A RESOURCE THEORY OF SELF-THINNING IN PLANT POPULATIONS

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The relation between mean individual weight w and growing density p in self-thinning plant populations has been given in the literature by the relation $w = kp^{-3/2}$. This -3/2 thinning "law" of Yoda et al. (1963) is seen here as a constraint on growth in the population caused by limitation of some resource. The property of the resource which defines the widely observed value of 3 in the -3/2 exponent is its dimensionality, its distribution in volume (three-dimensional space). Generalization of this interpretation explains thinning at low light levels where the limiting resource (light) is distributed over area (two-dimensional space). Such thinning has been observed to give an exponent of -1 (= -2/2). Further generalization explains the occurrence of the constant yield relation in which populations of a given age have a constant yield per unit area over a wide range of growing densities. The idea of the dimensionality of the exploited resource is extended from whole plants to plant parts, and constraints on plant biomass allocation in the form of allometric relations are predicted. The theory differs from all previous work on thinning in emphasizing the constraining role of a limiting resource and in proposing that the dimensionality of the limiting resource has quantitative implications. Plant geometry is seen as a consequence, not a cause of the -3/2 thinning pattern.

Predictions based on the theory which are corroborated by extant literature include: occurrence of -3/2 thinning in a wide variety of

plant species of various morphologies; occurrence of -1 thinning at low light levels; occurrence of the constant yield relation in a wide variety of plant species; the amount of thinning to take place in self-thinning stands of a given age; the slope of the allometric relation between sapwood weight and total tree weight; and the relation between mean individual weight and population density in some animal populations. Other predictions, described here, together with a discussion of experimental manipulations to test them include: reducing the belowground volume should lower the intercept and, under some circumstances, the steepness of the -3/2 thinning line, while a very shallow soil may change the slope to -1; the amount of thinning experienced by a population should depend upon the amount of variability in the size of individuals in the population; multiple species stands may be quantitatively described in terms of life history strategies and the constraints of the constant yield relation and -3/2 thinning; the thinning exponent may be changed if the dimensionality of the limiting resource is altered.

Experiments using leaf mustard, swiss chard, and buckwheat are reported. Experimental results testing key predictions of the theory corroborate that: a reduced level of fertilization lowers the position of the -3/2 thinning line (lowers the value of k); a reduced light level lowers the position of the -1 line of constant yield; a reduced light level lowers the steepness of the thinning line; a shallow soil at least lowers the position of the thinning line and perhaps also its steepness; thinning in mixed stands of species with comparable growth form is regular when the species identity of individuals is ignored; the allometric relations of roots and leaves on total plant weight are constrained by the dimensionality of the resources these organs exploit.

A RESOURCE THEORY OF SELF-THINNING IN PLANT POPULATIONS

A Thesis

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of Cornell University in Partial Fulfillment

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by

Richard Edward Furnas

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BIOGRAPHICAL SKETCH

Richard Edward Furnas was born 10 August 1952. His interest and
fascination for science generally and biology in particular were strongly
supported by his parents, Judith Louise O'Shea Furnas and Dr. Thomas
Coleman Furnas, Jr., and extend back to his earliest memories. Special
science projects in elementary school, and science fairs led in junior
high and high school to participation in the Future Scientist's program
at the Science Museum in Cleveland. He left high school from his junior
year to come to Cornell as a biology major, placing out of the first year
of biology. Four years at Cornell saw him a National Merit Scholar
majoring in biology with a concentration in ecology, and graduating in
1973 B.A. cum laude with distinction. From Cornell he went to Alaska
where he gained first hand experience in subarctic and wilderness living
while earning in 1975 master's degrees in both biology and mathematics
at the University of Alaska at College. After a brief return to the
lower forty-eight he went to West Germany in the fall of 1975 to attend
the Goethe Institute in Staufen on the edge of the Black Forest in
southern Germany. There he studied the German language intensively for
six months after which he went to Göttingen where he audited courses in
ecology, geology and mathematics at the University. He returned to the
United States in 1976 to commence graduate study at Cornell University of
which this thesis is the culmination. He is now in the process of
founding the Scarab Institute for creative resource management, an

Ithaca-based not-for-profit organization dedicated to scientific research and education in environmentally benign technologies and attitudes toward the management of energy, material, and human resources.

To Dr. Robert H. Whittaker

whose sublime influence on the paths I have taken

is greater than he knows.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

1. INTRODUCTION

Space has long been used as an organizing principle in defining how organisms interact. Notions of space have ranged from extremely informal observations about individuals displacing one another in territorial disputes to the elaborate and abstract ideas of multidimensional resource spaces used to describe the MacArthur or Hutchinsonian niche (Hutchinson 1958). Space is also the important organizing principle of this thesis. How a limiting resource is distributed in space can be seen as an important property allowing a synthesis of three important parts of plant population biology:

1) the -3/2 thinning "law," which states that self-thinning in overcrowded stands results in mean plant weight being proportional to the -3/2 power of the growing density p.

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

2) the constant yield relation which states that yield (biomass) per unit area Y_t after a period of growth t, is constant for a wide range of growing densities.

$$Y_t = k \quad \text{or equivalently, since } w_t p_t = Y_t$$

$$w_t = kp^{-1}$$

3) allometric growth relations among plant parts.

A theory is developed which integrates the above ideas and provides motivation for the experiments which were performed. The thesis is

organized as follows:

1) Introduction

2) Theory--wherein the theoretical developments and their relation to previous work are discussed.

