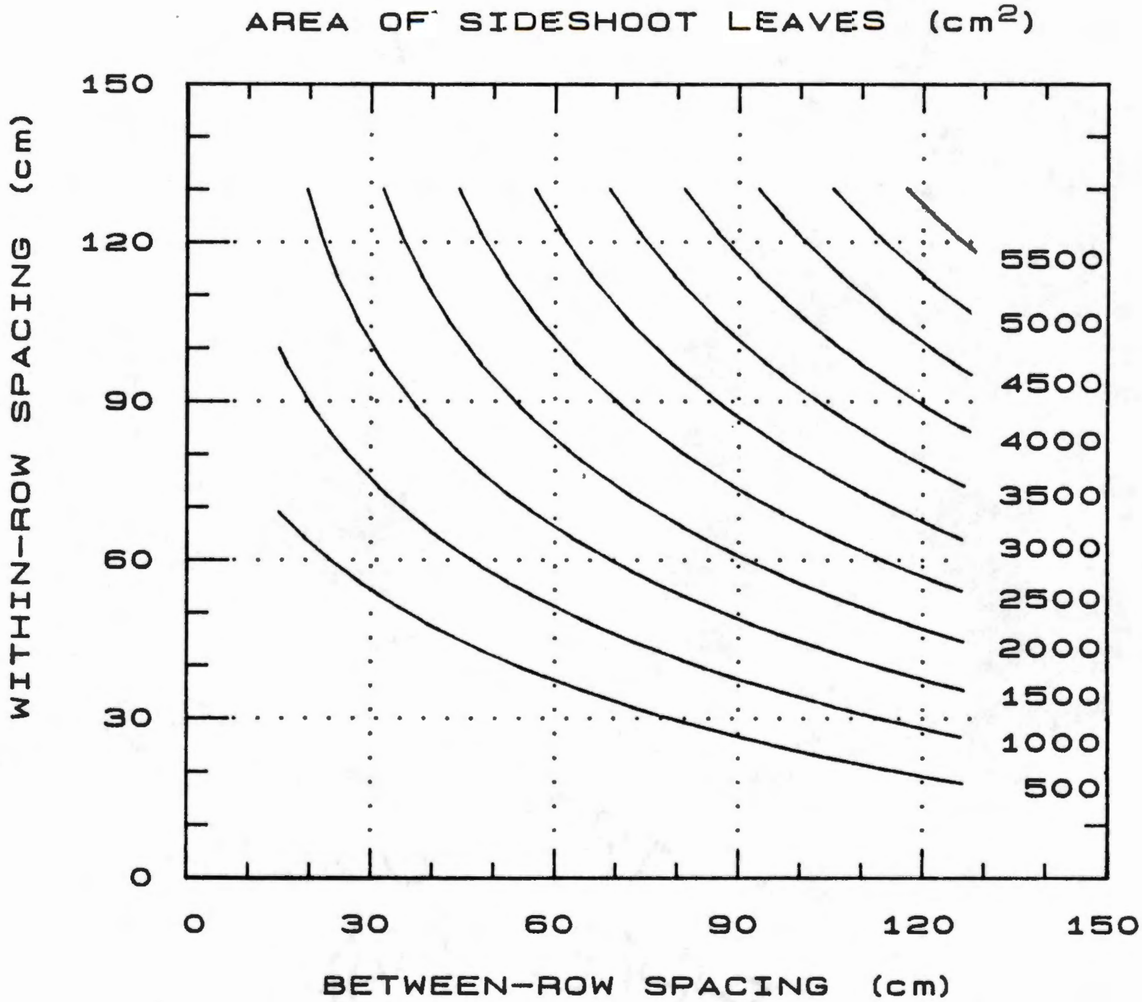

Figure 13. Effects of between-row and within-row spacing on the area of sideshoot leaves per plant. R^2=0.716263, Y=-1342.951064 + (5.11738689 x x_1) + (28,07138331 x x_2) + (0.0080108 x x_1^2) - (0.09415321 x x_2^2) + (0.26702263 x $x_1^2 x_2^2$), where Y = leaf area of sideshoots, x_1 = between-row spacings (cm), and x_2 = within-row spacing (cm).

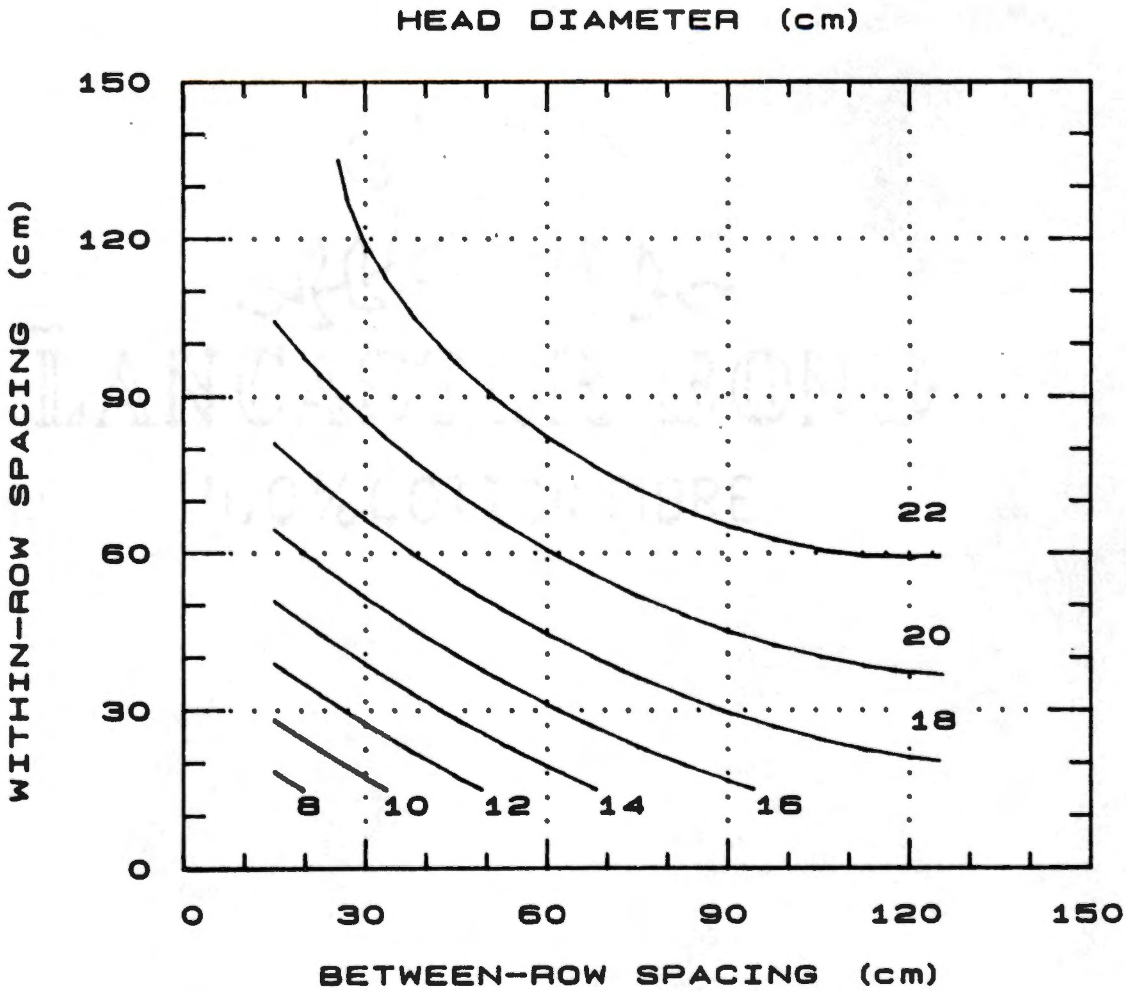

Figure 14. Effects of between-row and within-row spacing on the head diameter of broccoli, expressed in cm. Contour intervals are plotted at increments of 2 cm. R^2=0.870190, $Y=1.12877559 + (0.18841274 \times x_1) + (0.25419154 \times x_2) - (0.0006231 \times x_1^2) - (0.00085063 \times x_2^2) - (0.00067698 \times x_1^2x_2^2) - (0.00085063 \times x_2^2) - (0.00067698 \times x_1^2x_2^2)$ where Y = head diameter (cm), x_1 = between-row spacing (cm), x_2 = within-row spacing (cm).

