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Competition in natural and experimental monocultures of Xanthium strumarium L.

Jess Konrad. Zimmerman
University of Windsor

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COMPETITION IN NATURAL AND EXPERIMENTAL MONOCULTURES OF *XANTHIUM STRUMARIUM* L.

by

Jess Konrad Zimmerman

A Thesis
submitted to the Faculty of Graduate Studies
through the Department of Biology
in Partial Fulfillment of the requirements
for the Degree of Master of Science at
The University of Windsor

Windsor, Ontario, Canada

1983

792983

Dedicated

in memory of my mother

Vivian Jessie Zimmerman

ABSTRACT

COMPETITION IN NATURAL AND EXPERIMENTAL MONOCULTURES OF XANTHIUM STRUMARIUM L.

by

Jess Konrad Zimmerman

The effects of plant density on the performance of Xanthium strumarium were investigated in natural and experimental monocultures. X. strumarium is an herbaceous annual that naturally occurs along bodies of water but is also a weed of agricultural fields and waste places.

In a beach population of X. strumarium, seedling survival, plant growth, and fruit production were assessed in response to changes in plant density, seedling emergence date, and soil moisture. Growth and fruit production were significantly reduced with increased plant density, but survivorship was largely density-independent. Delayed seedling emergence reduced seedling survival, but had no effect on the fruit production of mature plants. Seedling survival, growth, and fruit production were positively correlated with soil moisture.

In an agricultural field, the growth of isolated plants of X. strumarium was compared to plants grown in dense stands at two different spacings. The effects of intraspecific

competition were compared to competition between X. strumarium and Abutilon theophrasti grown at the closest spacing of the monoculture treatments.

Plants grown under density stress suffered greatly reduced growth and reproduction compared to isolated plants. The effects of competition were a reduction in growth rate and unit leaf rate. A reduction in leaf area ratio occurred only for plants grown in the highest density monoculture. Seasonal patterns in biomass allocation indicated that plants grown under density stress allocated proportionately more biomass to stems and roots and less biomass to leaves than isolated plants. Mature plants exhibited an increased proportion of biomass allocated to fruits with increased density. This pattern was, in part, explained by an increase in mean fruit weight with increased density.

The role of limiting water supply was compared to light limitation. There were no significant differences in xylem pressure potential, leaf conductance, or photosynthetic rate among treatments, indicating there was no competition for soil water. Plants under density stress showed increased plant height, altered leaf area distributions, and increased specific leaf area suggesting light was a limiting factor for plants grown in competition. These patterns correlated well with differences in shading among treatments.

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GENERAL INTRODUCTION

Factors regulating natural populations of organisms have been a central focus of ecological study. Much of the discussion of factors affecting population dynamics has involved the relative importance of density-independent and density-dependent mechanisms. Density-independent factors (e.g. weather) have a constant effect on a population over a range of densities while density-dependent factors have increasing or decreasing effects with a change in population density. This controversy, which was prevalent in the late 1950's and early 1960's, is succinctly reviewed by Clark et al. (1967).

Intraspecific competition was proposed very early as an important density-dependent mechanism regulating natural populations (Nicholson 1933). Nicholson (1933) defined competition as "the state of reciprocal interference which occurs when animals (or plants) having similar needs live together and which influences their success (in survival and reproduction)". Intraspecific competition might be assumed to be more stringent than interspecific competition because members of the same species should have similar requirements for growth and reproduction.

Organisms can respond to changes in population density through changes in mortality, growth, reproduction, or some combination of all. To cite examples from the zoological

literature, Eisenberg (1966) showed that experimental manipulations of the density of adult pond snails (Lymnea elodes) resulted in no change in adult survivorship. However, changes in fecundity resulted in a complete absence of treatment effects on the number of young. The number of snails returned to the pre-manipulation levels in all treatments in a single generation because in nature all adults die before the second year. Food limitation was strongly implicated as the mechanism reducing adult fecundity. Wise (1975) found that experimental manipulations of the population density of the spider, Linphia marginata, resulted in reduced survivorship of immatures and reduced survival and fecundity of adult females. Females appeared to be limited by food supply. Density effects on growth and development (Istock et al. 1975, Hurd et al. 1978, Stiven and Kuenzler 1979) and proportional reproductive allocation (Wu et al. 1977) have also been reported. Increased density can also reduce the mating success of territorial species (Warner and Hoffman 1980, and references therein).

Although responses to a change in population density may be qualitatively similar for plants and animals, plants are more plastic in their growth than animals. A change in density which may result in, at most, an order of magnitude difference in growth in animals (see references above) might for plants produce a reduction in growth of two to three

orders of magnitude which would not be unexpected. Puckridge and Donald (1967) sowed wheat at a range of densities from 1.4 to 1078 plants per meter square. A 54-fold range in individual plant weights was recorded at the end of the season. The plants showed a 43-fold variation in the number of ears produced per plant while variation in the number of grains per ear was 2-fold. Variation in the weight of a single grain was only 1.05-fold. The lack of variation in seed weight in response to large changes in plant density in wheat and other species led Harper et al. (1970) to conclude that seed weight was the least plastic of all plant yield components. Harper (1977) has thoroughly reviewed the literature on the effects of density on the growth, form, and reproduction of plants.

The responses of plants to increasing density at the population level are well described (White 1980, Harper 1977). At very low densities, plants do not interfere with the growth of one another and are, therefore, not competing. Over a range of densities that will cause a reduction in growth (resulting from competition), but at which mortality is not density-dependent, the relationship between the log of mean plant weight and log density will have a slope of -1. That is, with increasing density, the growth of individual plants is compensated in a one to one ratio. At higher densities, density-dependent mortality will occur and the

slope of the relationship between log mean plant weight and log density will have a slope of -3/2. This is the 3/2 Thinning Law (Yoda et al. 1963). Its rationale has been based upon the geometry of packing three dimensional structures on a flat surface (White and Harper 1970), although it is not clear why this result is obtained only in the presence of density-dependent mortality.

Self-thinning populations also show a characteristic pattern of changes in the variation of individual plant weights with increasing density. Populations of plants growing at high density may show distributions that are highly negatively skewed, with numerous small plants and few, very large plants. Plants grown at low density often have normal distributions of plant weights (see Koyoma and Kira 1956, Obeid et al. 1967 for examples). Three factors can account for this pattern (summarized by Turner and Rabinowitz 1983): size selective mortality, variance in exponential growth rates among individuals, and dominance and supression - small individuals are competitively suppressed by the largest individuals. This pattern is not universal. Graminoids, for example, appear to be an exception (Turner and Rabinowitz 1983).

Studies of the responses of plants to increasing density are notably lacking in two aspects. Most studies have used crop species or crop weeds grown in agricultural

environments, while not enough attention has been given to studying naturally occurring populations. Moreover, although a reduction in growth with increasing density clearly indicates that resource deprivation has occurred, it is rare that an attempt has been made to describe the resources that were in limiting quantities.

In the present study, the responses of Xanthium strumarium L. to changes in plant density, in both natural and experimental monocultures, were investigated. In a naturally occurring beach population of X. strumarium the effect of density on survival, growth, and reproduction was compared to other potentially important factors such as soil moisture. Competition in experimental monocultures of X. strumarium grown at differing densities in an agricultural habitat was investigated with the goal of describing the resources that could potentially limit growth under competitive conditions.

DESCRIPTION OF XANTHIUM STRUMARIUM

Xanthium strumarium L., commonly known as cocklebur, is a member of the family Compositae (Asteraceae) in the tribe Ambrosiae. It is an herbaceous annual, growing to heights of 20 to 150 cm and has a stout tap root (Weaver and Lechowicz 1982). Its most distinquishing characteristic is the fruit, which is a hard, woody bur, 1-3.5 cm long, with hooked prickles (Gleason and Cronquist 1963).

X. strumarium naturally occurs along rivers and on lake and sea beaches. It is also a weed of agricultural fields and waste places. Naturally occurring populations are usually small, somewhat ephemeral, and homogeneous, while weed populations are larger and more heterogeneous (Weaver and Lechowicz 1982). Dispersal in naturally occurring populations is usually achieved by water while in weed populations, dispersal largely results because of human activities. X. strumarium can be found on a variety of soil types, but apparently prefers coarse, porous soils (Kaul 1965).

The genus Xanthium has been the subject of much taxonomic confusion. On the basis of bur morphology, more than 20 species of Xanthium had been described at one time (Weaver and Lechowicz 1982). Löve and Dansereau (1959) revised the genus, reducing the number of species to two, X. strumarium and X. spinosum L. X. strumarium is a highly

variable species, provisionally considered to have two subspecies one of which is further divided into six complexes based on bur morphology and geographic distribution. The two populations used in this study are apparently member of the pensylvanicum-italicum complex, based on descriptions in Löve and Dansereau (1959) although bur sizes differed greatly between populations.

X. strumarium is monoecious, wind pollinated, and self-compatible (Löve and Dansereau 1959). Inflorescences are small and green and occur in clusters in the leaf axils and at the end of branches and the main stem. Staminate (male) inflorescences contain 100-150 florets and tend to occur above the pistillate (female) inflorescences. Pistillate inflorescences contain two flowers in a spiny involucre. The mature fruit (or bur) contains two achenes (seeds), usually of differing size. Flowering is photoperiodically controlled, induced by short days in late summer. In southwestern Ontario, flowering generally begins in early to mid-August and fruit filling occurs in the following two weeks.

The arrangement of male and female inflorescences and self-compatibility leads to a great deal of inbreeding in X. strumarium. Moran and Marshall (1978) estimated the outcrossing rate in a natural population in Australia to be essentially zero with an upper confidence limit of 12%.

There was almost no allozymic variation within each of four complexes naturalized to Australia, but considerable variation among complexes. This pattern correlated well with patterns of bur morphology. However, Moran et al. (1981) found significant levels of genotypic variation within populations for 15 quantitative characters. Nevertheless, enviromentally induced variation was a larger component of the total phenotypic variation, indicating the importance of phenotypic plasticity in the species.

The two seeds within each fruit of X. strumarium have differing dormancy and germination requirements. These have been extensively studied (reviewed by Weaver and Lechowicz 1982). In general, the large seeds in each fruit are non-dormant and will germinate in the spring following dispersal while the small seeds will not germinate until later in the season or in the following year. However, twin seedlings arising from a single fruit have often been noted (Weaver and Lechowicz 1982, Zimmerman and Weis 1983).

Voucher specimens from each population of X. strumarium used in this study have been deposited in the herbarium at the University of Windsor and with Plant Biosystematics, Agriculture Canada, Ottawa, Ontario.

CHAPTER I

FACTORS AFFECTING SURVIVORSHIP, GROWTH, AND FRUIT PRODUCTION IN A NATURAL POPULATION OF *XANTHIUM STRUMARIUM*

CHAPTER I

INTRODUCTION

The manner in which density regulates populations of organisms has been the concern of botanists and zoologists alike (Antonovics and Levin 1980). In plant populations, two patterns of response to plant density have recieved considerable attention. First is the 3/2 Thinning Law (Yoda et al. 1963) describing the relationship among plant growth and density in the presence of density-dependent mortality. It has been shown for a variety of tree and herb species (Harper 1977, White 1980) that a self-thinning population will follow a 'trajectory' described by

$$w = Kd^{-3/2}$$

where w is mean plant weight, d is density and K is a constant. If there is no density dependent mortality in the population, then the density-yield relationship will have a slope of -1. Secondly, and apparently in conjuction with self-thinning (White and Harper 1970), plant populations growing at high density will form size hierarchies (Koyoma and Kira 1956, Obeid et al. 1967, Ford 1975; but see Turner and Rabinowitz 1983). A few individuals will become large and dominate a stand while most individuals are supressed and

less vigorous.

The vast majority of studies describing the above relationships have been made in agricultural settings (Harper 1977). A need has been seen to investigate naturally occurring populations (Solbrig 1980) because agricultural environments and the genetic structure of agricultural plant populations are typically quite uniform (Snaydon 1980). Quite clearly, natural populations face an array of factors affecting their dynamics. Although a search for single factor effects (e.g. density) will often be fruitful, it may not provide a complete understanding of observed population dynamics.

I have investigated the effects of density, seedling emergence time, and soil moisture on mortality, growth, and fruit production in a naturally occurring population of X. strumarium. I chose to investigate the effects of seedling emergence time in addition to density because of its well described effects on seedling mortality, plant growth and fecundity (Black and Wilkinson 1963, Ross and Harper 1972, Cook 1979, Weaver and Cavers 1979, Naylor 1980, Howell 1981). Soil moisture was investigated because of its relative ease in measurement in comparison to other critical plant resources, for example, nutrients. Also, as X. strumarium naturally inhabits beach sand (Löve and Dansereau 1959, Weaver and Lechowicz 1982), soil moisture was suspected to be

an important factor for plants growing in a soil with a low water holding capacity.

MATERIALS AND METHODS

Study Area

This study was conducted in Holiday Beach Provincial Wildlife Management Unit located in Section 58, Malden Township, Essex County, Ontario. All research took place along a section of beach facing Lake Erie approximately 75 m in length and separated from an adjacent marsh by a grove of Willows (*Salix* spp.) and Cottonwoods (*Populus deltoides* Marsh.). Most of the area (approximately 85%) consisted of open sand. Woody vegetation on the beach was predominated by *Salix* spp. and saplings of *Populus deltoides*. The herbaceous assemblage was dominated by Cocklebur (*X. strumarium*) and Sea Rocket (*Cakile edentula* (Bigel.) Hook), although Evening Primrose (*Oenothera biennis* L.) and *Polygonum* spp. occurred with moderate frequency.

Field and Laboratory Procedures

One quarter meter squared quadrats were used to sample portions of the population of *X. strumarium* occurring in the study area. Sampled quadrats were within 3 m of a transect approximately parallel to and 10 m from the shoreline, with the exception of one quadrat placed 9 m inland of the transect. Quadrat sites were chosen on May 10, 1982 approximately one week after seedling emergence began. Quadrat placement was made with consideration given only to sampling the range of observed seedling densities in each

area of the population.

In twelve quadrats, individual seedlings were mapped using a square plexiglas sheet (60 x 60 cm, 0.64 cm in thickness) supported by wood dowels attached at each corner. Seedling locations in each quadrat were recorded on clear vinyl sheets placed over the plexiglas sheet. Individuals were identified by their position in numbered 10 x 10 cm sub-quadrats. Quadrats were censused every 4 to 7 days through May and at longer intervals through the remainder of the growing season (see Fig. 1.3). On each census date, the death or emergence of individual seedlings was recorded. Survivorship for each quadrat was calculated as

$$\frac{\text{number of seedlings surviving}}{\text{total number of seedlings observed.}}$$

In separate quadrats, percent soil moisture was obtained using the probe from a commercial soil moisture meter (Agtronic Manufacturing) wired to a multimeter (Radio Shack, Inc.) capable of measuring resistances from 0 to 20 megohms. This device made it possible to obtain more precise resistance values than those provided by the meter included with the Agtronic device. The soil moisture probe was calibrated in the laboratory using 4 kg of sand collected at the study site. Distilled water was added to air dry sand in known quantities and the electrical resistance recorded. The

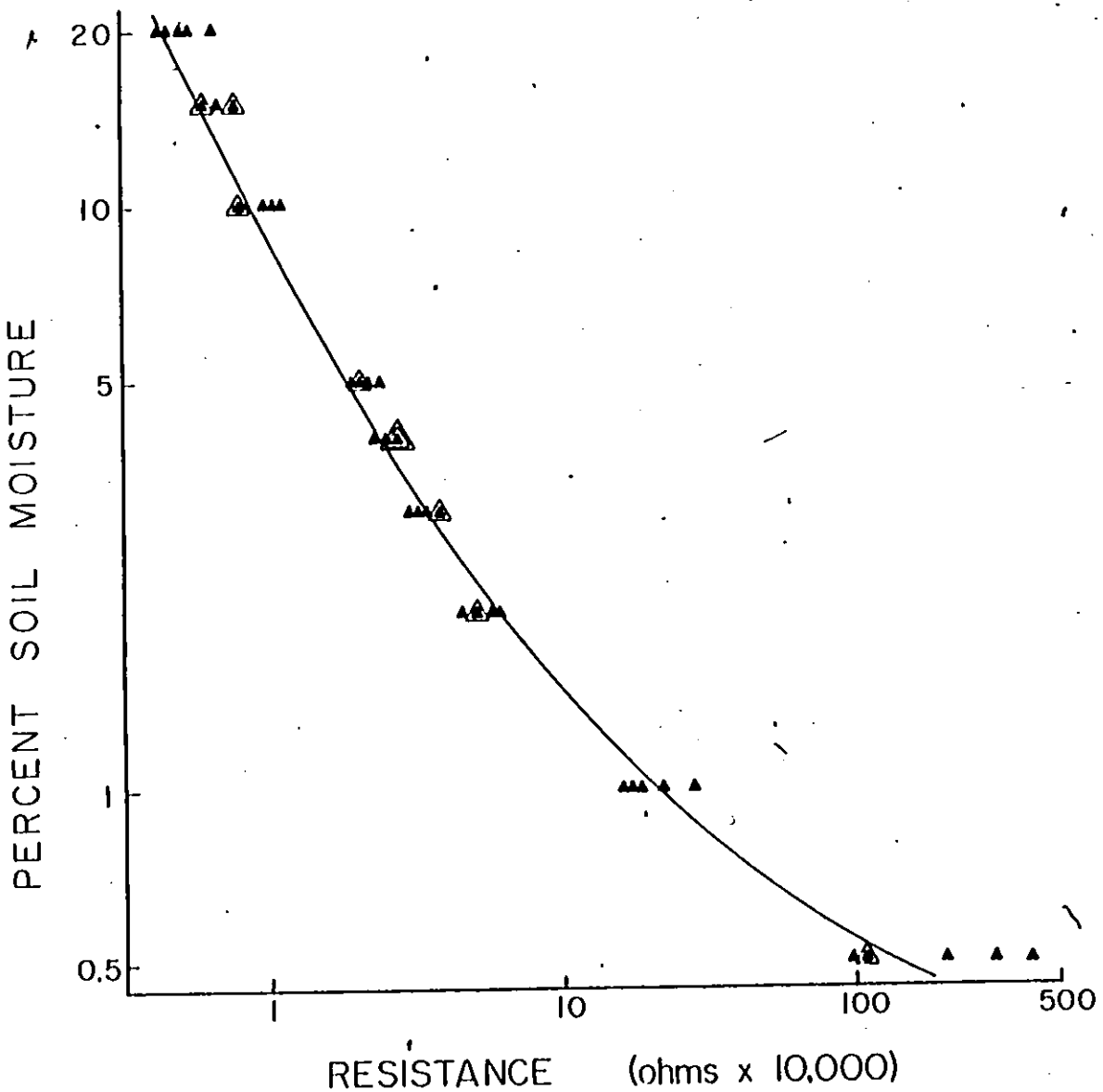
resultant relationship (Fig. 1.1) was used to convert resistance values obtained in the field to percent soil moisture (percent of soil dry weight).

On each sampling date, resistance readings were taken at each corner and the center of each quadrat at depths of 5, 10, and 20 cm. The five values for each quadrat at each depth were averaged and entered into the data set as a single value. Readings were taken at 4 to 7 day intervals through May and every one to three weeks thereafter until late September. Twelve soil moisture quadrats were established on May 10. On May 31 measurements at three quadrats were discontinued. Measurements continued at replacement quadrats established elsewhere to better represent the range of observed seedling densities. Thus, soil moisture data presented for the early growing season and the whole growing season represent somewhat differing sets of quadrats. Those quadrats sampled earlier were not included in the analysis of soil moisture effects on growth and reproduction. One other quadrat was discontinued on June 11 after all seedlings in it had died. Therefore, for the analysis of growth and reproduction patterns, there are soil moisture data for eleven quadrats sampled on 10 or 13 dates.