3) Experiments/Methods

4) Results/Discussion

5) Conclusions--a summary of the principal results and suggestions for further work.

2. THEORY

Grau, teurer Freund, ist alle Theorie
Und grün des Lebens goldner Baum.

--Goethe, _Faust_

2.1. Background

Yoda et al. (1963) observed that in plant stands of a single species of uniform age, there is a close mathematical relationship between the average size of the individuals in the stand and the number of individuals per unit area, once growth has progressed to the point that some individuals are dying due to crowding. In its simplest qualitative terms the population begins with many small plants and ends with just a few large ones. The mathematical form of the relationship is:

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

or equivalently $\log w = -3/2 \log p + \log k$

where	units
w is the mean weight of an individual in the population	g/indiv.
p is the number of plants per unit area (growing density)	$\#/m^2$
k is a constant	g/m^3

These units will be used throughout the thesis.

Although it is not surprising that there should be an inverse relationship between size and growing density, the regularity with which an

3

exponent close to -3/2 appeared in the fitted data of Yoda et al. is
remarkable. Subsequent work has shown the -3/2 thinning "law" to prevail
in about 70 species of plants (summarized in White 1975, 1979) ranging
from cultivars to wild species, annual to perennial, herbaceous to woody.

Although much empirical work has been done, some of it mathemati-
cally quite elaborate though largely descriptive (Hozumi 1977), the
biological theory has been weak. In their paper, Yoda et al. (1963)
observed that the exponent -3/2 suggests a conversion from area to
volume. They interpreted the area involved to be the projected canopy
area of the individual plants, which, in crowded stands, fills the area
of the stand. This is an unworkable concept in crowded stands because of
mutual shading. Similarly, the volume which they proposed to be impor-
tant was the volume of the plant itself. To the extent that plants grow
in a geometrically similar fashion--change only in size and not in shape
--the -3/2 power relation should obtain (given a roughly constant spe-
cific gravity of the plant tissues). This derivation yields the -3/2
relation exactly but, as Yoda et al. pointed out, plants simply do not
grow maintaining a constant shape. The theory elegantly produced the
right answer but a basic (and seemingly necessary) assumption was known
to be false. Perhaps as a result of this failing relatively little was
done to pursue the theoretical suggestions relating to plant shape except
to observe that -3/2 thinning was a more robust phenomenon than could be
predicted by existing theory (Yoda et al. 1963).

Different workers have taken several approaches to reconciling the
theoretical problems of plant form and crown projection. In 1970, White
and Harper, in discussing further empirical work relating plant size and

growing density, suggested that the notion of projected canopy area was not necessary. Drawing on the earlier work of Clark and Evans (1954) on nearest neighbor relations in plants, they concluded that the area involved, instead of being an average projected canopy area, could be taken as an average area per plant (the reciprocal of plants per area--the growing density) without losing the generality of the derivation. Other workers (Goodall 1960, Ross and Harper 1972) have also discussed relations based on the cube of a distance to a nearest neighbor. Mohler et al. (1978) used the -3/2 relation in association with suggestions from Kira et al. (1956) about plant allometry to document the failure of the theoretical model to satisfy its immediate corollaries. Mohler et al. (1978) suggested that an interplay of stand structure and allometry gives rise to the -3/2 "law," effectively removing the -3/2 relation from any theoretical basis whatsoever. Miyanishi et al. (1979) propose an alternative theory which attempts to accommodate different growth forms. It assumes that some geometric regularity in plant shape is necessary to achieve the numerical regularities of thinning. The regularity need not be complete preservation of plant shape but may be extended to include constant cross-sectional shape with extension growth or similar projected shape with constant height. The model thereby predicts different slopes for different growth forms. As will be shown later, their assumption is not necessary. Furthermore, the work by Gorham (1979) shows that both the exponent and the intercept of the thinning line are independent of plant morphology.

Before progressing to the derivation of the -3/2 thinning relation, some mathematical preparation is desirable. In the course of the thesis

I make extensive use of the log transformation. Such transformations are sometimes perceived as deformations of the data which may hide important variability, which may make purported relationships appear better than they really are, or which are done purely for convenience, with no biological justification whatsoever. My use of the log transformation asks a question of the data and portrays them in a manner which allows visual inspection of a graph to discern the answer. The -3/2 thinning "law" produces a curve when plotted on linear graph paper and it is difficult to assess by eye how well the curve describes a set of data. Use of the log transformation however renders the relationship a straight line of specific slope--a relation readily perceived by eye (Fig. 2.1). Because of the properties of the logarithm, the shape of the curve does not change with changes in units of measurement (grams, pounds, kilograms, square meters, hectares, etc.) and much information involving proportional inter-relationships among the data may be read directly from the graph without recalculating or replotting the data.