An allometric relationship (i.e., one in which the relative growth of a plant part is considered in relation to growth of the entire plant) between leaf size and curd size of cauliflower has previously been established (Salter, 1960). It should be noted, however, that Salter measured leaf size in terms of fresh and dry weights, rather than by leaf area as in the present study.

Increasing LAI during early phases of plant growth may enable the crop to intercept a greater total amount of solar radiation. Consequently, photosynthetic ability of the crop will be maximized, resulting in heightened yields (Frappell, 1979). Research in buckwheat has shown that crops planted at high densities attained their optimum LAI at an earlier stage than crops planted at low densities. Furthermore, the time required for the crop to achieve its maximum LAI appeared to be directly releated to yield of that crop (Iwaki, 1958). In the present study, average values for LAI at the time of harvest were lowest in the most closely spaced treatments (15 x 15 cm). Since no measurements of LAI were performed when the crop was in its early stages of growth, it was not possible to determine the times at which individual treatments achieved their optimum LAI. However, absolute highest total yields of 18,000 kg/ha were obtained from plants grown in the most closely spaced treatments, in contrast to maximum total yields of 5,400 kg/ha at the widest spacings tested (Figure 15).

Results of the present study indicate that spacing greatly influenced the horticultural production efficiency of individual

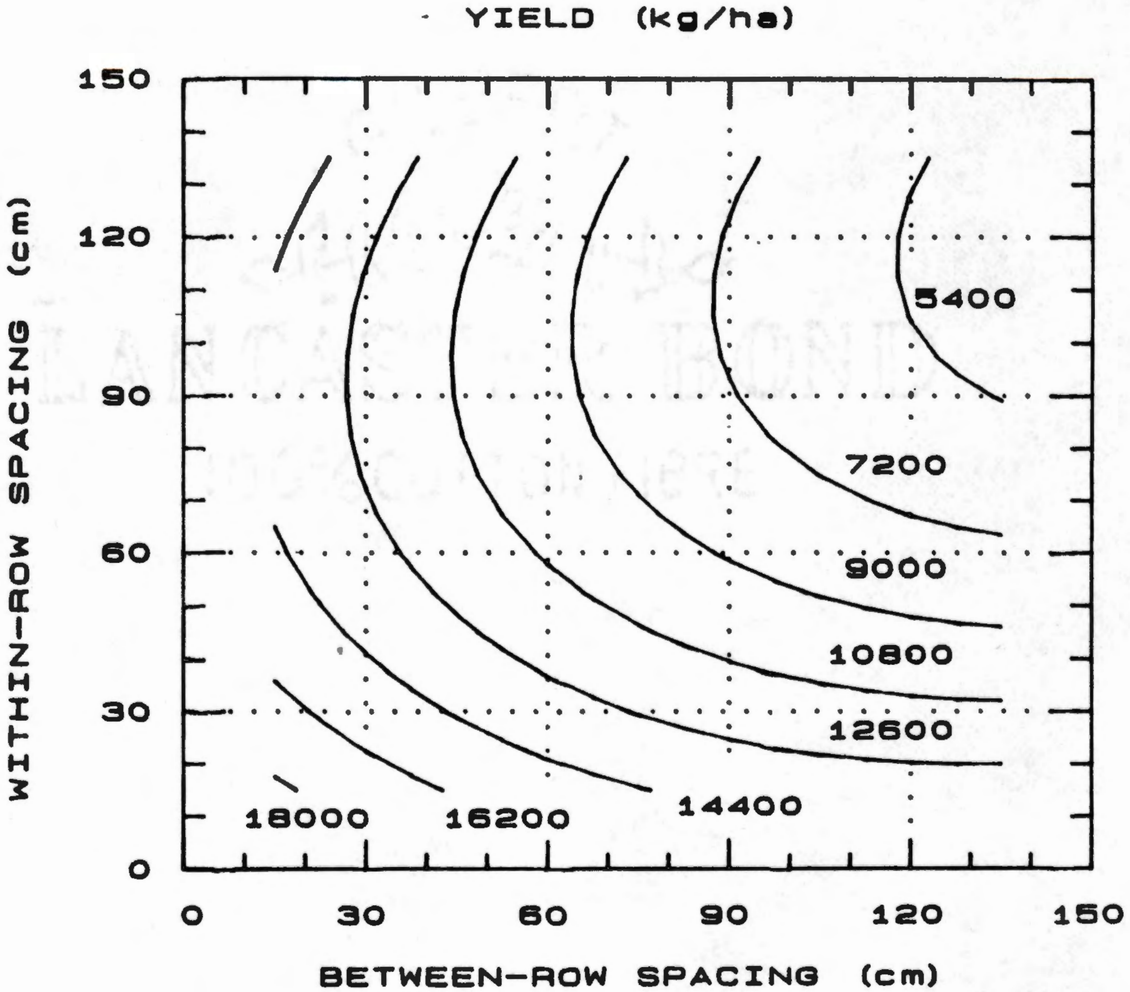

Figure 15. Effects of between-row and within-row spacing on the yield of broccoli, expressed in kg/ha. Contour intervals are plotted in increments of 1/10 of maximum total yield. $R^2=0.792499$, $Y=21533.09398 - (91.80137548 \times x_1) - (135.523795 \times x_2) + (0.3805981 \times x_1^2) + (0.79319811 \times x_2^2) - (0.40756464 \times x_1^2 x_2^2)$ where Y = yield (kg/ha), x_1 = between-row spacing, and x_2 = within-row spacing (cm).

plants. At the widest spacings tested, total leaf area per plant was ten times greater than that of plants grown at the narrowest spacings. However, head size of plants grown at the widest spacings was only three times greater than that of plants grown at the narrowest spacings. It is apparent from these comparisons that spacings which permitted almost unlimited vegetative growth did not result in proportionate increases in reproductive growth. Although sideshoots contributed substantially to the total leaf area per plant, this overall gain in leaf area showed no apparent benefit in terms of increased head size. Thus, horticultural production efficiency per unit leaf area was actually higher for plants grown at very close spacings (Table 3).