On each sampling date, the number of seedlings in each soil moisture quadrat was counted. Survivorship was calculated as

Figure 1.1

Calibration curve used to convert electrical resistance (ohms x 10^4) to percent soil moisture. Multiple data points indicated by outlines. $\text{Log}_{10}(\text{percent soil moisture}) = 0.951 - 0.948(\log_{10}(\text{ohms} \times 10^4)) + 0.172(\log_{10}(\text{ohms} \times 10^4))^2$ (R=0.995).


20
10
5
1
0.5
PERCENT SOIL MOISTURE
1
10
100
500
RESISTANCE (ohms x 10,000)

$$\frac{\text{number of seedlings surviving}}{\text{maximum number of seedlings observed.}}$$

This overestimates the actual survivorship as emergence of seedlings between sampling dates could have masked deaths of others. Demographic data from censused quadrats was used to estimate this error; the maximum number of seedlings observed underestimated the total number of seedlings in a quadrat, on average, by about 7.5%.

In mid-October, the number of fruits produced by each plant in each demography and soil moisture quadrat was recorded. Five plants in each quadrat were randomly chosen and harvested by clipping the stem at the level of the soil surface. These were dried at 80 C, allowed to equilibrate to air temperature and then weighed to the nearest 0.01 g.

Data Analysis

All statistical analyses were done using packaged programs provided by version 79.6 of S.A.S. (Ray 1982) except the multiway contingency table analysis, described below, which was performed by hand. For parametric statistical analyses, all variables were checked for normality and scedasticity (using an F-max test, Sokal and Rohlf 1981). If a variable did not satisfy these assumptions, an appropriate transformation was applied and the variables

rechecked. Appropriate non-parametric tests were used if transformation did not reduce heteroscedasticity and provide a normal distribution.

The relationships among density, seedling emergence time, and mortality were analyzed by collapsing the data into a 2x2x2 contingency table. Multiway contingency tables are best analyzed using log-linear models. Log-linear models have properties that are analogous to analysis of variance, except that one is concerned with interactions among variables rather than main effects. Log-linear models arise from the fact that each cell frequency in a contingency table is a product of the total sample size and the sums of respective row and column probabilities. By applying a log transform, the log of the cell frequency becomes the sum of the log of each of the terms in the above product. Thus for a three-way table, including all possible interactions among variables, the model is

$$\log m_{ijk} = u + u_i + u_j + u_k + u_{ij} + u_{jk} + u_{ik} + u_{ijk}$$

The similarity to models used in analysis of variance should be clear. For extended discussions of the use of log-linear models in the analysis of contingency tables, see Bishop et al. (1975), Feinberg (1977), and Knoke and Burke (1980). Colgan and Smith (1978) provide a good introduction and

describe some applications to ethological data.

A G-statistic was used to compare observed and expected frequencies. The distribution of G can be approximated by a X^2 distribution, but has several theoretical advantages over the typical X^2 (Sokal and Rohlf 1981). In the analysis of multi-way contingency table, it allows testing of conditional independence between variables. This is equivalent to a nested interaction in ANOVA.

I have analyzed the contingency table here following the method outlined in Sokal and Rohlf (1981) after Bishop et al. (1975). In this method, one begins with a saturated model, the model with all main effects and possible interactions as given above plus all conditional interactions. Individual terms in the model are tested in a hierarchical fashion beginning with the second-order interaction (for an example of an alternate approach, see Whittam and Siegal-Causey 1981). Expected frequencies are calculated with all terms in place except that being considered (or those previously rejected). Those terms showing significant departure from expectation are retained in the model. Testing continues until all terms have been accepted or rejected. If a particular term is found significant and retained, all lower order terms involving the variables in the term are, by definition, retained in the model. For example, in the case of a three-way table, if the second-order interaction was found significant, no further testing would be performed and

the saturated model would be the final model.

Freeman-Tukey deviates (Sokal and Rohlf 1981) were calculated to examine the degree of departure of individual cells from expected values. Freeman-Tukey deviates are calculated as

$$\sqrt{f_{ijk}} + \sqrt{f_{ijk} + 1} - \sqrt{4 \cdot \hat{f}_{ijk}}$$

and are compared to

$$\sqrt{\nu X^2_{.05(\nu)} / abc}$$

to determine an approximation of which deviates are significantly "large" for a test with ν degrees of freedom and a, b, and c classifications for each variable.

Recently, a new method for analyzing the degree of size hierarchy in a population of plants has been developed (Weiner and Solbrig unpubl. manuscript). This measure, the Gini Coefficient (G), has been drawn from the economics literature considering the distributions of wealth in societies (see Sen 1973). I have applied it to measure hierarchy of fruit production for each of the quadrats sampled. Its meaning can be shown graphically by ranking individuals in a population of plants by their fruit

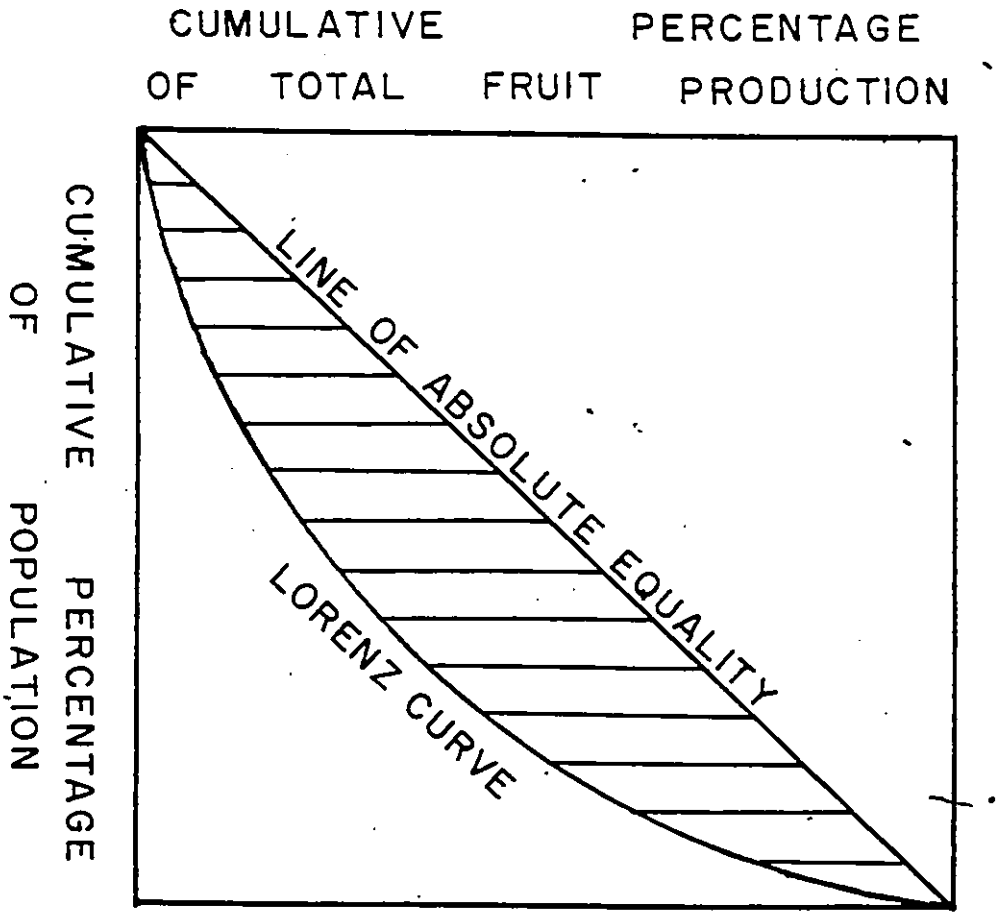
production and plotting the cumulative percentage of total fruit production in the population against cumulative percentage of individuals in the population (Fig. 1.2). Perfect equality in fruit production in the population would result in a diagonal line from the lower left hand to the upper right hand corners. Any inequality in fruit production would result in a curve below the diagonal, called the Lorenz Curve. The ratio of the area between the diagonal and the Lorenz Curve over the total area under the diagonal provides the Gini Coefficient. Computationally, G is calculated as

$$G = (1/2n^2u)\sum_{i=1}^{n}\sum_{j=1}^{n}|y_i - y_j|$$

where n is the number of plants in the population, u is the mean fruit production and y_i and y_j are fruit production values for individual plants. Thus, the Gini Coefficient is one half the arithmetic average of the absolute value of the differences between all pairs of plants.

Figure 1.2

Graphical representation of the Gini Coeffecient applied to fruit production hierarchies in plant populations. Gini Coefficient is the proportion of area between the diagonal and Lorenz Curve and total area under the diagonal (after Sen 1973).


CUMULATIVE PERCENTAGE
OF TOTAL FRUIT PRODUCTION
CUMULATIVE PERCENTAGE
OF POPULATION
LINE OF ABSOLUTE EQUALITY
LORENZ CURVE

RESULTS

Seedling Mortality

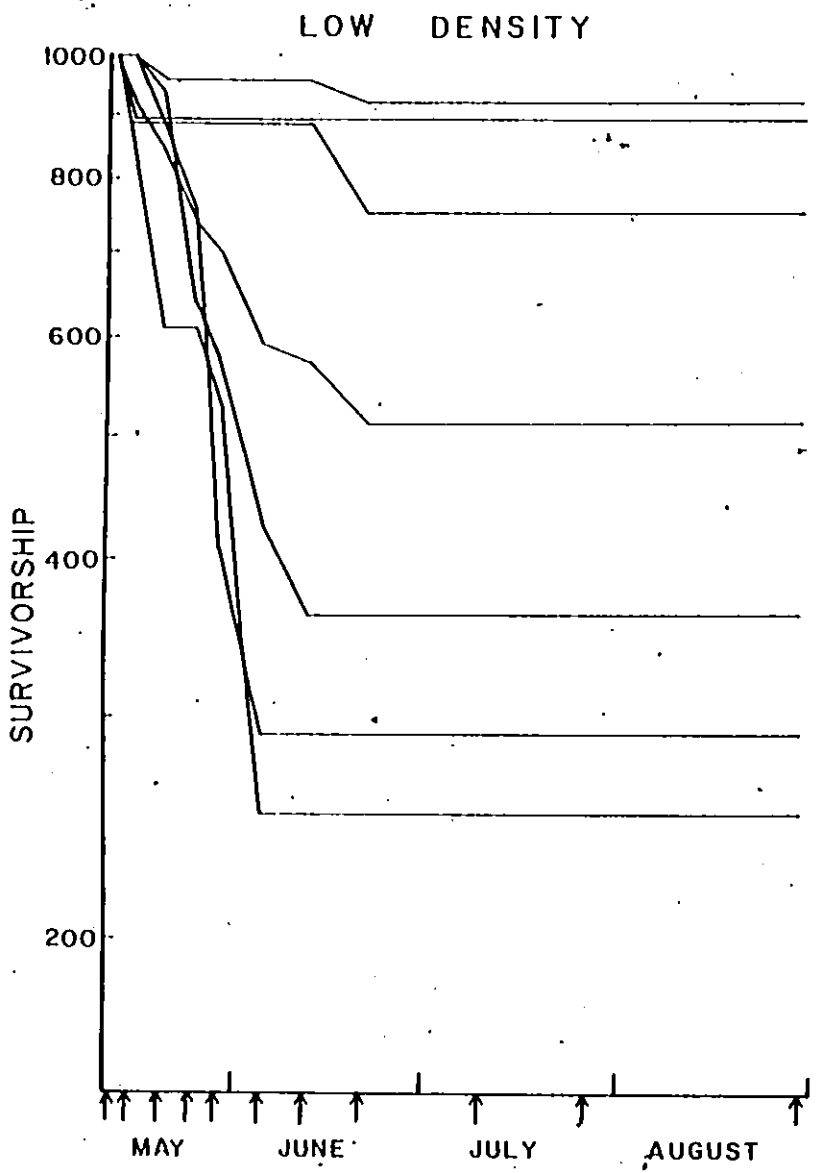
Seedling densities ranging from 36 to 368 per square meter were represented in the twelve quadrats for which detailed demography data were obtained. The survivorship curves have been grouped by density into those for quadrats with less than or greater than 50 individuals (Fig. 1.3). Survivorship is presented with all seedlings in a quadrat considered as a single cohort. Most mortality occurred early in the growing season; there was little or no mortality following mid-June. Furthermore, on average, there appeared to be greater mortality in low than in high density quadrats. But, most importantly, in both density groups there was great variation in seedling mortality among quadrats.

Field observations indicated two major causes of seedling mortality, damage by wind blown sand and dessication. The former effect seemed to predominate. Mortality from blowing sand resulted because of erosion of seedling hypocotyls at the level of the sand surface. Insect herbivore damage did not appear important; no insects were ever observed feeding on seedlings and damage was restricted to the area of the hypocotyl at the sand surface.

Most seedlings (approximately 82%) had emerged at the time of the first census (Fig. 1.4). Observations prior to the first census indicated most seedlings were not more than one week old. Late emergence of seedlings occurred up to May

Figure 1.3

Survivorship curves for twelve quadrats (0.25 m^2) for which detailed demography data were obtained. Results are divided into low density (<50 individuals, left hand graph) and high density (>50 individuals, right hand graph) quadrats. Arrows denote census dates.


LOW DENSITY
1000
800
600
400
200
SURVIVORSHIP
MAY
JUNE
JULY
AUGUST

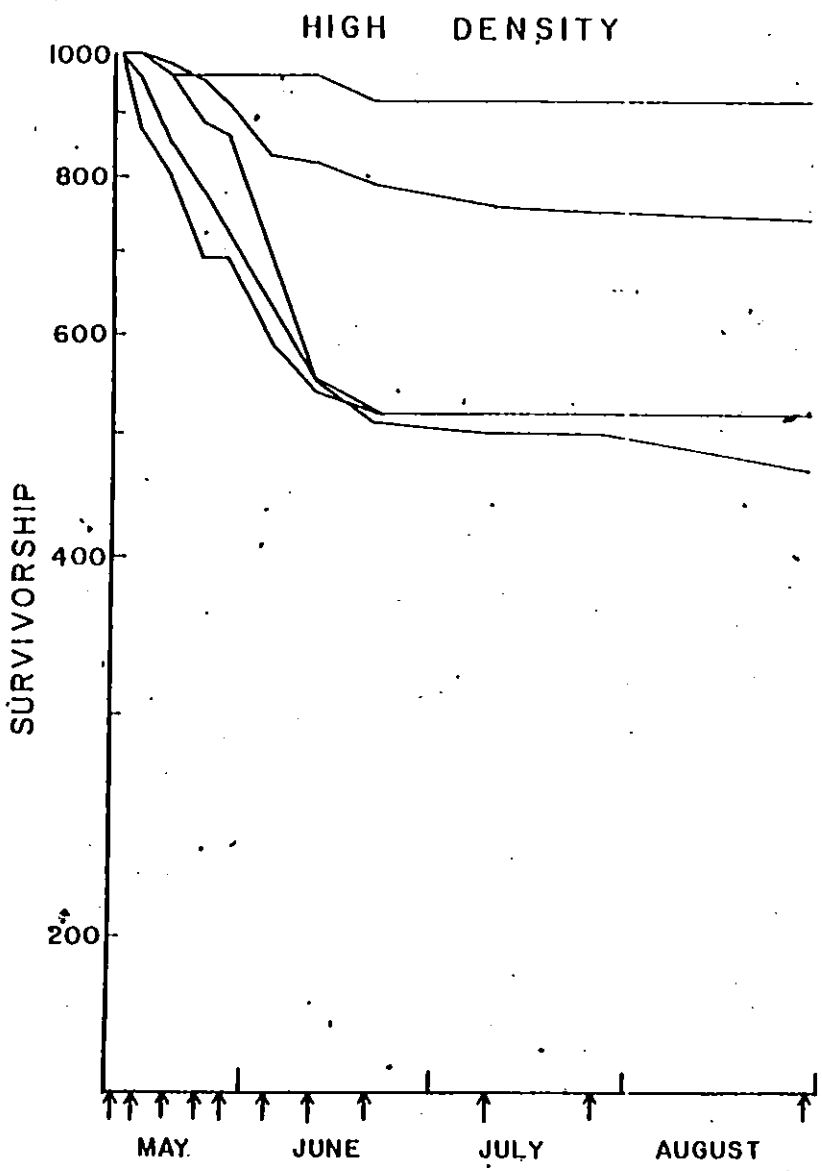
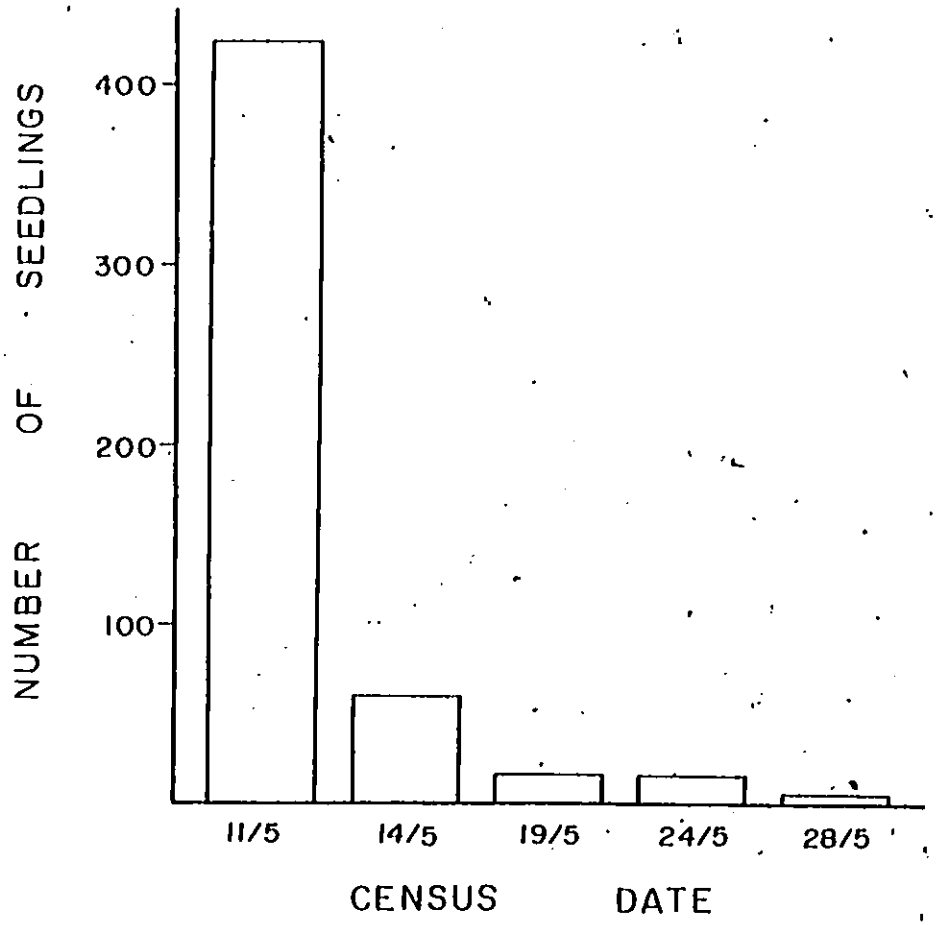

HIGH DENSITY
1000
800
600
400
200
SURVIVORSHIP
MAY
JUNE
JULY
AUGUST

Figure 1.4

Distribution of seedling emergence time.