While extensive use of the log-log graph has been made in the literature, the use of regression analysis (e.g., Yoda et al. 1963, White and Harper 1970, White 1975) and Principal Components Analysis (Mohler et al. 1978) has clouded the simple biological interpretations possible for certain lines of specific slopes. Starting with the initial thinning equation:

$$w = kp^{-3/2} \quad \text{or, in the log-transformed domain} \quad \log w = \log k - \frac{3}{2}\log p$$

$$\text{and rearranging we get:}$$

$$wp^{3/2} = k \qquad\qquad \log w + \frac{3}{2}\log p = \log k$$
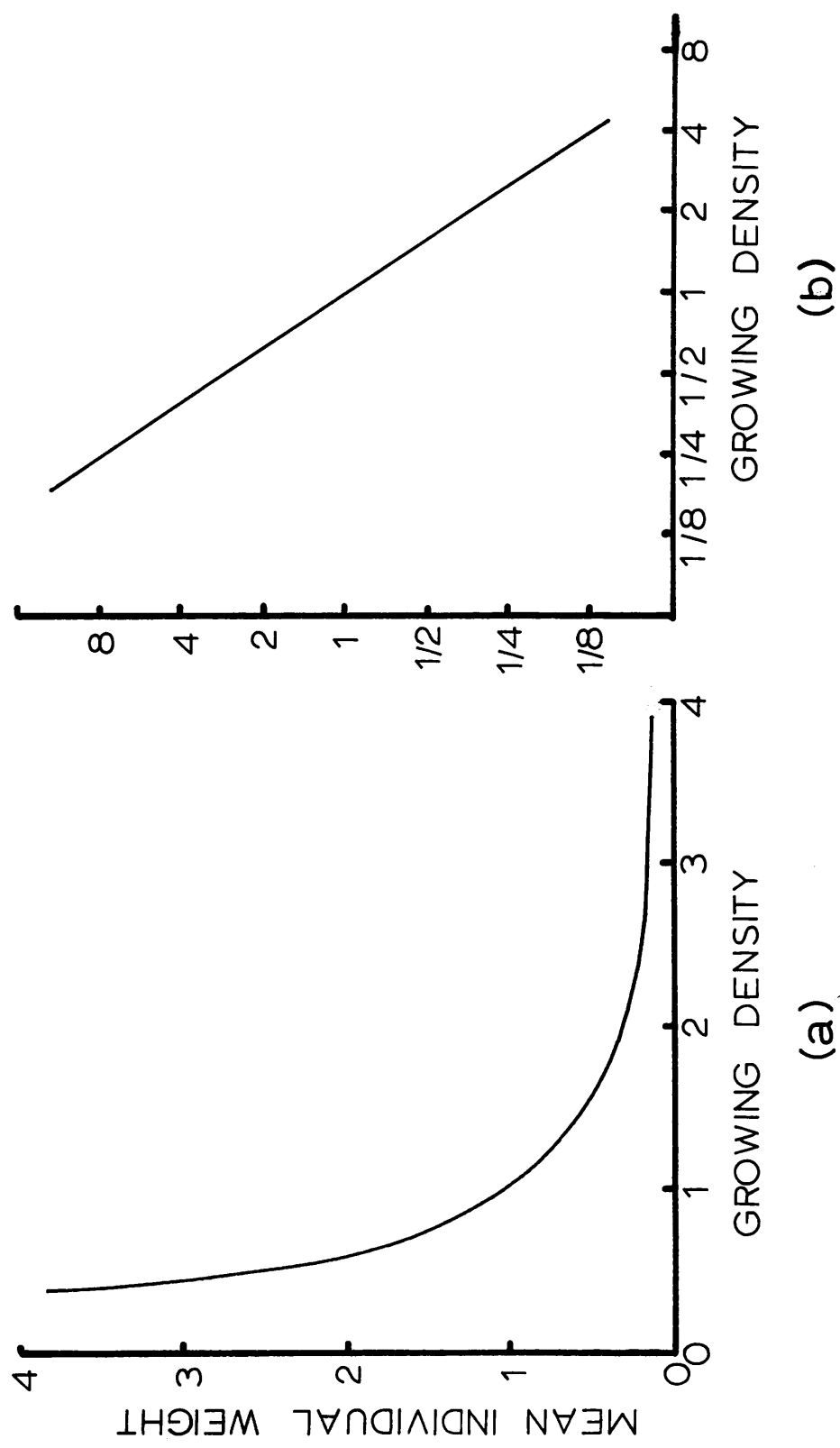
Fig. 2.1. The relation between mean individual weight w and growing density p given by $w = kp^{-3/2}$ in self-thinning populations. a) linear axes; b) logarithmic axes.

where k is constant with units of mass/volume. A line of slope -3/2 in the log-log graph of mean plant weight against growing density corresponds to the line of constant mass per unit volume.

In an analogous fashion, if we replace the -3/2 with a -1 we have:

$$w = kp^{-1}$$
$$or$$
$$wp = k$$

$$\log w = \log k - \log p$$
$$or$$
$$\log w + \log p = \log k$$

But wp is weight per individual times individuals per area and so in this instance k has units of mass/area. A line of slope -1 in the log-log graph corresponds to a line of constant mass/area--the yield (biomass) per unit area of the population is constant. The constants in these two cases which have such natural interpretations will be distinguished by the subscripts 3 and 2 signifying mass per unit volume (3 dimensions) and area (2 dimensions) respectively. When the associated exponent is unspecified, or is not one of these special cases, the constant will be written without subscript.

Note that the intercept (with p = 1 and therefore log p = 0) is the logarithm of the constant, be it k_3 or k_2. The value of k may be read directly from the graph. Note further that given a pair of lines of slope -1, for example, the one corresponding to the higher yield is the upper of the two lines, and the ratio of their yields is the exponential of the difference between the two values of k_2.