Spacing Effects on Whole-Plant Conformation and Hollow-Stem

Whole-Plant Size

As spacing increased, plants became visibly larger in size and more robust in appearance. The average circumference of the stalk of plants grown at spacings of 122 x 122 cm was 18.1 cm. Progressive decreases in spacing resulted in gradual changes in plant conformation. Similar observations have been reported by other workers (Zink and Akana, 1951; Zink, 1968). Plants grown at very close spacings were often tall and spindly in appearance. At spacings of 15 x 15 cm, stem circumference averaged 5.7 cm (data not shown). Many of the plants in this treatment exhibited a malformed shape, probably as a result of intense competition among plants for light and water.

Table 3. Horticultural Production Efficiency of Plants Grown in Narrow vs. Wide Spacing Arrangements.[a]

Spacing (cm)			Total Leaf Area Per Plant (cm^2)	Head Diameter (cm)	Leaf Area (cm^2) Per Unit Head Diameter (cm)
Within-Row		Between-Row			
15	x	60	2500	13	192
30	x	90	6000	18	333
45	x	120	10000	21	476
90	x	120	15000	23	652

[a]Comparisons of selected spacings, showing the increase in head size per plant relative to the increase in total leaf area per plant.

Hollow-Stem

Changes in spacing also influenced the incidence and severity of hollow-stem (Figure 16). This disorder was more prevalent at wide spacings, with approximately 90 percent of plants per treatment exhibiting measurable symptoms at the widest spacing tested, 122 x 122 cm. In contrast, occurrence of hollow-stem was minimized at close spacings, with fewer than 10 percent of plants showing measurable symptoms at the closest spacing tested, 15 x 15 cm (Figure 17). Many other workers have found the disorder to occur most frequently in plants grown at wide spacings (Zink and Akana, 1951; Zink, 1968; Cutcliffe, 1972; Hipp, 1974; Dufault and Waters, 1985). It has been suggested (Zink, 1968; Cutcliffe, 1972) that the condition may be related to accelerated development of plants as they approach maturity. The lack of plant competition at very wide spacings might particularly favor rapid, unrestricted growth, with the result that wide spacings tend to produce a higher proportion of plants affected by the disorder.

As previously discussed, stem circumference and overall size of individual plants became progressively larger in response to increases in spacing. In similar fashion, increases in spacing produced a concomitant increase in the actual size (i.e., length, width and volume) of hollow-stem damage (see Appendix).

Spacing Effects on Stomatal Conductance of Leaves and Moisture Content of Soil

Stomatal Conductance

Results of stomatal conductance measurements, performed in conjunction with soil moisture determinations, are presented graphically

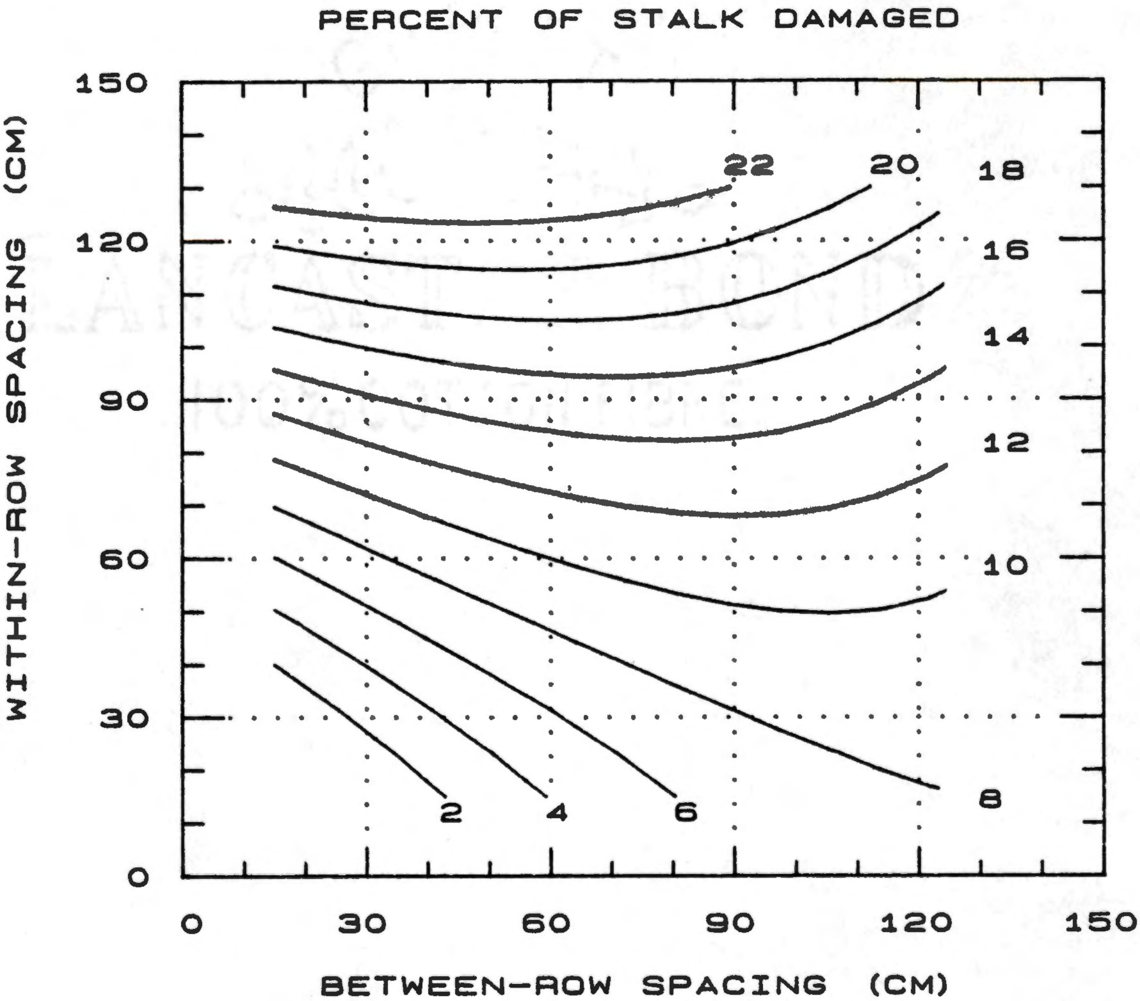

Figure 16. Effect of between-row and within-row spacing on percent of stalk damaged by hollow-stem. Contour intervals are plotted in increments of 2 percent. R^2=0.292891, Y= -7.686119293 + (0.21703082 x x_1) + (0.16172124 x x_2) - (0.00075719 x x_1^2) + (0.00052438 x x_2^2) - (0.00116605 x $x_1^2 x_2^2$) where Y = percent of stalk damaged, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

