PLANT COMPETITION, ROOT GROWTH
AND ETHYLENE EVOLUTION

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This is to certify that the

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AND ETHYLENE EVOLUTION

presented by

Stanley J. Kays

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_____PhD_____ degree in ___Horticulture___

_____
Major professor

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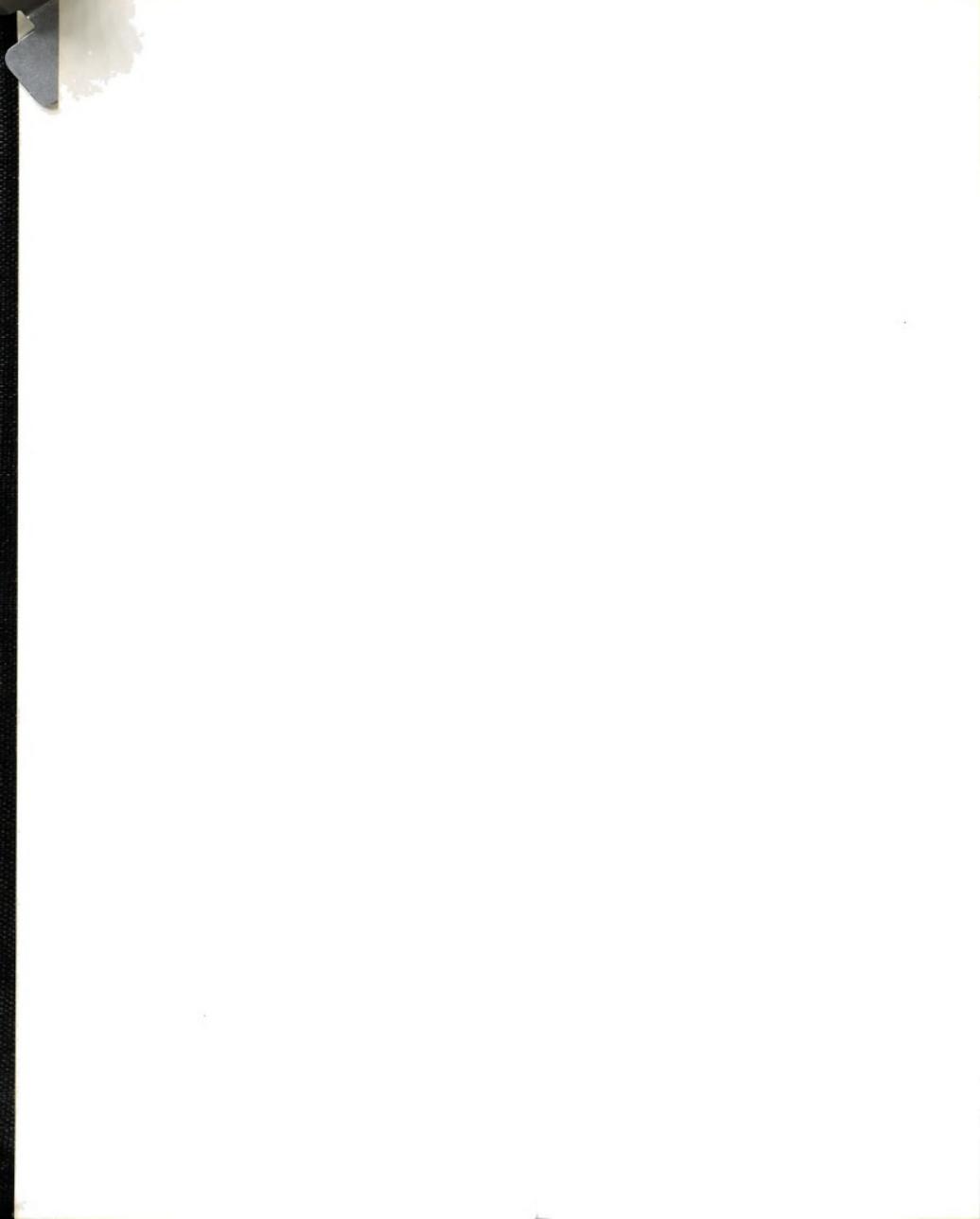
ABSTRACT

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By

Stanley J. Kays

The effect of increasing population pressure on the
variation between individuals within homogenous communities
of tomato plants, Lycopersicon esculentum Mill., was studied.
Plant populations of 5 x 5, 10 x 10, 20 x 20 inches between
plants were used. Population increases resulted in a decreas-
ing number of fruit per plant and clusters with fruit per
plant. As the population of plants increased, the variation
between plants within a stand became progressively larger.
The number of fruit per plant and the weight of fruit per
plant appeared to be more sensitive to population pressure
than the total plant weight or number of clusters with fruit
per plant. The variation in number and weight of fruit per
plant and the number of clusters with fruit per plant gener-
ally increased relative to the lowest or most stable popula-
tion upon approach of final harvest. Increased plant density
also results in a higher mortality rate among members of a
population. Increased plant population appeared to result in
both beneficial factors (e.g. decreasing number of clusters
with fruit per plant) and detrimental factors (e.g. increased
plant to plant variation) in relation to obtaining the highest
percent of ripe fruit using a once-over harvest technique.

If the total yield is fixed, one can predict that if other factors do not become limiting, the point of balance between increasing variation between members of a population and decreasing number of clusters will give the highest potential yield of ripe fruit/acre.

Three plant populations of tomato (5 x 5, 10 x 10 and 20 x 20 inches) were studied from the standpoint of changing water needs, alterations in the composition of their soil gas phase and changes in soil compaction. Increased populations of plants required progressively more water per unit area of land. Distinct changes in the soil gas phase also occurred with increased plant population, date of measurement and depth in the soil. A typical inverse relationship between CO_2 and O_2 concentrations occurred with increasing soil depth. Both CO_2 and O_2 decreased with increased population. An inverse relationship between CO_2 and O_2 occurred in the early part of the growing season, while a positive correlation was noted in the latter part. The O_2 concentration increased progressively during the growing season. The concentration of ethylene in the soil gas phase increased during the growing season, however, no significant population or depth effects were noted. There were no significant differences in soil compaction with increased plant population, however, a progressive consolidation with time was noted. Increases in population density of tomatoes results in both changes in requirements for production and distinct alterations in the plant communities environment.

Bean roots (<u>Vicia</u> <u>faba</u>, L., variety Broad Windsor) were enclosed in glass chambers where their axial growth was restricted by a hard plastic barrier. A perforated hard plastic tube enclosed the root to prevent curvature. Upon contacting the barrier, the level of ethylene evolution increased to as much as 6 times that of controls and was maintained for up to 30 hours after initiation, however, with a gradual decline. Removal of the barrier resulted in a decrease in ethylene evolution to near that of controls. Exogenous application of ethylene at very low concentrations stimulated growth in length while higher concentrations inhibited length growth. Exogenous ethylene also resulted in an increase in radial diameter. Ethylene found in the soils gas phase reached near physiologically significant concentrations late in the fall. Water from irrigation resulted in a temporary depression in the ethylene concentration in the soil gas phase. The results indicate that ethylene evolution by bean roots acts as an endogenous growth regulator in response to high mechanical resistance.

A technique was developed utilizing an electron microprobe x-ray analyser for the measurement of small changes in bulk density around plant roots or other below ground plant organs. The effective diameter (root diameter + the distance of deformation) of <u>Vicia</u> <u>faba</u>, L., variety Broad Windsor was approximately 6 times the original diameter of the root. The

potential for overlapping areas of deformation between neighbor roots was calculated from existing root density data for single plants and is substantial.

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                       Sections I, II, III and IV are segments of related thesis research information condensed into formats suited and intended for publication in the Proceedings of the American Society for Horticultural Science (sections I and II), Planta (section III) and Soil Science Journal (section IV).

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Plant Competition: Influence of density on
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Introduction

Much of the data available on plant populations concerns the influence of plant density on the community, generally measured as yield per unit area of land (10,14,15). With increasing population pressures it becomes desirable, however, to study the effect of density on individuals within the community, since total yield is a function of collective individual behaviors. This provides the potential for a greater understanding of controlling relationships in plant populations and may facilitate prediction of the problems arising with intensive cropping.

Plants display a high morphological "plasticity", responding in shape and size to the prevailing environmental conditions (5). Early competition with neighboring plants immediately results in a reduction of growth rate and the reduction increases with increasing intensity of competition (1). The timing of competition, relative to the morphological development of the plant, is important both to the physical aspects of the "plasticity" of response and in some cases, total yield per acre (4). In cereals, if competition is delayed until after florescence, a greater number of inflorescences are produced per plant and upon

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the onset of competition there is both competition between neighboring plants and between inflorescences within the same plant. This results in a decrease in the number and size of seeds per inflorescence. If, however, competition occurs before flowering, flower formation and flower number are a function of the stress and consequently there is not a decrease in seed size or number per inflorescence. Therefore, maximum yield is not only a function of the stress between plants in a community but also the competition within individuals of that community (4).

With increasing population pressure, homogenous communities move progressively toward a skewed distribution for size of the members of the community and generally the shift is toward an increasing proportion of smaller plants (7,9,13). For some crops (e.g. Zea mays) the shape of the height distribution curve of the population moves to the right with the shorter plants having a higher growth rate in length resulting in a net equalization of height (8).

Density or distance to the nearest neighbor also results in changes in the mortality rate (3,6,7). The highest plant mortality rate corresponds with the highest plant densities.

The purpose of this paper is to describe some of the responses of the individual within a community and their possible implications in production problems.

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Materials and Methods

Populations of direct seeded tomatoes, variety Heinz 1783, were studied utilizing spacings of 20 x 20 in., 10 x 10 in. and 5 x 5 in. The statistical design was a split plot with three replications. The plots were 8 x 8 feet square with guard rows around the edges. Fertilizer applications were made according to soil test results (M.S.U. Soil Testing Laboratory) for the production of tomatoes and a pre-emergence herbicide, diphenamid, at the rate of 5 pounds/acre was applied. Accurate spacing was obtained by using a dibble board with the appropriate spacing. At the cotyledon stage, extra plants at a single space were pinched off, leaving a 100% stand.

The plots were irrigated individually upon reaching 45% of the available soil moisture. Soil water status was measured with individually calibrated Bouycous soil moisture blocks placed in the center of the populations at depths of 8 and 16 inches. Irrigation (1/4 in.) was applied using a calibrated hand hose as a light spray for the necessary length of time.

Three harvest dates at approximately 30 day intervals were used. A once over harvest was utilized for total yield. The following data was taken: total weight of fruit in each class, plant weight, number of clusters with fruit, number of fruit per plant and number of plants remaining of the original population.

Results

As anticipated from previous work (2,11,12) both the number of clusters with fruit per plant and the number of fruit per plant were reduced with increasing population pressure (Fig. 1). However, looking at the progressive changes in variation or skewness of the populations yields additional information is obtained concerning the behavior of individuals, relative to their neighbors, within a given population. With increasing density of plants, the variation in number of fruit per plant and the weight of fruit per plant between members in a population increases (Fig. 2). There was a small increase in coefficient of variation between the low and medium populations but a dramatic rise was noted for the most intensively competing population. The variation in weight of the individual plants and the number of clusters with fruit per plant increased progressively, in a near linear fashion, with increasing plant density (Fig. 3).

As growth progressed toward final harvest, the variation between plants in the highest population continued to increase up to harvest with regard to the number of fruit per plant (Fig. 4). However, the variation decreased within the lower populations as they approach harvest. This may be demonstrated by the percent increase in coefficient of variation over the lowest or most stable population with time. The most intensively competing stands continued to

increase in variation compared with the variation of the lowest plant population. All populations tended to stabilize with respect to the variation in the number of clusters with fruit per plant as final harvest approached (Fig. 5). However, relative to the lowest population, the variation within the highest density of plants became progressively larger with time. As with number of fruit per plant, the variation in weight of fruit per plant was amplified with increasing population or decreasing area per plant (Fig. 6) while the variation within the lower populations tended to stabilize near harvest.

The mortality rate, expressed as deaths per hundred plants, increased with increasing plant population (Fig. 7). The variation in number of live plants left in a stand also increased with increasing population and with time (Fig. 8). While there was a continual increase in the variation of the number of live plants at the highest plant density, the lower populations were little affected (Fig. 8).

Discussion

The variability between individual plants was much greater at higher densities of plants than at lower densities. With this, the mortality rate also rose with increased population thus giving an overall effect of increased diversity. The rapid rise in variation between plants at the highest population with respect to the number

Fig. 1.--The change in number of fruit per plant and
number of clusters with fruit per plant with increasing
plant population. The significance probability of the F
statistic for population was 0.002 for the number of fruit
per plant and 0.0005 for the number of clusters per plant.
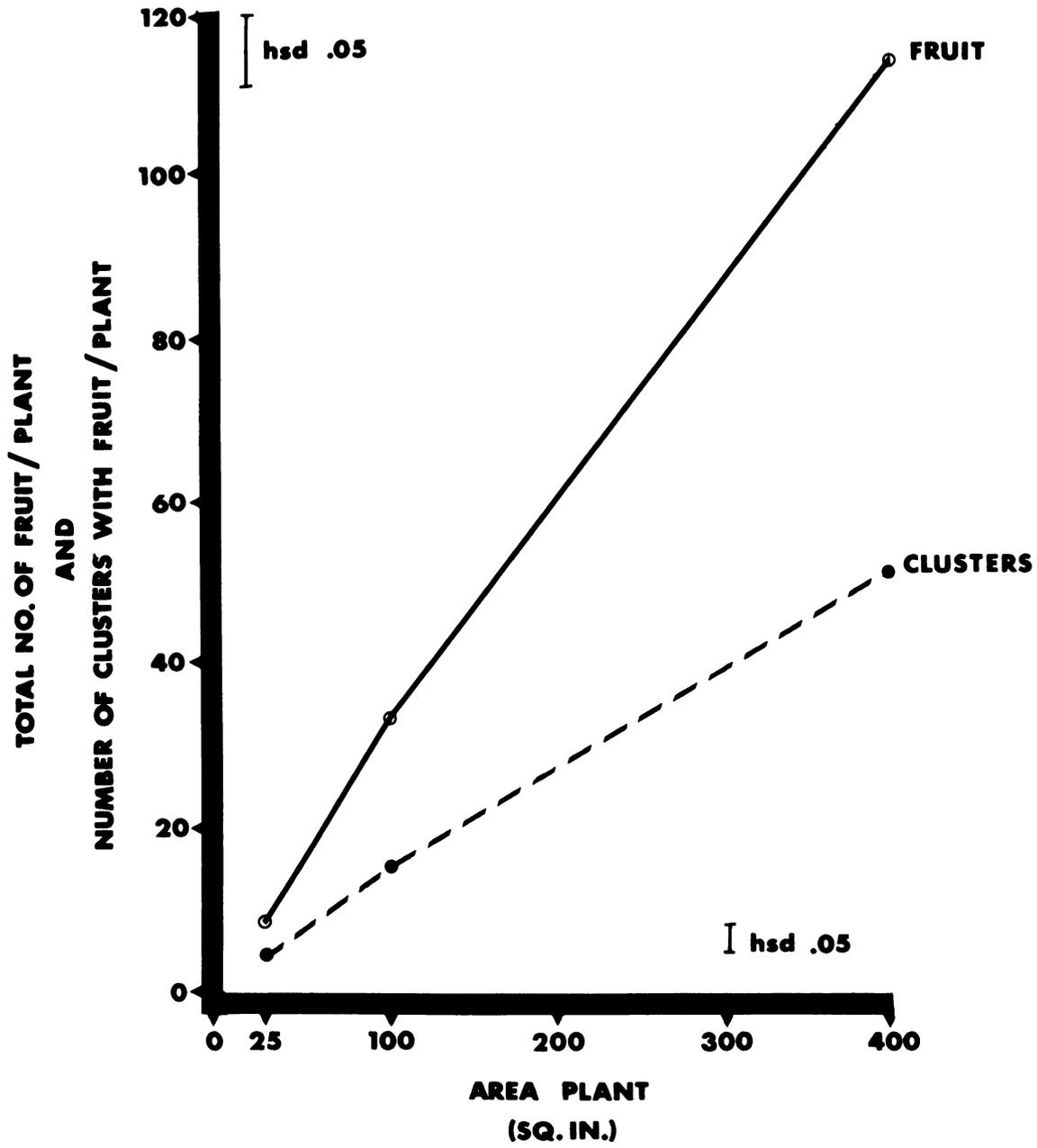
Fig. 2.--The change in coefficient of variation for
the number of fruit per plant and the weight of fruit per
plant with increasing plant population. The significance
probability for the F statistic for population was 0.002
for the number of fruit per plant and 0.0005 for the
weight of fruit per plant.
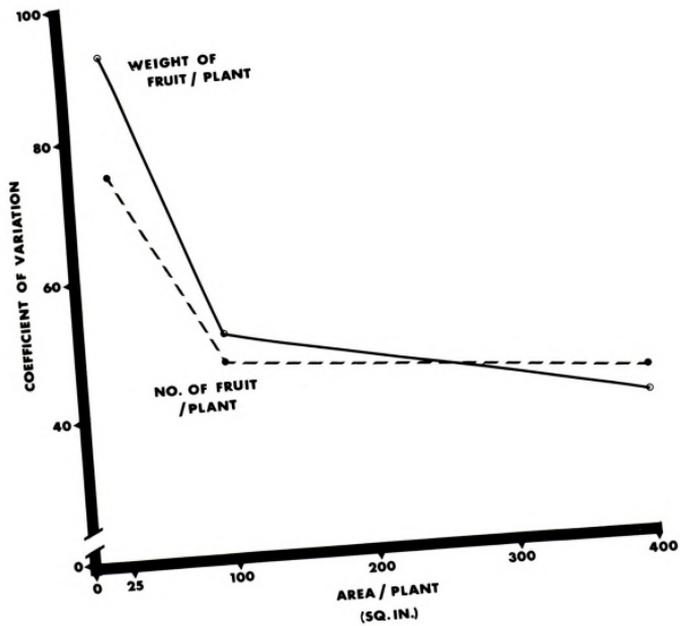
Fig. 3.--The change in coefficient of variation for
plant weight and the number of clusters with fruit per
plant with increasing plant populations. The significance
probability for the F statistic for population was 0.0005
for the number of clusters per plant and 0.0005 for the
plant weight.

Fig. 4.--The change in coefficient of variation for the number of fruit per plant with time for three populations and the percent change in coefficient of variation over the lowest population. The significance probability for the F statistic for population was 0.002 and 0.0005 for date. The standard deviations for the coefficients of variation are plotted on the figure. (----represents the % increase in coefficient of variation over the lowest population.)

Fig. 4.--The change in coefficient of variation for the number of fruit per plant with time for three populations and the percent change in coefficient of variation over the lowest population. The significance probability for the F statistic for population was 0.002 and 0.0005 for date. The standard deviations for the coefficients of variation are plotted on the figure. (----represents the % increase in coefficient of variation over the lowest population.)

Fig. 4.--The change in coefficient of variation for the number of fruit per plant with time for three populations and the percent change in coefficient of variation over the lowest population. The significance probability for the F statistic for population was 0.002 and 0.0005 for date. The standard deviations for the coefficients of variation are plotted on the figure. (----represents the % increase in coefficient of variation over the lowest population.)