Other lines of interest are lines of zero slope, which correspond to constant mean weight per individual, and vertical lines which correspond to a constant growing density (Fig. 2.2).
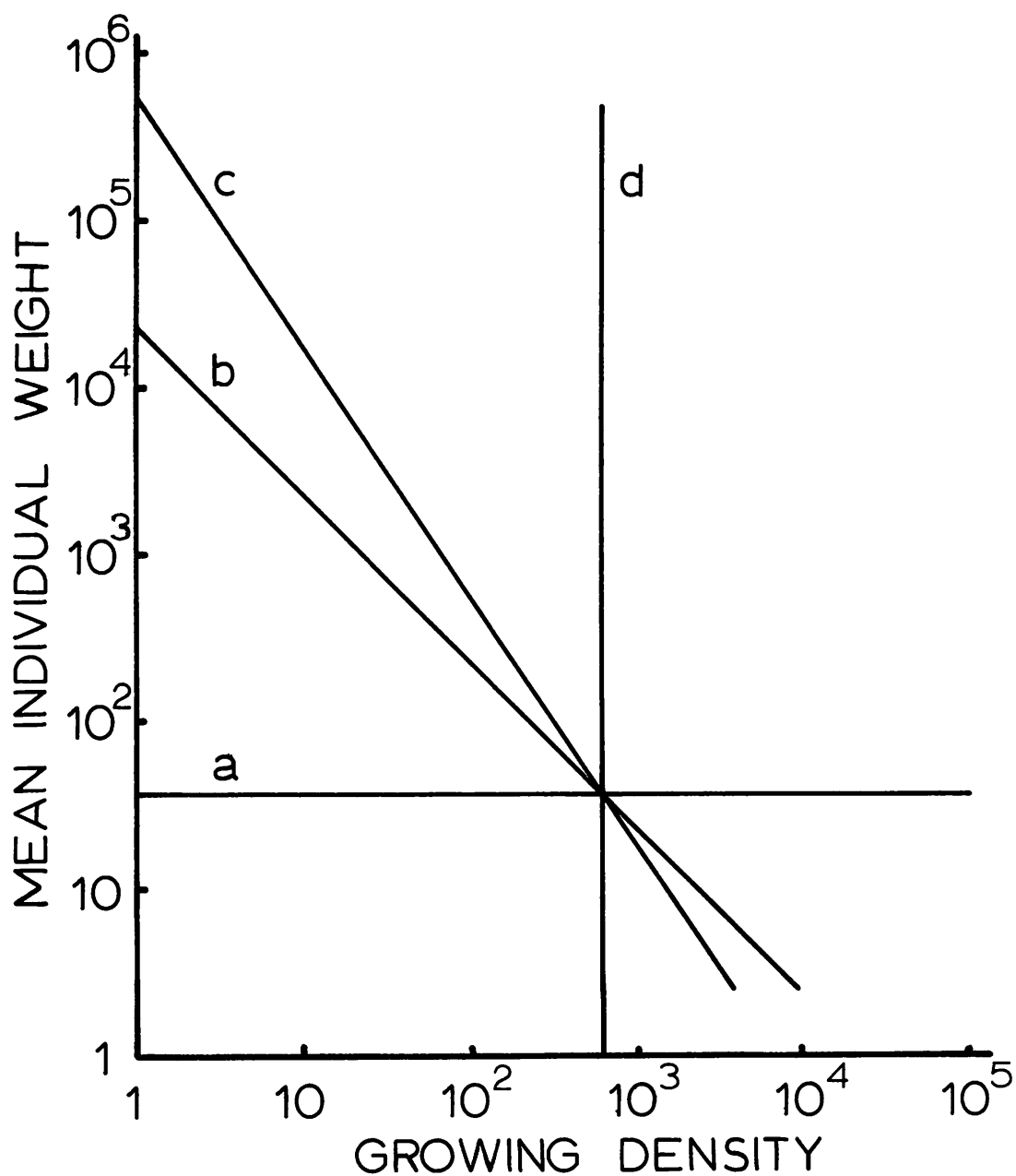
Fig. 2.2. Lines in the log-log domain of mean individual weight w
and growing density p with natural interpretations:
  a) constant mean individual weight (slope = 0)
  b) constant yield per unit area (slope = -1)
  c) constant biomass per unit volume (slope = -3/2)
  d) constant growing density (vertical line)

2.2. The Origin of -3/2 Thinning

As already discussed, existing theories to explain -3/2 thinning rely on a geometry of plants which is not observed. More importantly, there is no suggestion as to why some particular geometry should be adopted by plants. A classical view of plant growth limitation (Liebig 1840, Blackman 1905) would hold that limited availability of some resource limits or constrains the amount of growth (in terms of growing density and biomass) which can be achieved in the population. I propose that the fundamental property of a limiting resource which results in the widespread empirical observation of -3/2 thinning is its distribution in volume. If the weight a plant can achieve is proportional to its resource base (and therefore the volume from which the resource is drawn), -3/2 thinning according to the equation $w = k_3 p^{-3/2}$ results.

In summary we may consider -3/2 thinning to be the consequence of the following three approximations which are considered to be independent of time and growing density.

1) The biomass w of the plants is proportional to the amount of limiting resource exploited.

2) The amount of limiting resource exploited is proportional to the volume in the environment accessible to the plants.

3) The volume accessible to the plants is proportional to $p^{-3/2}$.