NUMBER OF SEEDLINGS
400
300
200
100
11/5
14/5
19/5
24/5
28/5
CENSUS DATE

28 (only one seedling emerged following this date). All seedlings emerging following May 11 were grouped into a single cohort of late emerging seedlings to be compared with the cohort emerging prior to May 11. By further collapsing the data into high and low density quadrats as in Figure 1.3 and comparing seedlings that survived to flower vs. those that died, the data can be presented as a 2x2x2 contingency table (Table 1.1A).

Analysis of the contingency table indicated the second-order interaction between emergence time, density, and seedling mortality was not significant (Table 1.1B, $p=0.252$). This indicates that density had no effect on the relationship between emergence time and mortality. The lack of any significant Freeman-Tukey deviates (Table 1.2A) for this analysis assures that this term was properly left out of the final model.

Conditional independence of emergence time and density was rejected (Table 1.1B, $p=0.010$). The values in the contingency table (Table 1.1A) and the pattern in Freeman-Tukey deviates (Table 1.2B) confirms that there were fewer late emerging seedlings at low than at high density. However, the number of late emerging seedlings in any one quadrat was not great enough to change the overall groupings of quadrats. The overall effect was to augment density differences between classes.

There was also a significant interaction between

Table 1.1. A. Contingency table showing seedlings classified by emergence time, quadrat density, and mortality.

EMERGENCE TIME	DENSITY	MORTALITY Alive	Dead
Early	Low	72	55
	High	200	95
Late	Low	3	14
	High	28	48

B. Results of contingency table analysis

EFFECT	DF	G	PROB.
Emergence Time x Density x Mortality	1	1.312	0.252
Emergence Time x Density (Mortality)	2	9.144	0.010
Emergence Time x Mortality (Density)	2	33.441	<0.001
Density x Mortality (Emergence Time)	2	7.224	0.027

Table 1.2. Freeman-Tukey deviates for contingency table analysis. Significantly large deviates indicated by asterisks.

A. Emergence Time x Density x Mortality

EMERGENCE TIME	DENSITY	MORTALITY Alive	Dead
Early	Low	0.209	-0.036
	High	-0.077	0.046
Late	Low	-0.635	0.281
	High	0.302	0.007

B. Emergence Time x Density (Mortality).

EMERGENCE TIME	DENSITY	MORTALITY Alive	Dead
Early	Low	0.583	0.690
	High	-0.311	-0.598
Late	Low	-1.398 *	-1.425 *
	High	0.965	0.955

Table 1.2. Continued.

C. Emergence Time x Mortality (Density)

EMERGENCE TIME	DENSITY	MORTALITY Alive	Dead
Early	Low	0.732	-0.734
	High	1.372 *	-1.805 *
Late	Low	-2.303 *	1.820 *
	High	-3.028 *	3.057 *

D. Density x Mortality (Emergence Time)

EMERGENCE TIME	DENSITY	MORTALITY Alive	Dead
Early	Low	-1.094	1.425 *
	High	0.723	-0.959
Late	Low	-1.133	0.808
	High	0.561	-0.343

emergence time and mortality (Table 1.1B, $p<0.0001$). Examination of Table 1.1A and the Freeman-Tukey deviates (Table 1.2C) clearly indicates that late emerging seedlings had greater mortality than early emerging seedlings.

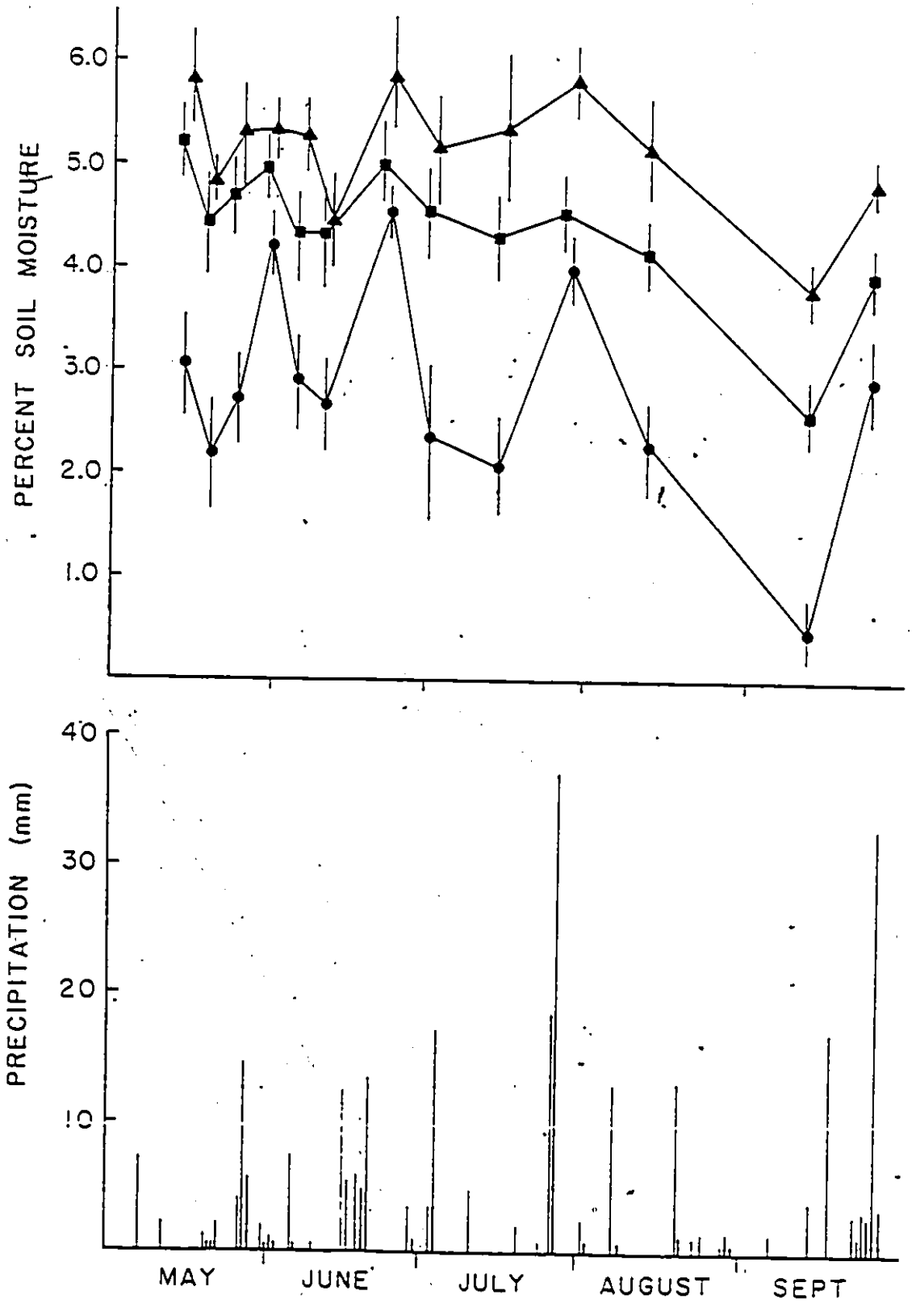
Conditional independence of density and mortality was also rejected (Table 1.1B, $p=0.027$). However, the Freeman-Tukey deviates indicated this result was due to a significant departure from the expected in only one cell (Table 1.2D). The suspicion that seedlings at high density suffered less mortality than those at low density appeared to be confirmed by this analysis, however the relationship was not strong.

No further testing of terms in the model was necessary because all tests of conditional independence of each pair of variables were rejected. In summary, results showed that density had no effect on the relationship between emergence time and mortality, but that late emerging seedlings had higher mortality than early emergers. High density quadrats had greater delayed emergence than low density quadrats, which tended to augment differences between density classes. Finally, low density quadrats, as a whole, had greater mortality than high density quadrats, although the relationship was not striking.

Soil moisture at the study site varied with both soil depth and time (Fig. 1.5). Percent soil moistures at 10 and 20 cm depths were most similar and, on average, much greater

Figure 1.5

Percent soil moisture at field site (upper graph) and daily precipitation (lower graph) in mm, recorded at Agricultural Canada Research Station, Harrow, Ontario. Circles, squares, and triangles represent percent soil moisture at depths of 5, 10, and 20 cm, respectively. Means are of 11 - 12 quadrats. Vertical bars indicate standard errors.


PERCENT SOIL MOISTURE
6.0
5.0
4.0
3.0
2.0
1.0
PRECIPITATION (mm)
40
30
20
10
MAY
JUNE
JULY
AUGUST
SEPT

than that for 5 cm. The seasonal pattern in percent soil moisture showed that at greater depths (10 and 20 cm), soil moisture was relatively constant from May through July, but declined during a period of low precipitation through August and early September. Values returned to those found for the early season with late September rains. Percent soil moisture at a 5 cm depth showed an overall pattern similar to that for greater depths, but varied over a larger range reflecting a greater response to rainfall events (Fig. 1.5). Using Spearman's rank correlation, percent soil moisture was found to be highly correlated among all depths within quadrats (Table 1.3; $r=0.731 - 0.781$, $p<0.0001$).

Data from the twelve soil moisture quadrats initially censused were used to detail the effect of soil moisture on seedling survivorship. During the period May 10 - 24, percent soil moisture was measured on three dates. Values for the 5 and 10 cm depths were found to be normally distributed and have equal group variances after an arcsin-square root transformation. Survivorship values were also arcsin-square root transformed. Values for the 5 cm depth are presented here because the regression using these values provided a higher correlation coefficient than those for the 10 cm depth. Most quadrats had similar percent soil moisture values (Fig 1.6), however one area of the population had consistently higher soil moisture and seedling survivorship. The relationship between survivorship and

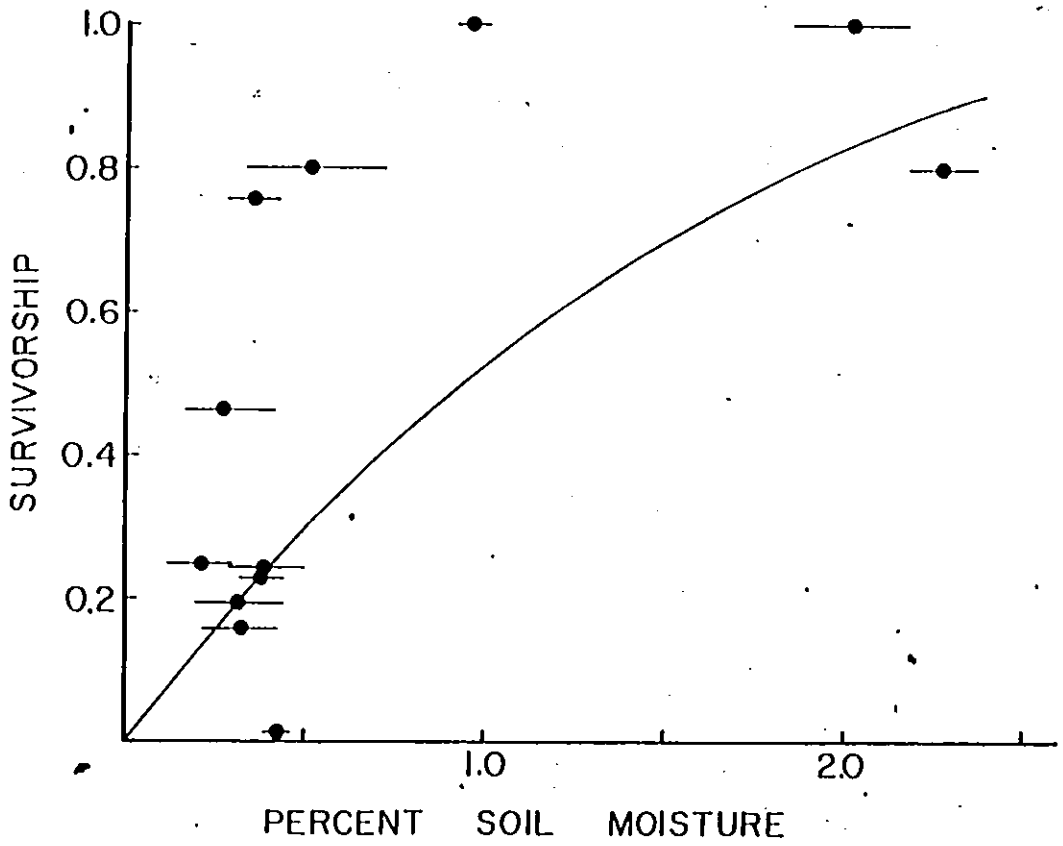
Table 1.3. Spearman rank correlations for percent soil moisture at depths of 5, 10, and 20 cm[1].

		PERCENT SOIL MOISTURE AT:		
PERCENT		5 cm	10 cm	20 cm
SOIL	5 cm	1.0000	0.7811	0.7303
MOISTURE	10 cm		1.0000	0.7500
AT:	20 cm			1.0000

[1]All correlation coefficients are significant at $p<0.0001$ (N=149).

Figure 1.6

Relationship of seedling survivorship from May 10 to 24 and percent soil moisture at a depth of 5 cm (back-transformed means ± std. errors) measured on three dates during the period.


1.0
0.8
0.6
0.4
0.2
SURVIVORSHIP
1.0
2.0
PERCENT SOIL MOISTURE

percent soil moisture was significant ($r=0.658$, $p<0.0001$). These results were confirmed by the high survivorship values found for the demography quadrats in the same area of the population.

Patterns of survivorship in the soil moisture quadrats were similar to those presented for quadrats in which detailed censuses were made (Fig 1.3). At low seedling densities, survivorship varied and reached values lower than those observed for high density quadrats. A multiple regression analysis of survivorship; percent soil moisture averaged for the three dates, and maximum quadrat density indicated that soil moisture had a significant effect on seedling survival (Table 1.4, $p=0.014$), but the effect of density was not significant ($p=0.243$). The regression accounted for roughly one-half of the variation in survivorship values among quadrats ($R^2=0.560$). These results conflict with those provided by the contingency table analysis which suggested that density and survivorship were related. Because the contingency table was obtained by collapsing data over all quadrats, among quadrat variation was ignored. If the variation among quadrats was considered, the effect of density was not significant, even after accounting for soil moisture differences among quadrats using multiple regression.

Table 1.4. Multiple regression analysis of variance for arcsin-square root survivorship for the period May 10-24.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Density	1	0.18324892	0.18324892	1.56 ns
Soil Moisture	1	1.09183854	1.09183854	9.31 *
Error	9	1.05544339	0.11727154	
Corrected Total	11	2.39964739		

Growth and Fruit Production

Field observations showed that as growth proceeded through the season, the plants did not form dense canopies except in the most moist area of the population and then only at the end of the growing season. Nevertheless, both plant dry weight measured at the season's end, and fruit production declined significantly with the density of reproducing individuals (Fig 1.7; $r=0.626$, 0.505 respectively, $p<0.0001$). Plant dry weight was log transformed and fruit production was log-log transformed to normalize the data and provide equal group variances. Although there appeared to be a curvilinear trend to these data after log transformation of either variable (the means of the fruit production values have been back-transformed to a single log transform in Fig. 1.7), neither log-log transformation of plant dry weights or using log density significantly increased the amount of variance explained by the regressions.

The effects of density and percent soil moisture on fruit production in the soil moisture quadrats were both significant (Table 1.5; $p<0.0001$ for both variables). For plant dry weight, the effect of density was significant ($p<0.0001$) while the effect of percent soil moisture was not ($p=0.076$; $R=0.728$). Seasonal means of arcsin-square root transformed values of percent soil moisture at a depth of 10 cm were used in these multiple regressions. The lack of

Figure 1.7

Relationship between plant dry weight, fruit production (means ± std. errors) and density of reproducing individuals. Fruit production means back-transformed from log-log transformed values.

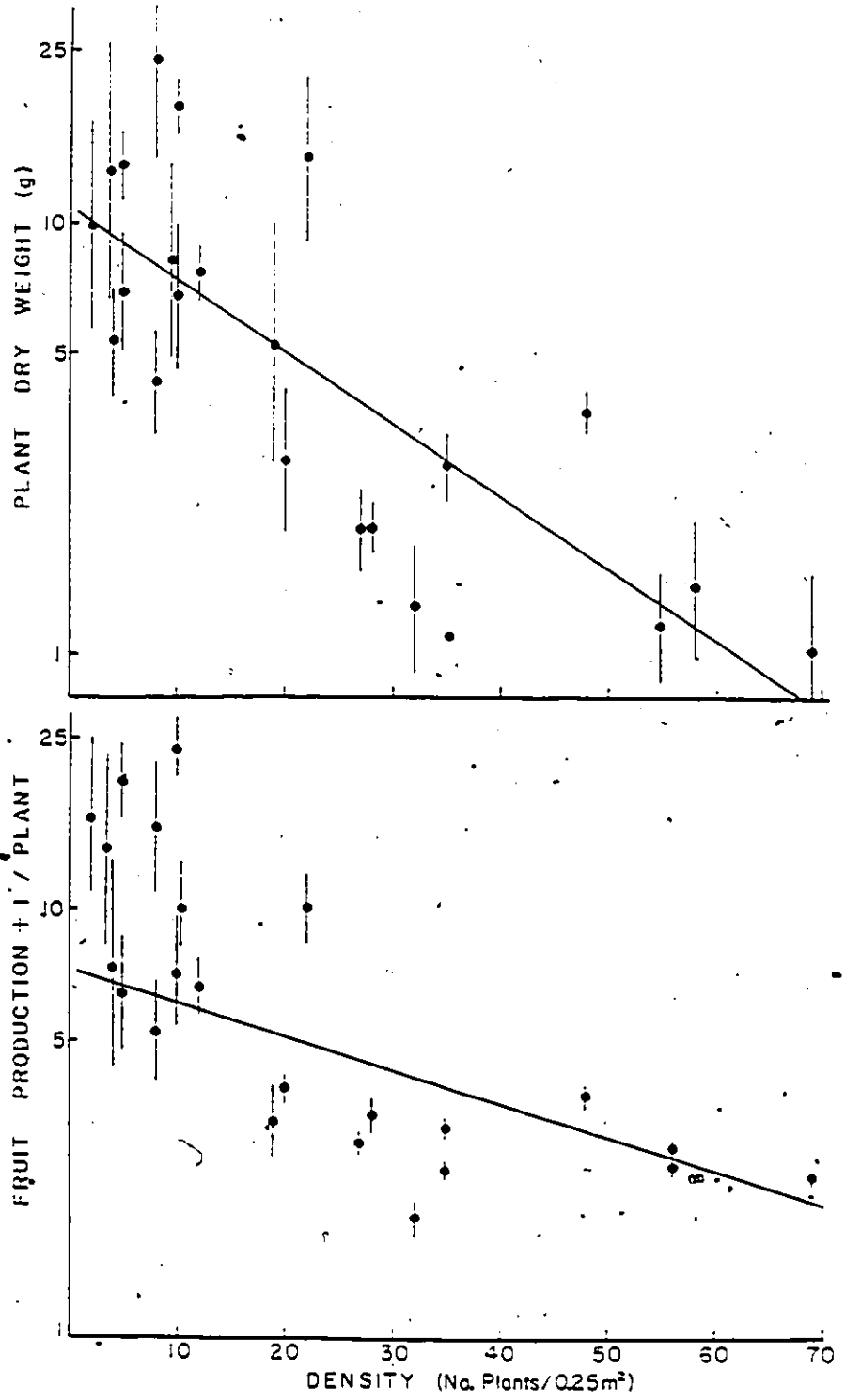

PLANT DRY WEIGHT (g)
25
10
5
1
FRUIT PRODUCTION + 1 / PLANT
25
10
5
1
10
20
30
40
50
60
70
DENSITY (No. Plants/0.25m²)

Table 1.5. Multiple regression analyses of variance for plant dry weight (g) and fruit production.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Plant Dry Weight (log transformed):				
Density	1	28.81122237	28.81122237	48.28 ***
Soil Moisture	1	1.97591858	1.97591858	3.31 ns
Error	44	26.25910880	0.59679793	
Corrected Total	46	55.82966588		
Fruit Production (log-log transformed):				
Density	1	9.08973441	9.08973441	139.97 ***
Soil Moisture	1	2.65343513	2.65343513	40.86 ***
Error	209	13.57273737	0.06494157	
Corrected Total	211	22.86480322		

significant correlation of plant dry weight with soil moisture may have been affected by the small sample sizes of plant weights; the correlation was nearly significant. The regression equation obtained for fruit production was

$$\log(\log(\text{fruit prod.} + 1) + 1) = 0.258 - 0.017(\text{density}) + 2.802(\text{soil moisture})$$

indicating fruit production was negatively correlated with density and positively correlated with percent soil moisture.