Fig. 5.--The change in coefficient of variation for
the number of clusters with fruit per plant with time for
three populations and the percent change in coefficient
of variation over the lowest population. The significance
probability for the F statistic for population and date
were 0.0005. The standard deviations for the coefficients
of variation are plotted on the figure.
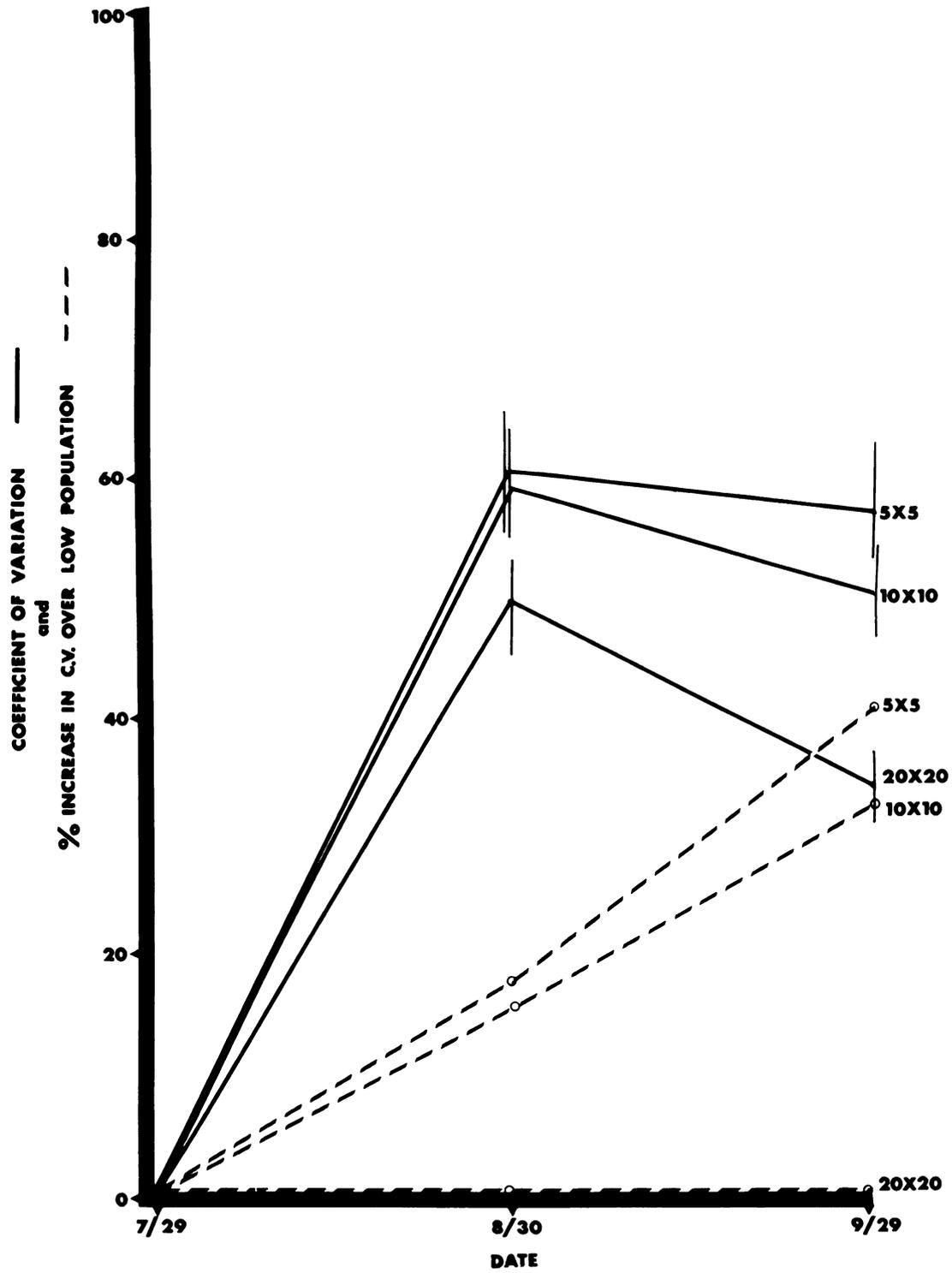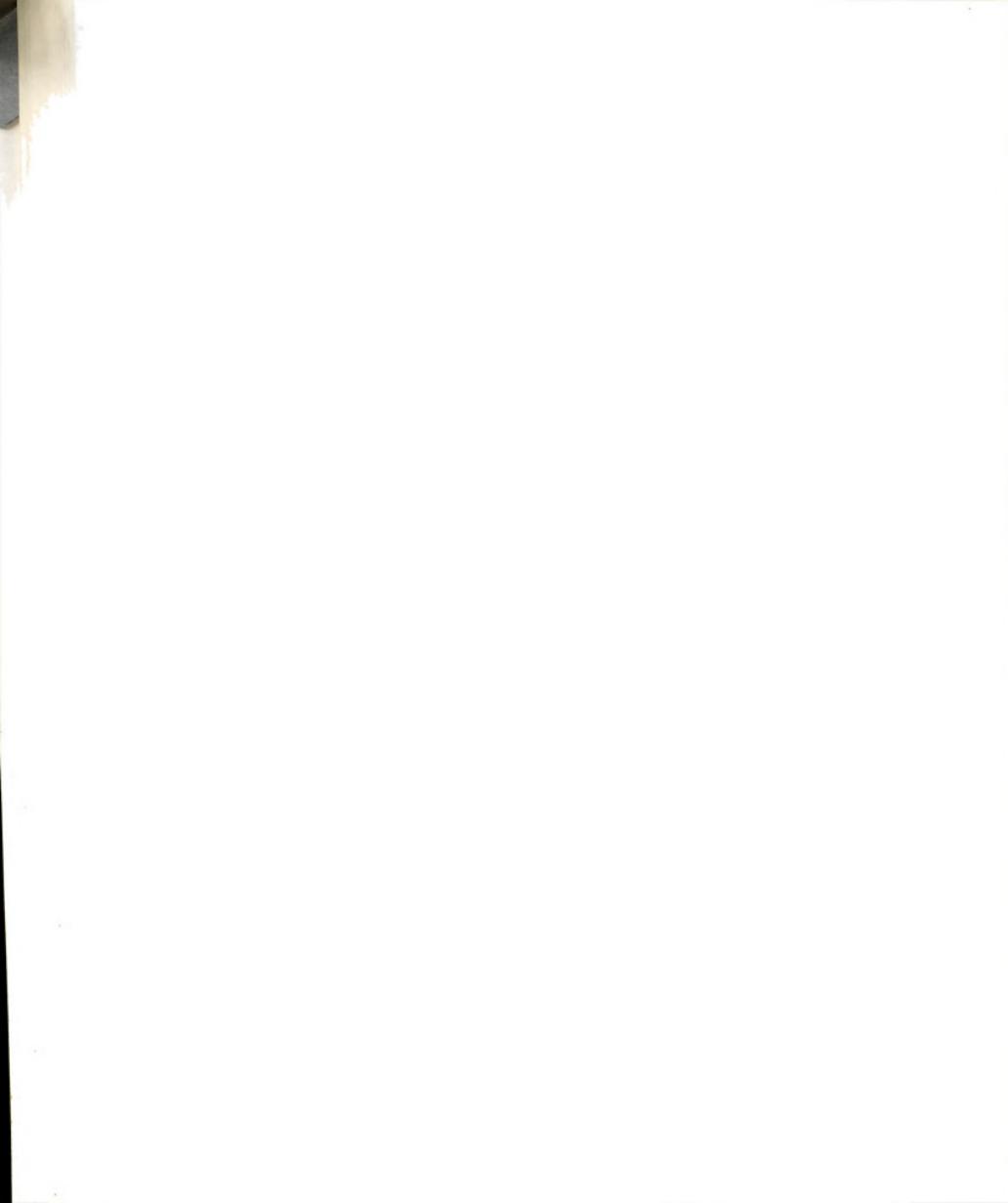
Fig. 6.--The change in coefficient of variation for the fruit weight per plant with time for three populations and the percent change in coefficient of variation over the lowest population. The significance probability for the F statistic for population and date were 0.0005. The standard deviations for the coefficients of variation are plotted on the figure. (----represents the % increase in coefficient of variation over the lowest population.)
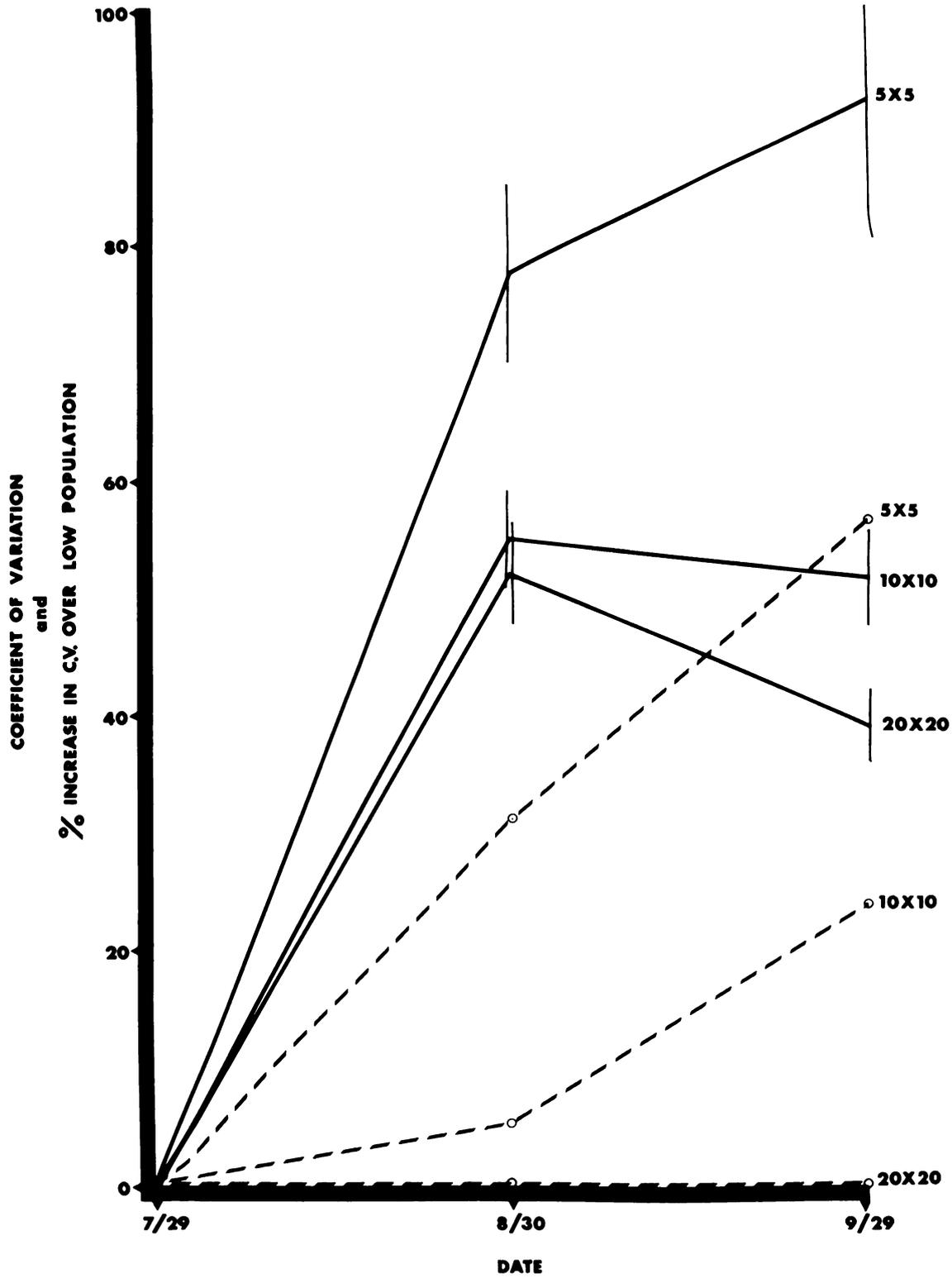
Fig. 7.--The change in number of deaths per 100 plants with increasing population. The standard deviation for each population is plotted on the figure.
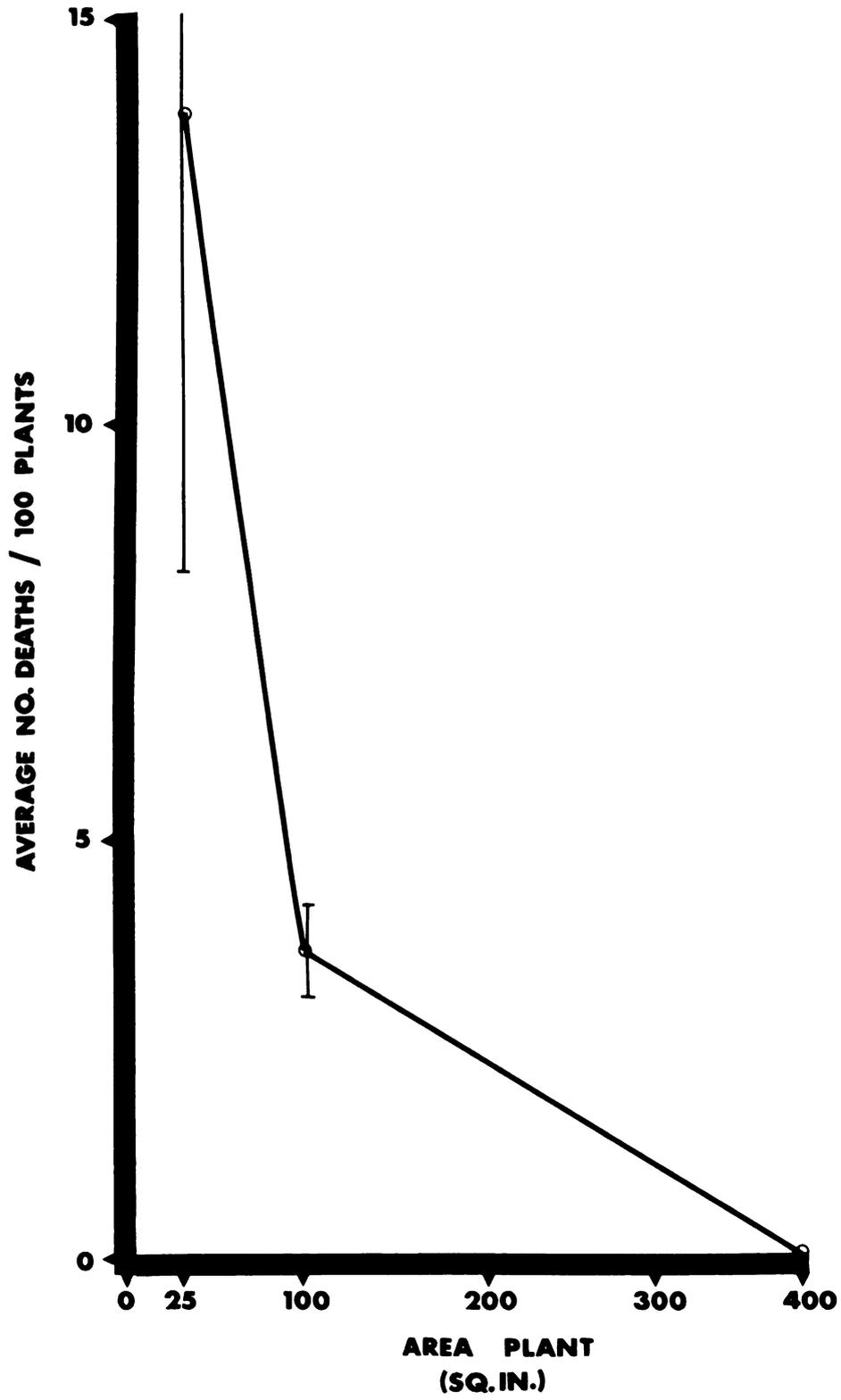
Fig. 8.--The change in coefficient of variation for the number of plants remaining of the original population with time for three plant populations. The standard deviations for the coefficients of variation are plotted on the figure.
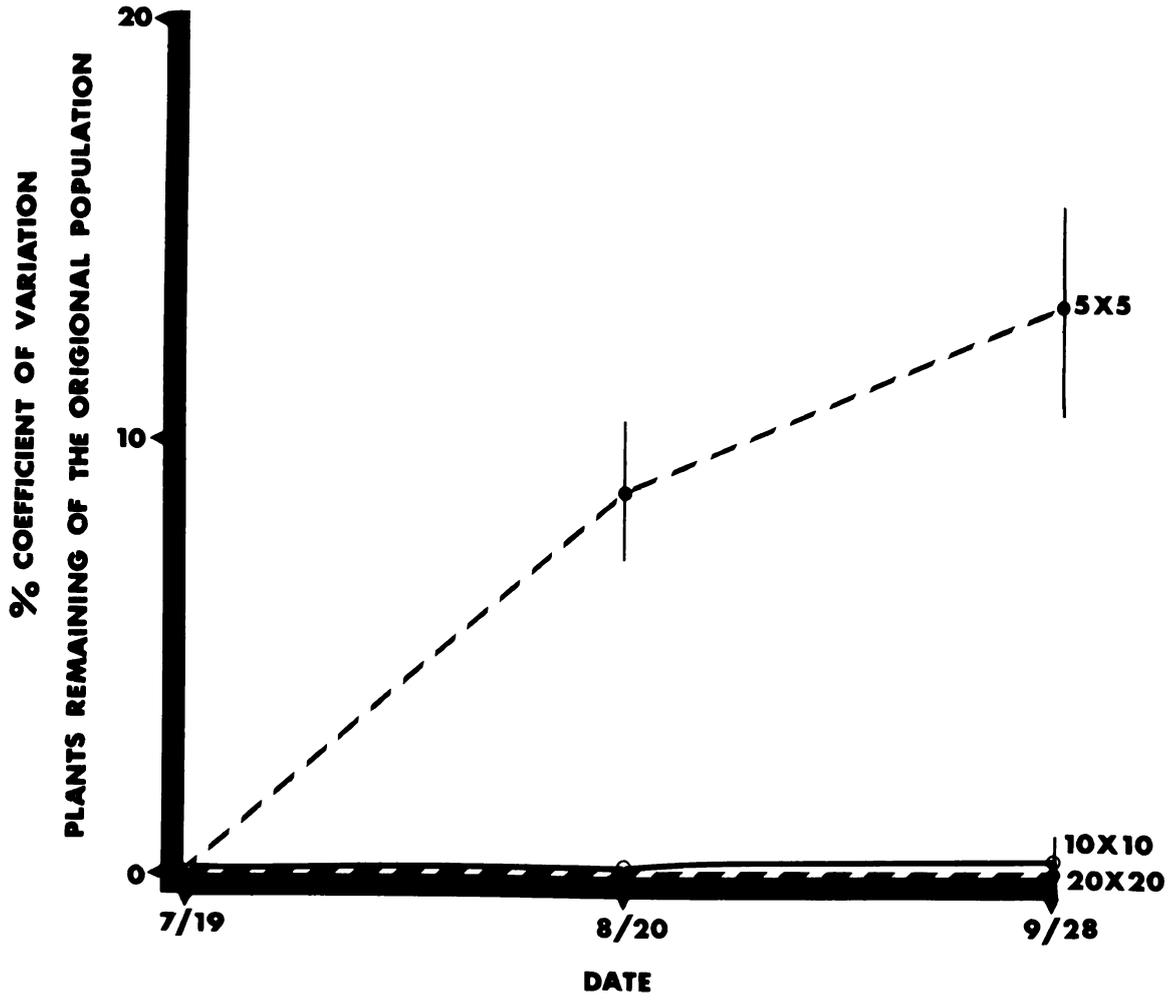
of fruit per plant and the weight of fruit per plant may
have been partially due to the dependence of these param-
eters on the number of clusters per plant. Therefore, any
diversity in number of clusters would have an additional
effect on the variation for the number and weight of fruit
per plant since normally one cluster has more than one
fruit. Consequently, anything that would decrease the
number of fruit per cluster, while not affecting cluster
number per plant, would force downward the variation be-
tween plants under intensive competitive stress. From this
it can be seen that number of fruit per plant and weight of
fruit per plant were much more sensitive to intensive popu-
lation pressure than the number of clusters per plant and
plant weight.

The critical question is: what effect do these param-
eters have on the uniformity of harvest when utilizing a
once over harvest technique? Because of the increase in
variation between plants at higher and higher populations,
it would seem that increased population works, from this
standpoint, against uniformity. However, at the same time,
the effect of increased plant density on the average number
of clusters with fruit per plant may force a decrease in
the potential for diversity and by doing so increase the
potential for uniformity. Consequently, increasing popula-
tion has both a positive (decreasing number of clusters with
fruit per plant) and negative (increased coefficient of vari-
ation) effect on the diversity of the members in the stand.

One may increase yields per acre for a given variety by more efficient utilization of the land area and/or more efficient utilization of the plants. If the potential yield (total tons of fruit per acre) for a given population of plants is considered fixed (Fig. 9), then any factor that decreases the distance between a and b (without affecting total yield or by affecting it less than the increase in benefit from decreasing the distance between a and b allows) will increase the tons of ripe fruit per acre. Population increases appear to do this (2), although land use efficiency also increases, mainly by decreasing the number of clusters per plant with fruit and subsequently the potential spread in harvest. However, any factor that forces the distance between a and b wider will have the opposite effect. As noted in the results, population increases also may increase the percent variation between plants which would tend to force the curve lower and wider; therefore, few tons of ripe fruit per acre. If the total yield is fixed, one could predict that, if other factors do not become limiting (e.g. depression of total yield), the point of balance between increased variation between members of a population and decreasing number of clusters will give the highest efficiency of plant use and consequently the highest potential yield/acre of ripe fruit.

Fig. 9.--A hypothetical curve for the optimum time of once-over harvest.
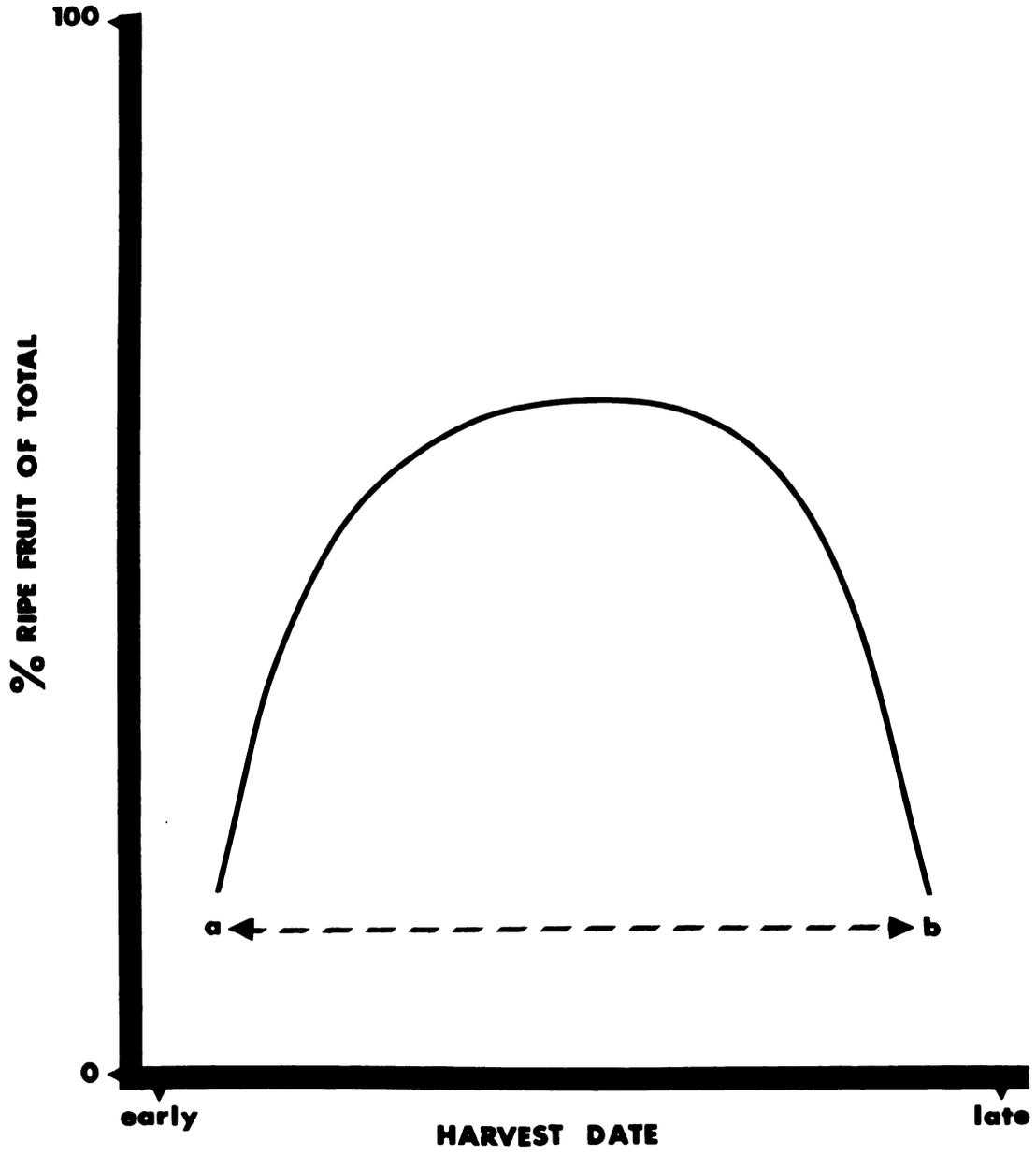
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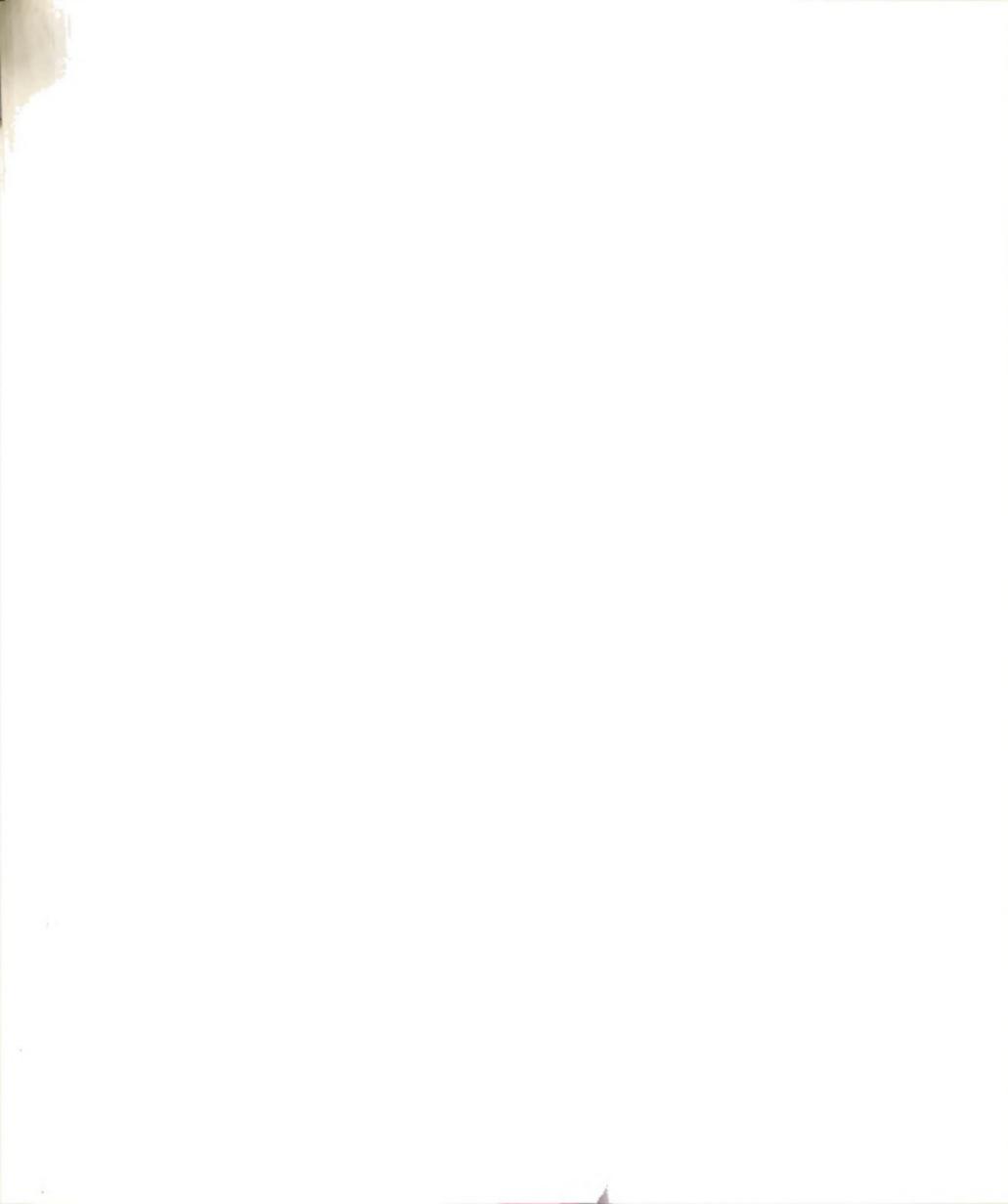
SECTION II

Plant Competition: Influence of density
on community phenomena

Introduction

Rising costs and labor shortages have forced changes in culture to achieve a high yield for machine harvest. One of these changes has been the use of higher plant populations (19,20). The typical response of tomato to increased plant population is an increase in total and early yield/acre (3,16,21,24,25,29,30), a decrease in fruit size (24,25,29,30) and a decrease in number of fruits/plant (18, 29,30).