The three approximate relations combine to insure that k_3, which has units of weight of plant per unit of volume in the environment, will be constant. The third approximation is consistent with the following sequence of mathematical transformations (stated here with a running example to emphasize their interpretation):

p is the growing density of the plants. It is directly measured and has units of plants per unit area.

e.g., 9 plants growing on $4m^2$ yield a value $p = 9/4$ plants per m^2.

It follows that on a per plant basis:

p^{-1} has units of area

Thus there is an average of $4/9$ m^2 for each plant,

$p^{-\frac{1}{2}}$ has units of length and

$2/3$ m is an index of interplant spacing, and its cube,

$p^{-3/2}$ has units of volume

$8/27$ m^3 is a proportionate index of the volume in the environment accessible to each plant.

Thus from the above three approximations we have $w = k_3 p^{-3/2}$. (Note here also that approximations 2 and 3 imply a dependence of the value of k_3 on the definition of individual, which in cloning populations for example may be vague, despite the absence of explicit mention of "individual" in the units of k_3.)

The principal departures from earlier theories are two:

1) -3/2 thinning is recognized as a constraint imposed on a population by limitations on the exploitation of a resource.

2) The empirical invariance of the -3/2 exponent is a consequence of a conversion from an area to a volume, both of which are in the environment. Neither the area nor the volume is directly related to structural features of the plants as postulated by earlier workers (Yoda et al. 1963, White and Harper 1970).

In the remainder of the thesis, these distinctions will be shown to allow a credible and testable basis for -3/2 thinning. They will also be shown to admit generalization, allowing a theoretical basis for understanding (1) some exceptions to -3/2 thinning, (2) the constant yield relation, and (3) some aspects of plant allometry (and hence resource allocation).

2.3. An Exception Leads to the Constant Yield Relation

The volume (3 dimensions) in which a limiting resource is distributed is thus seen as an important property of the resource (being the source of the "3" in the -3/2 thinning law). Are there resources which are distributed over an area (2 dimensions) giving rise to a -2/2 or -1 relationship rather than a -3/2 relationship? Light is a resource with a strongly two-dimensional character. The flux of light is described on a per area basis (watts/cm^2) and although there is a three-dimensional character to its exploitation by leaves in a canopy, the available resource is ultimately determined by the area over which the light is being intercepted. White and Harper (1970) reported that data from thinning populations grown at low light intensity by Hiroi and Monsi (1966) were better described by a slope of -1 than by a slope of -3/2. The occurrence of the -1 slope for low light intensities was a principal anomaly reported by White and Harper and has had no theoretical explanation. From the present development it can be viewed as an expression of the same underlying process as -3/2 thinning except that the important limiting resource is distributed over area rather than in a volume. As observed above, a line of slope -1 is a line of constant yield per unit

area. Thus, -1 thinning constitutes a population of constant yield as it ages; its biomass is constant; it is at compensation point, unable to increase its biomass further.

There is a common observation particularly well known from the agricultural literature (Hozumi et al. 1956, Wiley and Heath 1969, but see also Collins 1976 for a non-agricultural example) called the constant yield relation. In stands grown at different densities, the yield per unit area after a given period of growth tends to be constant over a wide range of densities. Although the data are usually not so portrayed, such populations must lie along a line of slope -1 on the log-log graph of mean plant weight vs. growing density.

We may now apply the basic theory to interpret this observation. Just as in the earlier discussion a line of slope -1 was seen to imply that a resource distributed over area constrains the growth of a thinning population, in populations which have grown for a specific period of time a line of slope -1 implies that a resource distributed over area constrains their growth. As before, light comes to mind as such a resource, suggesting that the limitation on the growth achieved by the plants is a consequence of light (Jennings and Aquino 1968) and the -1 form of the relation is due to light's two dimensionality.

A clear distinction must be made between two classes of curves:

1) In the classical context of thinning, a single population is observed as it undergoes mortality. At successive points in time, the population is examined and measurements taken to determine growing density and mean plant weight. When graphed on log-log paper, such points tend to lie alone a line of slope -3/2 (-1 for low light) (Line A, Fig. 2.3).
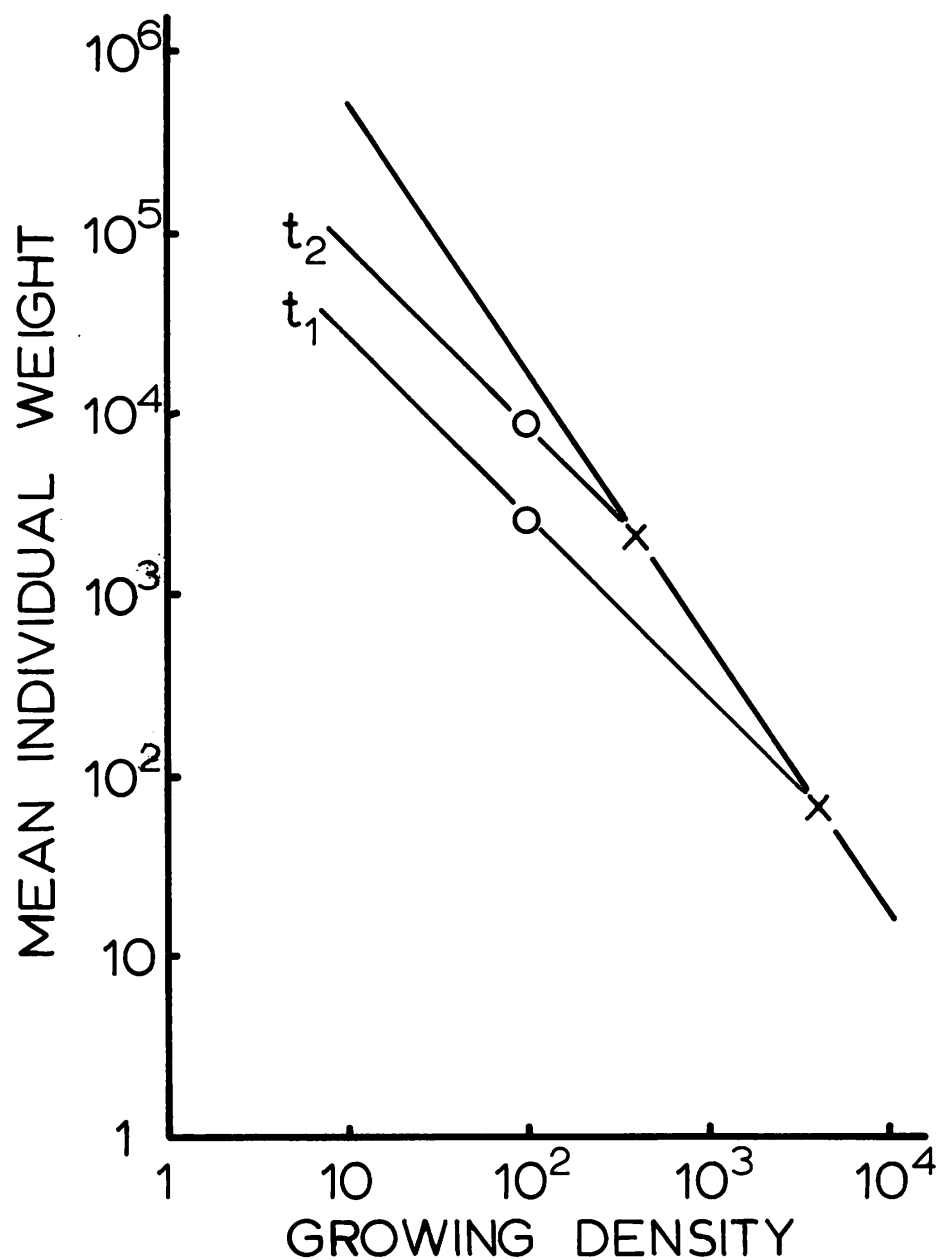
Fig. 2.3. The log-log relation between mean individual weight w and growing density p in two populations of different initial growing densities high (x) and low (o), sampled at two times t_1 and t_2. Lines of constant yield for times t_1 and t_2 as well as the -3/2 thinning line are shown. (simulated data)

2) In the case of the constant yield relationship, the points placed on
   the graph come not from the same population at successive points in
   time, but from different populations having different growing densi-
   ties at the same point in time (Line B or Line C, Fig. 2.3).

It is important to keep the distinction in mind when applying the
theory to the interpretation of observations: If we consider the basic
approximation, made by the theory, that the size (weight) of the organism
is a proportional response to its resource base, the common ground shared
by the two classes of curves emerges: In -3/2 thinning, a population is
being constrained by some finite resource distributed in space (volume),
say nutrients in the soil, and that resource (volume) is being parti-
tioned among the individuals in the population. In the constant yield
relation, we use the same words and say that the populations are being
constrained by some finite resource distributed over area (say light) and
that resource is being partitioned among the individuals in the popula-
tion. The importance of the distriction, however, is that at some later
time the population in the constant yield relation will lie along a
different -1 line: The yield will have increased because of the addi-
tional growing time, or, in the view of the theory, because of the addi-
tional light, the additional resource, to which the population has had
access.

The constant yield relation may now be integrated with -1 thinning.
Over a wide range of densities, the constant yield relationship tells us
that the populations lie along lines of slope -1 with successive points
in time producing successively higher lines corresponding to progres-
sively greater yields. As growth proceeds, the additional percent yield

accrued during a given time unit may be expected to decrease as the total maintenance costs of the accumulating biomass increase, and the successive lines of slope -1 become closer and closer together (Fig. 2.4). When the light is so limiting that the maintenance costs equal the productivity possible from the incoming light, the population has reached the compensation point, and yield stabilizes--the yield from the population can no longer increase. Whereas up to now the discussion has dealt with the population averages of weight and density, the importance of individual variation in the population now begins to manifest itself. Since further yield increases are precluded by the light level, the growth in the population is constrained to one of two alternatives:

1) Growth may stagnate completely, maintaining the size and growing density it has, or

2) Growth may continue in some individuals at the expense of others, reducing population density through mortality and giving rise to -1 thinning.

Since there are always differences among individuals in a population, we may expect alternative (1) above to be relatively rare although the suggestion arises that relative stagnation in such populations may arise if individual differences are small (see also sections 2.6 and 2.7).