In the past, density-yield relationships have been presented using the $\log_{10}$ of mean plant weight and $\log_{10}$ density. To provide comparable results, $\log_{10}$ mean plant weight in each quadrat was regressed against $\log_{10}$ density for the data on X. strumarium. The relationship obtained was

$$\log_{10}(\text{plant weight}) = 2.098 - 0.750(\log_{10}(\text{density})).$$

The slope of this regression was significantly different from -1.5 ($t=4.62$, $p=0.0002$), but was not significantly different from -1 ($t=1.54$, $p=0.138$).

The data from the demography quadrats allowed comparison of the effects of emergence time and density on fruit

production. As before, seedlings were separated into two cohorts, early and late emergers. Recall that there was a greater number of late emerging seedlings at high than at low density. To separate the effects of density and emergence time on fruit production, analysis of covariance was used. The analysis sought to determine whether there was a significant effect of emergence time on fruit production when density was held constant. The effect of emergence time was not significant ($p=0.721$), but as before, density had a strong effect on fruit production ($p<0.0001$; Table 1.6). The assumptions that regression slopes of the covariable (density) were separate and parallel were tested and found to be satisfied.

The Gini Coefficient was used to assess changes in the hierarchy in fruit production with increasing density of flowering individuals. Over the range of available quadrat densities, the data appeared to fall into three relatively distinct density groups. Combining the data into three groups provided large sample sizes and assured reasonable values for G (Table 1.7). These values should not be greatly biased by any differences among density classes (other than density) because a full range of quadrat densities was selected in each area of the population. Hierarchy in fruit production appeared to decline with increasing plant density (Table 1.7). Values for G for the two lowest density classes

Table 1.6. Analysis of variance for differences in log-log transformed fruit weight between emergence time classes, means adjusted for differences in density between classes (analysis of covariance).

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Emergence Time	1	0.00059696	0.00059696	0.13 ns
Density	1	0.46976120	0.46976120	100.02 ***
Error	308	1.44664403	0.00469690	
Corrected Total	310	1.95385140		

Table 1.7. Gini Coefficients for fruit production.

DENSITY CLASS[1]	2/12	19/35	48/69
GINI COEFFICIENT	0.523 (11, 78)[2]	0.581 (7, 197)	0.288 (4, 228)

[1] Density classes presented as range of number of flowering individuals per quadrat.
[2] Number of quadrats in each class and total sample size indicated in parentheses.

were similar and greater than that for the highest density class.

DISCUSSION

Seedling recruitment has been identified as one of the most critical stages in the life history of a plant (Cook 1979, Harper and White 1974). In this study, date of seedling emergence and soil moisture were found important to the recruitment of seedlings in a natural population of X. strumarium. Seedling survivorship appeared largely independent of density.

A decline of seedling survival with a delay in emergence time has been observed in other studies (Weaver and Cavers 1979, Cook 1979, Howell 1981). It is not clear that the reduced survivorship of late emerging seedlings found for X. strumarium was entirely due to competition from early emerging seedlings. Most mortality occurred early in the season before plants were well established. This appears to be in contrast to two of the above mentioned studies (Cook 1979, Howell 1981). Additionally, mortality appeared, in part, due to the effects of blowing sand. Finally, for the sample size provided, the relationship between emergence time and mortality appeared independent of seedling density. Perhaps the pattern of seedling survival with emergence time simply reflects increased susceptibility to changing environmental conditions, for example, the lack of substantial precipitation over part of the period of late emergence (see Fig 1.5). Clearly, delayed emergence did not

affect the level of fruit production and, presumably plant growth of surviving individuals, as found elsewhere (Black and Wilkinson 1963, Ross and Harper 1972, Naylor 1980 Howell 1981).

Blowing sand has been reported as an important source of mortality in annual grasses inhabiting the dunes at Aberffraw, Anglesey, North Wales (Mack 1976, Huiskes 1977, Watkinson and Harper 1978). There, many seedlings died because of uprooting or burial. In this population of X. strumarium, high soil moisture apparently reduced the amount of blowing sand while also reducing the dangers of dessication resulting in increased seedling survival.

Overall, seedling mortality appeared density-independent, although there was some indication that seedlings at high density were less susceptible to the causes of mortality. These results are consistent with field observations indicating that wind blown sand was an important source of seedling mortality. Watkinson and Harper (1978) noted similar patterns of mortality in Vulpia fasciculata where wind drag was a predominant cause of mortality. Exposure to wind blown sand may explain some of the variation in seedling mortality among quadrats.

In the past, researchers have measured size hierarchies in plant populations by skewness or the degree to which a size distribution appears lognormal. Weiner and Solbrig

(unpubl. manuscript) have argued that skewness is only one component of size hierarchies and that a large variation in the sizes of individuals and the fact that very few individuals contribute most of the biomass (and seed production) in the population must be taken into account. It is the concept of inequality rather than simple assymetry that makes the Gini Coefficient suitable to studying size hierarchies in plant populations.

That the slope of the density-yield relationship had a slope of -1 in this population of X. strumarium is consistent with the conclusion that mortality was largely density-independent. This may also explain the lack of increased hierarchy in fruit production with increased density, a pattern also associated with self-thinning populations (Harper and White 1970). In fact, the degree of hierarchy appeared lowest for areas of high density and may be explained by the limited canopy developement of the X. strumarium population. Competition for light has been implicated as an important component in the development of size hierarchies in plant populations (Turner and Rabinowitz 1983). Competition for resources in the soil may have a reversed effect.

Clearly, density, date of seedling emergence, and soil moisture explain only a portion of the variability in the three demographic parameters measured and may represent only

a subset of important factors affecting the dynamics of the population. Each of the three factors measured for their effects in this population of X. strumarium showed differing patterns of effect through the growth cycle of the plants. Soil moisture had significant effects throughout, contributing to both survivorship and growth and fruit production of individuals. Seedling emergence time had significant effects on survivorship, but did not affect fruit production. Plant density did not strongly affect seedling survival, but appeared important in determining plant growth and fruit production. These patterns emphasize the importance of considering all aspects of the life cycle of a plant in attempting to understand its population dynamics.

CHAPTER II

RESOURCE COMPETITION IN EXPERIMENTAL MONOCULTURES OF *XANTHIUM STRUMARIUM*

CHAPTER II

INTRODUCTION

Plants growing in the proximity of one another rely on a common pool of resources. When one or more of these resources becomes limiting such that the growth and reproduction of the plants is reduced, the plants are said to be competing. Plants are relatively plastic in their growth and they show well characterized responses to the presence of competing individuals (extensively reviewed in Harper 1977). In many cases, competitively stressed plants will exhibit a reduction in the proportion of biomass allocated to seeds or fruits in addition to a reduction in overall growth and reproduction. Presumably, this arises because the plants must allocate greater biomass to structures gathering the limited resource or resources.

The role of resources in competitive interactions among individual plants has been generally considered too complex to ever disentangle (deWitt 1960). Reduction in growth caused by limited availability of one resource automatically leads to reduced need for other resources, but also a reduced ability of the plant to gather them. Yet, advances have been made in the understanding of resource limitation in plant competition. Competition for water has probably received the least attention in studying competitive interactions among plants, while light, often the limiting resource for crop

plants (Donald 1961), has received the most.

The importance of light in competition among and within species of Trifolium is well established (Black 1958,1960, Davidson and Donald 1958, Harper and Clatworthy 1963, Williams 1963). Competition between two varieties of barley was found to be affected by water and nutrients (Hartmann and Allard 1964) and not by light (Edwards and Allard 1963). Other good examples of the role of nutrients in competitive interactions between plant species can be found in Weiner (1980) and Hall (1974a, 1974b).

An elegant method of investigating the roles of shoot and root interactions in plant competition was independently developed by Donald (1958) and Aspinall (1960). Pairs of species were grown in pots with aerial or soil partitions, both partitions or neither. In this way the relative importance of competition for above or below ground resources could be compared. Donald however, was quite aware of the limitations of this approach in field situations.

The simplest approach to understanding competitive interactions under field conditions is to compare plants grown at spacings in which resources are not limiting to those grown at densities where competition is assured. Thus, the former plants serve as a 'control' treatment to be compared to the competition treatments. Resource abundances are then monitored in the different treatments to determine

whether a reduction in resource availability occurs under conditions of competition. If plants show any response (Harper (1977), terms these symptoms) to changes in resource availability, then the nature of the competitive interaction should be revealed. Furthermore, growing plants in monoculture eliminates the complexity of sorting out inter- and intraspecific interactions. Yet, it would be interesting to know if these effects are qualitatively similar.

The role of competition for light and water in experimental monocultures of Xanthium strumarium grown at three different densities was investigated using this approach. A single treatment of competition between Xanthium and Abutilon theophrasti was used to compare the effects of intra- and interspecific competition. Light and soil moisture levels were monitored for plants grown with and without competitors. Responses to changes in light level were characterized using several morphological variables, while responses to soil moisture were measured using physiological variables indicative of moisture stress. Quantitative analysis of plant growth, seasonal patterns of biomass allocation, and data for cumulative growth and fruit production indicate the patterns of response to competition in X. strumarium and provide a basis for understanding its selective importance.

MATERIALS AND METHODS

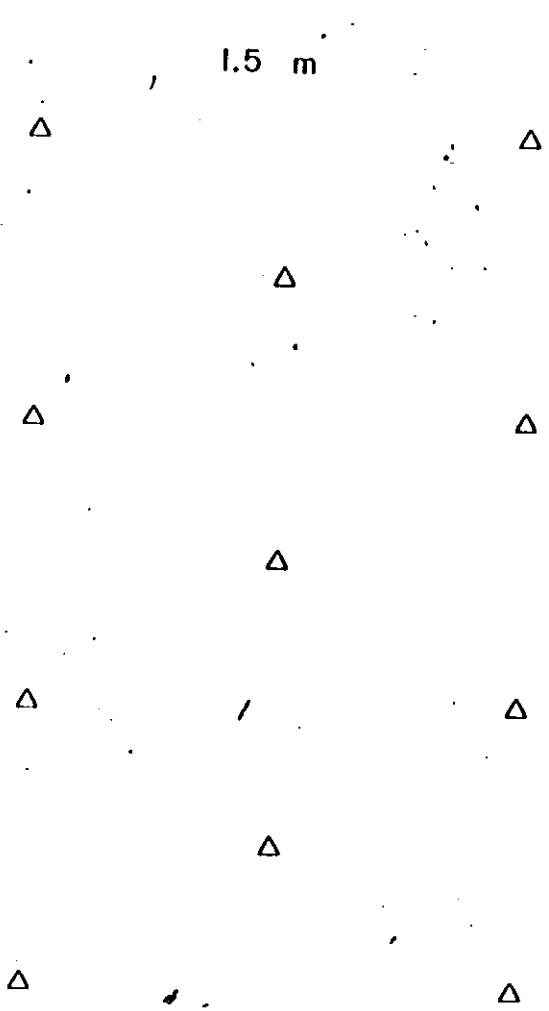
General Field and Laboratory Procedures

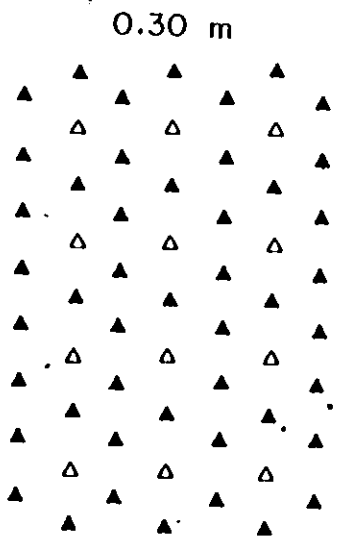
Experiments were performed on a Granby sandy loam soil at the Agriculture Canada Research Station, Harrow, Ontario. The soil had an organic matter content of 2.5-2.6 % and a pH of 5-5.2. Fertilizer (8, 32, and 16 % N, P, and K, respectively) was broadcast over the soil at a rate of 224 kg/ha on May 3, 1982. Similar applications of fertilizer had been made in previous years. Fruits of X. strumarium used in the study were collected in the fall of 1980 or 1981 as bulk samples from plants used in experiments on Research Station grounds.

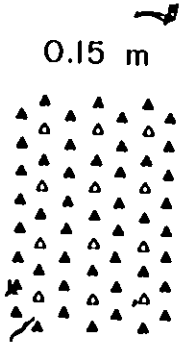
Fruits were placed in the soil on May 21,1982 in hexagonal arrays (Sakai 1956) at three different spacings, 1.5 m, 0.3 m, 0.15 m. These are equivalent to densities of 0.51, 12.8, and 51.3 plants per meter square, repectively. There were four treatments (Fig 2.1). One treatment served as a control; X. strumarium was planted at spacings of 1.5 m so that adjacent plants would not compete. This is near the 1.8 m spacing which Wapshere (1974) found would prevent X. strumarium from interfering with the growth of neighbors. Two treatments using X. strumarium at 0.3 m (low density monoculture) and 0.15 m (high density monoculture) spacings were used to assess the effects of intraspecific competition. In these treatments, only plants at the center of a hexagon

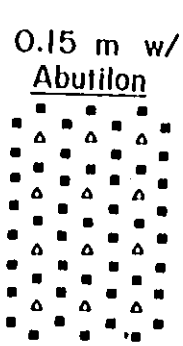
Figure 2.1

Schematic diagram of treatments showing relative planting densities and plants used for harvesting. Open symbols are plants that were harvested, triangles denote X. strumarium, and squares denote A. theophrasti.


1.5 m


0.30 m


0.15 m


0.15 m w/
Abutilon

of competitors were harvested (see Fig. 2.1) to maintain competitive effects on remaining experimental plants. For comparison of inter- and intraspecific competition, a final treatment consisting of a mixture of X. strumarium and Abutilon theophrasti was planted at a spacing of 0.15 m. The two species were arranged such that each X. strumarium was placed at the center of a hexagon of A. theophrasti (see Fig. 2.1). Only X. strumarium was harvested from this treatment. Treatments in which plants were spaced at 0.3 and 0.15 m will be collectively referred to as the interaction treatments. Each treatment was replicated five times and laid out in a randomized block design.

Infection of X. strumarium by rust (Puccinia xanthii) was controlled using a fungicide (Mancozeb) sprayed at approximately ten day intervals through late July and August. Although some infection did occur, it did not appear to differentially affect the treatments.

Randomly chosen plants in each cell of the design were harvested at intervals of 6 to 14 days from late June to mid-September. In general, harvest intervals were longer towards the end of the season. At each harvest, plants were removed from the soil retaining as much of the root biomass as possible. Each plant was separated into roots, stem, living leaves, dead leaves, and male and female inflorescences. On eight of eleven harvest dates, the number

of leaves and the total leaf area, including petioles, of each plant was measured (Li-Cor model Li-3100 area meter). Plant material was dried at 75 C for at least 72 hrs. and then weighed to the nearest 0.01 g (to the nearest 0.001 g if a sample was small) after being allowed to equilibrate to room temperature.

On two harvest dates, July 23 and September 1, the above ground portion of each plant was harvested using the stratified clip method (Monsi and Sakai 1953). Plants were divided into 10 cm (July 23) or 25 cm (September 1) horizontal strata. During harvesting, stem and petioles were clipped along planes separating each strata. Leaf blades were not subdivided, but were harvested whole to facilitate counting. Leaf blades occurring at the margin of a harvest stratum were subjectively assigned to one of the adjacent strata based upon the apparent relative mass in either stratum. Plant material in each harvest stratum was divided into stem, petioles, leaf blades, dead leaves, and if present, male and female inflorescences, then dried and weighed as described above. The total leaf blade area, petiole area, and leaf number in each harvest stratum was also measured.

Prior to each stratified clip harvest, light levels within the canopy surrounding each plant to be harvested were measured. Light levels (phototsynthetically active

radiation, Li-Cor model Li-185B) as proportions of full sunlight were measured at intervals of 10 cm (July 23) and 12.5 cm (August 28) through the canopy. Measurements were taken within one hour before or after solar noon. For plants grown without competition, self shading was measured at three points evenly spaced about the plant and one-half the distance from the central stem to the furthest expanse of leaves on a plant. For the interaction treatments, light levels were measured at 3 points midway between harvest and alternate competitor plants. Weather conditions differed on the two days light levels were measured; July 23 was a cloudless day while August 28 was uniformly overcast.

In early July, two plants in each cell of the design were randomly selected for seasonal measurements of soil moisture, leaf conductance, and photosynthetic rate described below. These plants were harvested in mid-October after the plants had matured. Because some leaf material and fruits had fallen from the plants prior to harvest, leaf material and fruits immediatedly beneath each plant were collected with it. Mature fruits were separated from the rest of the plant. Plant material, other than fruits, was dried as described above or allowed to dry in paper bags in the laboratory over several weeks time. All material was then weighed to the nearest 0.01 g.