Competition begins earlier in the growing season as the plant density increases (6). The intensity of competition increases as the season progresses and may, in some crops (e.g. _Lolium rigidum_), result in the complete cessation of growth. Consequently, the yield at extremely low plant densities tends to approach, with time, the yield at extremely high densities (5).

The yield of vegetative dry matter/unit area often reaches a relatively constant level (1), however, the total yield of reproductive parts may be depressed at high densities (13). A considerable range of densities appear to give near-maximal yields (3,16) but this varies from year to year (21).

Several less pronounced community induced phenomena that under certain conditions may critically influence plant growth and subsequent yield, have been ivestigated.

Materials and Methods

Populations of direct seeded tomatoes, varieties New Yorker and Heinz 1783, were studied in 1969 and 1970, respectively. Spacings of 20 x 20 in., 10 x 10 in., and 5 x 5 in. were utilized. The statistical design was completely randomized with 3 replications in 1969 and a split plot with 3 replications in 1970. The main plots were for date of harvest with plant population within. The plots were 8 x 8 feet square with guard rows around the edges. Fertilizer application was made according to soil test results (M.S.U. Soil Testing Laboratory) for the production of tomatoes and a pre-emergence herbicide, diphenamid, at the rate of 5 pounds/acre was applied. Since soil gas composition, compaction and water utilization data were to be taken, to avoid compacting or disturbing the soil, hand seeding and all subsequent thinning and weeding were done from a temporary overhead platform. Accurate spacing was obtained by using a dibble board with the appropriate spacing. At the cotyledon stage, any extra plants were pinched off, leaving a 100% stand.

Water Use: Individually calibrated Bouycous soil moisture blocks were placed in the center of each population
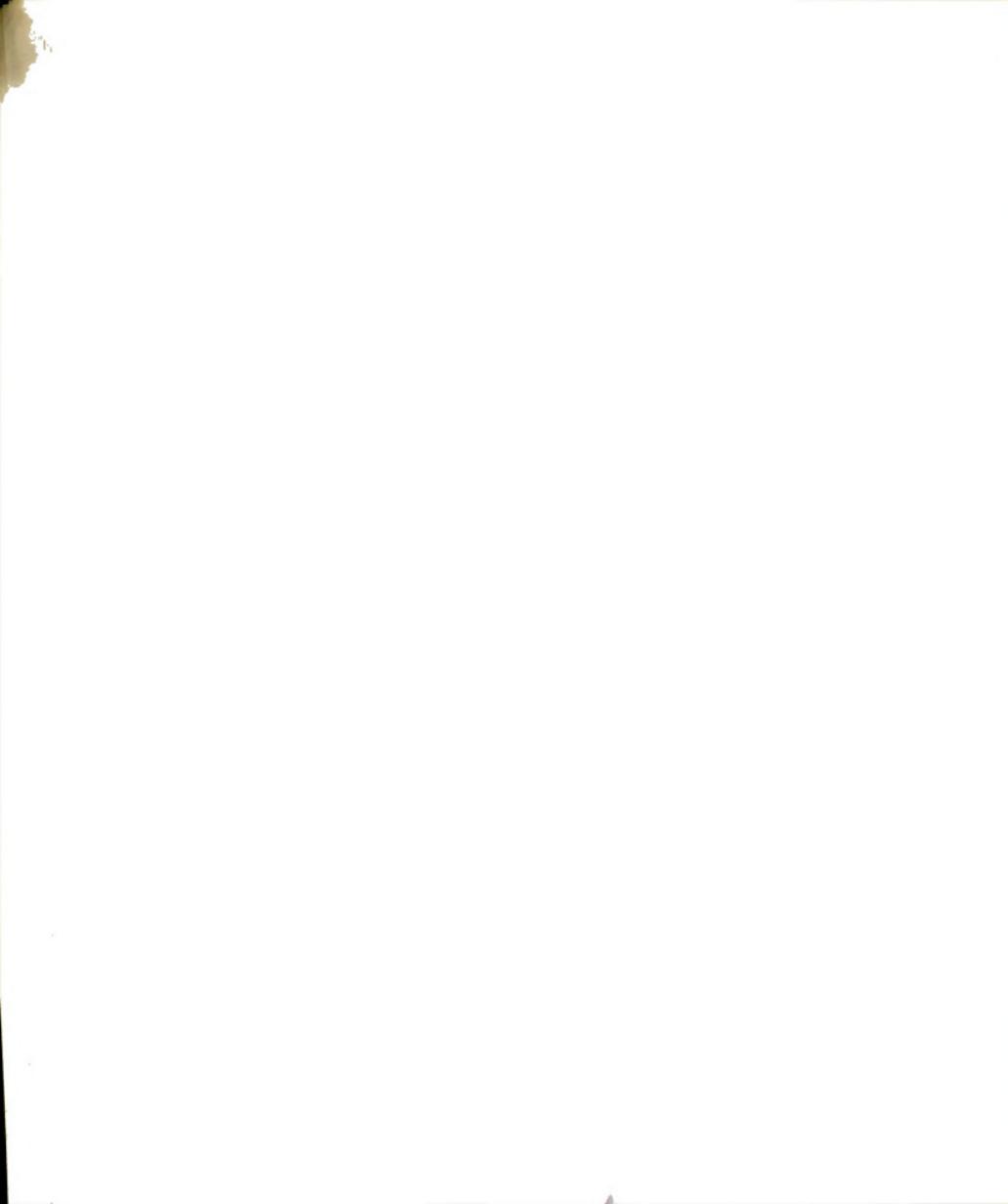
at 8 and 16 in. depth prior to planting. Soil moisture was
measured on alternate days and individual plots were irri-
gated when the soil contained 45% of the available water.
Irrigation (1/4 in.) was applied using a calibrated hand
hose as a light spray for the necessary length of time. Any
run off from rain or irrigation was prevented by a 3 in.
dike around the edge of the individual plots.

Soil Compaction: Compaction of the upper 2 in. of soil
was measured using a polished point probe (1/8 in. diameter
x 2 1/2 in., 22° point angle) attached to a Hunter Spring
mechanical force gauge giving a measure of resistance in
grams. The probe was polished to decrease skin friction and
a uniform entry rate was maintained. One hour prior to
measurement, each plot was irrigated with 1/2 in. of water
to eliminate differences in resistance due to differences in
percent soil moisture. Fifteen measurements were taken per
plot per date. The measurements were taken at random in the
population and equidistant between two neighboring plants.

Soil Gas: Glass tubes (5, 9 and 17 in.), sealed at the
apex with a serum vial stopper and open but covered with a
fine copper grid at the base, were placed in each plot. A
smaller glass tube was placed through the serum vile cap at
the top and extended down to 2 cm from the copper grid.
This second tube was also sealed with a serum vile cap. The
soil gas phase at the depth of the open end was allowed to
equilibrate with the gas in the tube. The second, internal,

tube was used to take the bulk of the sample as close to the open end as possible. Three sampling tubes per plot were placed in the soil, one each at 4, 8 and 16 in. depth, using a soil core sampler. The tops were covered with aluminum foil to minimize any sun mediated effects. Gas samples (10 ml.) were taken with a syringe and subsamples were analysed by gas chromatography within 30 minutes of sampling. O_2 and CO_2 were determined on the same 5 ml. samples with a thermal conductivity detector while 2 ml. samples were used for ethylene with a flame ionization detector.

Harvest: A once over harvest was utilized for total yield.

Results

As noted in previous studies (3,16,21,24,25,29,30), total yield increased with increasing plant population (i.e. decreasing area per plant) (Fig. 1). Although the total yields were considerably higher in 1970 as compared with 1969, the yield response to plant population was similar each year.

The water requirement also increased with increasing plant populations (Fig. 2). The greatest requirement for irrigation corresponded with periods of low rainfall. Part of the variation in total water requirement between years was due to a 42% increase in rainfall in 1970. Consequently,
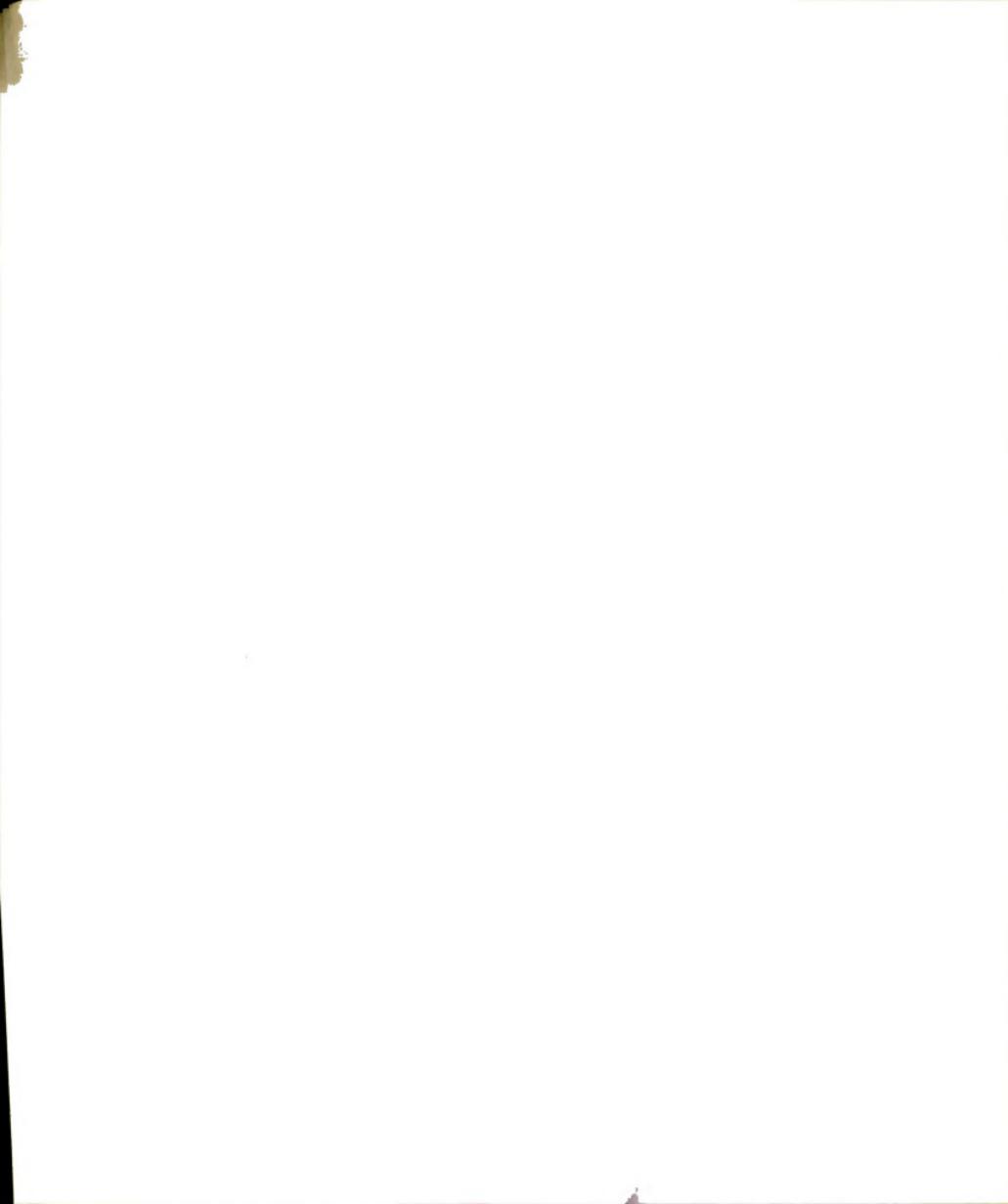
the differences in water requirement between populations in
a year of high rainfall (1970) were less pronounced than
during the 1969 growing season. The increasing populations
of plants responded with the same trend each year with re-
spect to their water requirements (Fig. 3). This is demon-
strated by the similarity in shape of the curves for the
two years and the linearity of the difference in water re-
quirements between years. Consequently, although the total
rainfall and total irrigation varied considerably with year,
the populations of plants responded similarly in their need
for additional water.

The soil in the upper 2 inches, became more compacted
with time (Fig. 4A). Plant population did not appear to
have a significant effect. However, this was confounded
by the requirement of greater amounts of water by higher
plant populations. Irrigated soil, devoid of plants, was
more compacted than soil not irrigated (Fig. 4B). There-
fore, the population effect could be substantially masked
by the increasing amount of water applied with increased
populations.

The levels of soil O_2 and CO_2 in the soil gas phase
significantly decreased with decreasing area per plant or
increasing plant population per acre (Fig. 5). The com-
plexity of the relation of population to its soil atmos-
phere, however, is suggested by the absence of the 1:1
reciprocal relationship normally noted between oxygen and
carbon dioxide in biological systems. Ethylene levels in

the soil gas phase were not significantly affected by the number of plants per unit area of soil. Soil O_2 decreased with increasing soil depth while CO_2 increased with increasing soil depth (Fig. 6). The fact that there was a typical reciprocal relationship between the two gases with depth adds credibility to the population effect noted previously. Also, the levels of soil O_2 were higher and CO_2 lower in soil without plants than in soil with growing plants.

Ethylene in the soils gas phase tended to be pocketed and highly random, consequently no significant depth effect was noted. The concentration of ethylene in the soil increased during the growing season (Fig. 7). The response of oxygen and carbon dioxide with time suggested the interaction of several controlling factors (Fig. 8). An inverse relationship existed during the first part of the growing season, however, this reversed to a direct relationship in the latter part of the season.

Discussion

The results obtained in this study indicate a definite increase in water requirement with increasing density of plants. Karper (14) demonstrated the relationship between rainfall and optimum plant density over a 10 year period. For one genotype (Kafir) the optimum density in a wet season was 10 times that of a dry season. The optimum plant density has also been increased with increased irrigation (12).
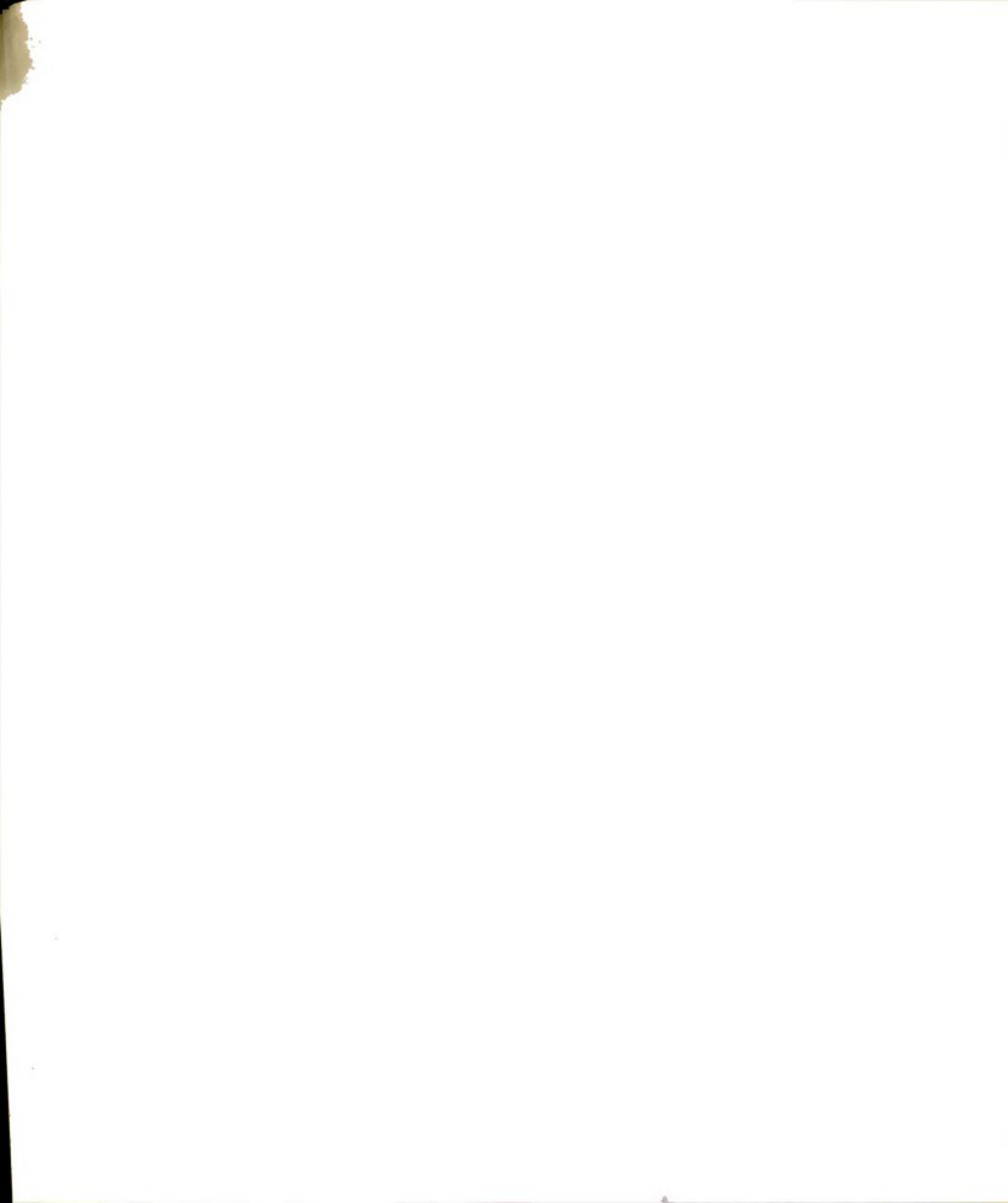
Fig. 1.--The effect of increasing plant population on total yield in tons of fruit per acre. The significance probability for the F statistic was 0.001 for both population and year.
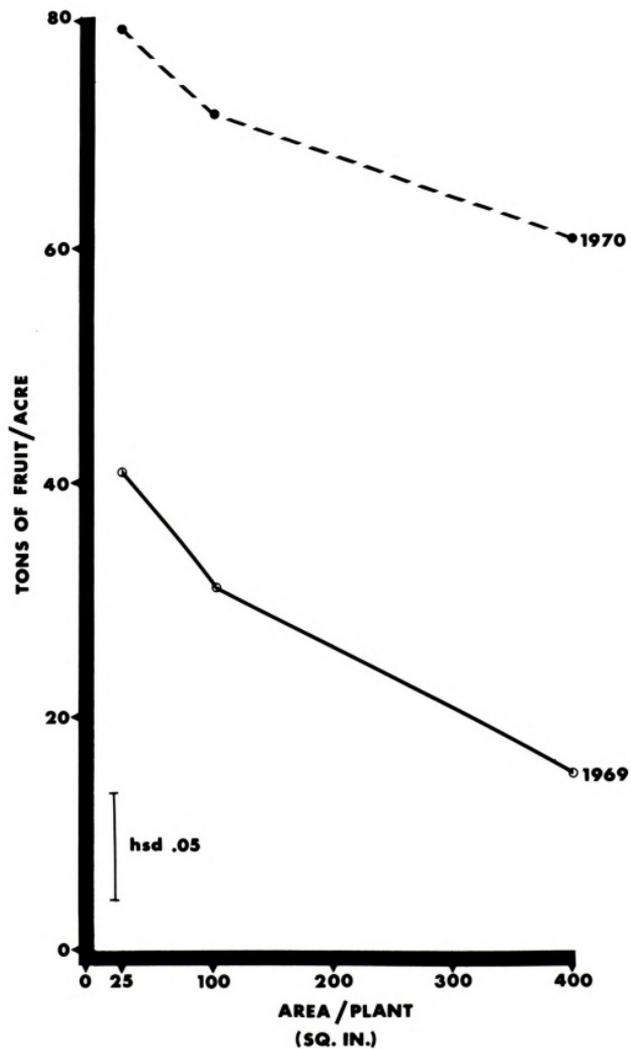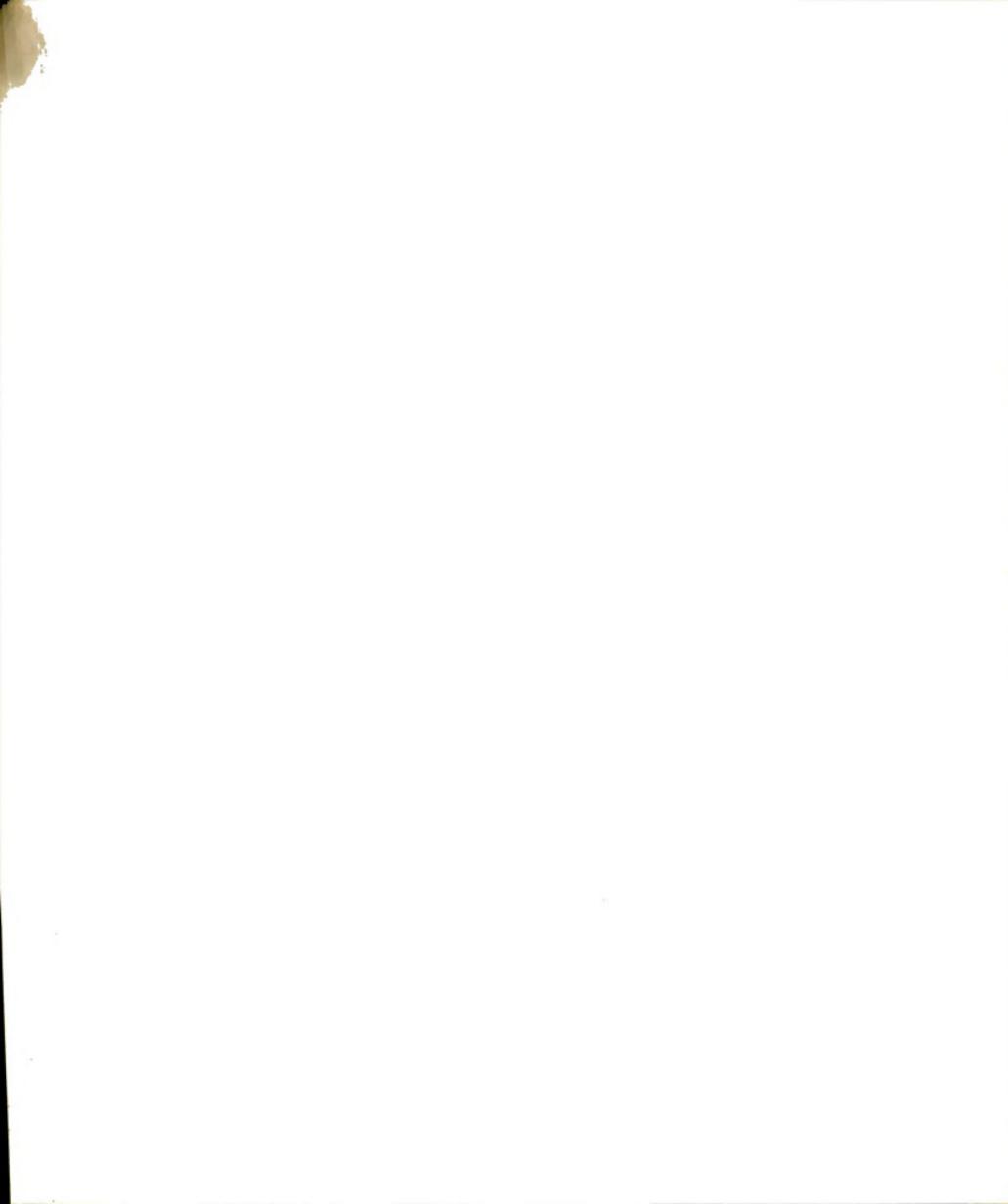
Fig. 2.--The cumulative inches of water (rain and irrigation) per plot for each population during the growing season. The significance probability of the F statistic for water use was 0.05 in both 1969 and 1970.