We may now consider how the constant yield relation can interact with -3/2 thinning itself. Note first that if a population is to exhibit -3/2 thinning, its yield must be increasing with time: for a given population on the -3/2 line, it also may be thought of as lying on a line of slope -1. If we look again at the same population at some later time and discover that thinning has proceeded, the population lies farther up on
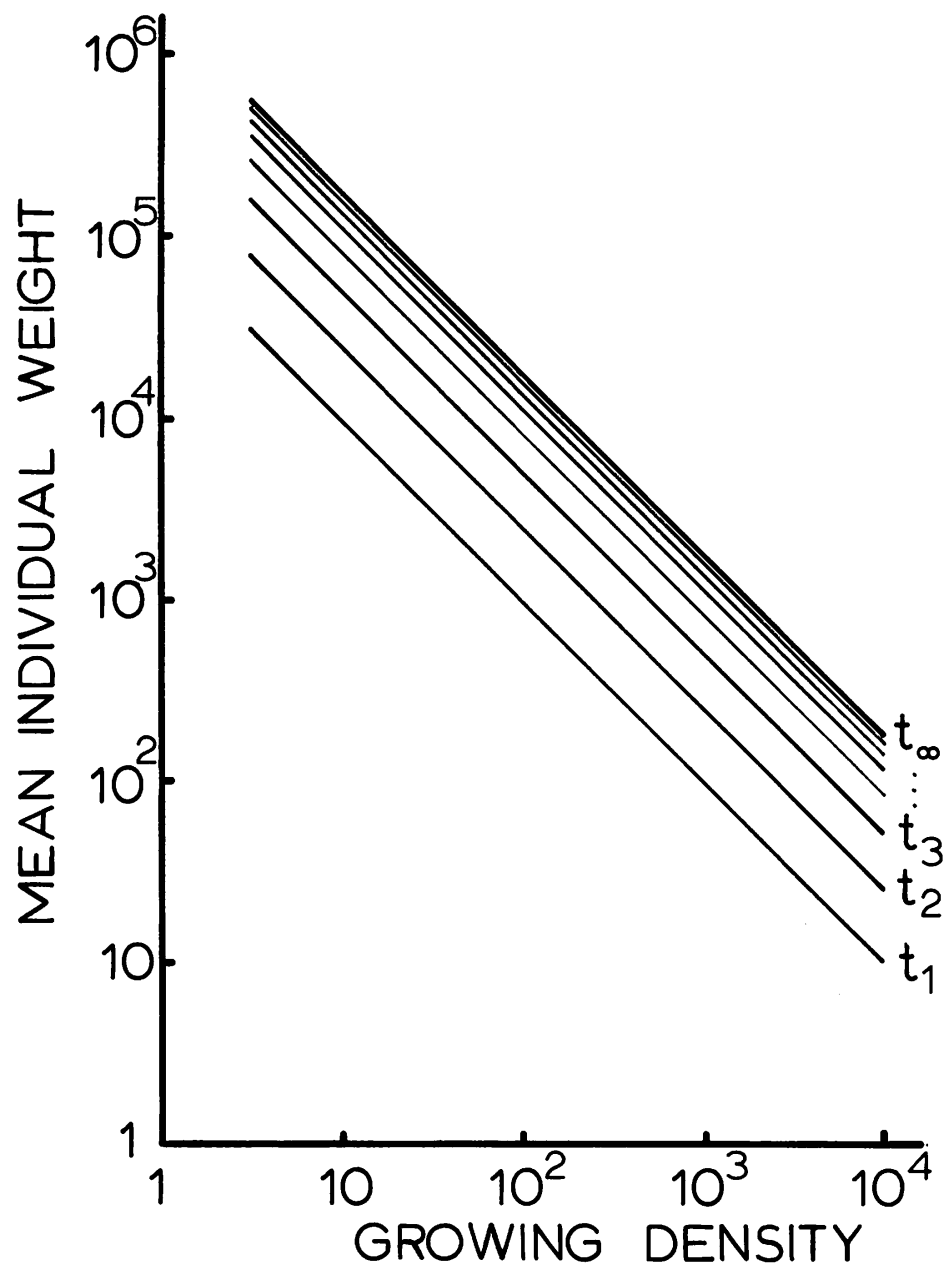
Fig. 2.4. The log-log relation between mean individual weight w and growing density p for populations following the constant yield relation at any given time t_1, t_2, t_3, and approaching compensation as they mature. (simulated data)

the original -3/2 line and therefore on a higher line of slope -1; the yield has increased. How is such a population different from one undergoing -1 thinning? Something is limiting the population or mortality due to crowding would not occur. The constant yield relation may even extend to include such thinning populations. The difference lies in the limiting resource being based on volume rather than area. In populations undergoing -3/2 thinning, the differences among individuals within the population may still give rise to some individuals which grow larger at the expense of others. Note that the proximate cause of mortality to individuals need not be the constraining resource. They may die from various causes but the constraining resource limits the relation between size and growing density among the survivors. Once again, however, there is the suggestion that individual differences, especially differences in size, play an important role in the dynamics of the thinning process.

White and Harper (1970) observed that in stands of forest trees there is a switch from -3/2 to -1 thinning as the trees matured. The stand may be seen as having undergone -3/2 thinning, accumulating ever more biomass which is increasingly expensive to maintain. When the maintenance costs equal the productivity, the stand is at compensation and the subsequent biomass remains constant as further mortality occurs.

Thinning has often been referred to as a type of density-dependent mortality (e.g. White and Harper 1970, White 1975, Mohler et al. 1978). While it is clear that density is involved in -3/2 thinning, there is no useful sense in which mortality is density dependent. The mortality is related to three parameters only one of which is growing density (others being (2) time and (3) mean plant weight). For a given density no

mortality will take place until the mean plant size has reached the level determined by the -3/2 thinning line. Thus mortality is initially independent of density, there being no mortality. Once thinning has begun the per capita mortality rate can also be density independent. If motion of the population along the thinning line is at a constant rate, for example, the instantaneous per capita mortality rate is constant and also independent of density. The pattern of mortality in thinning populations is therefore only partially related to density and references to it as density-dependent obscure the other important parameters.