For plants grown in the interaction treatments, fruits

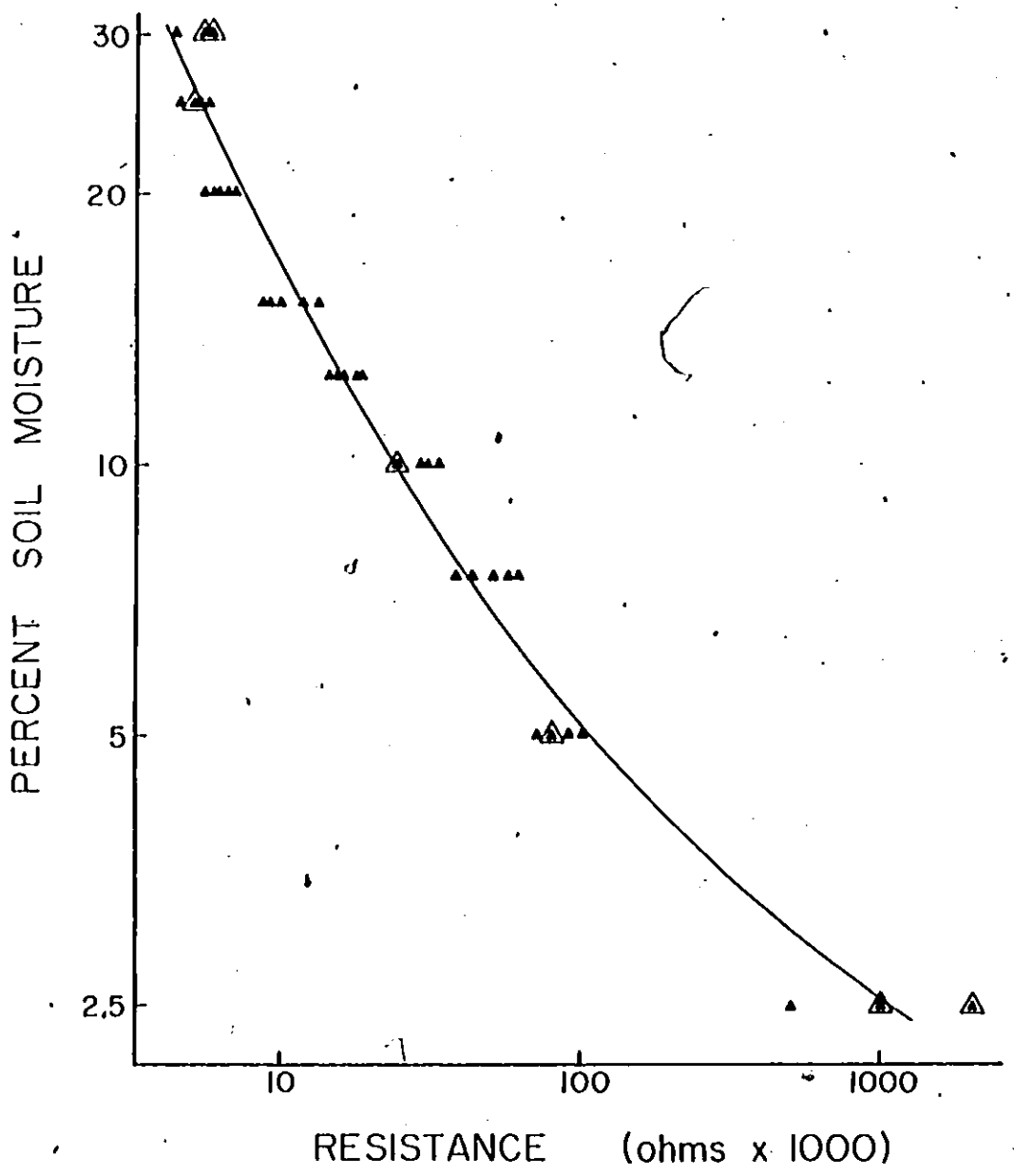
were individually counted and up to 240 (depending upon the number of fruits produced by a plant) were randomly selected and weighed to the nearest 1 mg. For isolated plants, 240 fruits from each plant were randomly selected and weighed as described and the fruit production of each plant estimated by dividing the total fruit mass by the mean fruit weight.

Soil moisture was measured around each pair of plants in each cell of the design on nine dates between early July and early September. Measurements were taken at a depth of 10 cm using the device described in Chapter One. A calibration curve (Fig. 2.2) was obtained in the same manner as described in Chapter One using soil obtained at the experimental site. For isolated plants, the electrical resistance of the soil was measured at three evenly spaced points 0.75 m from the central stem of the plant. In all other treatments, measurements were taken at 3 points between experimental and alternate competitor plants and equidistant from each.

Leaf conductance was measured using a transient porometer (Li-Cor model Li-700, see Kanemasu et al. 1969) following the precautions of Morrow and Slayter (1971) regarding field use. Photosynthetic rates were measured by labelling leaves with $^{14}CO_2$ using a method modified from Shimshi (1969) and Tieszen et al. (1974) described in the following section. Leaf conductance and photosynthetic rates were measured in close conjunction on the same leaf on each

Figure 2.2

Calibration curve used to calculate percent soil moisture from field measurements of soil electrical resistance. Multiple data points indicated by outlines. $\text{Log}_{10}(\text{percent soil moisture}) = 1.941 - 0.834(\log_{10}(\text{ohms} \times 10^3)) + 0.108(\log_{10}(\text{ohms} \times 10^3))^2$ (R=0.989).


30
20
10
5
2,5
PERCENT SOIL MOISTURE
10
100
1000
RESISTANCE (ohms x 1000)

experimental plant: To control for leaf age effects, the third fully expanded leaf from the top of the plant was used in all cases. Most measurements were taken between 1000 and 1300 h EDT except on one day when measurements continued until almost 1400 h. All days were cloudless or nearly so. If an experimental plant was shaded by nearby competitors, the competitors were parted to expose the experimental plant to full sunlight at least ten minutes before measurements were taken.

A reduced data set representing eight of ten possible dates has been presented for photosynthetic rate. Reliable values for the specific activity of the radioactive gas used on two dates could not be obtained. Furthermore, unreliable leaf conductance data were obtained on four dates and were eliminated from the analysis. Photosynthetic rate and leaf conductance data were concurrently available for five dates.

Leaf xylem pressure potential was measured for one plant in each cell of the design on 7 dates from July through early September using a pressure bomb (Sholander et al. 1965). Measurements were made using the third fully expanded leaf from the top of a plant and were made as rapidly as possible between 1300 and 1500 hr EDT on each date. All days were cloudless. Because this method required removing a leaf from each plant, only plants scheduled for harvest the following day were used; if there was no scheduled harvest the

following day, the plants were tagged and not used for subsequent harvests. Leaves from harvested plants were refrigerated overnight to be included in leaf area measurements the following day.

Measurement of Photosynthetic Rate

The radioactive gas used to label leaves for measurement of photosynthetic rate was generated from $NaH^{14}CO_3$ in a stainless steel chamber. The lid of the chamber contained intake and outtake valves. The intake valve was fitted with a circular tube on the interior of the lid in which was placed 2.7 ml of 70% perchloric acid. The bicarbonate (1 ml, 1 mCi $^{14}CO_2$) was placed in the bottom of the cylinder and the cylinder lid sealed with care not to spill acid into the bottom of the chamber. The intake valve was connected to the regulator of a cylinder containing air with a CO_2 concentration of 306 ul/l. Similarly, a hose connected the outtake valve of the chamber to a lecture bottle. This apparatus (chamber and connecting hoses) was designed to withstand at least 6.8 atm (=100 p.s.i.) of internal pressure. Air was allowed into the chamber in bursts by alternatively closing the intake valve, increasing the pressure from the air cylinder with the regulator and the opening the intake valve. This was done two to three times to ensure that all the perchloric acid had been blown into

the bottom of the chamber. The chamber was then swirled several times and allowed to sit for several minutes before the pressure was increased to move the radioactive gas into the lecture cylinder. The air cylinder and lecture bottle were then closed and disconnected from the chamber. The lecture bottle was connected to the air cylinder with a high pressure transfer hose and brought up to the pressure of the air cylinder.

The specific activity of the gas mixture was measured by introducing 1 ml of the radioactive gas into a scintillation vial containing 5 ml of NCS (Amersham) , a solubilizing solution that can act as a CO_2 trap, and sealed with a serum stopper. The gas was introduced into the vial using a 5 ml plastic syringe. The vials were allowed to stand overnight, then the NCS was diluted to the full capacity of the vile with TEG, a 1:1 mixture of toluene and methanolamine, and placed immediately into a scintillation counter (Beckman model LS-3105P). This procedure was replicated five times and the results averaged after counts had been corrected for quenching using the internal standards channels ratio method (Wang et al. 1975). The gas was found to have a specific activity of 3.18 uCi/mmol CO_2 (0.118 GBq/mmol CO_2) and a calculated CO_2 concentration of 325 ul/l.

The apparatus used to label leaves with $^{14}CO_2$ in the field consisted of the lecture bottle containing the

radioactive gas, a regulator, a flowmeter, and a plexiglas cylinder containing a CO_2 absorbant (Ascarite II, A.H. Thomas Co.) all mounted on a plywood board. A plexiglas chamber measuring 1 cm in dia. and allowing a clearance of 1 mm on each side of a leaf and mounted on a pair of vice grip pliers was used to expose leaves to the radioactive gas. Leaves were exposed to air containing $^{14}CO_2$ for 40 s at a flow rate of 0.1 l/min. A 1 cm dia. leaf disc was immediately excised using a #5 cork borer and placed in a scintillation vial containing 0.5 ml of a soulution of NCS and 10% water. Leaf discs were allowed to remain in NCS at room temperature for at least two days before processing for scintillation counting.

Samples were prepared for counting by first decolorizing the samples with a solution of benzoyl peroxide in toluene. This solution was prepared by adding 1 g benzoyl peroxide to each 5 ml of toluene, heating the solution to 60 C, allowing it to cool to room temperature and then filtering. To each sample was added 0.5 ml of this solution; this amount of decolorizing solution appeared to provide the greatest amount of decolorization and minimal quenching in trial experiments. If the samples appeared dry after extended storage time, excess toluene was added to the decolorizing solution after cooling in a ratio of 1:1 and 1 ml of this solutiom was added to the sample. Samples were then heated at 50 C for 1 hr.

After the samples had cooled, 15 ml of scintillation fluid was added (OCS, Amersham) and the samples were placed in the scintillation counter. Photosynthetic rates were calculated from the radioactive counts using the following equation (Tieszen et al. 1974):

$$P = \frac{(CPM)(44 \text{ mg mmol}^{-1}CO_2)}{(E)(T)(2.22 \times 10 \text{ DPM mCi}^{-1})(SA)(A)},$$

where CPM is the counts per minute, E is the counting efficiency (c.p.m. per d.p.m.), T is time (minutes), SA is the specific activity, and A is the area of the leaf disc.

Growth Analysis

The analysis of plant growth can involve a variety of analytical techniques (Radford 1967, Evans 1972, Hunt 1978), however I chose to analyze three of the most common measures of plant growth, relative growth rate, leaf area ratio, and unit leaf rate (commonly referred to as net assimilation rate). Relative growth rate is usually defined as

$$R = dW/dT \times 1/W$$

where W is the weight of a plant at time T. Leaf area ratio

is simply the ratio of the leaf area of a plant (L) to its total weight, that is

$$F = L/W.$$

By definition, the unit leaf rate (E) is related to the two above measures by the relationship

$$R = F \times E.$$

Thus,

$$E = 1/W \times dW/dT \times W/L$$

$$= (dW/dT)/L$$

The unit leaf rate is the efficiency of the leaves in producing plant biomass on a per area basis.

Practically, relative growth rate over a period of time is estimated by harvesting many plants at the beginning and end of the period and calculating

$$R = (\log W_2 - \log W_1)/(t_2 - t_1).$$

where W_1 and W_2 are the mean plant weights at times t_1 and t_2. Similarly, leaf area ratio over the time period is estimated as

$$F = (F_1 + F_2)/2$$

assuming that F changes linearly with time. E is then found by dividing R by F. The assumption that F changes linearly with time does not often hold and Evans (1972; see also Radford 1967) describes a method of finding the relationship between F and time so that meaningful estimates of E can be obtained. However, with the advent of modern computers, a less complicated method of deriving R, F, and E from plant growth data have been developed. Hunt (1978) has described the development of this method. Basically, this method uses polynomial regression to develop a model describing the change in logW and logL over time (these variables are log transformed to avoid problems of heteroscedasticity). R, F, and E are then derived from these regression models.

For X. strumarium polynomial regression models of plant dry weight and leaf area (log transformed) over time were

developed for each treatment producing equations of the form

$$\log W = a + bT + cT^2$$

$$\log L = a' + b'T + c'T^2.$$

The increase in variance of logW and logL explained by the inclusion of the quadratic term in these models was significant in all cases while cubic terms were not significant. Instantaneous estimates of R over the season were found by simply taking the first derivative of the relationship of logW over time for each treatment. Thus,

$$R = b + 2cT$$

The leaf area ratio at any time was found as

$$F = \text{antilog}(\log L - \log W)$$

with logL and logW obtained from the poynomial regression models described above. Finally, for unit leaf rate over time,

$$E = R/F.$$

To provide an indication of the variation in values about these estimates, this process was repeated for data in each block in each treatment. Values at each harvest date were averaged and standard errors calculated for each treatment (Vernon and Allison 1963).

Statistical Analyses

Statistical analyses were performed as described for Chapter One. Non-parametric analyses were performed using the MRANK procedure from S.A.S. (Sarle 1981).

RESULTS

Growth Analysis

Plants in all treatments showed a characteristic logistic pattern of growth (fig 2.3); there was a linear increase in dry weight through the early part of the season, followed by a leveling off to constant values by the season's end. The seasonal growth of isolated (1.5 m spacing) plants was much greater than that observed for plants under density stress; isolated plants achieved dry weights one to two orders of magnitude greater than those in the interaction treatments (Fig. 2.3). In general, plants in low density monoculture (0.3 m spacing) had greater growth than plants in high density monoculture (0.15 m spacing), while those grown with Abutilon attained growth intermediate between that of the other two interaction treatments. Differences among the interaction treatments did not appear significant. However, it will be seen later that the increased replication afforded by the final harvest in October showed some of the differences among the competition treatments to be significant.

Polynomial regressions of logW (fig 2.3) and logL over time using linear and squared terms provided good fits to the data (Table 2.1). Changes of logL over time were similar to those seen for logW. R^2 values ranged from 0.708 to 0.927 among treatments for regressions of logW, while for logL ,

Figure 2.3

Seasonal patterns of growth (plant dry weight in g ± std. errors; upper graph) and relative growth rate (R, day^{-1}; lower graph) in each treatment. Filled circles, filled squares, and open circles are for X. strumarium at spacings of 1.5 m, 0.3 m, and 0.15 m, respectively. Open squares indicate X. strumarium grown with A. theophrasti. For R, means and std. errors calculated from separate analysis of each block; curves calculated from combined data. See text.

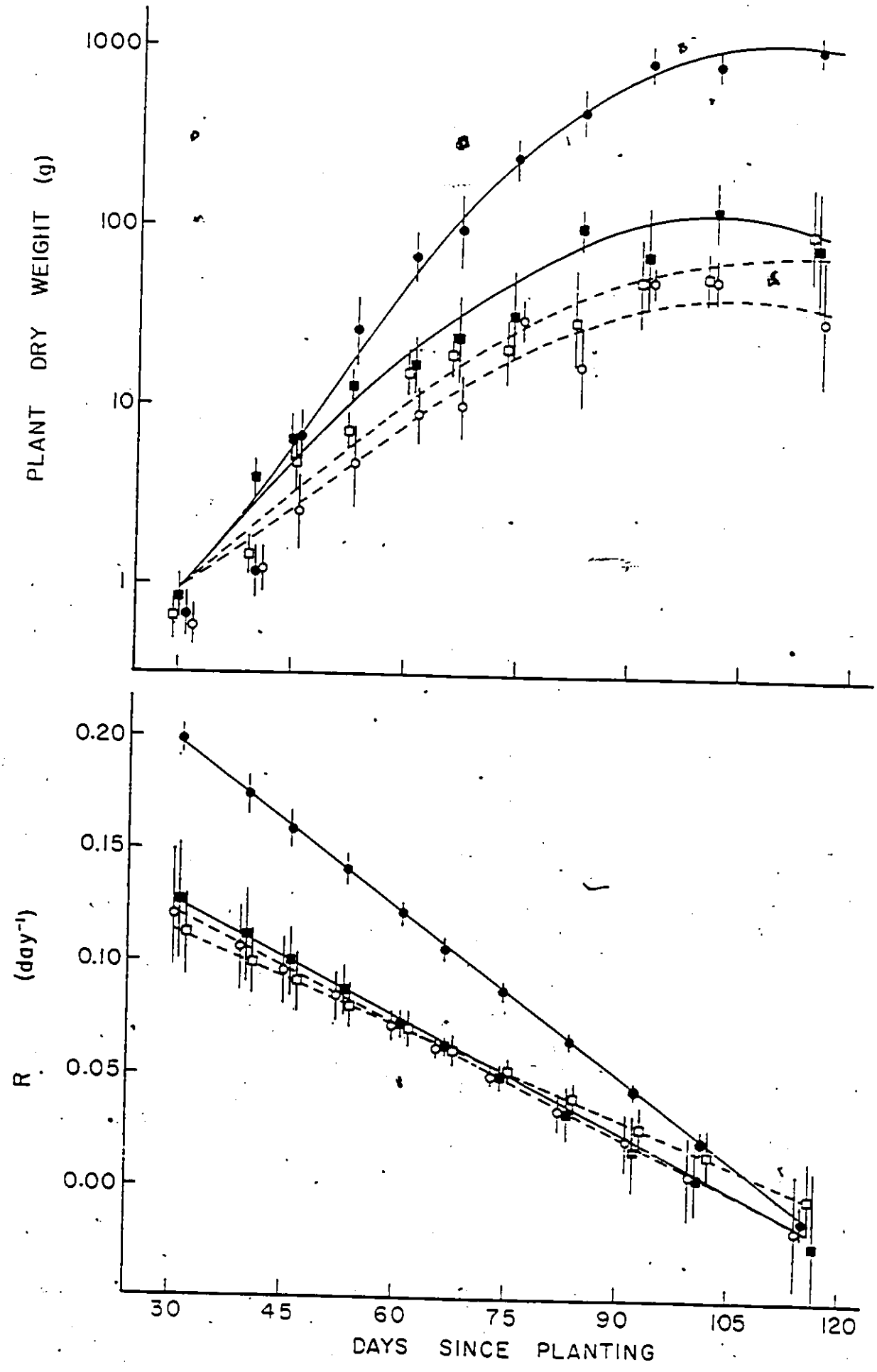

1000
100
10
1
PLANT DRY WEIGHT (g)
0.20
0.15
0.10
0.05
0.00
R (day⁻¹)
30
45
60
75
90
105
120
DAYS SINCE PLANTING

Table 2.1. Regression equations of plant dry weight (g) and leaf area (cm^2) over time (days).

TREATMENT	EQUATION	R^2
Plant dry weight:		
1.5 m	$\log W = -8.076 + 0.275(T) - 0.0013(T^2)$	0.927
0.30 m	$\log W = -4.795 + 0.183(T) - 0.0009(T^2)$	0.708
0.15 m	$\log W = -5.273 + 0.173(T) - 0.0008(T^2)$	0.748
0.15 m w/ Abutilon	$\log W = -4.396 + 0.154(T) - 0.0007(T^2)$	0.738
Leaf area:		
1.5 m	$\log L = -4.155 + 0.299(T) - 0.0015(T^2)$	0.892
0.30 m	$\log L = -1.280 + 0.223(T) - 0.0013(T^2)$	0.756
0.15 m	$\log L = -0.034 + 0.150(T) - 0.0008(T^2)$	0.666
0.15 m w/ Abutilon	$\log L = -1.382 + 0.210(T) - 0.0011(T^2)$	0.761

the R^2 values ranged from 0.666 to 0.892. In general, higher R^2 values were obtained for regressions for open grown plants than for the competition treatments.