CUMULATIVE INCHES OF WATER/PLOT

DATE
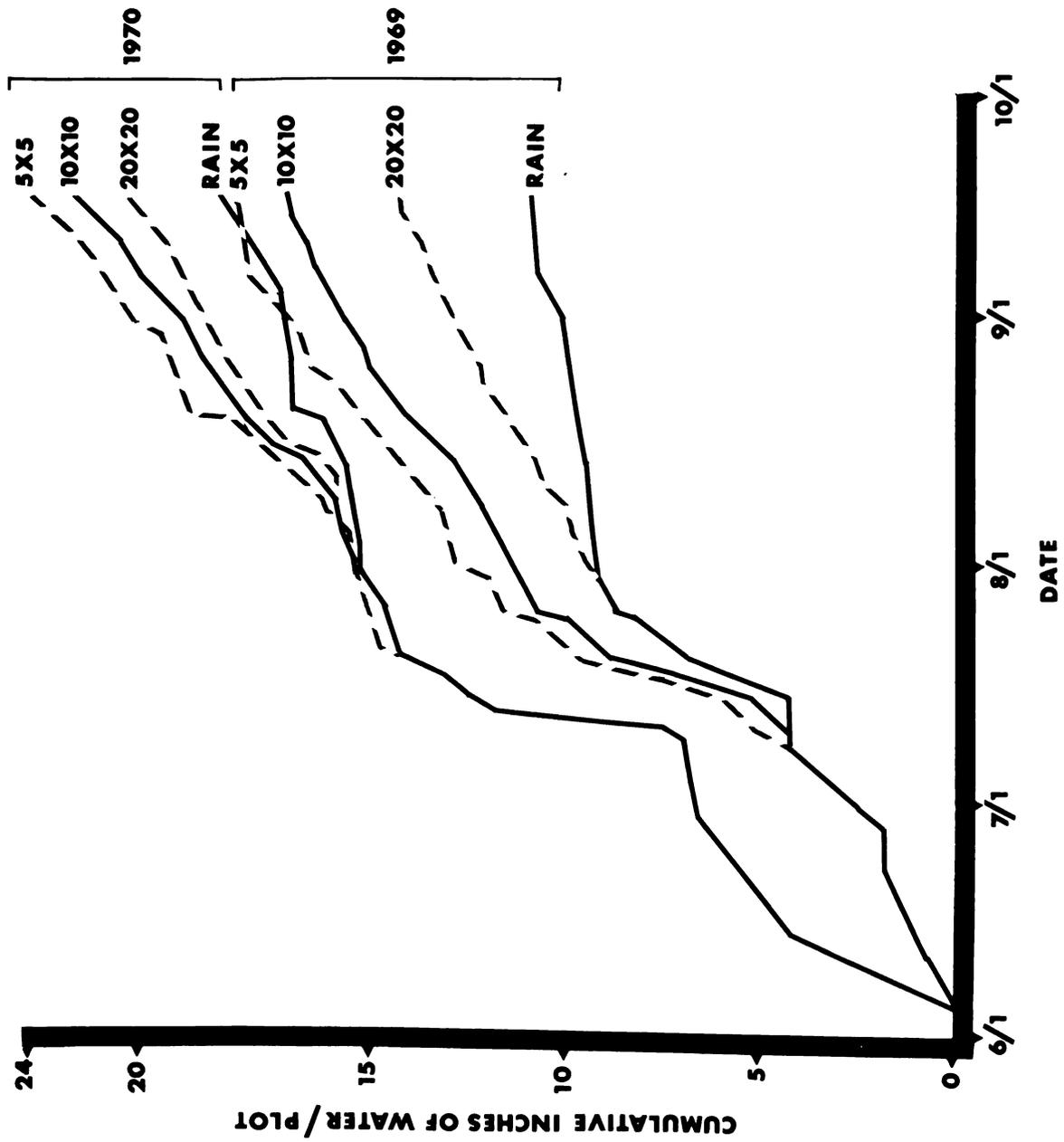
Fig. 3.--The inches of water required per plot with increasing population during the 1969 and 1970 growing season. The significance probability of the F statistic for water use was 0.05 in both 1969 and 1970.
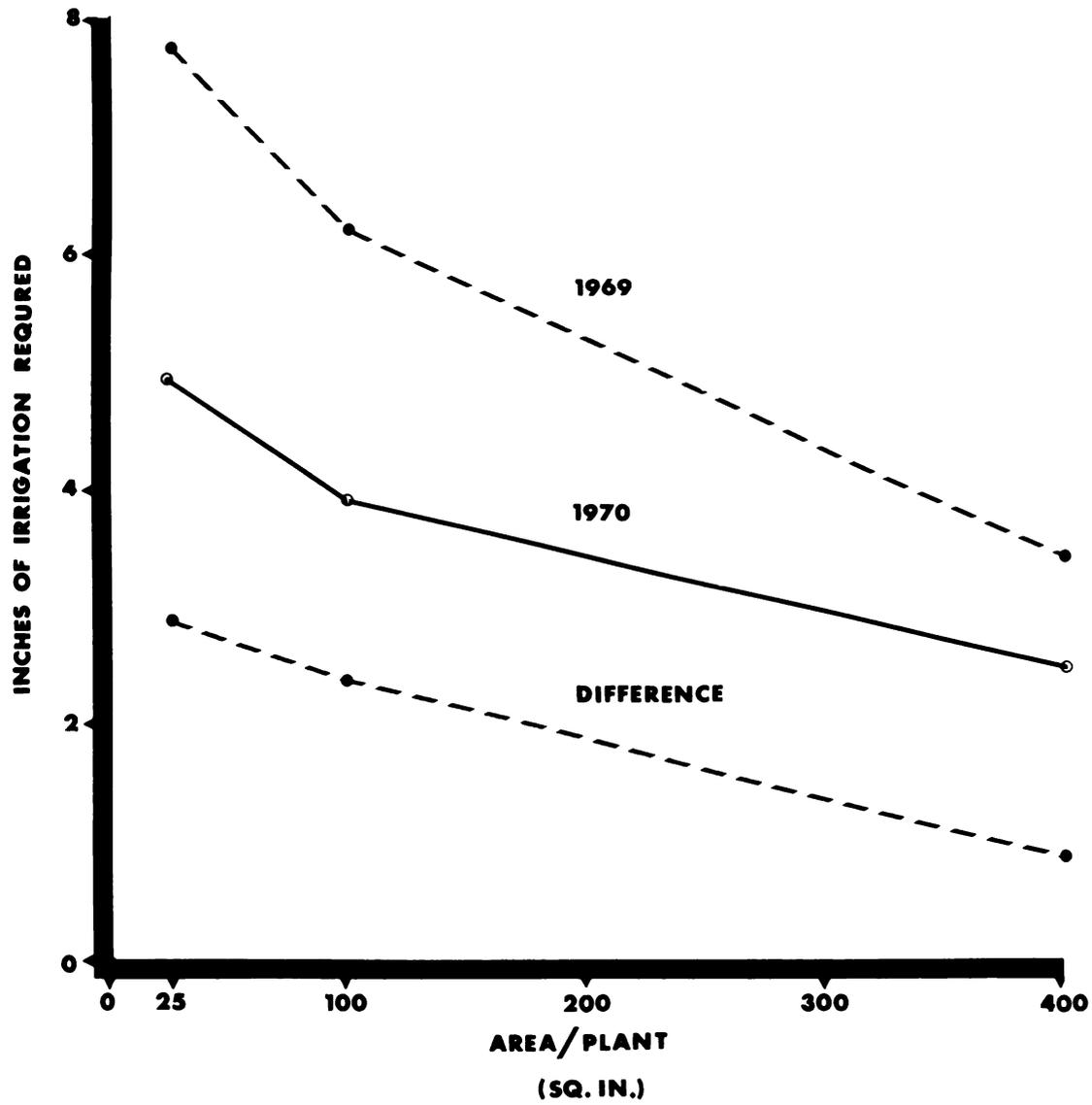
Fig. 4A.--The increase in soil compaction for all populations during the growing season.

Fig. 4B.--The change in soil compaction for plots devoid of plants, with and without irrigation, during the growing season. The significance probability for the F statistic for date was 0.0005.
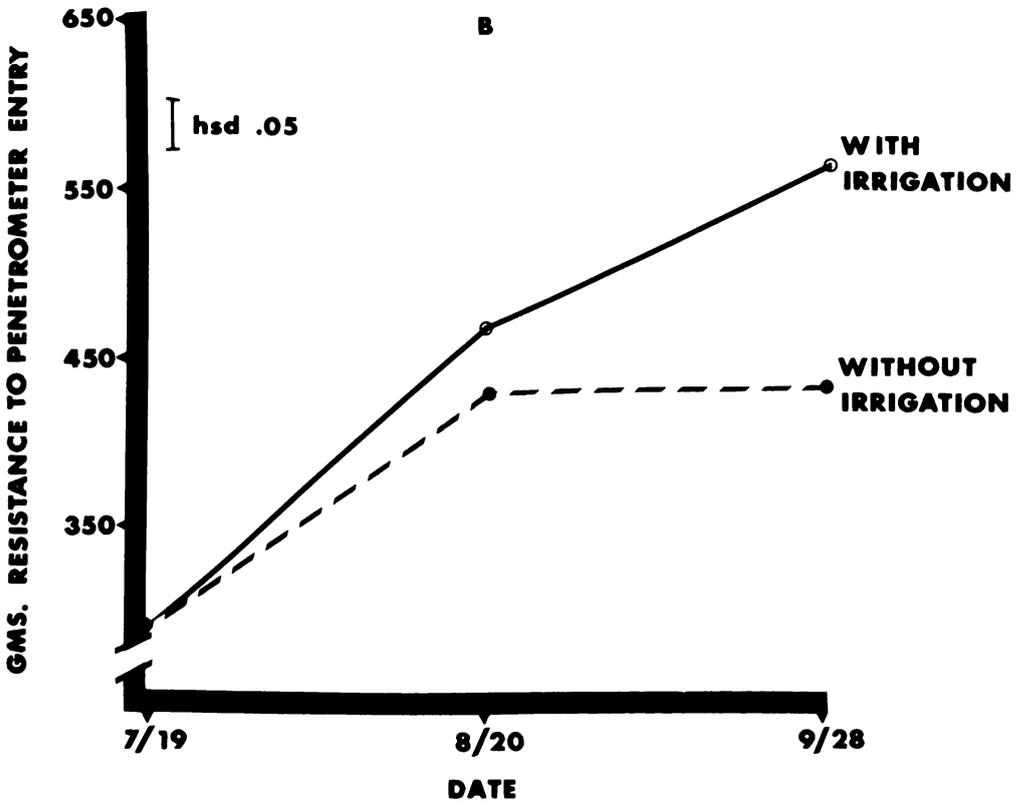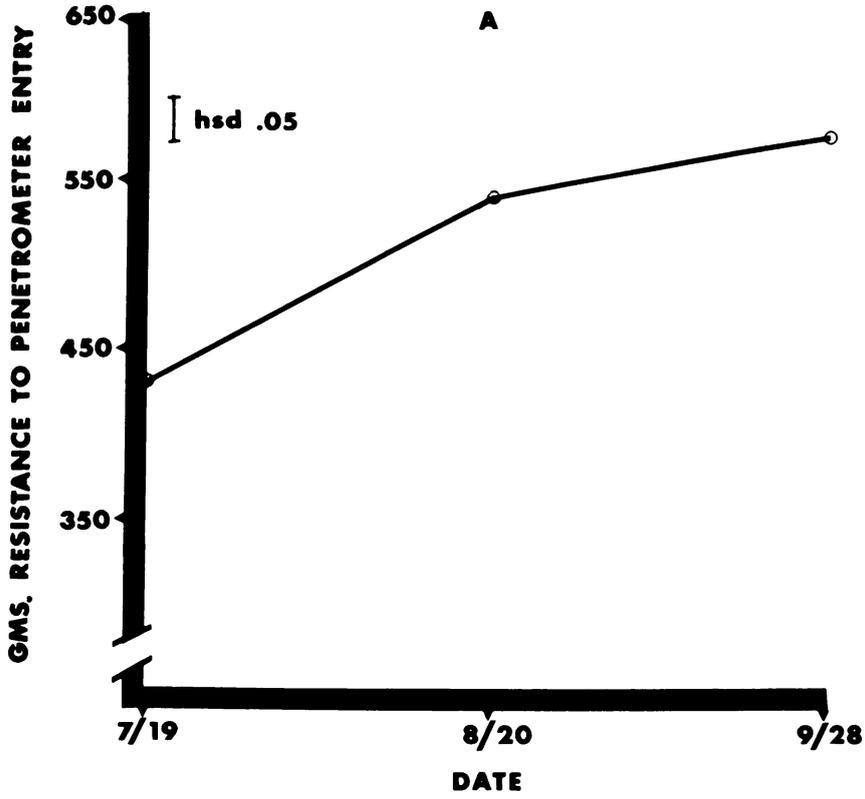
Fig. 5.--The change in concentration of CO_2 and O_2 in the soils gas phase with increasing plant population. The significance probability of the F statistic for population was 0.0005 for both CO_2 and O_2.
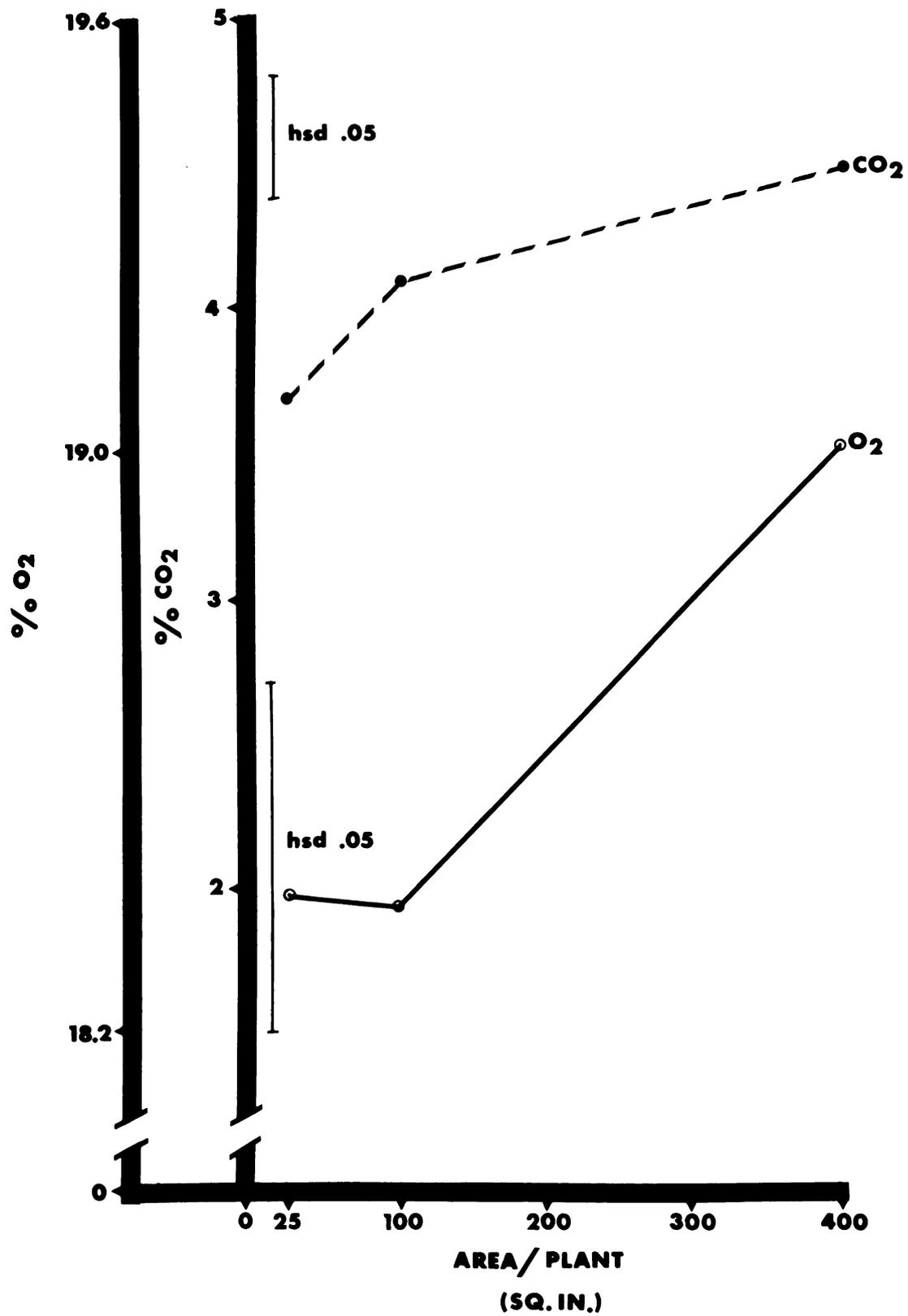
Fig. 6.--The change in concentration of CO_2 and O_2 with increasing depth in the soil, with and without plants. The significance probability of the F statistic for depth was 0.0005 for both CO_2 and O_2.
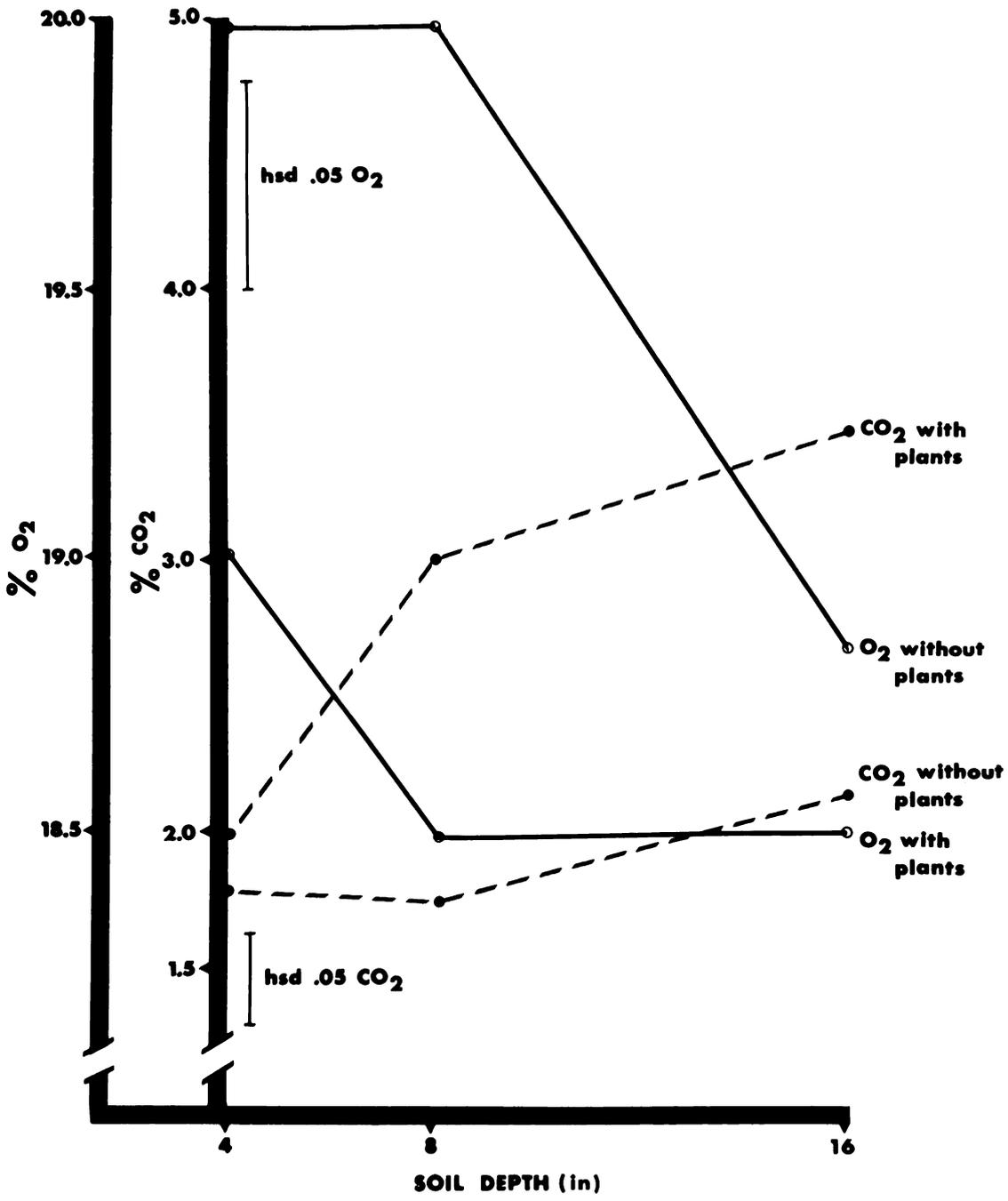
Fig. 7.--The increase in concentration of ethylene in the soils gas phase with time during the growing season. The significance probability for the F statistic for date was 0.0005.
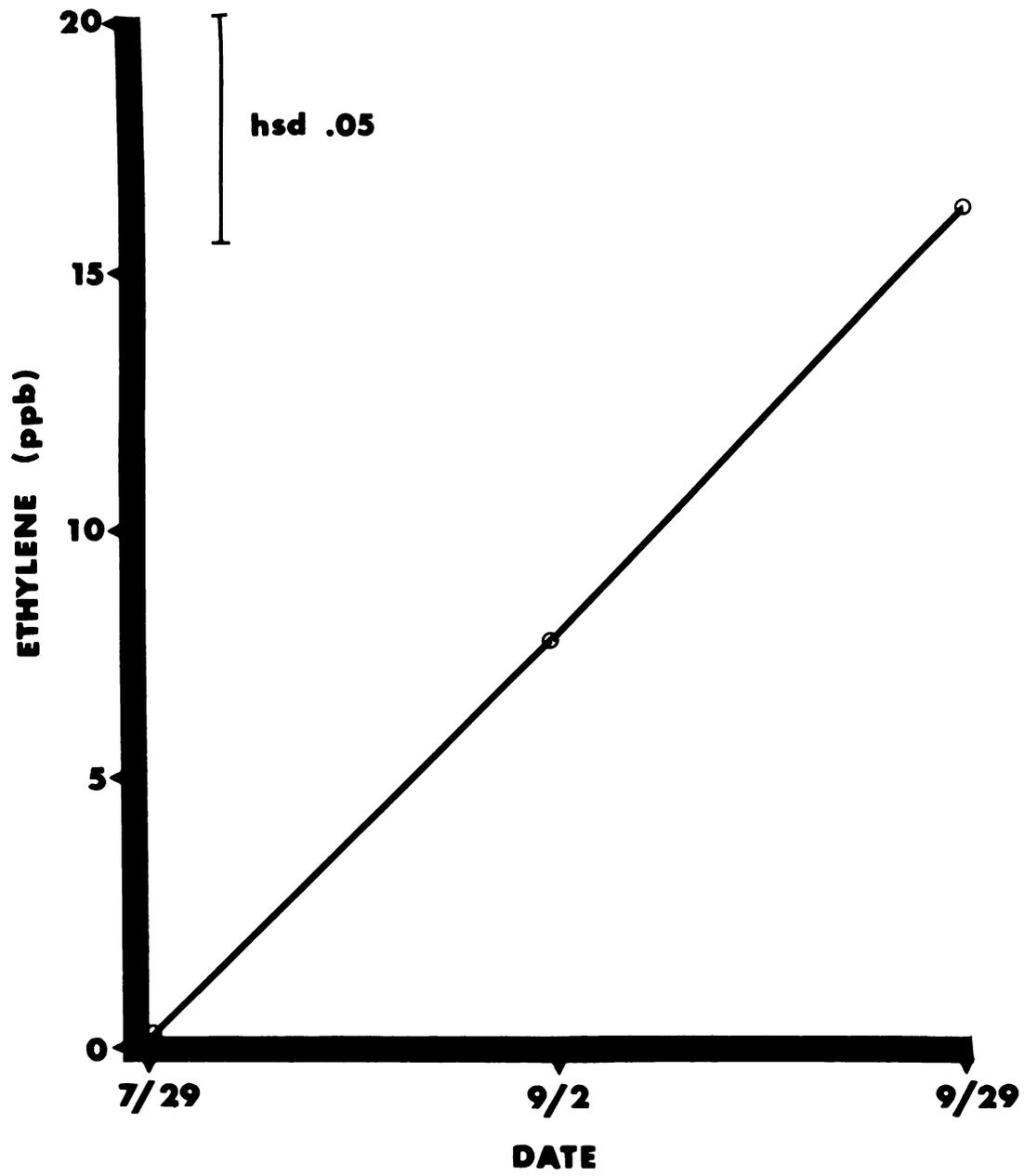
Fig. 8.--The change in concentration of CO_2 and O_2 in the soils gas phase during the growing season. The significance probability of the F statistic for date was 0.0005 for CO_2 and 0.003 for O_2.
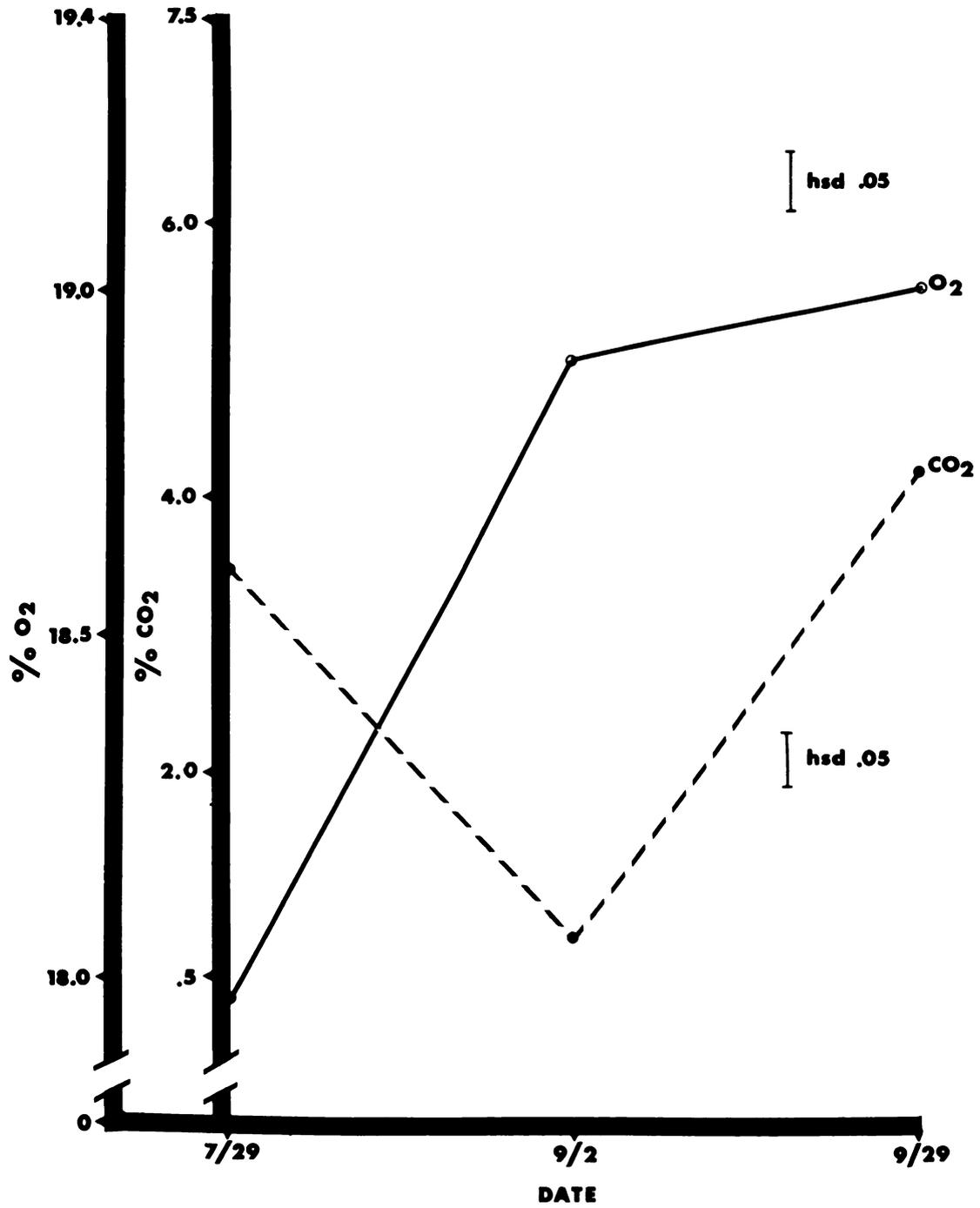
Carolus, et al. (5) found the growth of tomatoes to be both a function of available soil water and degree of atmospheric stress. The greater the leaf area the plant develops before extensive plant to plant competition, the greater was the root system and the less likely was the plant to suffer from drought (17). Consequently, as the water requirement of a population increases the potential for stress also increases. This relative to the decreasing number of fruit per plant and the relationship of water stress to the occurrence of blossonend rot of tomato accentuates the need for increased control over the water requirements at high plant populations.