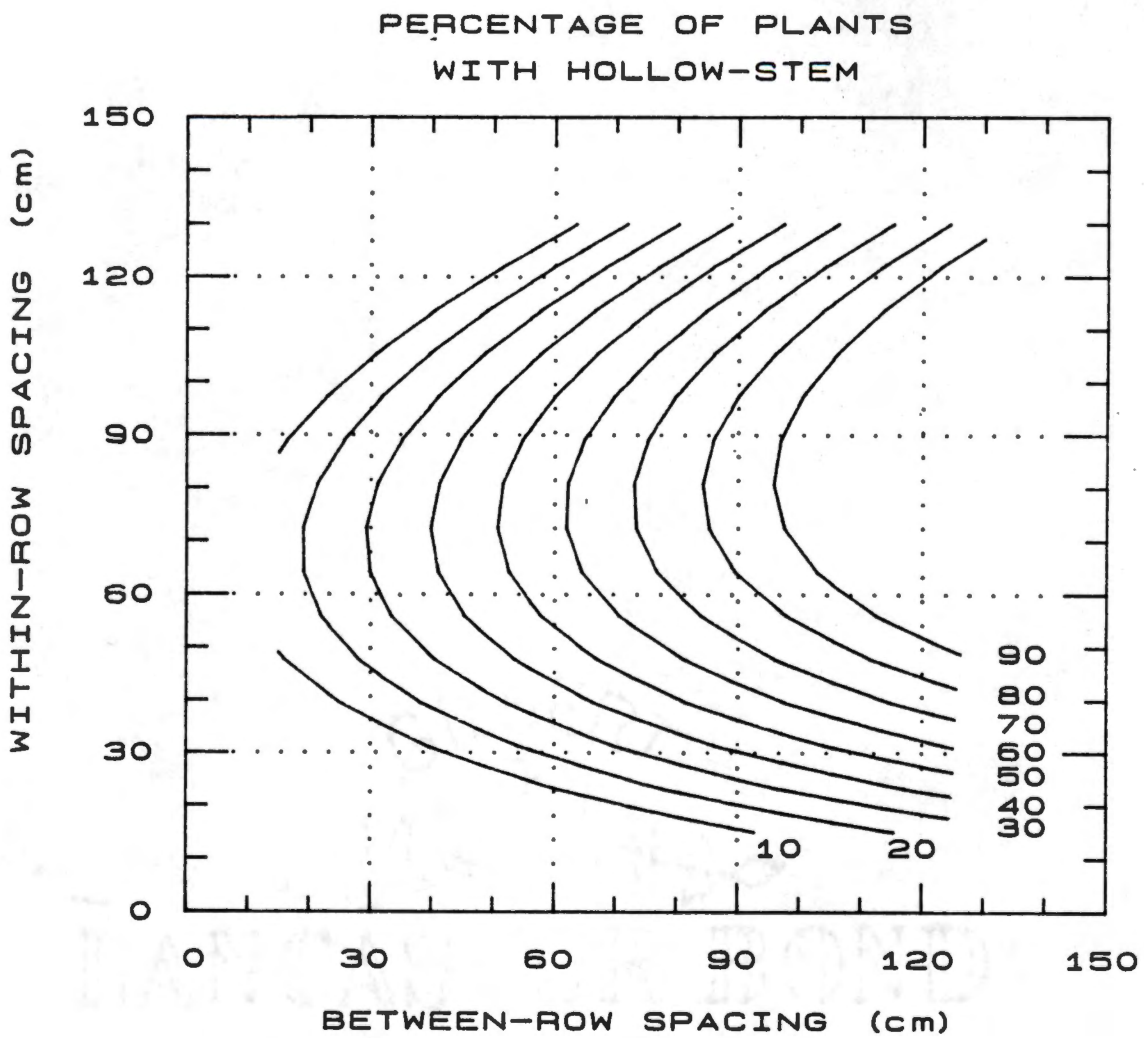

Figure 17. Effect of between-row and within-row spacing on percent of plants with hollow-stem. Contour intervals are plotted in increments of 10 percent. R^2=0.821860, Y=-74.1079494 + (0.59257788 x x_1) + (2.32481996 x x_2) - (0.00116306 x x_1^2) - (0.01778466 x x_2^2) + (0.00598579 x $x_1^2 x_2^2$) where Y = percent of plants with hollow stem, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

in Figure 18. Stomatal conductance readings were highest at close spacings and gradually decreased thereafter, with lowest readings obtained at the widest spacings. These findings imply that intense competition pressures present at very close spacings might have caused plants to transpire at unusually high rates. As a result, soil moisture would have been depleted more rapidly at narrow spacings than at wide spacings. Stomatal behavior is known to be directly influenced by changes within the environment and within the plant. Specifically, the water potential of the plant is the fundamental factor involved in the regulation of pore width (Larcher, 1980). Stomatal conductance may also influence photosynthetic capability of the plant. It has been shown that the stomatal conductance of a leaf is an indicator of its capacity to assimilate CO_2 (Farquhar and Sharkey, 1982).

Soil Moisture Content

Figure 19 shows soil moisture content in relation to plant spacing. Increases in spacing were accompanied by increases in percent soil moisture. Highest values for soil moisture content (19 to 21 percent) were obtained at the widest spacing tested, 122 x 122 cm. Likewise, lowest values for soil moisture (16 percent) were associated with the closest spacing tested, 15 x 15 cm.

These results were somewhat contradictory to visual observations made during the course of the experiment, as the soil surface of widely-spaced treatments appeared to dry out more rapidly and