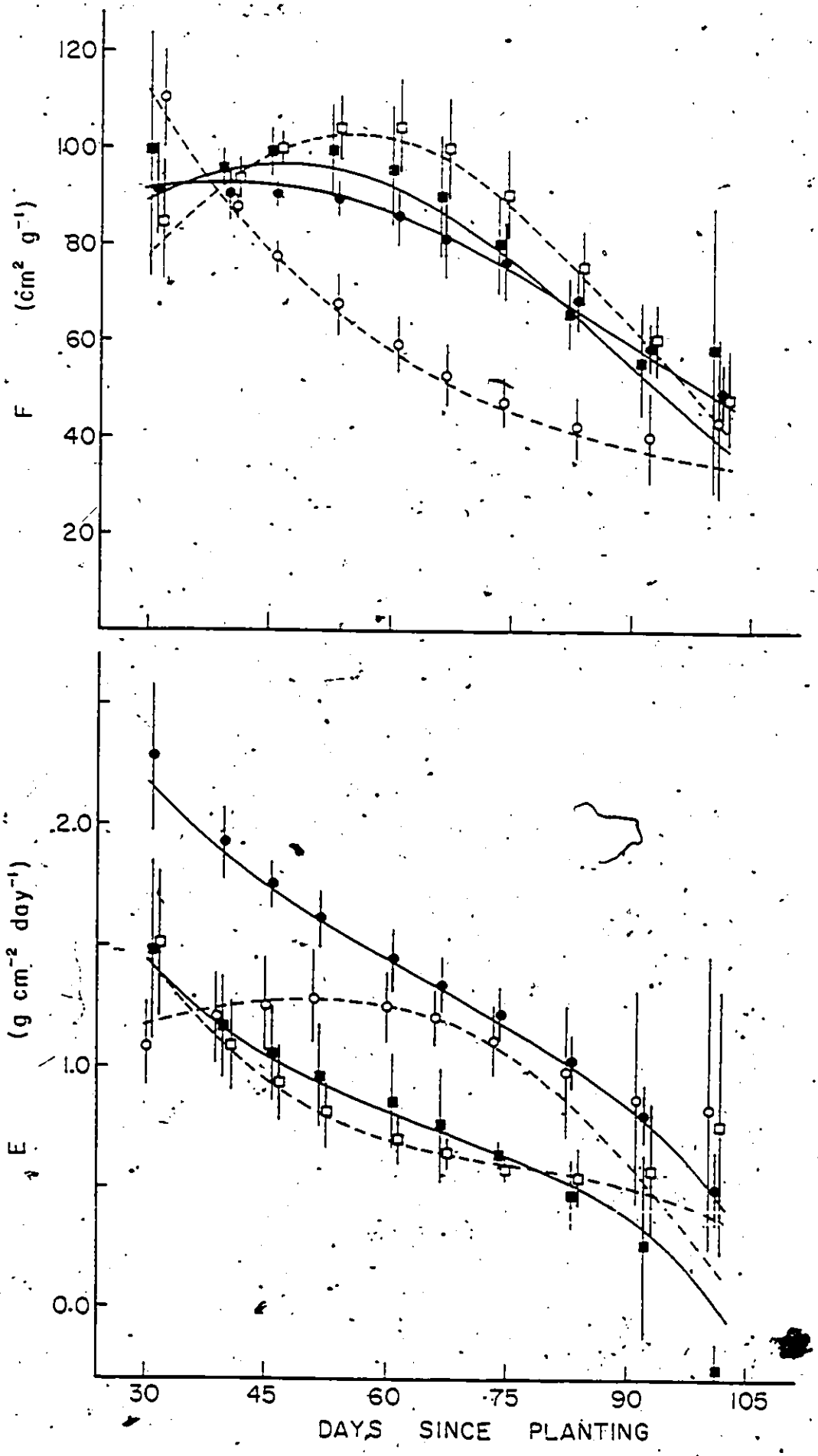
Relative growth rates (R) of plants in all treatments declined over the season (fig 2.3) and were all essentially 0 by season's end. As would be expected from the patterns in seasonal growth, R was much greater for plants grown without competition than for plants grown in the interaction treatments over much of the season. Therefore the decline in R for open grown plants was more rapid than for the competition treatments. For the three interaction treatments, temportal patterns in R were essentially identical over the season.

Leaf area ratio (F), the ratio of leaf area to plant weight, also declined over the season in all treatments (fig 2.4). The pattern in decline for isolated plants, those in low density monoculture and those grown with Abutilon were similar. Values of F were constant (or perhaps increased) through the early season and declined thereafter. In contrast, F declined throughout the early season and appeared constant through the latter part of the season for plants in high density monoculture and appeared to be significantly smaller than in the other treatments over much of the season.

Unit leaf rate (E), the efficiency of leaves in producing biomass, (fig 2.4) was highest for isolated plants,

Figure 2.4

Season patterns of leaf area ratio (F, $cm^2\ g^{-1}$; upper graph) and unit leaf rate (E, $g\ cm^{-2}\ day^{-1}$; lower graph). Symbols are as described for Fig. 2.3. Means and std. errors calculated from separate analysis of each block; curves calculated from combined data. See text.


120
100
80
60
40
20
F
(cm² g⁻¹)
2.0
1.0
0.0
E
(g cm⁻² day⁻¹)
30
45
60
75
90
105
DAYS SINCE PLANTING

particlularly at the beginning of the season. Similar to the pattern in the other growth indices, E declined over time in these plants. For the low density monoculture and plants grown with Abutilon, E appeared significantly less than control plants and had a less marked decline over the season. Values of E for the high density monoculture appeared largely constant over the season (the late season decline did not appear significant) and at mid season appeared more similar to the open grown plants than the other competition treatments.

In general, treatment patterns in the three growth indices were similar when obtained by averaging the results from regressions using each block, which was done to provide an indication of variation in the indices, and those obtained from regression of all data for a treatment as a whole. Differences between these two methods occurred most frequently at the temporal extremes and were most apparent for unit leaf rate, the index requiring the most derivation.

Analysis revealed that plants grown under competitive stress had suppressed growth rates, although differences in growth rates among interaction treatments were not apparent. The low growth rates for low density plants and those grown with Abutilon appeared to result from reduced values of E, because values of F were similar to that for open grown plants. Conversely, the high density monoculture had a

reduced F while E was at times more similar to that of open grown plants.

Proportional Allocation

Proportional allocation data were obtained to provide an indication of the way in which the plants altered the distribution of assimilates to various plant parts in response to the effects of competition. There were clear differences in the proportions of biomass allocated to leaves, stems, roots, and dead leaves among treatments over the season (Fig 2.5, Table 2.2; $p<0.001$). Analysis of variance also showed there were significant treatment x date interactions for each of these variables ($p<0.05$; Table 2.2) or nearly so (for dead leaves, $p=0.054$). This indicates that the changes in allocation to these components among treatments were not parallel over time. To assess the differences in allocation patterns among treatments over time, one way analysis of variance was performed using data from five dates over the season. Because this procedure could have inflated the probability of obtaining a significant result (Type I error), a significance level of 0.01 was used. Tukey's Studentized Range Test was used to test differences among individual treatments, again using a significance level of 0.01.

Allocation to living leaves declined over the season in

Figure 2.5

Seasonal patterns of biomass allocation to various plant parts. Means (± std. errors) are back-transformed from arcsin-square root transformed values. Symbols are as described for Fig. 2.3. Means with same letter are not significantly different (Tukey's Studentized Range Test, $p<0.01$) for dates indicated.

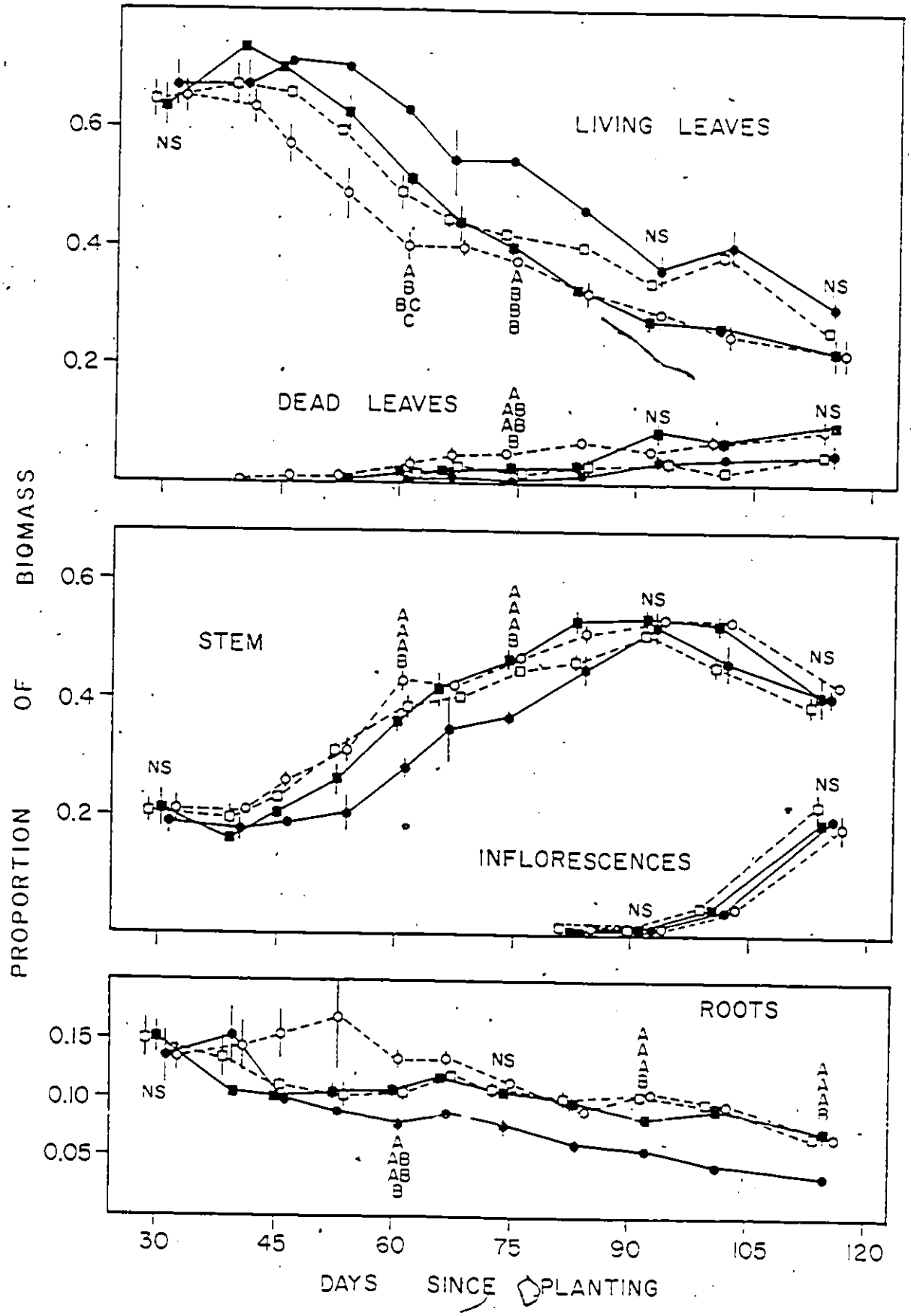

LIVING LEAVES
DEAD LEAVES
STEM
INFLORESCENCES
ROOTS
PROPORTION OF BIOMASS
DAYS SINCE PLANTING
0.6
0.4
0.2
0.15
0.10
0.05
30
45
60
75
90
105
120
NS
A
AB
ABC
B

Table 2.2. Analyses of variance for arcsin-square root transformed proportions of biomass allocated to various structures.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Living Leaves:				
Treatment	3	0.48144014	0.16048005	46.95 ***
Date	10	4.75318431	0.47531843	139.07 ***
Block	4	0.00997514	0.00249379	0.73 ns
Treatment x Date	30	0.23983647	0.00799455	2.43 ***
Error	169	0.57762691	0.00341791	
Corrected Total	216	6.09328509		
Stem:				
Treatment	3	0.13066922	0.04355641	18.40 ***
Date	10	3.45457274	0.34545727	145.97 ***
Block	4	0.02012993	0.00503248	2.13 ns
Treatment x Date	30	0.11326161	0.00377539	1.60 *
Error	169	0.39995181	0.00236658	
Corrected Total	216	4.12387272		
Roots:				
Treatment	3	0.12791780	0.04263927	26.65 ***
Date	10	0.32384242	0.03238424	20.24 ***
Block	4	0.00516111	0.00129028	0.81 ns
Treatment x Date	30	0.09578313	0.00319277	2.00 **
Error	169	0.27042959	0.00160018	
Corrected Total	196	0.83039442		

Table 2.2. Continued.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Dead Leaves (days 67-115):				
Treatment	3	0.17654233	0.05884744	20.07 ***
Date	5	0.20084899	0.04016980	13.70 ***
Block	4	0.01296611	0.00324153	1.11 ns
Treatment x Date	15	0.07740726	0.00516472	1.76 ns
Error	90	0.26387927	0.00293199	
Corrected Total	117	0.73153140		
Inflorescences (days 92-115):				
Treatment	3	0.00147134	0.00049045	0.66 ns
Date	2	1.29345799	0.64672900	872.09 ***
Block	4	0.01614327	0.00403582	5.44 **
Treatment x Date	6	0.00671103	0.00111851	1.51 ns
Error	43	0.03188820	0.00074159	
Corrected Total	58	1.37877003		
Female Inflorescences (days 92-115):				
Treatment	3	0.00085676	0.00028559	0.30 ns
Date	2	1.64324518	0.82162259	876.07 ***
Block	4	0.01576348	0.00394087	4.20 **
Treatment x Date	6	0.01070756	0.00178459	1.90 ns
Error	43	0.04032775	0.00093785	
Corrected Total	58	1.74575301		

all treatments ($p<0.001$; Fig 2.5). This decline occurred earliest for plants in the interaction treatments and appeared most pronounced for plants in high density monoculture. By mid-season (day 74), there were clear differences in leaf allocation between open grown plants and plants in the interaction treatments, but no significant differences appeared for later harvests. Dead leaves began accumulating in the high and low density monocultures earliest. By mid-season, the proportion of dead leaves in the high density monoculture was significantly greater than all other treatments, but no significant differences were observed thereafter.

The decline in allocation to leaves over the season was paralleled by an increase in stem allocation in all treatments ($p<0.001$; Fig. 2.5). On days 61 and 72, plants in the interaction treatments had greater allocation to stem than open grown plants. Differences among the interaction treatments, as well as differences among all treatments on any other dates, were not significant.

Plants in the interaction treatments also had greater allocation to root tissue, a pattern that tended to develop first in the high density treatment (Fig. 2.5). A large variance in root allocation in the high density monoculture for one date (day 53) was a source of significant heteroscedasticity in the data set. Deleting all data for

this date produced a homoscedastic data set and yielded results very similar to those for all dates combined. Therefore, results are presented from the analysis of all dates.

Development of inflorescences and fruits occurred late in the season (Fig 2.5). There was a tendency for male inflorescences to develop first such that all inflorescence tissue on day 83 was male (although male and female inflorescences appeared to mature synchronously). Most fruit filling, and the die back of male inflorescences occurred between dates 101 and 115, such that most inflorescence tissue was filled fruits on the latter date. An analysis of variance for allocation to female inflorescences revealed no differences among treatments for days 92 to 115 (Table 2.2). Similar results were obtained for male inflorescence allocation over days 83 to 101.

In summary, there were significant treatment differences in the allocation of biomass to leaves, stem, roots, and dead leaves. Differences in the allocation to leaves, stem, and dead leaves occurred predominantly during mid-season; plants in the competition treatments had decreased allocation to leaves and increased allocation to stem tissue. Dead leaves accumulated most rapidly in the high density monoculture. Differences in root allocation between isolated plants and the interaction treatments were most apparent late in the

season. No differences in the allocation to inflorescences were apparent.

Fruit Production, Allocation to Fruits and Mean Fruit Weight

Data collected for mature plants harvested in October provide a summary of the effects of competition on growth. In addition, data are presented for the effects of competition on fruit production, proportion of biomass allocated to fruits and mean fruit weight.

As indicated by the growth analysis, plants grown without competition achieved much greater growth than plants under competition ($p<0.001$), either in monoculture or in competition with Abutilon (Tables 2.3 and 2.4). Moreover, differences among the competition treatments, not apparent in the patterns of seasonal growth (Fig. 2.3), became evident with the increased replication provided by the final harvest. Growth was most suppressed in the high density monoculture (Table 2.2). Plants in low density monoculture and those grown with Abutilon achieved similar growth even though those grown with Abutilon were planted at the same density as the high density monoculture.

As would be expected, the pattern in fruit production among treatments was similar to that for plant biomass (Table 2.3). Fruit production for plants grown without competition was at least an order of magnitude greater than than that of

Table 2.3. A. Mean biomass, fruit production, proportion of biomass allocated to fruits, and individual fruit weights (± std. error; means are for untransformed data) for plants in each treatment[1].

TREATMENT	BIOMASS (g)	N	FRUIT PRODUCTION	N	ALLOCATION TO FRUITS	N	FRUIT WEIGHT (mg)	N
1.5 m	1205.72^{A} ±234.65	10	2143.8^{A} ±501.9	10	0.248^{C} ±0.018	10	136.73^{C} ±1.53	1200
0.30 m	161.76^{B} ±29.81	9	238.9^{B} ±40.6	10	0.269^{BC} ±0.009	9	201.13^{B} ±2.01	970
0.15 m	31.38^{C} ±7.58	10	44.5^{C} ±11.3	10	0.300^{B} ±0.010	10	228.42^{A} ±4.42	179
0.15 m w/ Abutilon	155.64^{B} ±62.02	8	309.0^{B} ±130.0	8	0.384^{A} ±0.012	8	203.19^{B} ±2.35	797

[1]Means with same letter are not significantly different ($p<0.05$, Tukey's Studentized Range Test).

Table 2.4. Analyses of variance for biomass, fruit production, proportion of biomass allocated to fruits, and individual fruit weights for plants in each treatment.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Biomass (log transformed):				
Treatment	3	76.72858429	25.57619476	28.70 ***
Block	4	3.85374484	0.96343621	1.08 ns
Error	29	25.84539116	0.89122038	
Corrected Total	36	106.22945338		
Fruit Production (log transformed):				
Treatment	3	82.81313828	27.60437943	32.45 ***
Block	4	3.17126200	0.79281550	0.93 ns
Error	30	25.51958130	0.85065271	
Corrected Total	37	111.44351361		
Proportional allocation to fruits (arcsin-square root transformed):				
Treatment	3	0.11288121	0.03762707	20.49 ***
Block	4	0.01264667	0.00316167	1.72 ns
Error	29	0.05325428	0.00183635	
Corrected Total	36	0.17555031		
Fruit Weight:				
Treatment	3	3196947.439	1065649.146	319.81 ***
Block	4	807827.163	201956.791	60.61 ***
Error	3138	10456236.867	3332.134	
Corrected Total	3145	14783072.959		

plants grown in the interaction treatments ($p<0.001$). Plants grown in low density monoculture and those with Abutilon produced significantly greater numbers of fruits than those grown in high density monoculture.

Despite suppression of fruit production for plants grown in competition, the proportion of biomass allocated to fruits in these treatments was greater than that for isolated plants ($p<0.001$; Tables 2.3 and 2.4). Plants grown in competition with Abutilon allocated the greatest proportion of biomass to fruits, while in all other treatments, allocation to fruits increased with increasing plant density. This pattern in reproductive effort is, in part, explained by patterns in mean fruit weight among the treatments (Table 2.3). In monoculture, mean fruit weight also increased with increasing density. For plants grown with Abutilon, mean fruit weight was similar to that for plants in low density monoculture.