The effect of increasing plant density on soil compaction presents a complex problem. Wollny (31) attributed the lower percent decrease in soil volume with increasing population to the additional protection from rain drops afforded by the increased canopy. The results reported herein support this well-known effect of water on compaction. Since the soil tends to consolidate in volume with time, a beneficial effect of an earlier connecting matrix of roots under high populations might also be expected. However, at the same time the effect of root pressure on the consolidation of soil into aggregates is well-documented (4,26), and with an increase in root volume per unit volume of soil with population (23), localized increases in density would be anticipated. The results obtained for population in this study were confounded with water application

increasing with population, consequently the population effect may have been masked. The fact that water has a definite effect on compaction and that no apparent effect was realized even though the total amount of water applied increased with population supports this possibility.

Changes in soil aeration mediate an array of diverse biological and chemical responses. Morphogenic alterations, nutrient availability, pH, redox potential and resistance to disease are but a few that have the potential to reduce yields or cause total crop failure (10).

It is important to note that because of the soil's diversity and dynamic state of flux many important factors (e.g. water status, gas diffusion rates, partitioning coefficients, physical conditions, etc.) are in constant interplay and are of critical importance in the determination of the quantity and quality of the soils atmosphere at a given instant. It is generally accepted that O_2 deficiency is of greater importance than CO_2 toxicity (10). Flooding of tomatoes results in a rapid inhibition of respiration and metabolism in the entire plant and inhibition of the TCA cycle in the roots (8). Anaerobic metabolism may result in two moles of CO_2 and ethanol for every mole of glucose metabolized (10). Fulton, et al. (7), in fact, found an accumulation of ethanol in xylem exudate shortly after flooding tomatoes. Evidence of Patrick, et al. (22), indicated the degree of sensitivity of tomatoes in relation to root oxygen. 21% oxygen was needed to obtain maximum growth.

CO_2 is fixed and is generally stimulatory to roots at low levels (11,27,33) although some plants (e.g. pea, bean and sunflower) have been reported to be inhibited by 1.0 to 1.5% CO_2 (28). Stemmit (27) noted both an increase in root and shoot growth with absorption of $C^{14}O_2$ from solution compared to plants given insufficient carbon dioxide levels. Consequently, soil CO_2 levels were not independent of shoot growth and high root fixation may, in some cases, result in increased production. Therefore, it is not surprising that CO_2 fixation by roots would shift O_2 and CO_2 away from a 1:1 ratio in the soil.

CO_2 and O_2 responded in an inverse relationship with depth in the soil. Also, areas with plants were higher in CO_2 and lower in O_2 than those without plants. The increased utilization of oxygen with population may be accounted for by the increased mass of metabolically active roots. This is also supported by the difference in concentration of these gases between soil with and without plants.

The response of CO_2 and O_2 concentration to date, may be indicative of the interaction of at least two control systems. If one considers the increased aeration and decreased water content in the soil with time (resulting in a decreased CO_2 concentration) interacting with increased respiration due to increasing root mass with time, a curve with depression then recovery would be anticipated.

The sensitivity of plants to low levels of ethylene has been known for some time (32). Recent work (9.15) has

indicated that ethylene is a natural growth hormone in grow-
ing plants and has several important biological functions.
Roots and hypocotyls give off low levels of ethylene during
growth. The absence of a population effect, however, would
indicate that the ethylene produced by roots does not signif-
icantly effect the soil atmosphere. Water has been shown to
have a definite, at least transitory, effect on soil's ethyl-
ene concentration (15); however, it is doubtful that this
alone could account for the increase with time.
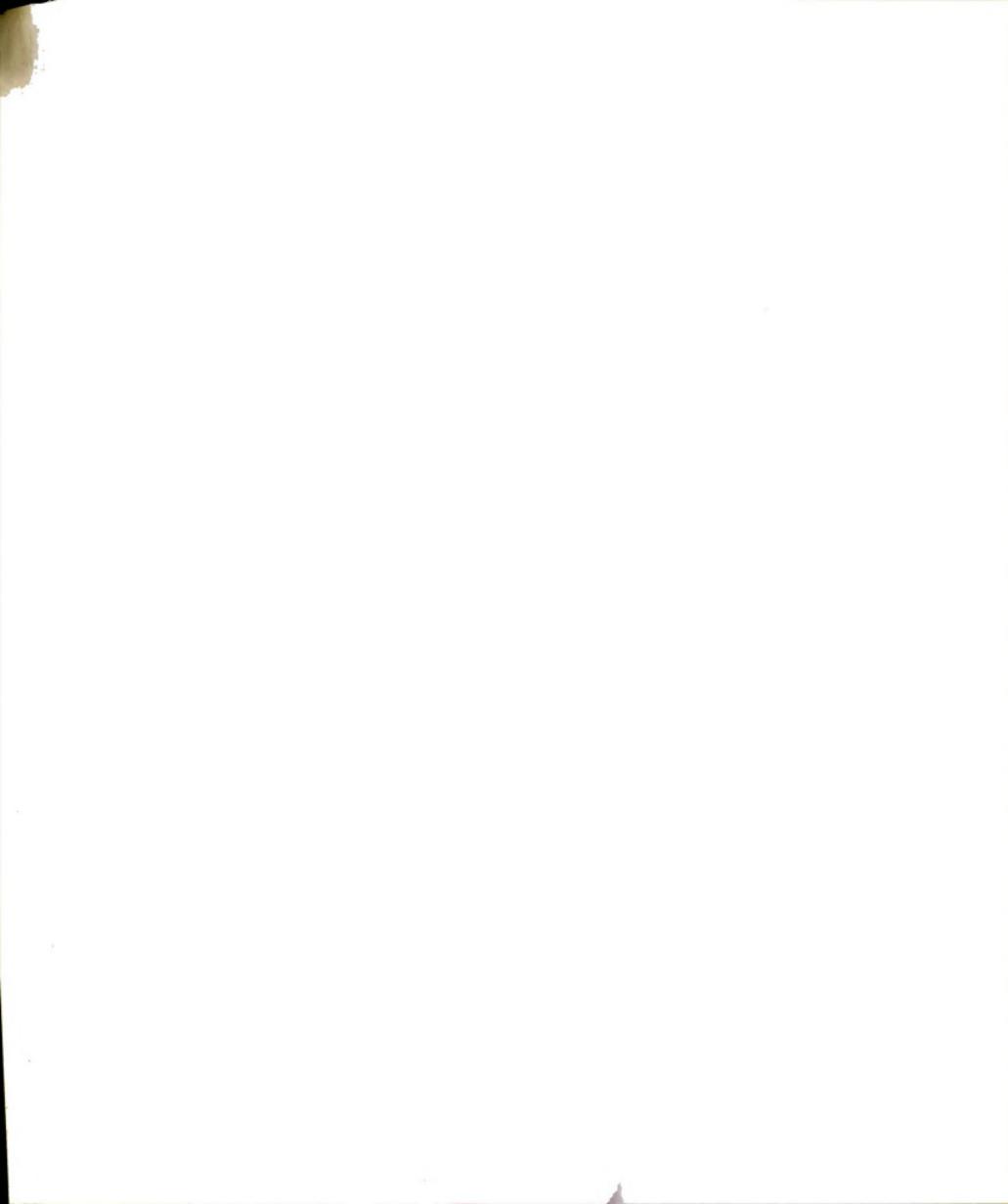
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SECTION III

Ethylene in Relation to the Response of
Roots to Physical Impedance

Introduction

It has been proposed that certain auxin effects on plant growth and development are mediated through their stimulation of ethylene synthesis (Zimmerman and Wilcoxon, 1935; Hall and Morgan, 1964). The possibility of a natural regulatory role of ethylene in roots is suggested by the similarity in response of roots to exogenous application of ethylene, auxin and mechanical resistance. Each has been shown to decrease the rate of elongation (Richards and Mac-Dougal, 1904; Ekdahd, 1953; and Eavis, 1965), increase radial expansion (Richards and MacDougal, 1904; Ekdahd, 1953; and Eavis, 1965), and induce the formation of root hairs and/or lateral roots (Zimmerman and Wilcoxon, 1935; Eavis, 1965; Hitchcock and Zimmerman, 1940; and Zimmerman and Hitchcock, 1933).

The evolution of ethylene has been noted in diseased, senescing, wounded and pharmacologically induced tissues (review by Burg, 1962). The work of Goeschl et al. (1966 and 1967) demonstrated that ethylene does act as a natural growth regulator in intact healthy plants.

The following paper deals with the ethylene control of root growth in response to mechanical impedance in the soil.

Materials and Methods

Seeds of the test plant, <u>Vicia</u> <u>faba</u>, L., variety Broad Windsor were imbibed in aerated water for 8 hours, planted in trays containing 15 cm of moist vermiculite, and grown in continuous dark for either 48 or 72 hours. All operations were at 18°C.

Ethylene Evolution: The apparatus used for measurement of ethylene evolution (Fig. 1A) consisted of a hollow glass tube (2.1 cm ID X 15 cm length) covered with black electrical tape to exclude light. Gas tight seals were made at the ends of the tube with soft neoprene stoppers. A hard plastic tube (2.3 cm in length with an ID slightly larger than the diameter of the root) was inserted in the base of the upper stopper perpendicular with the plastic barrier. This was used to simulate the radial restriction presented by the soil. The tube was perforated to insure adequate ventilation of the root. The adjustable hard plastic barrier was placed at the base of the tube or 3 cm below it in the case of unobstructed controls. Background measurements were made on identical apparatus, however, a glass plug was placed in the root hole in the neoprene stopper. A small piece of moist filter paper was placed around the glass just under the upper neoprene stopper. Seedlings with roots 2.2 to 2.4 cm long were carefully removed from the vermiculite and placed through a hole in the upper stopper and into the plastic tube. The stopper with seedling was then inserted

Fig. 1A.--Apparatus for measurement of endogenous ethylene evolution: 1) air inlet and exhaust, 2) moist vermiculite, 3) wire restrainer, 4) seedling, 5) neoprene seal, 6) root, 7) moist filter paper, 8) perforated plastic tube, 9) plastic barrier, 10) glass rod for raising and lowering barrier, and 11) basal neoprene seal.

Fig. 1B.--Apparatus for exogenous application of ethylene: 1) air inlet and exhaust, 2) moist vermiculite, 3) seedlings, 4) neoprene seal, 5) roots, and 6) moist filter paper.

Fig. 1C.--Apparatus for measurement of soil gas atmosphere: 1) serum cap, 2) glass tubing, 3) copper grid, and 4) open basal end.
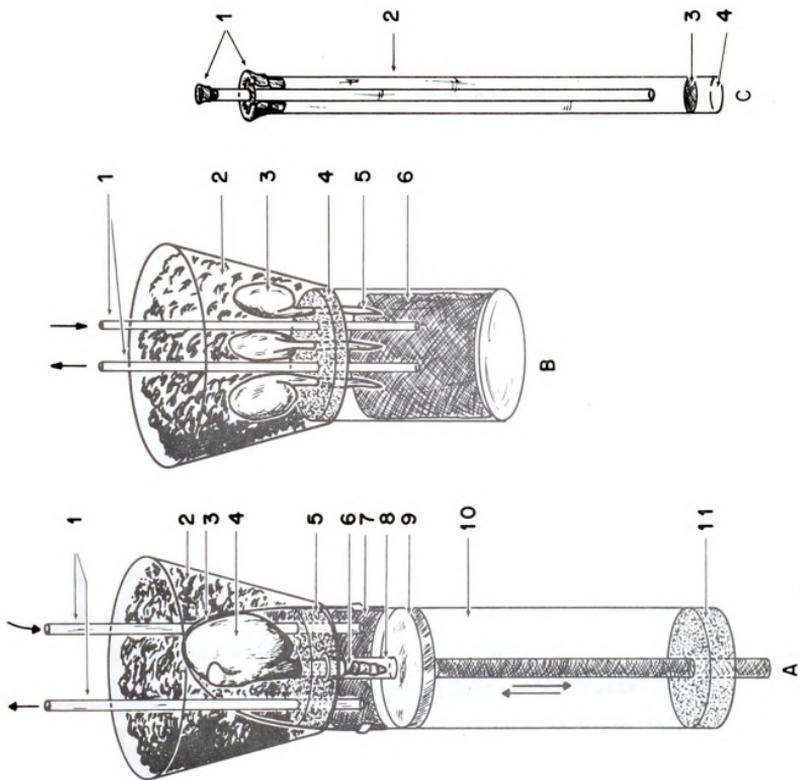
into the glass tube and secured with wire taped to the glass tube. This was necessary to prevent the root from simply lifting the seed out of the vermiculite when it contacts the obstruction. A polystyrene pot was then taped around the seedling and upper portion of the glass tube. Moist vermiculite was placed around the seedling. The plants were allowed to equilibrate 1 hour before measurements were taken.

A flow rate of 1 ml./min. was selected since relatively low gas exchange rates are characteristic of the soil. A 10 ml./min. capillary was placed at the exhaust to minimize any back diffusion of ethylene from the surrounding air. The air stream had ethylene removed with a potassium permanganate scrubber and was humidified before entering the chamber.

Two ml. gas samples were collected by closing the exhaust and withdrawing at the same rate as the air was entering. Ethylene concentrations were determined by flame ionization gas chromatography using an alumina column. CO_2 and O_2 concentrations were periodically monitored and did not deviate substantially from the norm.

Ethylene Treatment: Three plants with roots 2.0 to 2.5 cm long were placed with their roots through holes in a neoprene stopper and inserted in a glass jar (4.5 cm ID X 10 cm deep) containing moist filter paper (Fig. 1B). The jars were painted on the outside to exclude light. Polystyrene pots were then fitted around the top and filled with moist vermiculite covering the seedlings. Air flow into the

jar was 30 ml./min. Ethylene was applied by the method of Pratt et al. (1960), in a concentration range from 0 to 1236 ppb. Four replications per concentration were used for each experiment. After 48 hours, the roots were cut off at the lower surface of the neoprene stopper and shadow graphed for measurement. Measurements of diameter were made with an optical stage micrometer and a 10X stereomicroscope.

Soil Ethylene Levels: Glass tubes (Fig. 1C) were placed vertically in a field (devoid of plants) at soil depths of 4, 8 and 16 inches. The surface end of the tube was sealed with a serum vile stopper and the lower end covered with a copper screen. Samples were removed through a second smaller tube, also serum stoppered, to obtain the gas from as near the soil surface at the appropriate depth as possible. The samples were chromatogramed within 20 minutes after removal. The possibility of ethylene evolution from the serum vile stoppers was tested and found not to be a factor. The plot had 1/2 inch of irrigation just prior to the first measurement.

Results

Upon reaching a physical obstruction, ethylene production by roots increased to as much as 6 times that of controls (Fig. 2). This increase normally started within 1 hour of contacting the obstruction. The rate of increase in ethylene evolution appeared to be partially related to the rate of root growth into the impeding zone; however,

the maximum rate of evolution was similar, irrespective of
the rate of increase. Upon removal of the obstruction, the
rate of ethylene production decreased to near that of con-
trols. If the physical barrier is not removed, the high
level of ethylene evolution was maintained for up to 30
hours after its initiation; however, during this time there
was a gradual decline of about 25%.

Exogenous application of ethylene at very low concen-
trations stimulated growth in length (Fig. 3). Stimulation
occurred at two distinct ethylene levels and may indicate a
dual effect of ethylene on root growth. The second stimula-
tion was less pronounced and consequently not conclusive.

Ethylene also resulted in an increase in radial en-
largement of the root (Fig. 4) reaching 20% above the control
in 1236 ppb ethylene. The rate of increase in diameter was
greatest at low levels (100 ppb) but occurred over the con-
centration range tested. The most pronounced increase in
diameter occurred 20 mm from the tip, however, the swelling
at 10 mm and 30 mm was substantial.

Ethylene found in the soil gas phase reached near physio-
logically significant levels (Table 1A) late in the fall
(10/1/70). The concentrations were pocketed and increased
during the growing season (Kays and Nicklow, 1971). On the
plots measured, which were devoid of higher plants, there was
no apparent depth effect for ethylene as typically noted for
O_2 and CO_2 (Kristensen and Enoch, 1964). Water from irriga-
tion or rain results in a temporary depression of the level
of ethylene in the soils gas phase (Table 1B).
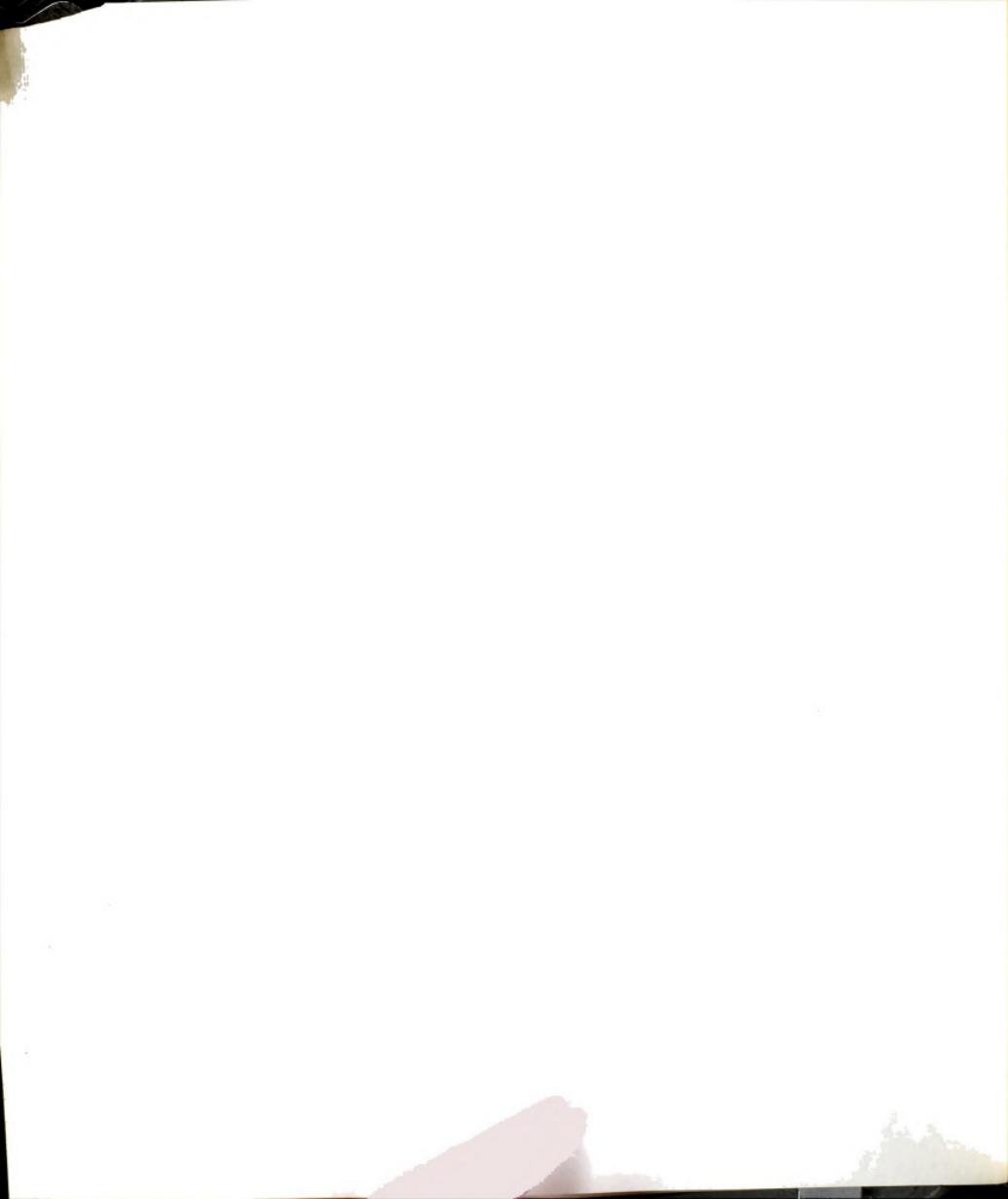
Fig. 2.--The increase in rate of ethylene evolution from <u>Vicia</u> <u>faba</u>, L. roots upon contacting a physical barrier.