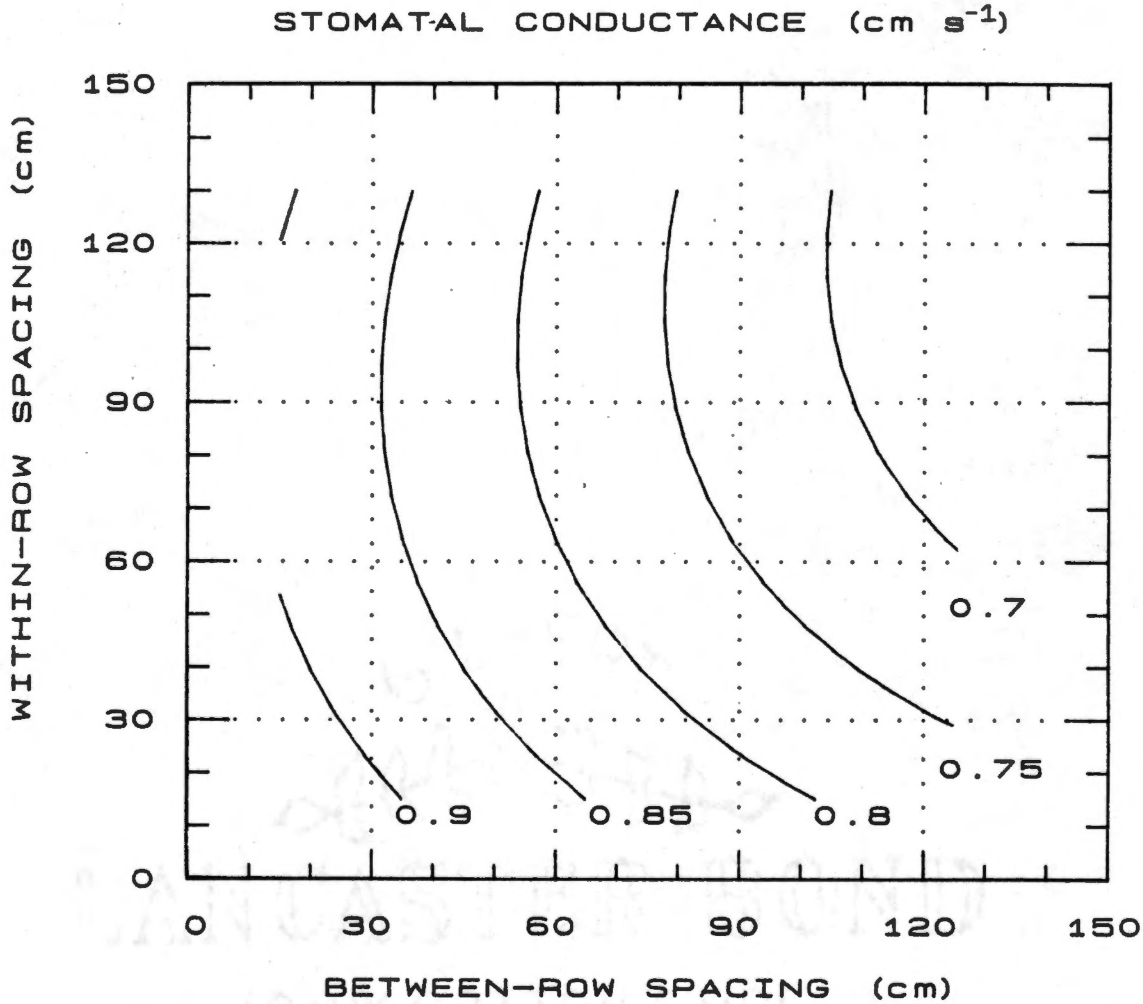

Figure 18. Effect of between-row and within-row spacing on leaf stomatal conductance. R^2=0.078478, Y=0.770147875 - (0.01359314 x x_1) + (0.01173672 x x_2) + (0.00012504 x x_1^2) - (0.0000781 x x_2^2) - (0.0000648 x $x_1^2x_2^2$) where Y = stomatal conductance in cm s^{-1}, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

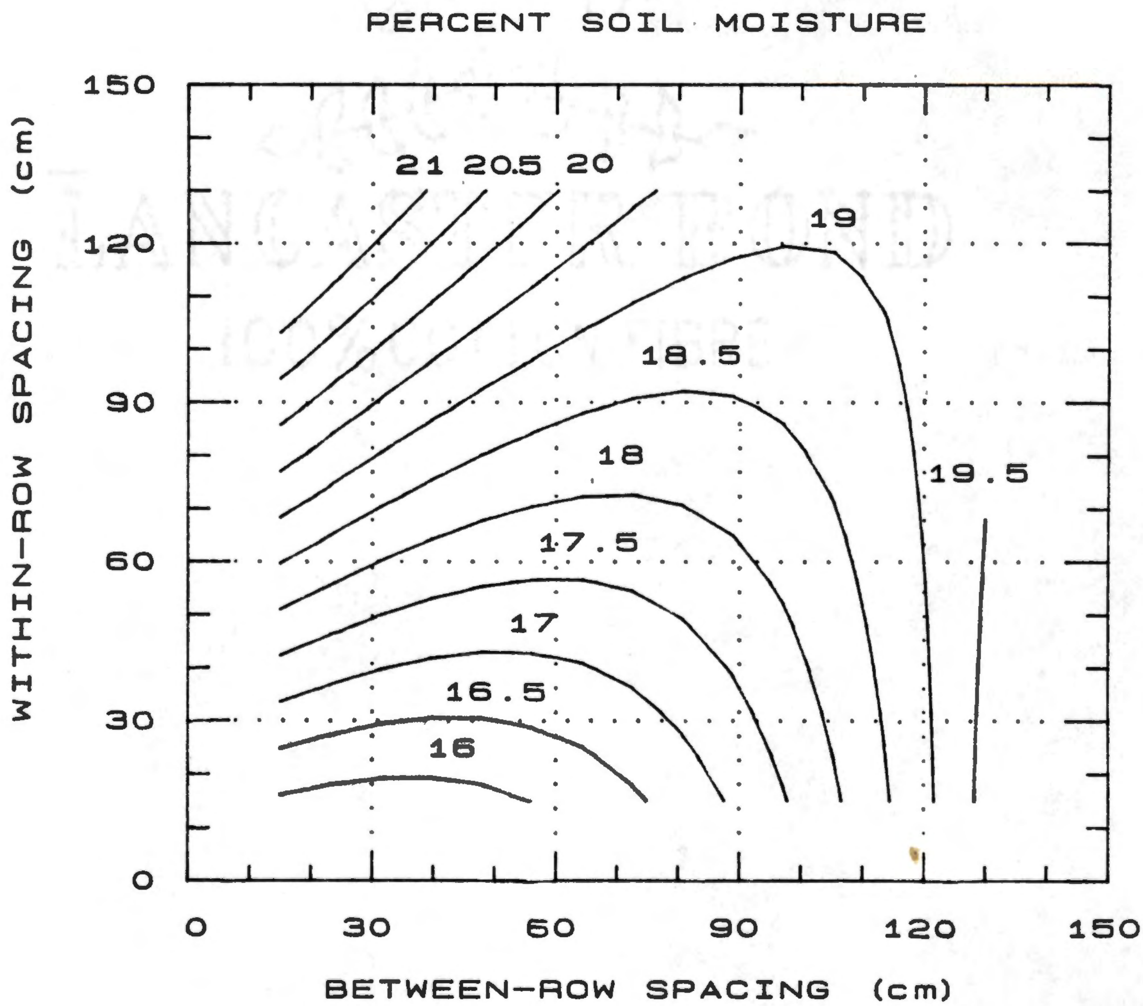

Figure 19. Effect of between-row and within-row spacing on soil moisture content. $R^2=0.395605$, $Y=17.22263669 - (0.03912964 \times x_1) + (0.03804482 \times x_2) + (0.00018775 \times x_1^2) - (0.00041325 \times x_2^2) + (0.0000613 \times x_1^2 x_2^2)$ where Y = percent soil moisture, x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

completely than the soil surface of closely-spaced treatments. It had therefore been assumed that the dense plant canopies associated with close spacings effectively prevented any substantial evaporative losses from the soil below. Holliday (1960) proposed that plant competition at very high densities might restrict the depth to which roots could penetrate. Consequently, less water would be absorbed from the soil profile.

A number of interrelated factors may be responsible for these discrepancies between observed and measured responses. First, density of the vegetative canopy would be influenced by the proximity and arrangement of the individual plants within each treatment. In very dense stands the amount of precipitation which actually reaches the ground is that which falls through gaps in the plant canopy, drips off leaves or runs down the stem (Lundegardh, 1974). Therefore, differences in soil moisture content among treatments could be at least partially attributable to a local unevenness in the initial distribution of precipitation.

At the widest spacings, the extreme distances between individual plants prevented formation of a dense vegetative canopy. Therefore, it appeared that these treatments lost a substantial amount of soil moisture due to surface evaporation from the topmost layer of soil. However, the actual amount of water present in the root zone was shown to be greater at wide spacings. It is possible that less precipitation was initially intercepted by vegetation, resulting in higher total water absorption by the soil (Lundegardh, 1974).

Physical disturbance of the soil surface could also affect the amount of water present in the root zone. When the top layer of soil is broken up by mechanical tillage or hoeing, the natural process of evaporative water loss via soil capillarity is altered. The cultivated soil layer results in a greater amount of moisture being conserved by the underlying soil. At very narrow spacings, competition with crop plants effectively prevented weeds from being a major problem. Any weeds in those treatments were controlled by means of pulling, and consequently the soil surface was left relatively undisturbed. At very wide spacings, however, weeds became sufficiently noxious to merit the use of mechanical cultivation and hoeing. These procedures disturbed the top layer of soil considerably. The tendency of the narrow spacings to experience more soil water loss by capillary action may have contributed to the differences in soil moisture content between narrow and wide spacings.