A final component in the interaction between fruit production, proportional allocation to fruits, and mean fruit weight is the number of fruits produced per gram of total plant biomass. Ratios of means from Table 2.3 showed that the plants grown with Abutilon produced the greatest number of fruits per gram (1.99) while this ratio declined with increasing density in the other treatments. Values for isolated plants, those in low density monoculture, and high density monoculture were 1.78, 1.48, and 1.42, respectively.

While confirming the trends seen in the growth analysis, these data have allowed finer resolution of differences in growth among competition treatments. Patterns in fruit production were similar to those for biomass accumulation; plants without competition greatly outgrew and outproduced those under competition. Plants in low density monoculture and those grown with Abutilon were similar in growth and fruit production while plants grown in high density monoculture had the least growth and fruit production. In general, mean fruit weight was highest for plants grown in the competition treatments, although in monoculture, fruit production per gram biomass was less than that for isolated plants. Nevertheless, the proportion biomass allocated to fruits was greater for plants grown in competition than that for isolated plants.

Analysis of Competition for Light.

The role of light as a limiting resource explaining the reduction of growth for plants grown in competition was investigated using a dual approach. Light profiles were measured to indicate whether there were differences in the amount of shading in each treatment. Differences in the morphology of plants among treatments were measured to determine whether plants were responding to any difference in shading among treatments. Morphological variables measured

Figure 2.6

Light profiles in each treatment on two dates, July 23 (left graph) and August 28 (right gragh). Mean light levels (± std. errors) presented as proportions of full sunlight. Symbols are as described for Fig. 2.3.

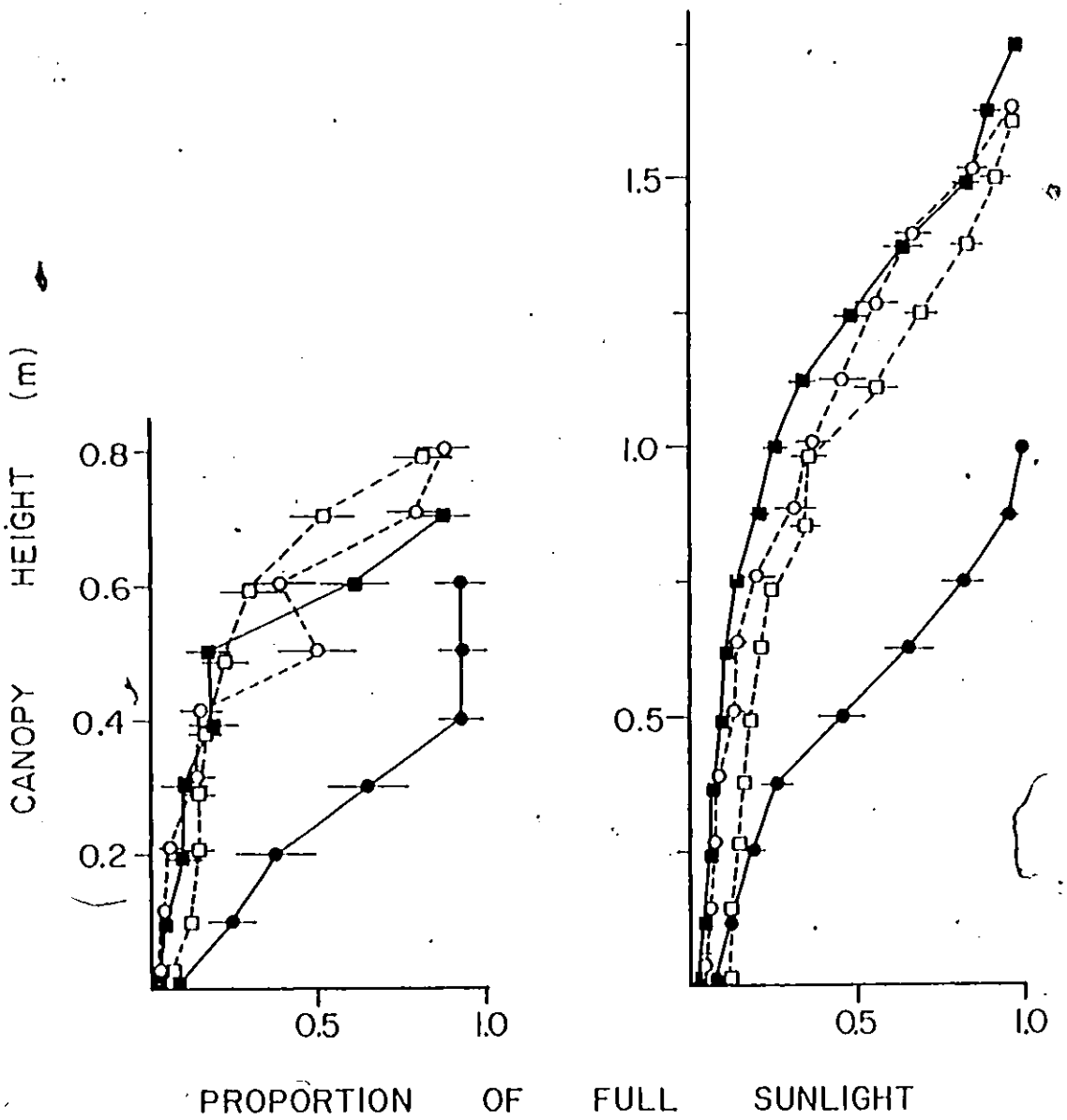

CANOPY HEIGHT (m)
0.8
0.6
0.4
0.2
0.5
1.0
1.5
1.0
0.5
0.5
1.0
PROPORTION OF FULL SUNLIGHT

Table 2.5. Mean light levels (proportion of full sunlight) at ground level (± std. error) on two dates in each treatment and results of Friedmans test for differences between dates and treatments.

	LIGHT LEVELS ON:	
TREATMENT	23/7	1/9
1.50 m	0.087 ±0.011	0.084 ±0.010
0.30 m	0.031 ±0.005	0.046 ±0.003
0.15 m	0.030 ±0.006	0.057 ±0.011
0.15 m w/ Abutilon	0.074 ±0.024	0.121 ±0.007

Freidmans Test:

EFFECT	X^2	DF	PROB.
Date	15.826	1	<0.0001
Treatment	40.140	3	<0.0001
Full Model	60.702	7	<0.0001

were the heights of the plants and vertical distributions of leaf area, leaf number and specific leaf area for plants in each treatment.

Light profiles in the canopies of the interaction treatments differed from those within plants grown without competition (Fig 2.6). Plants grown in competition with other plants were shaded to a much greater extent than self-shading occurred in plants grown without competition. This pattern was apparent on both dates light levels were measured. Within the interaction treatments, light profiles were similar. Because of the methods used to measure light levels these results overstate the amount of self-shading in the isolated plants; even for the lowest levels of the canopy, many leaves received full sunlight.

There were also significant differences in the reduction of light at the ground level among treatments and between dates ($p<0.0001$; Table 2.5). In general, the low density and high density monocultures had similar values and were lower than those for plants grown without competition and those grown with Abutilon.

Plants grown in competition were significantly taller than those grown without competition (Table 2.6). Although on individual dates the interaction treatments were not all significantly different than those grown without competition, the pattern was evident in data for all dates over the season

Table 2.6. Mean height (± std. error) in cm of plants in each treatment for the stratified clip harvest dates and over the entire season[1].

	PLANT HEIGHT (cm)					
TREATMENT	JULY 23	N	AUGUST 28	N	ALL DATES[2]	N
1.50 m	34.0[B] ±4.0	5	108.7[B] ±5.8	5	55.4[B] ±5.6	55
0.30 m	51.4[B] ±3.1	5	162.3[A] ±7.7	5	80.1[A] ±8.0	55
0.15 m	55.5[A] ±6.5	5	142.7[A] ±8.1	5	72.6[A] ±7.2	55
0.15 m w/ Abutilon	58.6[A] ±4.9	5	127.8[B] ±12.6	5	73.5[A] ±6.8	55

[1]Means with same letter for each sample period are not significantly different (Tukey's Studentized Range Test, $p<0.05$).
[2]Analysis of variance for data representing the entire season required a log transformation.

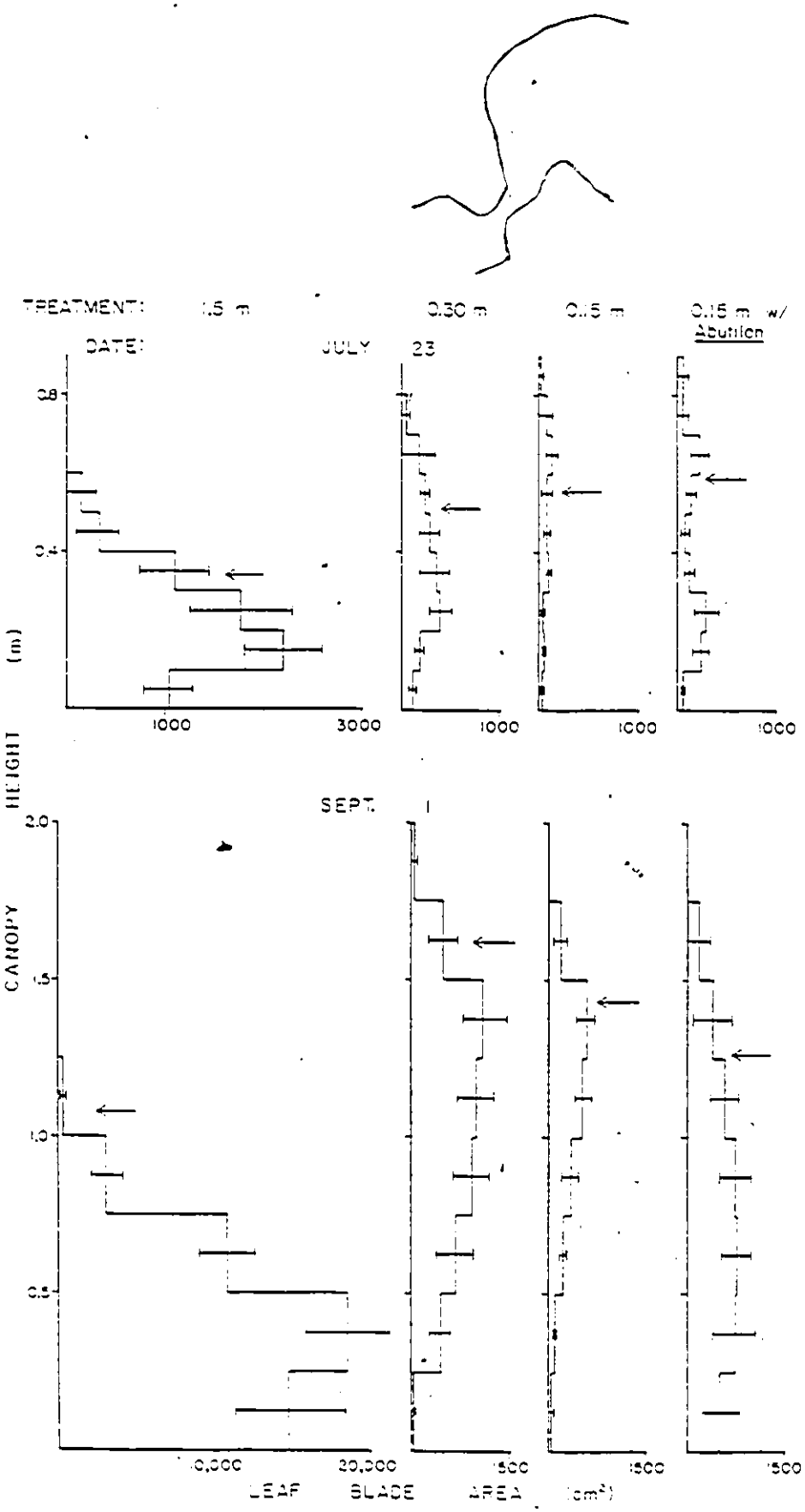
($p<0.001$).

There were clear differences in the patterns of leaf area distributions between plants facing no competition and those in the competition treatments (Fig. 2.7). The vertical distribution of leaf area was relatively uniform for plants in the competition treatments compared to isolated plants, which showed a strong peak in leaf area near the base of the plant. These patterns were apparent for both harvest dates, although there were clear differences in growth between dates in all treatments. Differences in leaf area distributions are largely explained by the fact that isolated plants produced large branches arising from the base of the plants, while branching of plants in the competition treatments was greatly suppressed.

For plants in the high and low density monocultures, there was a tendency towards increased leaf area in the upper portions of the canopy on the later harvest date (Fig 2.7). This results in part, because leaf death occurred in the lowest harvest strata. However, this pattern would be more apparent if a method of accounting for height differences among plants within treatments had been devised. Shorter plants are not represented in the upper most strata. Therefore, mean values for these strata are strongly affected by zeros obtained for some plants and misrepresent the fact that most plants had peak leaf areas near the top of the

Figure 2.7

Vertical distribution of leaf blade area (cm^2) in each treatment on two dates, July 23 (upper graph) and September 1 (lower graph). Horizontal bars indicate std. errors. Arrows denote mean plant height in each treatment.


TREATMENT:
1.5 m
0.30 m
0.15 m
0.15 m w/ Abutilon
DATE:
JULY 23
SEPT. 1
CANOPY HEIGHT (m)
0.8
0.4
2.0
1.5
1.0
0.5
1000
3000
20,000
1500
LEAF BLADE AREA (cm²)

plant.

Maintenance of leaf area in the lowest harvest strata for plants grown with Abutilon (Fig 2.7) probably reflects the tendency of some plants to send branches into adjacent walkways. Abutilon did not maintain as dense a canopy as Xanthium did, particularly in the lower portions of the canopy. This result is owed to the fact that Abutilon readily dropped its lower leaves and rarely regenerated new ones within the canopy. In contrast, Xanthium maintained the lower leaves longer and was able to grow new ones within the canopy.

Comparing Figures 2.7 and 2.8, it is clear that differences in leaf area distibution among treatments resulted largely from differing distributions of leaf number rather than mean leaf area. However, in the lowermost portions of plants in the low and high density monocultures there is some indication that there was a reduction of mean leaf area as well.

The tendency of Xanthium to grow new leaves within the canopy allows a final analysis indicating differing reponses to light levels among treatments. Regressions of specific leaf area on harvest stratum height (Table 2.7) indicated, in general, that specific leaf area declined with height at a greater rate for plants facing competition compared to those that did not. Differences in regression intercepts confirm

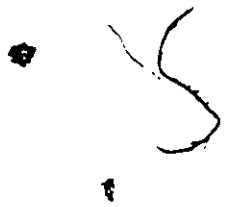


Figure 2.8

Vertical distribution of leaf number in each treatment on two dates, July 23 (upper graph) and September 1 (lower graph). Horizontal bars indicate std. errors.

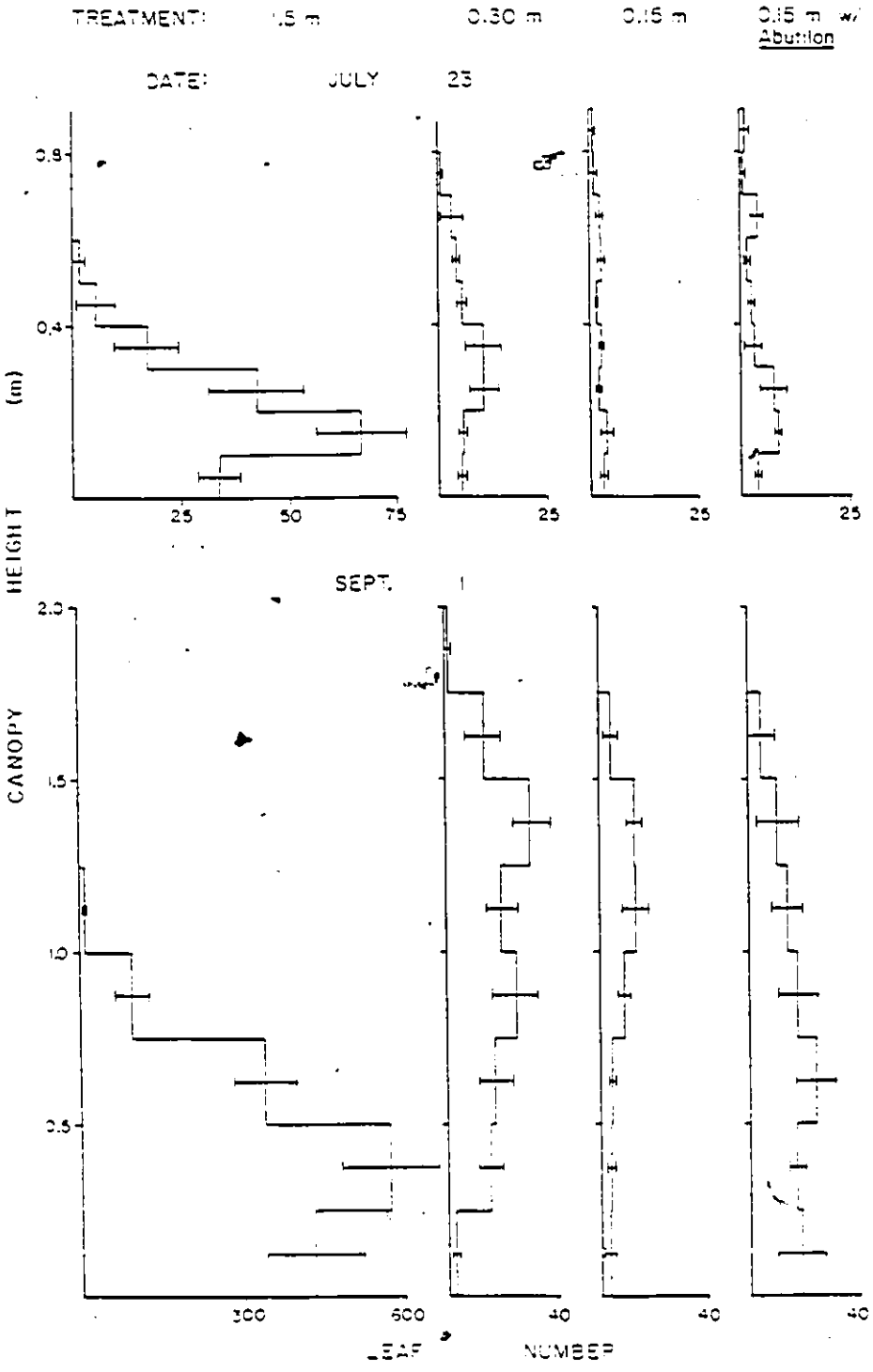

TREATMENT:
.5 m
0.30 m
0.15 m
0.15 m w/ Abutilon
DATE:
JULY
25
0.8
0.4
(m)
HEIGHT
25
50
75
25
25
25
SEPT.
1
2.0
1.5
1.0
0.5
CANOPY
300
600
40
40
40
LEAF
NUMBER

Table 2.7. Regression equations for specific leaf area ($cm^2 g^{-1}$) vs. canopy height class on two dates in each treatment. Five percent confidence limits are presented for comparison.

DATE	TREATMENT	INTERCEPT	SLOPE	R	PROB F
23/7	1.50 m	184.97 ±8.74	-1.236 ±0.484	0.833	<0.0001
	0.30 m	267.20 ±25.50	-1.690 ±0.733	0.652	<0.0001
	0.15 m	288.66 ±34.97	-2.250 ±0.897	0.704	<0.0001
	0.15 m w/ Abutilon	233.14 ±17.77	-0.974 ±0.465	0.603	0.0002
1/9	1.50 m	169.04 ±16.26	-0.541 ±0.265	0.668	0.0004
	0.30 m	297.87 ±17.59	-1.244 ±0.178	0.937	<0.0001
	0.15 m	297.61 ±40.75	-1.261 ±0.464	0.732	<0.0001
	0.15 m w/ Abutilon	260.29 ±32.77	-0.962 ±0.452	0.652	0.0002

that leaves in the lowermost harvest strata were thinnest in the competition treatments. These patterns were most evident for plants in the low and high density monocultures.