ETHYLENE EVOLUTION (μl./kg./day)

TIME (hr.)

CONTROL

▼ barrier removed
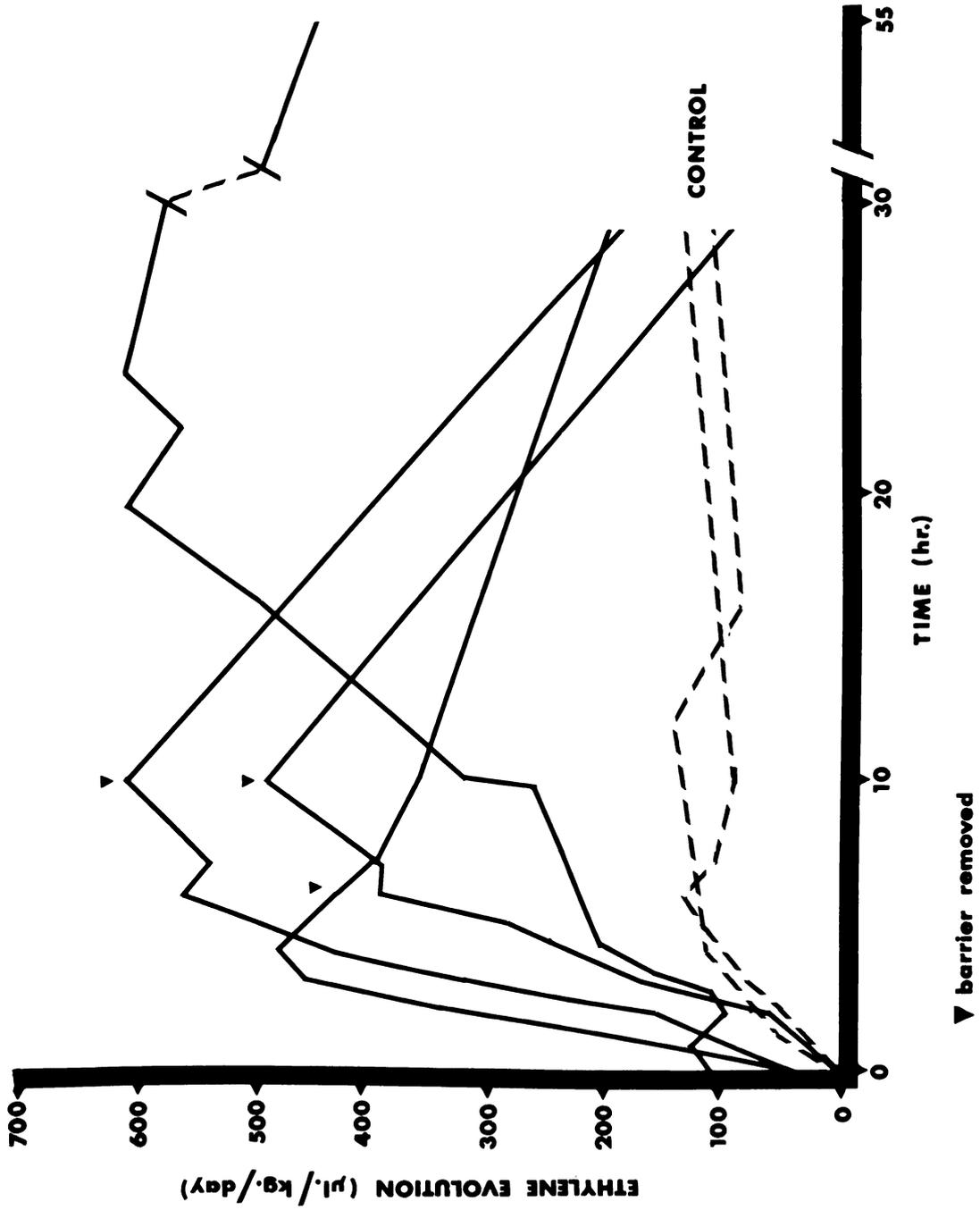
Fig. 3.--The effect of exogenous concentrations of ethylene on the increase in length of _Vicia faba_, L. roots after 48 hours. Each point represents an average of 36 roots.

CONTROL

ETHYLENE CONCENTRATION
(ppb)

CHANGE IN LENGTH OVER CONTROL (mm)
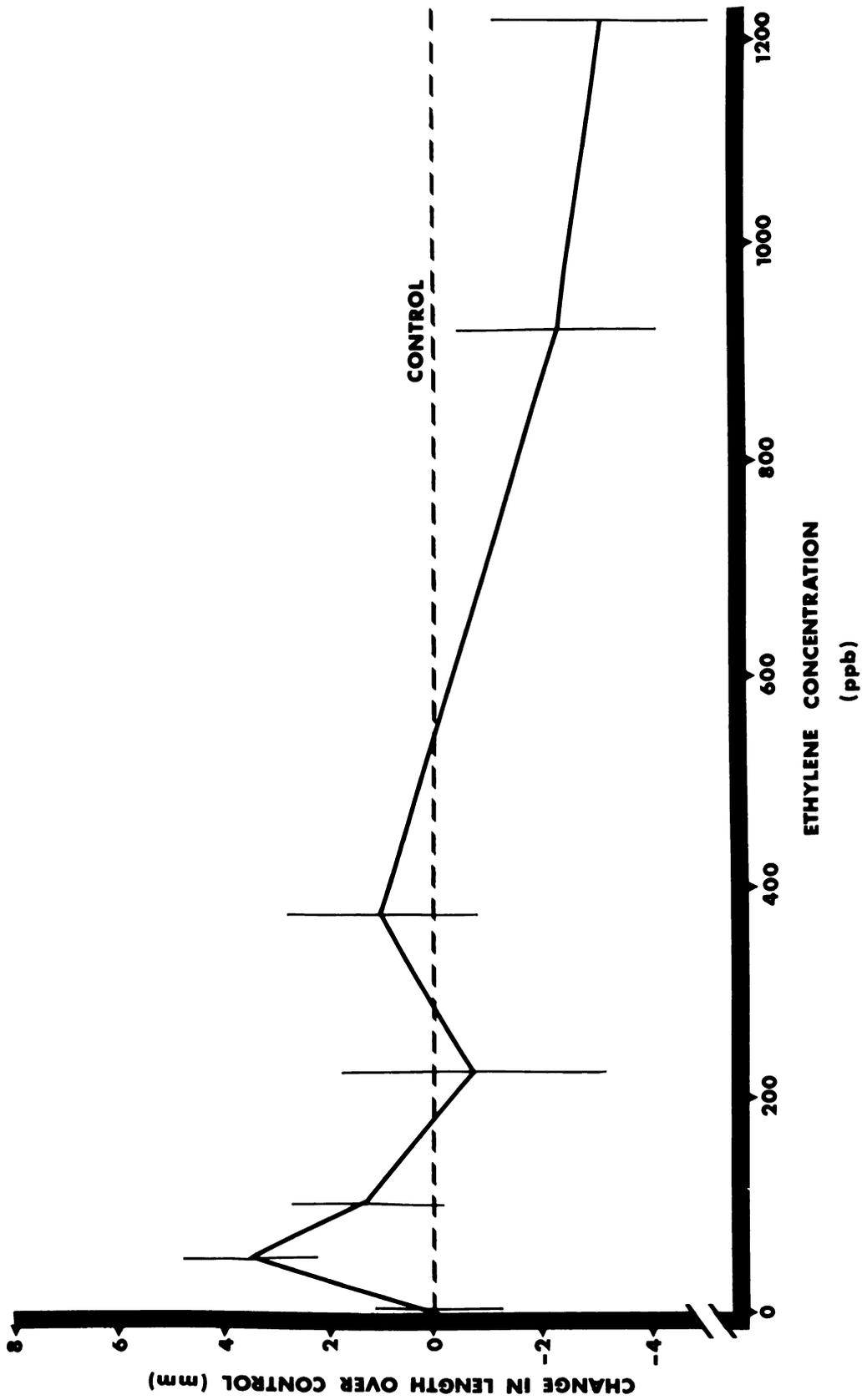
Fig. 4.--The effect of exogenous concentrations of ethylene on the increase in diameter of <u>Vicia</u> <u>faba</u>, L. roots after 48 hours. Each point represents an average of 36 roots.
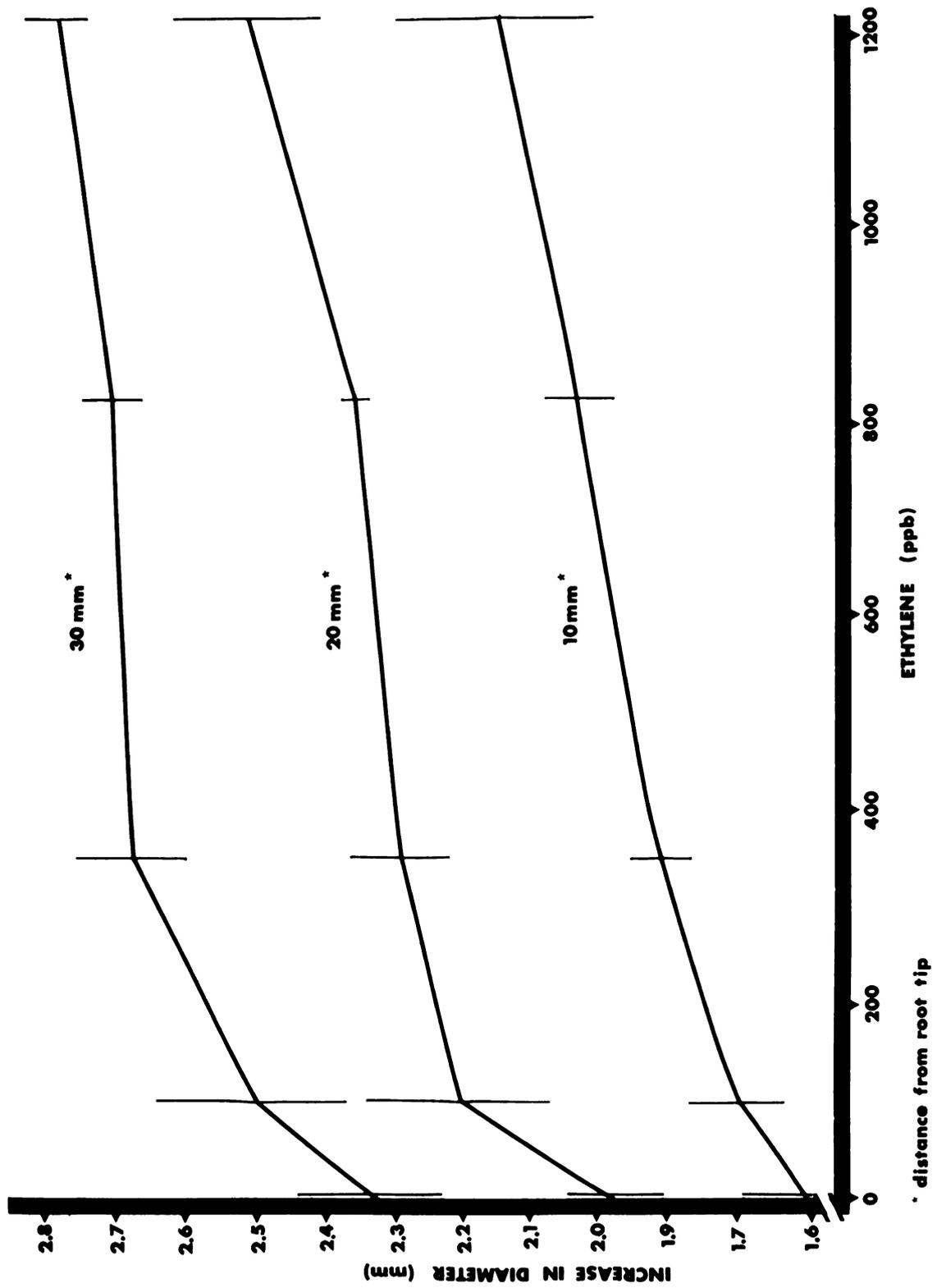
Table 1A.--Change in ethylene concentration in soil gas
         phase during the growing season.*

Date	Concentration of Ethylene (ppb) *(average of 3 soil depths of 4, 8 and 16 inches)
8/1	Not Detectable
9/2	8.67 ± 2.16
10/1	15.67 ± 2.61

Table 1B.--Percent change in the ethylene concentration in
         the soil gas phase after irrigation (1/2 in.).

Days From Time Irrigation	% Decrease From The First Measurement
0	0
3	66.6
11	45.0

Discussion

Roots and underground shoots deform the soil by tensile failure, shear failure without compression and shear failure with compression (Barley and Greacen, 1967). The radial force exerted by a root is substantial. Measurements up to 6.1 bar have been made for _Vicia faba_ (Pfeffer, 1893). Small changes in root diameter can mediate a substantial increase in shear failure potential in a soil or ped of high mechanical impedance thus enhancing the root's chances of overcoming the restriction. Resistance to radial expansion also greatly increases the longitudinal force potential. Consequently, radial and longitudinal resistances are closely related to radial and longitudinal expansion and subsequent growth.

The results indicate that axial mechanical resistance mediates an increase in ethylene evolution from roots and this in turn results in radial expansion. An increased force potential could result in a resumption of elongation and/or an increase in elongation. The physiological changes in size and shape of the root are closely tied to the nature of the resistance and the root's potential to mediate shear failure. It should be noted that Radin and Loomis (1969) using cultured radish roots found the opposite effect on radial expansion. However, the swelling response was apparent when ethylene was applied to excised roots (Chadwick and Burg, 1967).

As with the response of hypocotyls to physical stress (Goeschl et al., 1969), the area of ethylene evolution appears to be localized. This is indicated by the uniform level of evolution of control roots even though their total weight and mass increases with time.

The root swelling response occurred after the increase in rate of ethylene evolution. If the roots were not grown through tubes, upon reaching the barrier, they bent rapidly without a detectable increase in ethylene production or noticeable change in diameter. One might anticipate that a certain minimum resistance must be present before high levels of ethylene are produced. Goeschl et al. (1967) found the level of ethylene evolution from hypocotyls to be a function of resistance rather than total load.

Ethylene in the soil atmosphere has in the past been largely neglected. The fact that it can be found and in significant amounts opens a series of new questions and problems. As indicated by Table 1B, transient water changes appear to cause fluctuations in the ethylene level in the soil atmosphere, possibly reflecting the high partitioning coefficient of ethylene into water. Since the soil where the samples were taken was devoid of plants, the increase in ethylene concentrations during the growing period cannot be ascribed to increasing number of plant roots. Consequently, one might anticipate the role of soil micro-organisms and organic matter to be of considerable interest and importance.

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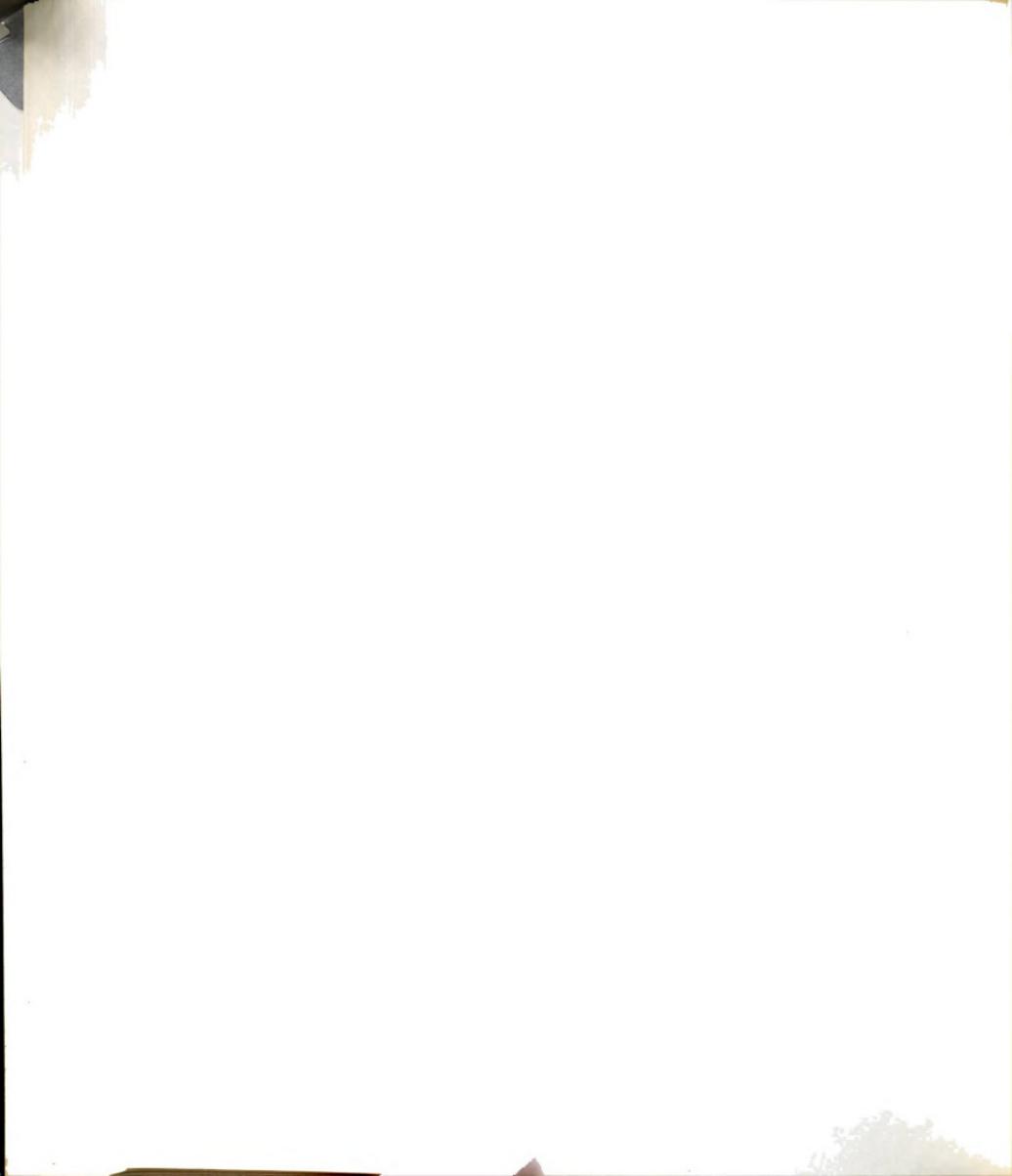
SECTION IV

A Sensitive Technique for Measuring Root Mediated
    Soil Deformations and Their Potential for
       Overlap Between Neighboring Roots

Introduction

Roots, hypocotyls and other below ground plant parts
alter existing structure of the soil that is in close
proximity with the organ (5). Shear failure with compres-
sion and shear failure without compression are the primary
means of channel formation by plant roots (3). The degree
of soil consolidation is a function of both the properties
of the soil and the plant root. Furthermore, the soil ex-
erts a pronounced influence on root growth (9). Root growth
can be restricted in cemented or indurated horizons (12).
Soil strength appears to be a primary factor in the pene-
tration and growth of roots into the soil (4). Where the
soil strength is sufficiently high, crop yields may in turn
be significantly depressed (1,10).

Several methods of measuring density changes in simu-
lated soil systems have been developed (7,11). Greacen's
technique (11) has the greatest precision and consists of a
photographic determination based on the relationship between
film density and bulk density of the medium. Although the
technique appears reasonably accurate for a large diameter
deforming penetrometer (in this instance a 3 mm steel probe),
the optical properties of soils would present substantial
accuracy problems when measuring the effect of small roots.

The objective of this study was to develop a technique for measuring small changes in bulk density around plant roots or other below ground plant organs and determine the effective root diameter.

Materials and Methods

Vicia faba, L., variety Broad Windsor, seeds were imbibed for 8 hours in aerated distilled water and planted singly in 50 ml. plastic beakers containing washed sand of either 18.27 µ or 49.09 µ average diameter. The perforated bases of the beakers were covered with filter paper before sand was added. A seed was placed at 40 ml. level, covered with sand and then wetted from the base with distilled water. The seeds were grown in the dark at 18°C for 96 hours. At this time the seedling was fixed in situ for 24 hours with 5% gluteraldehyde, also taken up from the base of the beaker. The beakers with seedlings were dried at 60°C for 48 hours and vacuum impregnated (Fig. 1) with methacrylate (30% ethyl and 70% butyl) with 2% benzoyl peroxide catalyst. The beaker was placed under a particle vacuum (717 mm. Hg) and lowered slowly to a point where the methacrylate in a container below moved up into the beaker with seedling from the base by capillary action. Methacrylate was utilized as the embedding medium because of its viscosity properties, similar to water, which minimized structural alterations due to front movement during embedding. After the methacrylate

front reached the surface of the sand the entire container was slowly lowered into the beaker of methacrylate to a point 1 cm from the top. The vacuum was released and the container placed in a nitrogen gas atmosphere and dried at 60°C for 48 hours.

The embedded samples were cut vertically, parallel to the main root, using a diamond circular saw, and ground to the center of the root with silicon carbide grinding paper. The samples were polished with a progressive series of silicon carbide grinding paper (grits 120 through 600).

The polished sample was carbon coated. Point scans using an EMXS-M electron microprobe x-ray analyser[1] were run for Si and Ca. Ca scans were used to give the exact location of the root edge. Data was collected with a strip chart recorder. Six to 8 scans were made for each density measurement. The scans were made at set intervals of approximately 1/2 the average diameter of the media parti-cles progressing down the root. Knowing the probe scan speed and the chart speed, the distance of any point, on the print out, from the root could be calculated. The ratio of the solids to the voids was measured at 1/2 peak height. Measurements were made for 1 mm distances, however, 250 or 500 μ distances can also be made.

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[1] Applied Research Laboratories

Fig. 1.--Apparatus for the embedding of samples:
a) glass rod for lowering sample, b) vacuum barostat,
and c) line to vacuum pump.

a.

b.