Spacing Effects on Mineral and Fiber Content

Mineral Content

Results of this study indicated that there was no significant influence of plant spacing on nutrient composition of broccoli. Furthermore, all plant tissue samples tested contained moderate to high levels of the elements in question. Calcium content ranged from 32,000 ppm to 77,000 ppm; potassium, 5,400 ppm to 11,800 ppm, and magnesium, 500 to 1,000 ppm. It has been reported that nitrogen became a limiting factor in cauliflower crops grown at very close spacings (Salter, 1961). No such deficiencies were observed in the present study, with nitrogen content of leaf tissues ranging between 2.60 percent and 4.70 percent at all spacings tested. There were no statistical differences among treatments in regard to N content of tissue.

Crude Fiber Content

Crude fiber content of broccoli stalk tissue ranged between 33.5 g and 60.2 g (expressed as mg of dried fiber per g of fresh tissue). A general trend toward higher fiber content was seen in broccoli grown at wide spacings. Fiber content of plants grown at intermediate and narrow spacings was approximately the same (see Appendix).

LITERATURE CITED

LITERATURE CITED

Aldrich, Thomas M., Marvin J. Snyder, and Thomas M. Little. 1961. Plant spacing in broccoli--affects yield, head size, earliness. Calif. Agric. 15:10-11.

Armitage, A. M., W. H. Carlson, and C. E. Cress. 1981. Determination of flowering time and vegetative habit of _Tagetes patula_ through response surface techniques. J. Amer. Soc. Hort. Sci. 106:632-638.

Army, T. J. and F. A. Greer. 1967. Photosynthesis and crop production systems. pp. 321-332. In: A. San Pietro, F. A. Greer and T. J. Army (eds.). Harvesting the sun--Photosynthesis in Plant Life. Academic Press, Inc., New York.

Berdahl, J. D., D. C. Rasmusson, and D. N. Moss. 1972. Effect of leaf area on photosynthetic rate, light penetration and grain yield in barley. Crop Sci. 12:177-180.

Bhagsari, A. S. and R. H. Brown. 1986. Leaf photosynthesis and its correlation with leaf area. Crop Sci. 26:127-132.

Cutcliffe, J. A. 1972. Effects of plant spacing and nitrogen on incidence of hollow-stem in broccoli. Can. J. Plant Sci. 52:833-834.

Cutcliffe, J. A. 1975. Effect of plant spacing on single-harvest yields of several broccoli cultivars. Hortscience 10:417-419.

Dufault, Robert J. and Luther Waters, Jr. 1985. Interaction of nitrogen fertility and plant populations on transplanted broccoli and cauliflower yields. Hortscience 20:127-128.

Farguhar, G. D. and T. D. Sharkey. 1982. Stomatal conductance and photosynthesis. Ann. Rev. Plant Phys. 33:317-345.

Hipp, Billy W. 1974. Influence of nitrogen and maturity rate on hollow-stem in broccoli. Hortscience 9:68-69.

Iwaki, Hideo. 1958. The influence of density on the dry matter production of _Fagopyrum esculentum_. Jap. J. Bot. 16:210-226.

Karami, E. and J. B. Weaver, Jr. 1972. Growth analysis of American upland cotton, _Gossypium hirsutum_ L., with different leaf shapes and colors. Crop Sci. 12:317-320.

Larcher, W. 1980. Physiological Plant Ecology. Springer-Verlag, Berlin.

Lundegardh, H. 1974. Environment and Plant Development. Hafner Press, London.

Mandl, F. A. and G. R. Buss. 1981. Comparison of narrow and broad isolines of soybean. Crop Sci. 21:25-27.

Massey, P. H., Jr., James F. Eheart, R. W. Young, and G. E. Mattus. 1962. The effect of soil moisture, plant spacing, and leaf pruning on the yield and quality of broccoli. Proc. Amer. Soc. Hort. Sci. 81:316-323.

Nichols, M. A. 1972. Letters to the editors. Can. J. Plant Sci. 52:415-416.

Salter, P. J. 1960. The growth and development of early summer cauliflower in relation to environmental factors. J. Hort. Sci. 35:21-33.

Salter, P. J. 1961. The irrigation of early summer cauliflower in relation to stage of growth, plant spacing and nitrogen level. J. Hort. Sci. 36:241-253.

Salter, P. J., D. J. Andrews, and Jayne M. Akehurst. 1984. The effects of plant density, spatial arrangement and sowing date on yield and head characteristics of a new form of broccoli. J. Hort. Sci. 59:79-85.

Stone, J. F., P. I. Erickson, and A. S. Abdul-Jabbar. Stomatal closure behavior induced by row spacing and evaporative demand in irrigated peanuts. Agron. J. 77:197-202.

Thomas, R. L., R. W. Sheard, and J. R. Moyer. 1967. Comparison of conventional and automated procedures for nitrogen, phosphorus and potassium analysis of plant material using a single digestion. Agron. J. 59:240-243.

Van Slyke, D. D. and A. Hiller. 1933. Determination of ammonia in blood. J. Biol. Chem. 102:499-504.

Wong, S. C., J. R. Cowan, and G. D. Farquahar. 1979. Stomatal conductance correlates with photosynthetic capacity. Nature 282:242-246.

Zink, F. W. and D. A. Akana. 1951. The effect of spacing on the growth of sprouting broccoli. Proc. Amer. Soc. Hort. Sci. 58:160-163.

Zink, F. W. 1968. Hollow-stem in broccoli. Calif. Agric. 22:8-9.