These results indicate that competition for light may explain a large portion of growth reduction in plants facing competition. There were clear differences in light levels among treatments. Plants in the competition treatments responded to lower light levels by growing taller and branching less than isolated plants. The result was a greatly altered distribution of leaf area within the canopy, largely resulting from differing distributions of individual leaves rather than mean leaf area. Morever, leaves in the lower portions of the canopies in the interaction treatments were thinner than those on plants grown without competition.

Analysis of Competition for Water

Similar to the analysis of light competition, competition for water was analyzed by monitoring levels of soil moisture in each treatment and determining if plants were responding to any soil moisture differences among treatments. Xylem pressure potential, leaf conductance, and photosynthetic rate were measured to indicate if plants were suffering moisture stress as a result of any soil moisture differences among treatments.

Differences in percent soil moisture between the

treatment with isolated plants and the competition treatments (Fig 2.9) were evident. In general, percent soil moisture was much higher for plants grown without competition than those grown with competition; any difference among the competition treatments was apparent only at the beginning of the season. As soil moisture measurements were repeated around individual plants over time, the data were analyzed as a split plot design (Table 2.8). F values for treatment and block effects were calculated using the plant(treat x block) mean square as the error mean square. This design has the advantage that treatment and block effects were tested with the error due to using different plants on different dates removed resulting in a more sensitive test of these effects. Treatment effects were significant ($p<0.001$), as was the treatment by date interaction ($p<0.001$). There were also significant soil moisture differences among blocks ($p=0.017$). Thus, plants in the competition treatments significantly reduced the amount of soil moisture compared to plants grown in isolation.

If soil moisture differences among treatments resulted in greater moisture stress in some treatments, those plants would be expected to have reduced (more negative) xylem pressure potentials. This, in turn, would result in lower leaf conductance and photosynthetic rate. Since photosynthetic rate was always measured in full sunlight, a

Figure 2.9

Seasonal pattern of percent soil moisture in each treatment. Means are back-transformed from arcsin-square root transformed values. Symbols are as described in Fig. 2.3.

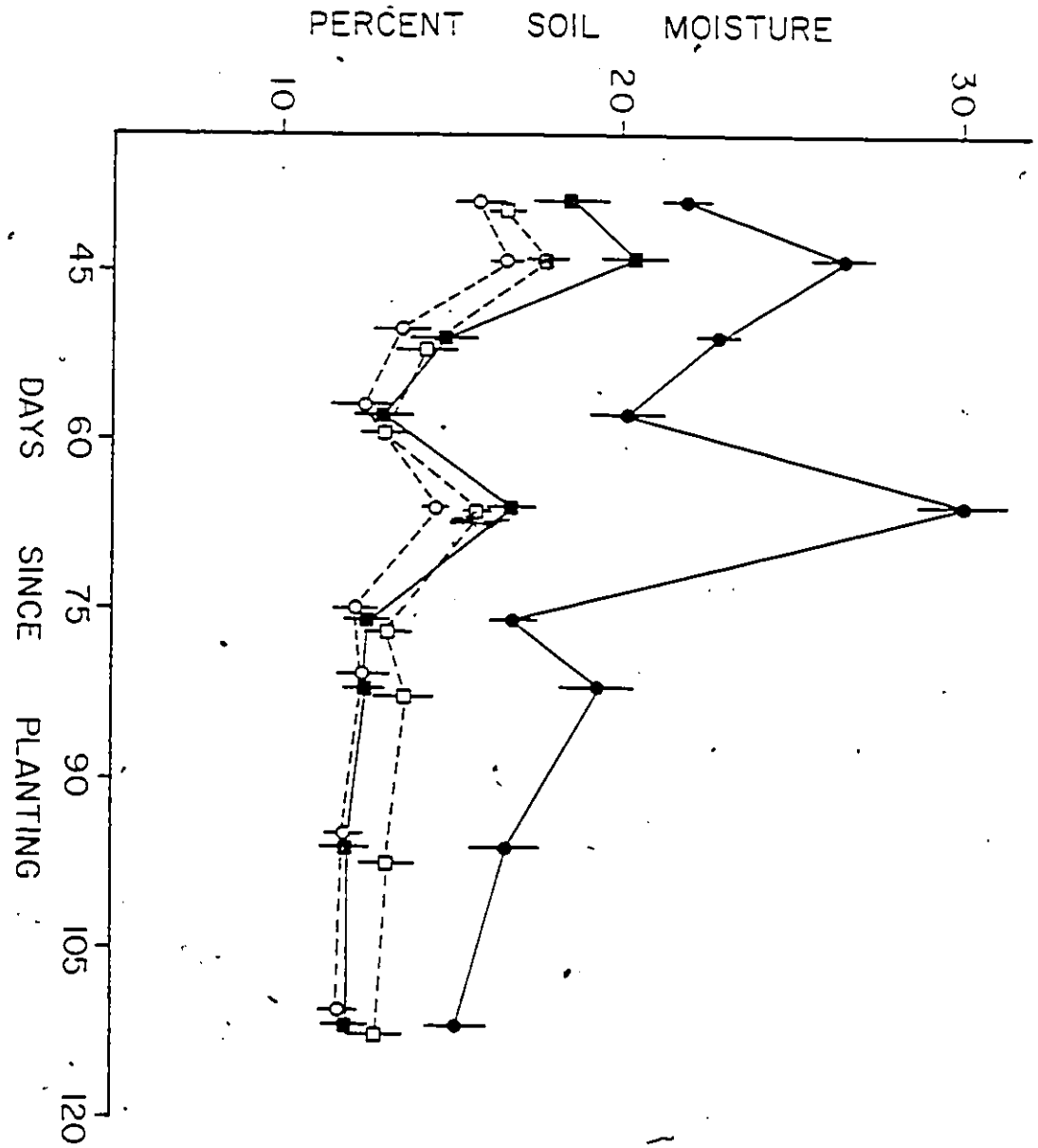

PERCENT SOIL MOISTURE
10
20
30
45
60
75
90
105
120
DAYS SINCE PLANTING

Table 2.8. Analysis of variance for percent soil moisture measured over nine dates.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Treatment	3	0.54453254	0.18151085	34.76 ***
Block	4	0.07398909	0.01849727	3.54 *
Date	8	0.41288187	0.05161023	145.65 ***
Treatment x Date	24	0.10203886	0.00425162	12.00 ***
Plant (Treatment x Block)	32	0.16711978	0.00522249	14.74 ***
Error	278	0.09850817	0.00035435	
Corrected Total	349	1.42060044		

lowered photosynthetic rate should indicate only that a plant was water stressed. Despite clear soil moisture differences among treatments, this apparently had no effect on the water relations of the plants (Table 2.9); no significant differences in the three physiological variables among treatments were evident (Table 2.10). For leaf conductance, also measured as a split plot design, there was a significant date by treatment interaction ($p=0.039$).

As would be expected, photosynthetic rate and leaf conductance were positively correlated for the five dates concurrent data were available ($p=0.008$). However, the correlation is weak ($r_s=0.190$). High variability in the photosynthetic rates is evident from the standard errors of treatment means (Table 2.9) suggesting these data were the source of the poor correlation between photosynthetic rate and leaf conductance. The source of this variability was not immediatedly evident. Nevertheless, as there were no treatment differences for xylem pressure potential and leaf conductance, the conclusion that there was no treatment effect on photosynthetic rate appeared justified. Apparently, soil water was not present in limiting quantities in any of the treatments.

Table 2.9. Mean values (± std. errors) of xylem pressure potential (MPa), leaf conductance (cm s^{-1}), and photosynthetic rate (mg CO_2 dm^{-2} h^{-1}) for plants in each treatment.

TREATMENT	XYLEM PRESSURE POTENTIAL	LEAF CONDUCTANCE	PHOTOSYNTHETIC RATE
1.50 m	-1.30 ±0.04	1.57 ±0.10	3.64 ±0.23
0.30 m	-1.37 ±0.05	1.61 ±0.08	3.72 ±0.22
0.15 m	-1.37 ±0.05	1.33 ±0.07	3.04 ±0.21
0.15 m w/ Abutilon	-1.29 ±0.04	1.51 ±0.08	3.54 ±0.21

Table 2.10. Analysis of variance for leaf xylem pressure potential (MPa) and leaf conductance (cm s^{-1}, split plot design) and Friedman's Test for photosynthetic rate (mg CO_2 dm^{-2} h^{-1}).

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F VALUE
Leaf Xylem Pressure Potential:				
Treatment	3	20.3914286	6.79714287	1.74 ns
Date	6	363.4940000	60.58233333	15.52 ***
Block	4	22.1518471	5.53769178	1.42 ns
Treatment x Date	18	97.9265714	5.44036508	1.39 ns
Error	108	421.6001429	3.90370503	
Corrected Total	139	- 925.5640000		
Leaf Conductance:				
Treatment	3	2.78602756	0.92867585	2.28 ns
Date	5	30.95705951	6.19151902	24.88 ***
Block	4	0.67790036	0.16947509	0.42 ns
Treatment x Date	15	6.53378461	0.44355856	1.79 *
Plant (Treatment x Block)	32	13.04903127	0.40778223	1.68 *
Error	172	41.80762011	0.24306756	
Corrected Total	231	95.81948726		

Photosynthetic Rate:

EFFECT	X^2	DF	PROB
Date	156.00	7	<0.0001
Treatment	7.07	3	0.0696
Full Model	179.48	31	<0.0001

DISCUSSION

In many ways the effects of increasing density on X. strumarium are similar to those reported for crop and weed species (reviewed by Harper 1977). There was a severe reduction in growth and fruit production of individual plants with increasing density. Changes in allocation to leaves, stems, and roots also occurred, but were more apparent during growth than at season's end. Leaf death occurred more rapidly for plants grown under density stress than those grown without competition. However, there was no mortality in any of the treatments and all plants produced at least a few fruits.

What is most atypical about these results is that allocation to fruits increased with increasing density. Most plants suffer reduced proportional allocation to seeds or fruits with increasing density (Harper 1977). Although the number of fruits produced per gram biomass declined with increasing density when Xanthium competed in monoculture, the increase in mean fruit weight with density resulted in increased proportional allocation to fruits. In competition with Abutilon, Xanthium produced more fruits per gram biomass than in any of the monocultures. With a moderate increase in fruit weight, plants under interspecific competition allocated proportionately more biomass to fruits than the other treatments.

Seed weight is regarded as the least plastic of all plant components (Harper et al. 1970). Nevertheless, effects of plant density on the sizes of seeds (Palmblad 1968, Snell 1967; Weis in prep.) and the distributions of dimorphic seeds (Baker and O'Dowd 1982, MacLaughlin and Weis, unpubl. data) have been demonstrated. Most of these studies show a decline in seed size with increasing density. In Xanthium, the weight of each seed within a fruit is highly correlated with fruit weight (Zimmerman and Weis 1983) such that the alteration of seed size accompanying changes in fruit size with plant density reported here is of a much larger magnitude than previously demonstrated. In X. strumarium, large fruits germinate more rapidly and in a larger proportion than small fruits (Zimmerman and Weis 1983). Although there is compensatory growth among seedlings from different sized fruits resulting in little difference in seedling size after 15 days growth, the importance of fruit size to seedling establishment, particularly under competitive conditions, cannot be disregarded. Thus, the differences in mean fruit weight produced by plants at different densities may represent real differences in the quality of these fruits.

The growth of Xanthium in the presence of Abutilon differed qualitativey and quantitively from that when Xanthium was grown in monoculture. Qualitative differences

in allocation to fruits have already been noted. Although grown at the same density as the high density monoculture, biomass accumulation, fruit production, seasonal patterns in growth indices and biomass allocation were more similar to Xanthium grown in low density monoculture. The choice of Abutilon as an interspecific competitor was based on practical concerns (the availability of seed and its low dormancy) and is of no purported evolutionary importance. However, the results for Xanthium grown with Abutilon are consistent with the widely held view that intraspecific competition is often more severe than interspecific competition. In this particular situation, this result appears to be explained by a lessened ability of Abutilon to maintain a dense canopy compared to Xanthium, therefore competitive conditions were more similar to a Xanthium monoculture at a lower density.

In general, unit leaf rate (E) declined with increasing plant density in X. strumarium although the results for the high density monoculture were somewhat enigmatic. Plants in the high density monoculture appeared to have leaves with efficiencies more near isolated plants than the other interaction treatments. This pattern may result from the early death of older, less efficient leaves in this treatment. An effect of plant density on leaf area ratio was only seen in high density monoculture, which had values of F

lower than the other treatments over much of the season. The results for specific leaf area are consistent among all interaction treatments. Plants grown in competition had significantly thinner leaves within the canopy than plants grown without competition, a pattern that correlates well with changes of light intensity within canopies among treatments.

Blackman (1968), on the basis of the responses of different plant species to changes in light level, soil fertility, and water supply, has indicated the changes in unit leaf rate, leaf area ratio, and plant height that should occur with increased plant density. If light was the sole limiting factor for plants, E should decline with increased density, while F and plant height should increase. If there are limiting supplies of nutrients or water, E and plant height should decrease with increased plant density. Finally, limiting water will cause an increase in F with increasing density and limiting nutrients will cause a decrease.

Increasing plant density has been shown to result in lowered unit leaf rates (E) in crop plants (Watson 1958, Blackman 1968, Buttery 1969, Bazzaz and Harper 1977) and in one species of tropical tree (Coombe and Hadfield 1962) although Abul-Fatih and Bazzaz (1979) found no effect of plant density on E in the weed species Ambrosia trifida. In

the example provided by Coombe and Hadfield (1962), plants were grown in separate pots at two different spacings and the results can be attributed to competition for light. They found that F increased with increasing density, a pattern also indicated by Watson (1958). Bazzaz and Harper (1977) found little change in F with increasing plant density under normal light levels. In one example where root competition was investigated, values of E and F for Impatiens parviflora were decreased in the presence of Agropyrons repens (Welbank 1961, cited by Hughes 1966). An increase in specific leaf area with increasing density frequently occurs (Watson 1958, Davidson and Donald 1958) and is regarded as "a sensitive indication of competition for light" (Williams 1963).

The patterns of leaf area distribution and canopy light levels in Xanthium grown in competition are similar to those reported for Trifolium spp. (Black 1958,1960, Harper and Clatworthy 1963, Williams 1963). These patterns were attributed to the prodominance of light competition in these studies. The importance of light interception in the upper canopy has been stressed (Black 1958, Williams 1963). The increase in plant height of plants in the competition treatments (and concurrent increase in allocation to stem biomass through the mid-season) in association with altered leaf area distributions is consistent with this view and Blackman's (1968) speculations.

The role of light competition in these results for Xanthium is clear. However, no account of competition for nutrients has been made in this study, except to note that none of the plants showed symptoms of nutrient deficiency. Plants grown in competition did show increased allocation to roots suggesting a response to reduced soil resources. Competition for water can apparently be excluded as none of the interaction treatments produced any significant changes in water relations. The reduction in leaf area ratio for plants in the high density monoculture also indicates that nutrients may have been limiting to these plants. Thus, competition for nutrients cannot be disregarded. Similarly, a possible reduction in CO_2 levels in the canopies of the competition treatments cannot be ignored (Wright and Lemon 1966).

Despite these caveats, much of the evidence from the analysis of resource competition among the plants in this study indicates a predominant role of competition for light in the reduction in growth and fruit production with increasing plant density. Thus, in this particular situation, competitive interactions may have been dominated by a single limiting resource.

GENERAL CONCLUSION

In this study of intraspecific competition among plants of X. strumarium, I have focused on two areas of limited understanding in plant population biology: factors affecting the dynamics of natural populations of plants and the role of limiting resources in plant competition. My work provides several general conclusions about plant competition in natural and experimental settings and suggests many avenues of further study.

In a natural population of X. strumarium, soil moisture and seedling emergence date were identified, in addition to plant density, as important factors affecting the performance of plants in the population. Density affected the growth and reproduction of plants while survivorship was largely density-independent. Soil moisture affected survivorship, growth and reproduction of plants while seedling emergence date did not affect fruit production but had significant effects on survivorship. That these three factors exhibited differing patterns of effect through the growing season indicates the importance of considering all aspects of the life cycle of a plant when seeking to understand its population dynamics.

Density is only a crude measure of the competitive stress experienced by individual plants. Models considering the mass, distance, and angular dispersion of neighbors would

undoubtedly better explain the variation in growth and reproduction of individual plants (Mack and Harper 1977, Weiner 1980a). Furthermore, there may be other equally important factors affecting the dynamics of the X. strumarium population. In view of the differing germination requirements of the two seeds within fruits of X. strumarium and limited knowledge of seed longevity in the soil (Weaver and Lechowitz 1982), an investigation of dormancy and mortality of buried seeds would be of interest. Finally, S.C.H. Barrett (personal communication) has suggested that time of floral initiation may be an important factor regulating the reproductive capacity of a determinately flowering species such as X. strumarium. Plants achieving greater growth by flowering later in the season would be expected to have a greater reproductive output than those flowering earlier. Variation in the timing of flowering was observed in the X. strumarium population.

For X. strumarium grown in an experimental setting in agricultural soil, intra- and interspecific competition resulted in reduced growth and reproduction. These results, as well as the alteration of patterns of growth indices and proportional allocation of biomass to vegetative parts, were similar to those found for other plant species (see references in Discussion of Chapter II). However, plants grown under density stress exhibited an increased proportion

of biomass allocated to fruits owing, in part, to the increased mean weight of fruits (and correlated changes in seed weight) produced by plants grown in competition. This result distinguishes this study from previous studies that generally show a reduced proportion of biomass allocated to reproduction and constant mean seed weight with increased density.

Analysis of resource competition in monocultures of X. strumarium grown in agricultural soil revealed plants competed for light but not soil water. Interpretation of the results is hampered by a lack of consideration of competition for nutrients. There were indications from the patterns in biomass allocation to roots and leaf area ratio that limiting nutrients may have explained some of the responses of plants to competitive stress. It is difficult to define the nutrient requirements of plants (Loneragan 1968) and one would be able to consider only a subset of the 17 known essential nutrients of plants. However, the monitoring of soil and tissue concentrations of critical nutrients (e.g. nitrogen) in this study would have provided a more well-balanced understanding of competitive interactions among X. strumarium plants.

In the natural population, observations suggested that plants did not compete for light but for soil resources. This is in contrast with the results from the experimental

population and indicates that competitive interactions among plants can change drastically with changes in habitat.

Weaver and Lechowicz (1982) have noted some general ecological differences between naturally occurring and agricultural populations of X. strumarium. In southwestern Ontario, these populations differ in the size of fruits (personal observation); beach populations tend to have larger fruits than agricultural populations. Zimmerman and Weis (1983) have investigated the effects of fruit size on germination and seedling growth for the agricultural population at Harrow. Extending this work to fruits from the beach population would be of interest. Further consideration of ecotypic differentiation of the populations could be undertaken in a common garden situation. This would allow a separation of enviromental and genetic effects on growth and morphology and would be a first step to a better understanding of ecological differences between the two populations.

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