60 cm

c.
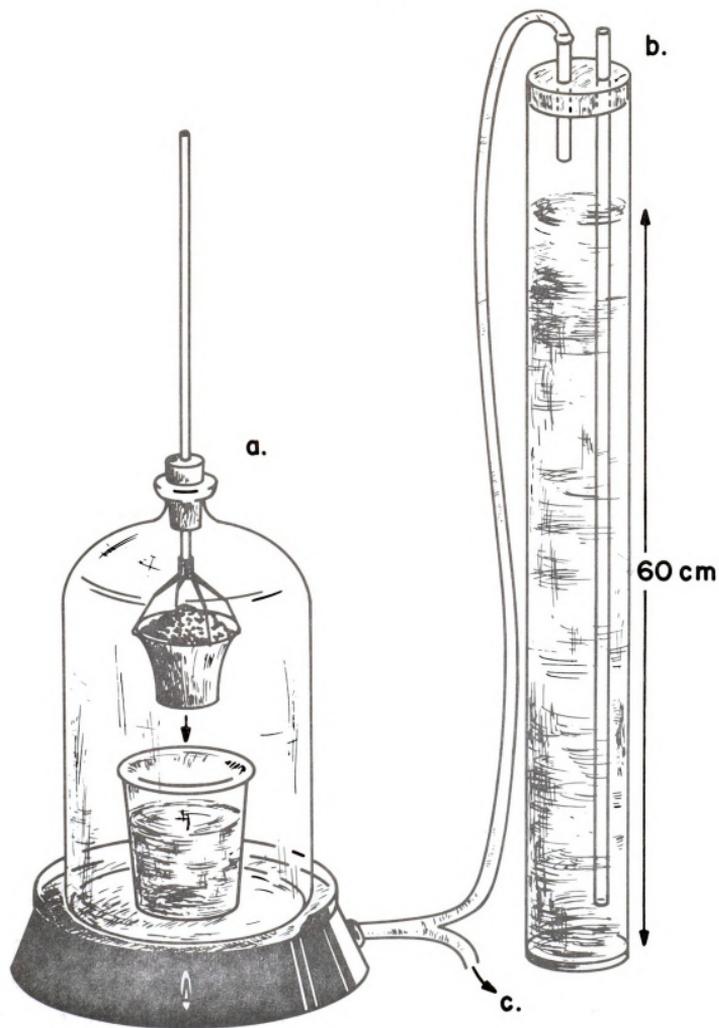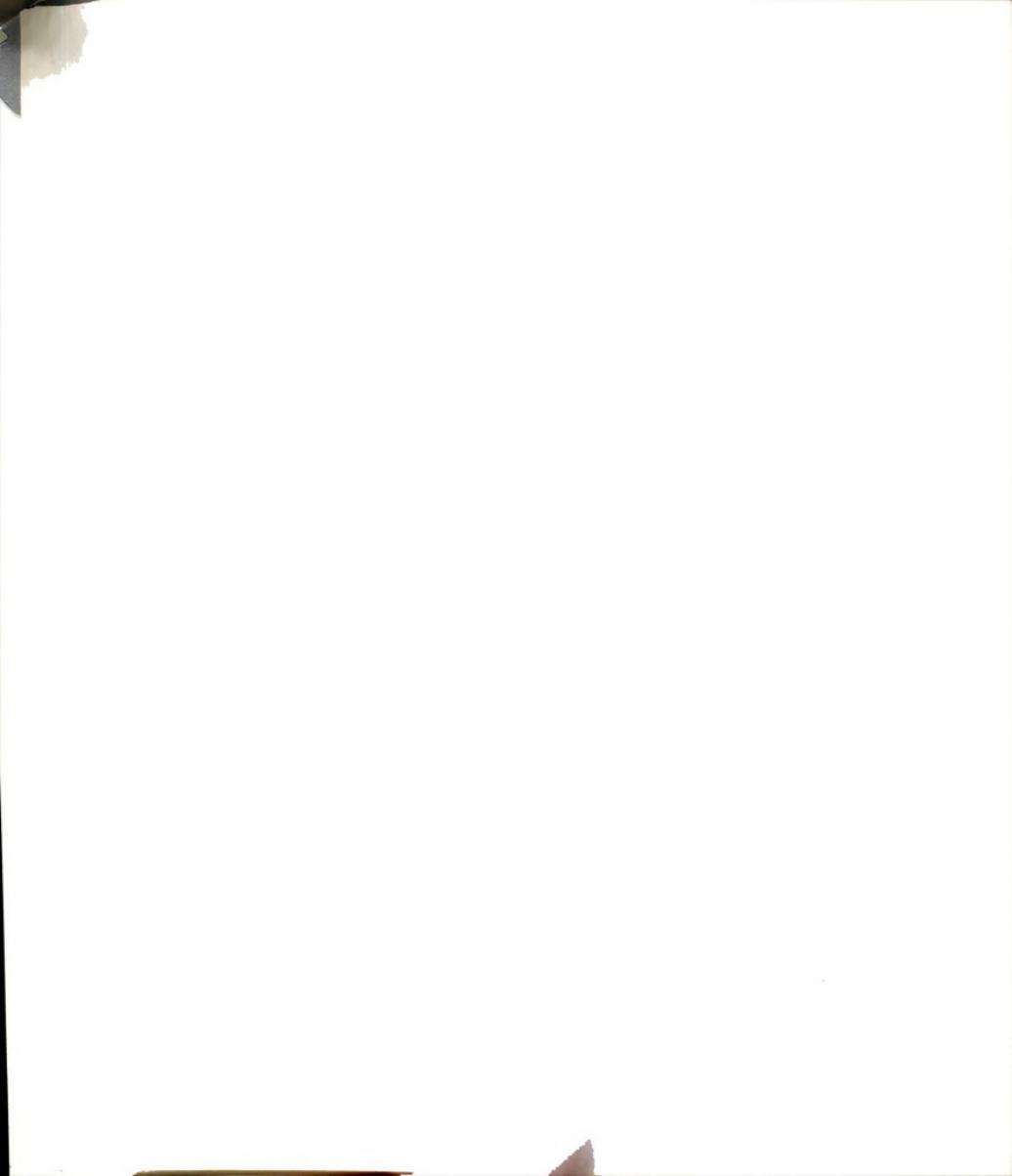
Results

A single scan for both Si and Ca is presented in Fig.
2. Calculating the voids ratio at 1/2 peak height, the
ratio of solids to voids is plotted vs the distance from
the root (mm) in Fig. 3. The density increased out to about
5 mm in fine sand in comparison with a distance of about 6
mm in coarse sand. Therefore, the effective diameter (root
radius + distance of deformation x 2) increased approxi-
mately 6 times.

Discussion

The results indicate that the effective root diameter
(root radius + distance of deformation x 2) is increased to
approximately 6 times the diameter of the root in coarse
sand. Greacen (11) reported a 4 fold increase in effective
diameter with a steel probe which, unlike plant roots, ex-
hibits no radial increase from swelling or secondary growth.

The question that arises is: under high populations of
plants or other areas with substantial root densities, do the
effective diameters of neighboring roots overlap? If one
assumes that roots of rye exhibit the same percent increase
in effective diameter as Vicia faba, L., then the effective
diameter, based on previous measurements of the average root
diameter (.23 mm) (2), can be calculated. Substituting the
effective diameter for d in the following equation for the
average distance between roots,

Fig. 2.--Line profile analysis run perpendicularly to a vertical root, showing the distribution of Si and Ca.
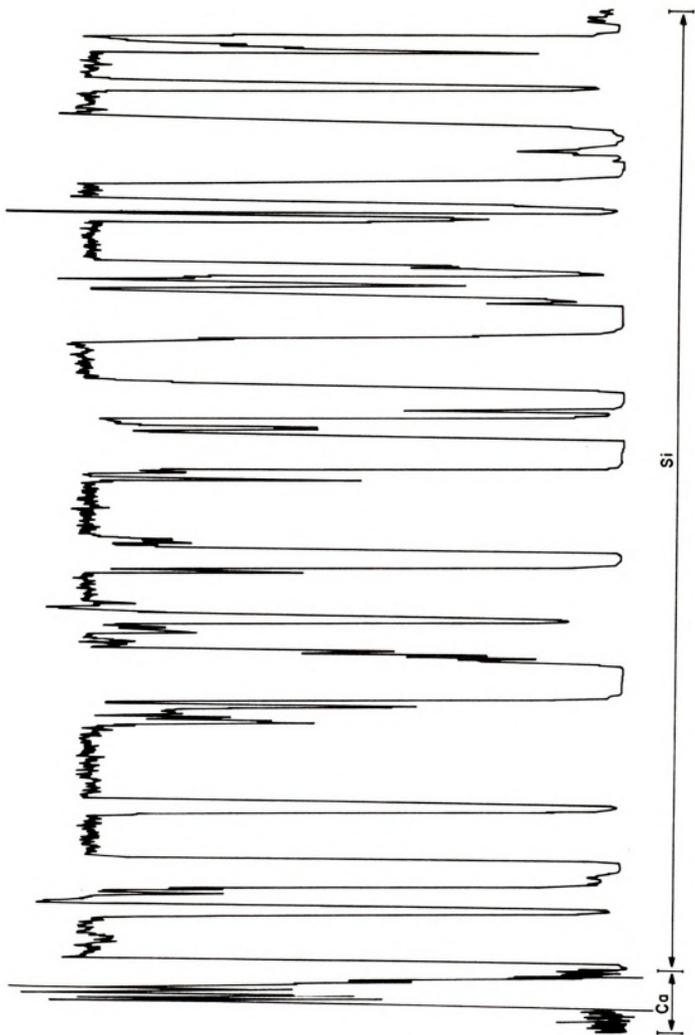
Fig. 3.--Change in voids ratio with distance from the root.
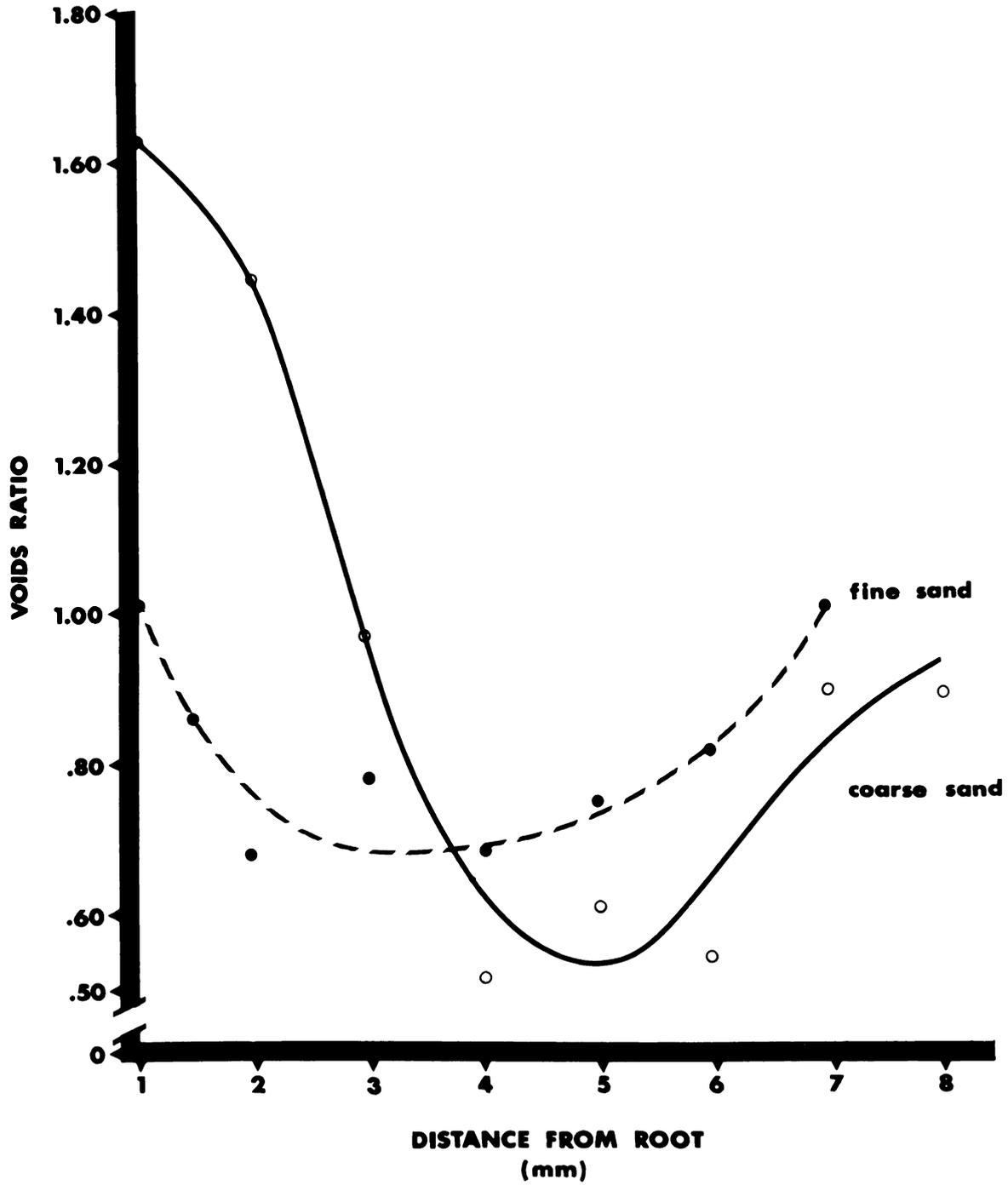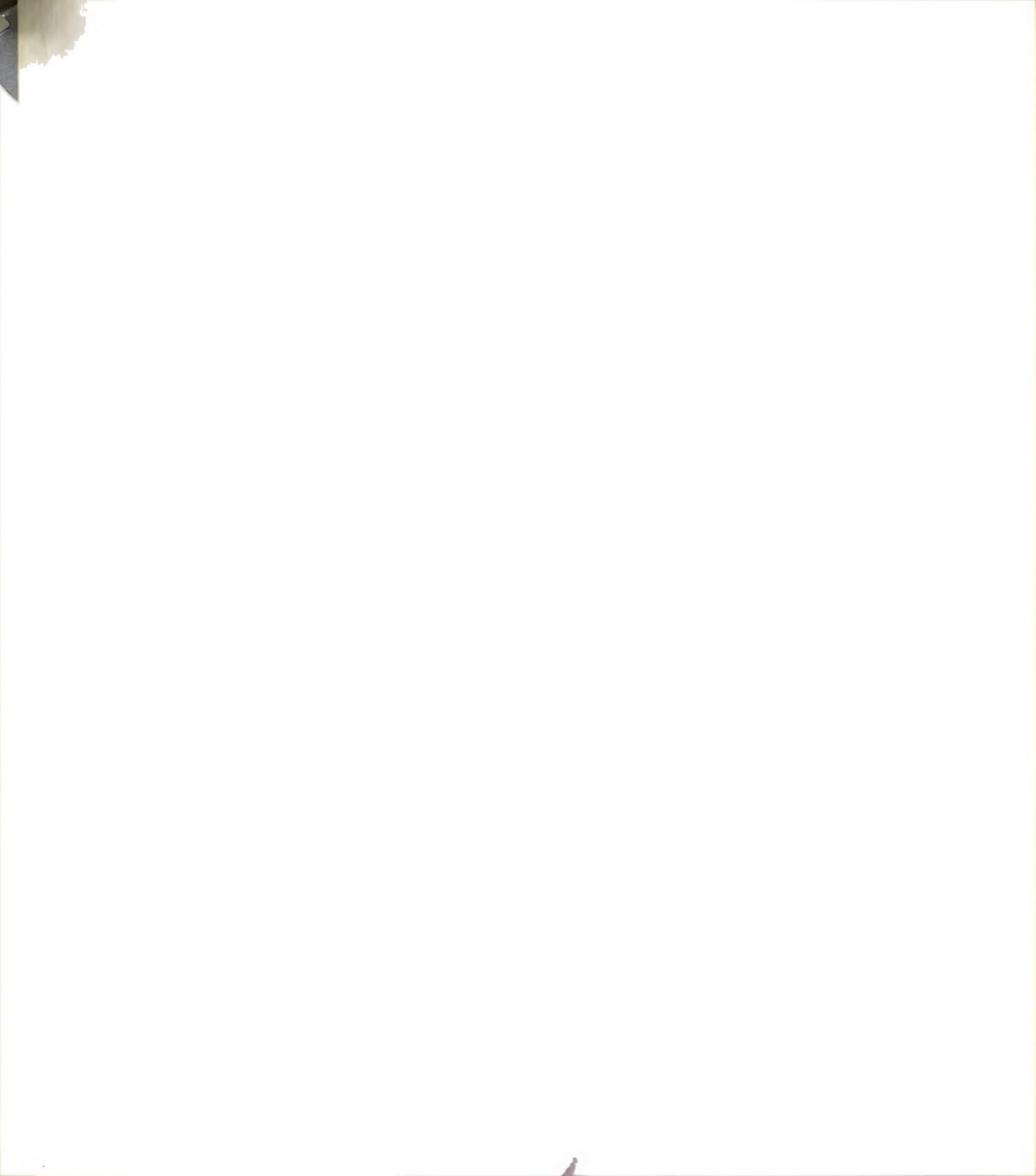
$$d = 1/(Lv \pi)^{1/2} \tag{1}$$

where d represents the average distance between roots and Lv is the root density (cm^{-2}), and solving for density, a value of 33.4 cm^{-2} is obtained. Therefore any density of roots greater than 33.4 cm^{-2} could have overlapping effective diameters or areas of deformation. A comparison of this value with actual measurements of root density for rye and/or wheat (Andrews, 53 cm^{-2} (2), Pavlychenko, 53 cm^{-2} (14), Dittmer, 50 cm^{-2} (8)) indicates that a single rye or wheat plant exhibits approximately twice the density of roots required to have their areas of deformation overlap.

Although this provides an excellent indication that roots have the potential for their areas of deformation to overlap, there are several considerations that must be kept in mind. (A). This method assumes that the root system is perfectly symmetrical. Work of Melhuish (13) and Barley and Sedgley (6) indicates that this is not the case. Since estimates were calculated under an ideal situation or perfect root distribution, then any move away from a perfect distribution would tend to increase the significance of the overlap potential. (B). The estimate assumes the same relative percent deformation regardless of the root diameter and particle size distribution. The results in Fig. 3 indicate, as one would anticipate, that particle size is of importance in relation to the distance of deformation. (C). It neglects, at present, changes in bulk density, vertical and radial resistances, and plasticity and elasticity changes in the soil.
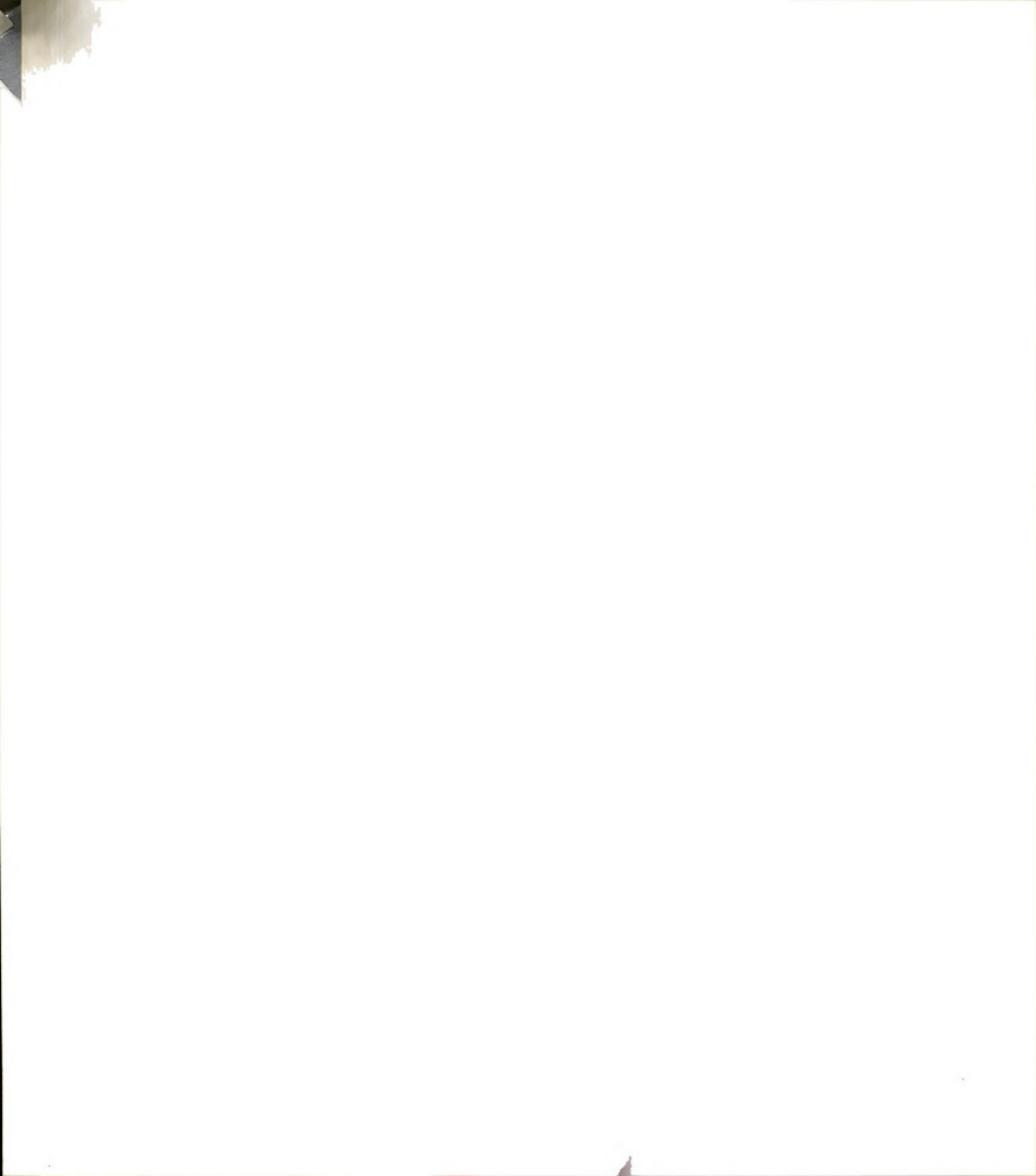
The magnitude of the difference in estimates of essential and actual root density, indicates the potential for overlap of physical deformations of roots. The physical and biological factors which determine if this competition for space by the roots actually results in a changed size and shape of the root system remain to be tested.