APPENDIX

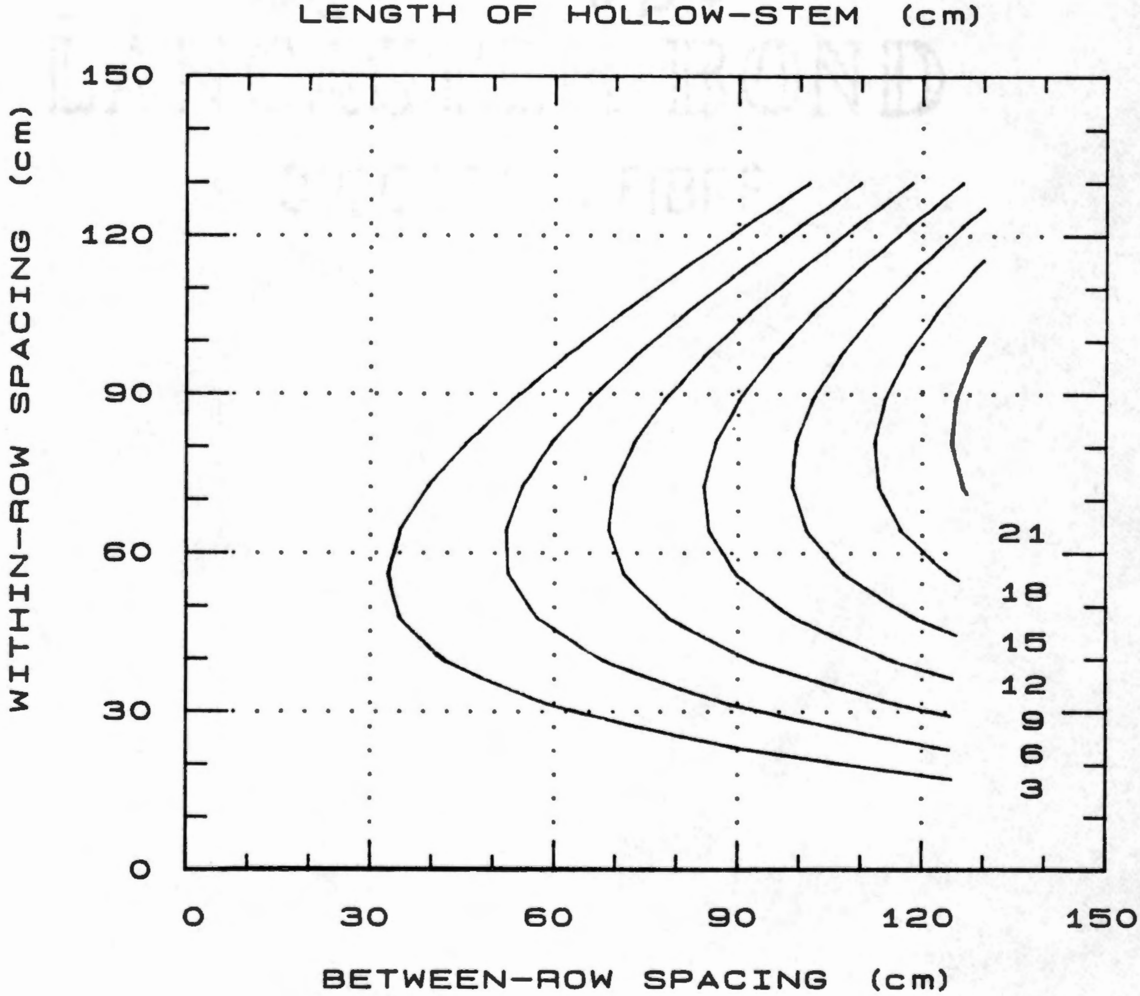

Figure 20. Effect of between-row and within-row spacing on length of hollow-stem. R^2=0.569299, Y=-5.70628976 - (0.02103573 x x_1) + (0.35651731 x x_2) - (0.00390399 x x_1^2) - (0.00390399 x x_2^2) + (0.00249823 x $x_1^2x_2^2$) where Y = length of hollow-stem (cm), x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

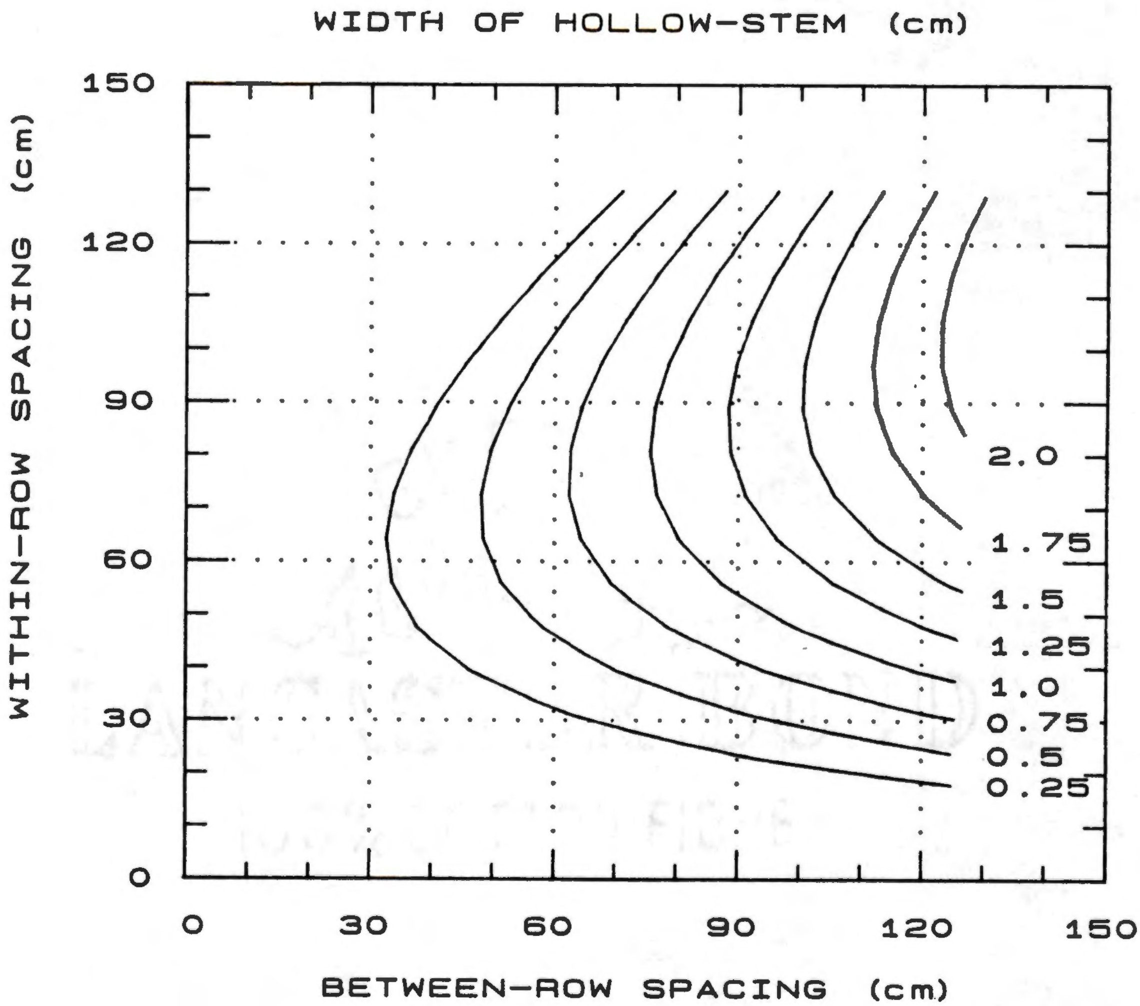

Figure 21. Effect of between-row and within-row spacing on width of hollow-stem. R^2=0.554869, Y=-1.028812588 + (0.00582893 x x_1) + (0.02507186 x x_2) - (0.0000048 x x_1^2) - (0.00016719 x x_2^2) + (0.00011048 x $x_1^2 x_2^2$) where Y = width of hollow-stem (cm), x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