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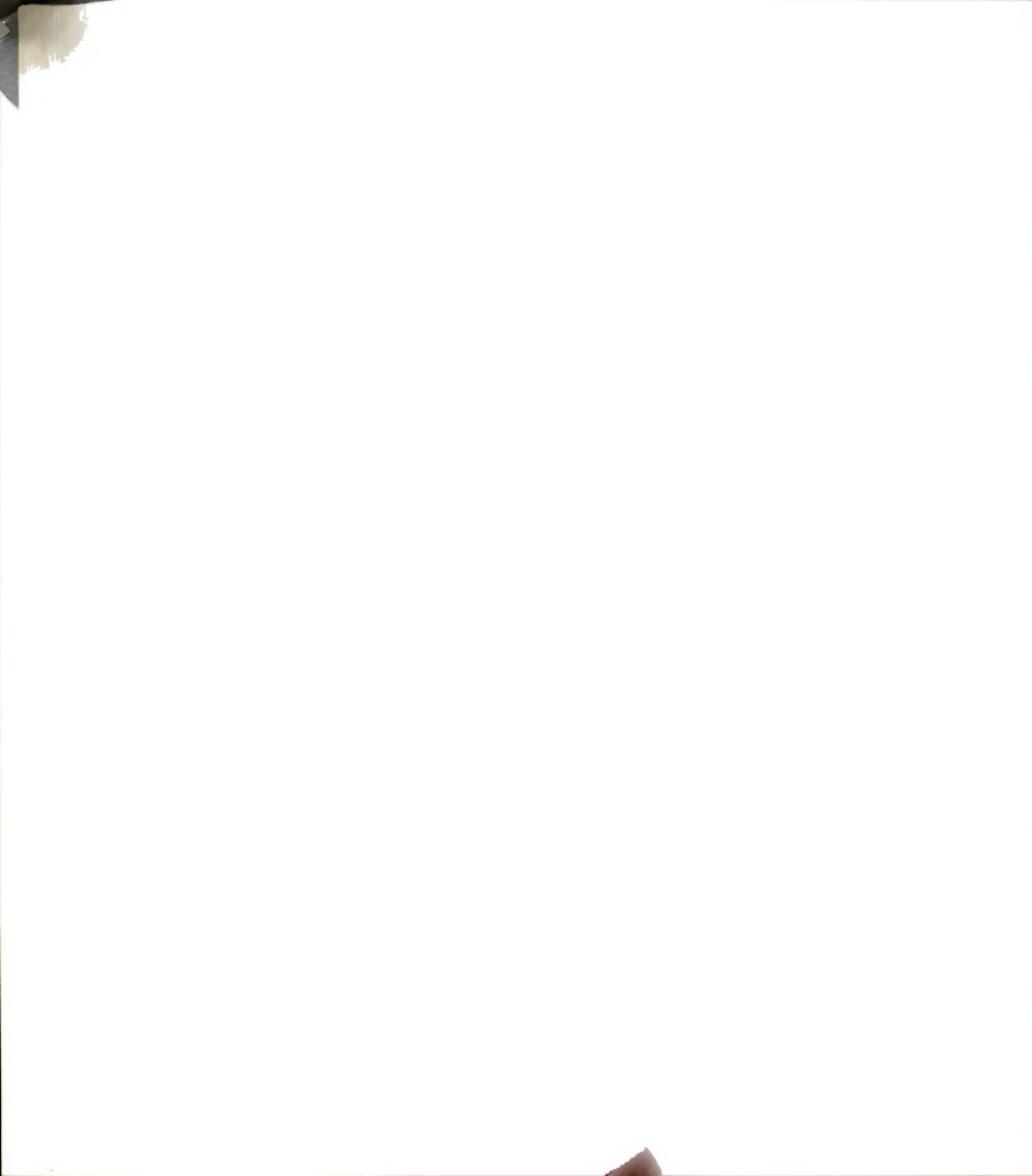
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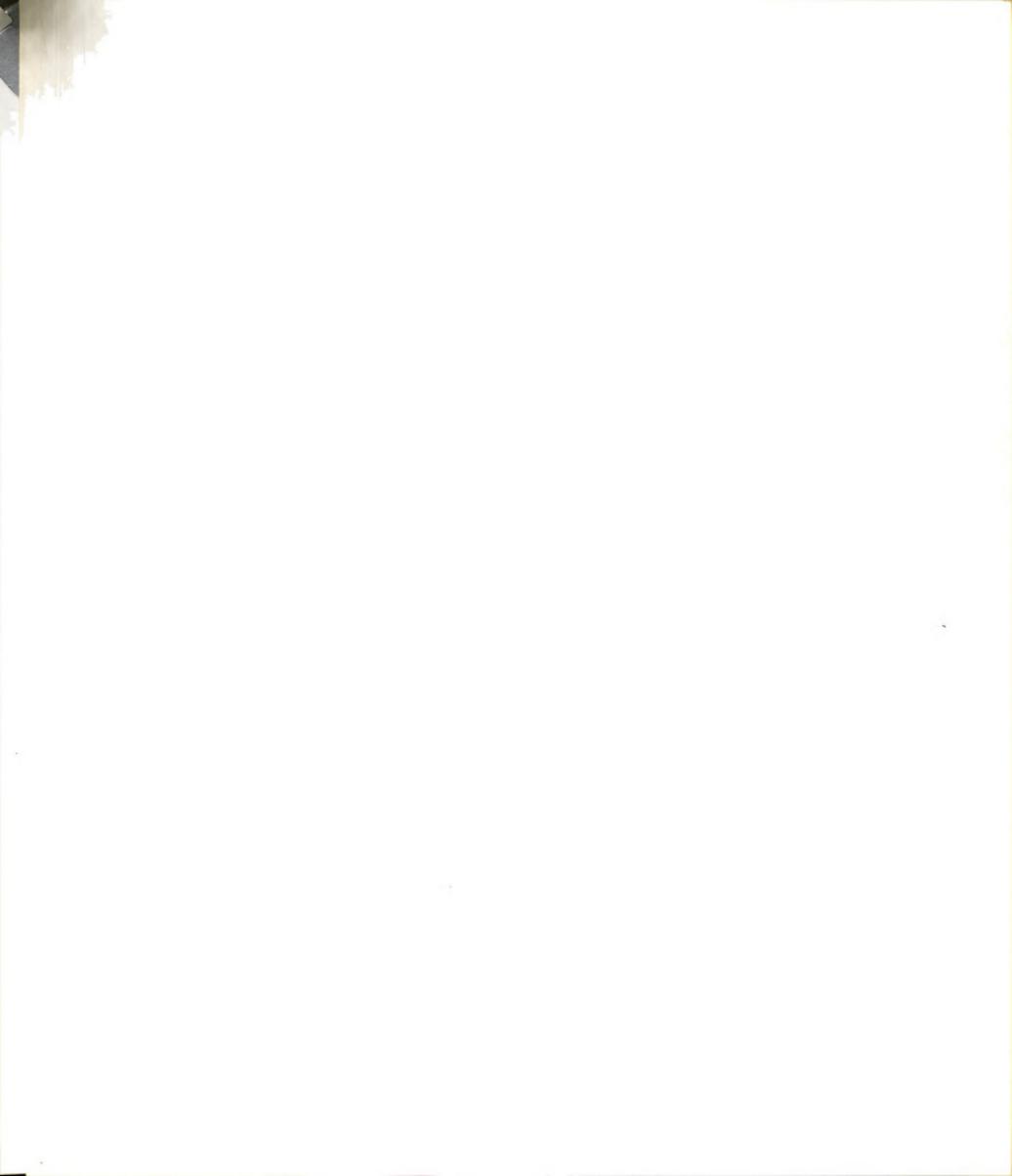
APPENDICES
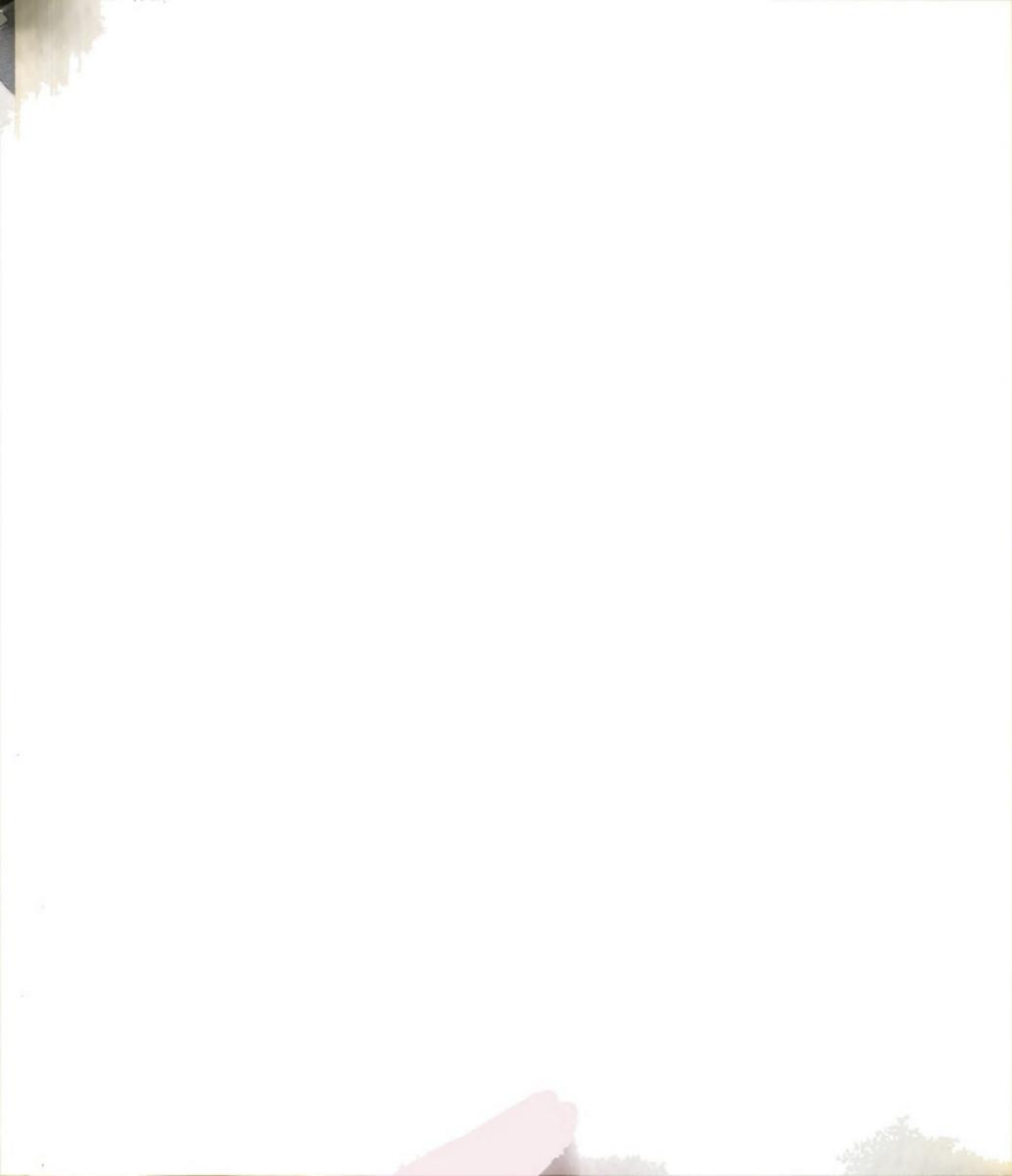
Appendix Table 1.—Harvest data for the number of fruit/
plant, number of clusters with fruit/
plant, fruit weight/plant and total
plant weight.

X_1	X_2	X_3	X_4	X_5	X_6	X_7
1	1	1	0	0	0	0.20
1	1	2	7.2	3.6	0.44	0.62
1	1	3	8.7	4.4	0.60	0.76
1	2	1	0	0	0	0.67
1	2	2	35.3	16.0	0.97	3.07
1	2	3	34.6	16.2	2.40	2.83
1	3	1	0	0	0	1.67
1	3	2	61.0	28.2	2.43	5.83
1	3	3	110.6	53.0	8.03	10.95
2	1	1	0	0	0	0.25
2	1	2	11.2	6.2	0.26	1.08
2	1	3	7.4	3.8	0.53	0.19
2	2	1	0	0	0	0.18
2	2	2	22.9	15.1	0.75	2.25
2	2	3	36.3	16.7	2.50	3.32
2	3	1	0	0	0	1.17
2	3	2	96.3	32.8	3.72	6.59
2	3	3	125.7	54.3	8.29	12.10
3	1	1	0	0	0	0.30
3	1	2	11.6	6.1	0.45	0.89
3	1	3	10.3	4.6	0.59	0.19
3	2	1	0	0	0	0.84
3	2	2	14.9	7.3	0.72	1.01
3	2	3	29.3	12.4	1.87	2.48
3	3	1	0	0	0	1.19
3	3	2	43.7	22.3	2.01	3.20
3	3	3	109.4	47.1	7.53	9.83

X_1 = Replication

X_2 = Plant population: 1 = 5 x 5 inches
                          2 = 10 x 10 inches
                          3 = 20 x 20 inches

X_3 = Date: 1 = 7/29
              2 = 8/30
              3 = 9/20

X_4 = Number of fruit per plant

X_5 = Number of clusters with fruit per plant

X_6 = Fruit weight per plant (in pounds)

X_7 = Total plant weight (plant + fruit) (in pounds)
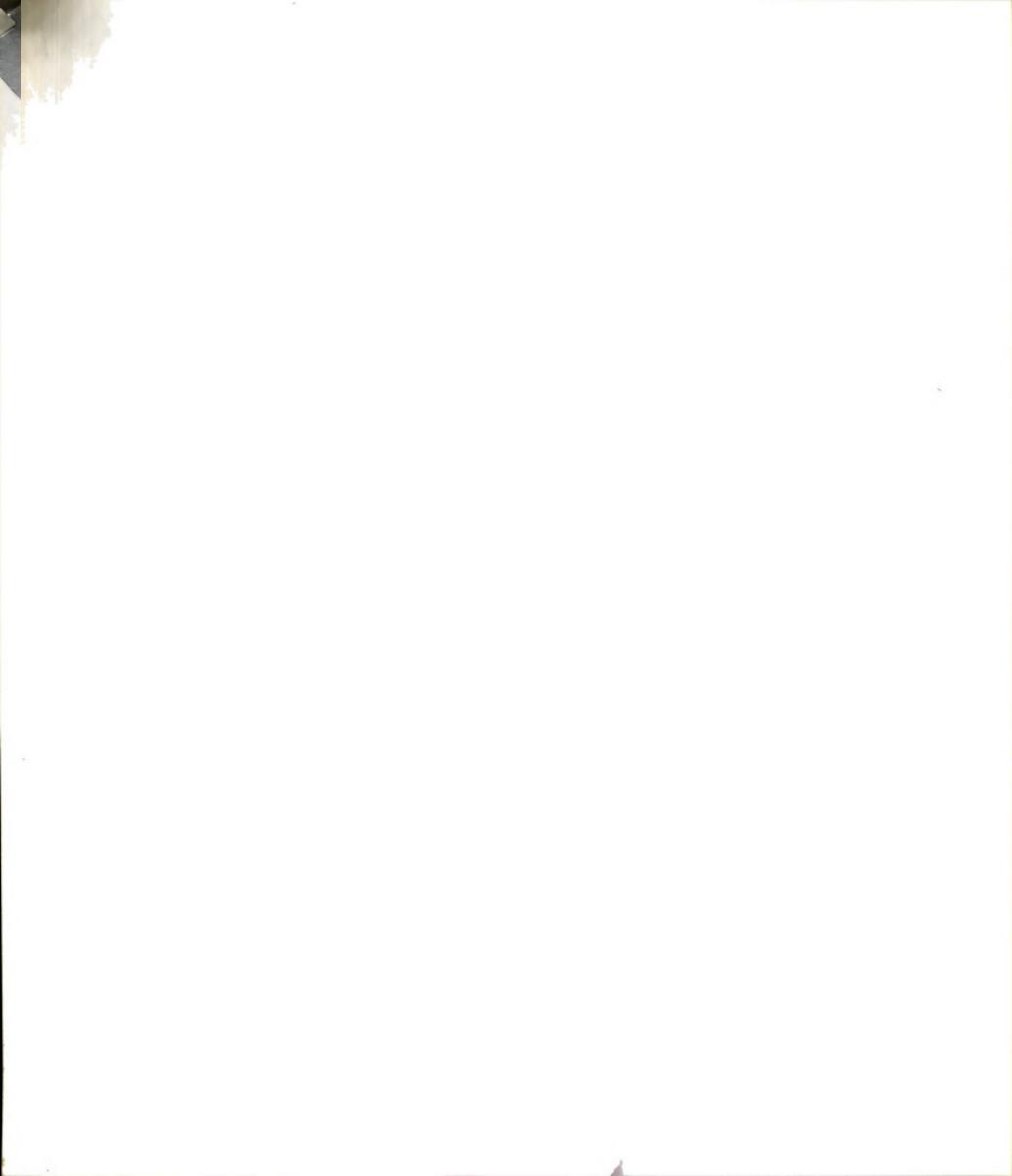
Appendix Table 2.—Soil gas atmosphere data for CO_2, O_2 and ethylene.

X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}	X_{11}	X_{12}
1	1	1	1.98	2.64	4.13	16.75	15.89	16.75	0	0	0
1	2	1	1.10	3.41	3.03	20.19	15.46	16.32	0	0	0
1	3	1	2.68	2.81	3.47	16.18	17.18	17.18	0	0	0
2	1	1	2.35	3.38	5.54	19.76	18.28	16.30	0	0	0
2	2	1	2.11	5.00	6.36	20.75	17.78	18.28	0	0	0
2	3	1	4.95	5.20	5.15	16.30	16.30	17.29	0	0	0
3	1	1	3.81	6.22	5.05	20.25	19.76	17.78	0	0	0
3	2	1	1.48	5.05	2.11	20.75	19.76	19.76	0	0	0
3	3	1	2.79	5.34	5.00	18.77	17.78	18.28	0	0	0
4	1	1	1.81	2.60	2.55	21.24	19.76	18.28	0	0	0
4	2	1	1.96	2.16	2.01	19.76	20.25	19.27	0	0	0
4	3	1	1.91	1.52	2.31	20.75	21.24	18.77	0	0	0
1	1	2	0.32	0.44	0.57	19.28	18.81	19.28	12	05	21
1	2	2	0.34	0.92	1.34	19.30	18.38	18.38	00	00	00
1	3	2	0.34	0.51	0.67	19.28	19.28	18.81	02	07	07
2	1	2	0.65	0.65	1.03	18.81	19.28	18.81	05	06	16
2	2	2	0.48	0.67	0.88	19.30	16.54	18.38	05	02	00
2	3	2	0.26	0.33	0.75	18.95	18.55	18.14	11	14	10
3	1	2	0.21	0.46	0.86	19.76	19.76	19.35	12	11	20
3	2	2	0.75	1.76	2.00	19.28	18.34	19.28	09	10	07
3	3	2	0.47	0.59	1.03	19.28	18.81	19.28	03	10	10
4	1	2	0.72	0.50	0.84	19.35	19.76	19.35	10	08	16
4	2	2	0.37	0.95	0.90	19.35	20.16	18.96	08	12	11
4	3	2	0.92	0.42	0.92	19.76	19.76	19.35	00	07	06
1	1	3	3.55	4.95	4.79	18.66	18.22	18.44	12	13	24
1	2	3	3.21	4.42	4.63	20.88	18.66	18.66	11	21	30
1	3	3	1.87	3.41	4.95	19.55	19.55	18.22	18	23	19
2	1	3	2.54	4.42	5.09	19.11	18.66	18.66	49	15	12
2	2	3	5.22	5.22	5.42	18.66	18.66	18.66	24	166	14
2	3	3	3.21	5.02	5.35	18.66	18.66	18.66	12	12	22
3	1	3	3.88	5.69	5.42	18.66	18.66	18.66	11	20	11
3	2	3	2.01	3.41	5.09	19.99	19.11	19.99	10	06	11
3	3	3	1.34	3.28	6.09	19.99	19.66	19.11	06	10	06
4	1	3	3.28	2.27	2.34	19.55	19.55	19.11	16	10	12
4	2	3	2.21	1.87	3.21	19.99	19.55	18.66	16	24	20
4	3	3	2.74	3.29	4.01	19.55	19.55	18.22	21	09	13

X_1 = Plant population: 1 = 20 x 20 inches
                               2 = 10 x 10 inches
                               3 = 5 x 5 inches
                               4 = without plants

X_2 = Replication

X_3 = Date: 1 = 7/29
               2 = 9/2
               3 = 9/29

X_4 = CO_2 at 4 in.

X_5 = CO_2 at 8 in.

CO_2 as %
O_2 as %
C_2H_4 as ppb

X_6 = CO_2 at 16 in.

X_7 = O_2 at 4 in.

X_8 = O_2 at 8 in.

X_9 = O_2 at 16 in.

X_{10} = C_2H_4 at 4 in.

X_{11} = C_2H_4 at 6 in.

X_{12} = C_2H_4 at 8 in.
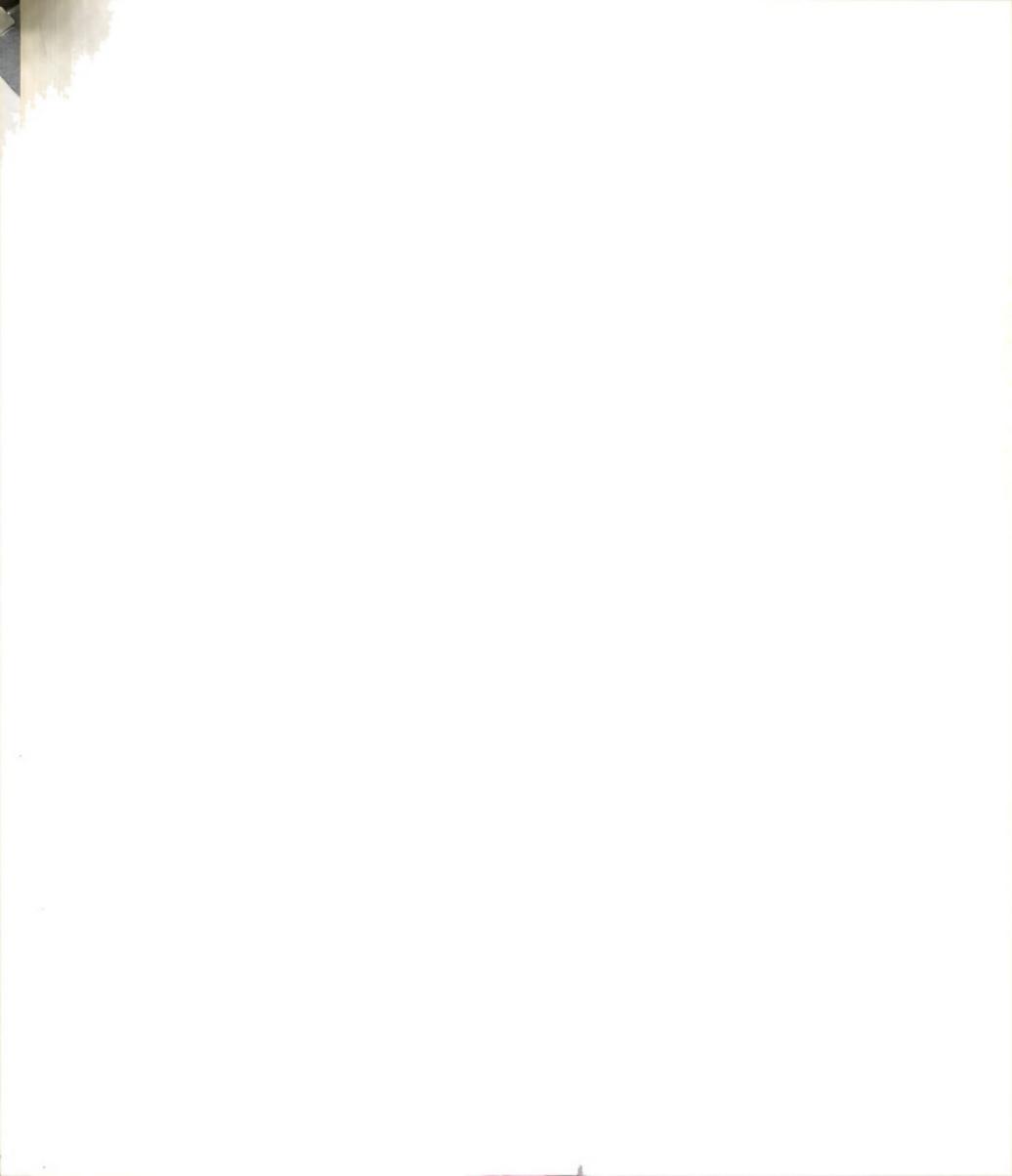
Appendix Table 3.—a) Soil probe resistance (gm); b) Ethylene concentration in the soils gas phase after irrigation; c) total fruit yield (tons/acre).

A				B				C			
X_1	X_2	X_3	X_4	X_1	X_2	X_3	X_4	X_1	X_2	X_3	X_4
1	1	1	422.0	1	1	1	58.5	1	1	1	58.10
1	2	1	478.6	1	2	1	62.2	1	1	2	80.89
1	3	1	468.0	1	3	1	52.1	1	2	1	44.80
2	1	1	439.0	2	1	1	100.6	1	2	2	75.23
2	2	1	482.0	2	2	1	20.1	1	3	1	17.93
2	3	1	424.0	2	3	1	29.3	1	3	2	40.34
3	1	1	401.0	3	1	1	42.1	2	1	1	53.22
3	2	1	395.3	3	2	1	41.1	2	1	2	75.38
3	3	1	452.0	3	3	1	5.9	2	2	1	46.80
1	1	2	589.0	1	1	2	20.7	2	2	2	67.00
1	2	2	542.0	1	2	2	20.7	2	3	1	23.33
1	3	2	546.0	1	3	2	14.1	2	3	2	41.64
2	1	2	570.0	2	1	2	12.5	3	1	1	55.22
2	2	2	623.0	2	2	2	7.1	3	1	2	76.41
2	3	2	696.0	2	3	2	21.8	3	2	1	46.39
3	1	2	502.0	3	1	2	15.8	3	2	2	47.99
3	2	2	489.0	3	2	2	18.5	3	3	1	25.06
3	3	2	537.0	3	3	2	10.9	3	3	2	37.80
1	1	3	609.3	1	1	3	42.7				
1	2	3	678.6	1	2	3	22.2				
1	3	3	592.0	1	3	3	39.8				
2	1	3	636.6	2	1	3	14.2				
2	2	3	587.3	2	2	3	43.8				
2	3	3	576.6	2	3	3	29.0				
3	1	3	457.3	3	1	3	15.9				
3	2	3	513.0	3	2	3	9.7				
3	3	3	588.0	3	3	3	9.1				

A:

X_1 = Plant population: 1 = 20 x 20 inches
                          2 = 10 x 10 inches
                          3 = 5 x 5 inches

X_2 = Replication

X_3 = Date: 1 = 7/19
               2 = 8/20
               3 = 9/28

X_4 = Soil probe data

B:

X_1 = Depth: 1 = 16 inches
                2 = 8 inches
                3 = 4 inches

X_2 = Replication

X_3 = Date: 1 = 0
               2 = 3 days
               3 = 11 days

X_4 = C_2H_4 - water data
               (ppb)

C:

X_1 = Replication

X_2 = Plant population:
        1 = 5 x 5 in.
        2 = 10 x 10 in.
        3 = 20 x 20 in.

X_3 = Date: 1 = 1969
               2 = 1970

X_4 = Total yield