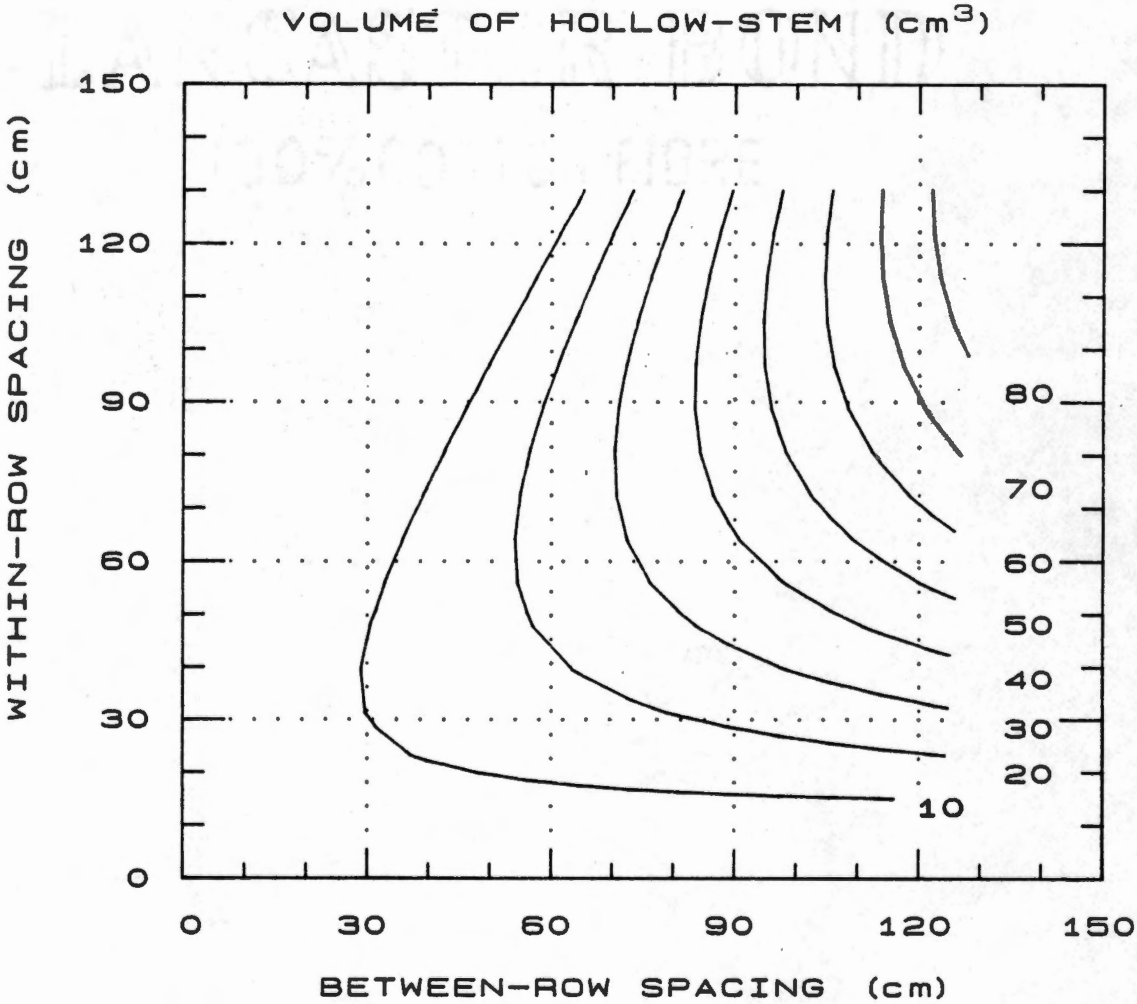

Figure 22. Effect of between-row and within-row spacing on volume of hollow-stem. R^2=0.457183, Y=-12.69652105 + (0.01175499 x x_1) + (0.14187003 x x_2) - (0.00017565 x x_1^2) - (0.00282354 x x_2^2) + (0.00669480 x $x_1^2 x_2^2$) where Y = volume of hollow-stem (cm^3), x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

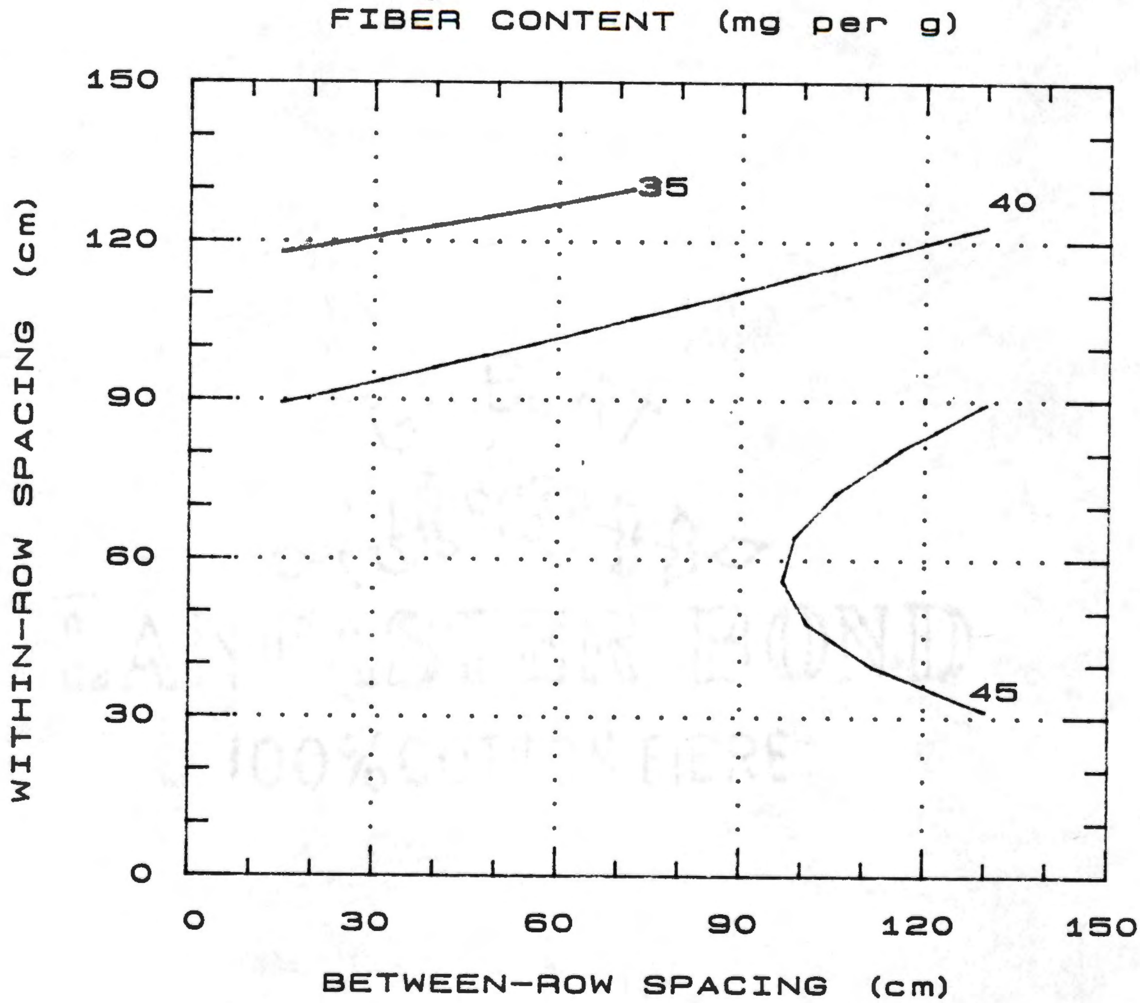

Figure 23. Effect of between-row and within-row spacing on fiber content of broccoli. R^2=0.213056, Y=38.44784927 + (0.00418098 x x_1) + (0.15721088 x x_2) + (0.0000874 x x_1^2) - (0.0016234 x x_2^2) + (0.00029727 x $x_1^2x_2^2$) where Y = fiber content (mg fiber/g fresh tissue), x_1 = between-row spacing (cm), and x_2 = within-row spacing (cm).

VITA

Julie Ann Hale was born in Hendersonville, TN in 1959 and received her Bachelor of Science degree with a major in Plant Science from The University of Tennessee at Martin in 1982. After graduation, she was employed by a landscaping firm where she held the position of landscape crew supervisor.

The author returned to graduate school in 1984 at The University of Tennessee, Knoxville. She was employed as a graduate research assistant for the duration of her Master's program. Upon graduation, the author will be employed by Ciba-Geigy Corporation.