2.4. Thinning in Animals

The derivation of the -3/2 power law presented above contains nothing which requires that it refer to plants. The emphasis on the interaction between organism size, growing density, and a limiting resource could apply to any organism although it is most interesting when the species considered can have a wide range of body sizes. In a population of organisms having a comparatively fixed body size, the population number is an adequate representation of the resources the population has exploited. The -3/2 relation in effect allows generalization of a notion of carrying capacity in terms of numbers, to one in which individual size and numbers may vary in a complementary fashion, while the intensity of resource exploitation remains unchanged.

Data from Brook Trout, Salvelinus fontinalis (McFadden 1961) in Lawrence Creek in central Wisconsin, U.S.A. are shown in Fig. 2.5a. The model of -3/2 thinning in this population is a remarkably good summary of the principal trend, accounting for 97% of the variation in the data.
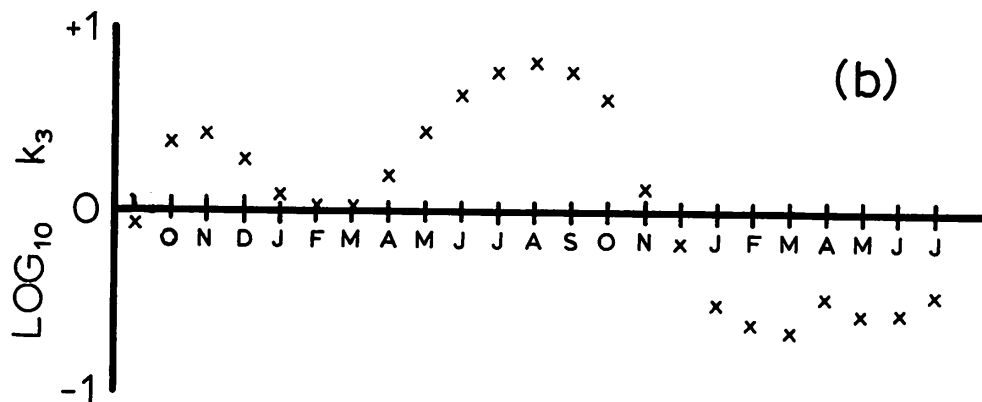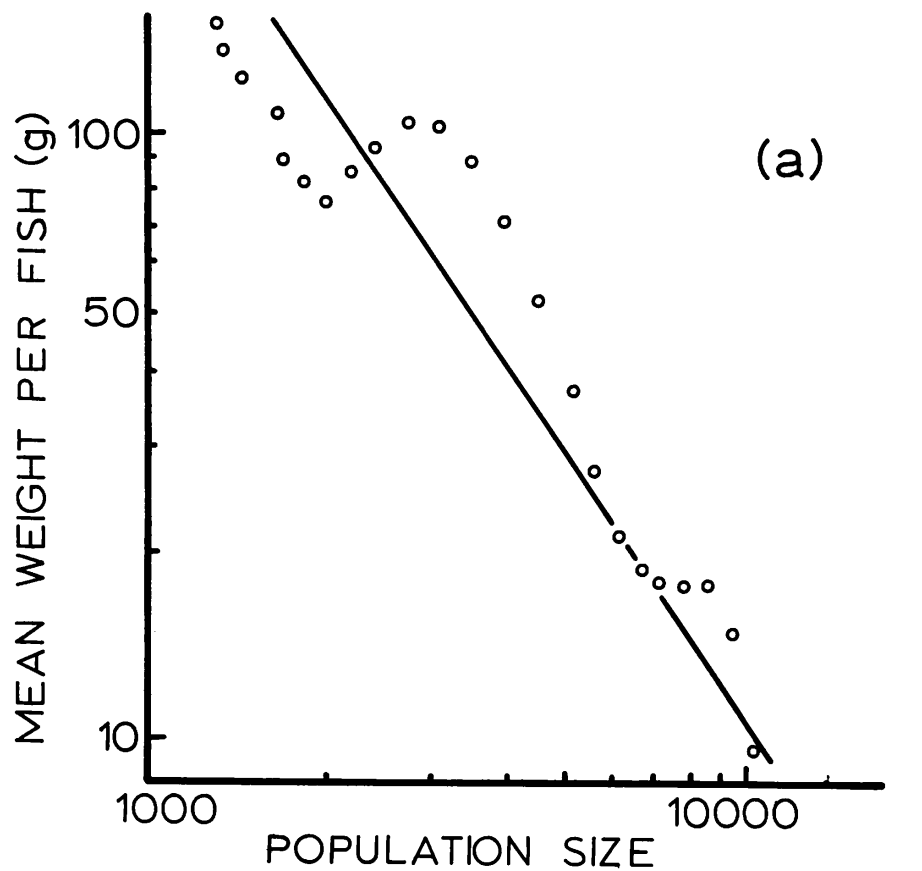
Fig. 2.5. (a) The log-log relation between mean individual weight and the size of the trout population in a Wisconsin stream (data from McFadden 1961). A line of slope -3/2 is shown. (b) The variation around the -3/2 line (expressed as log k_3 in relative units) as a function of time.

The trout data do show a variation around the line which seems to be related to the seasonality of food and growth relations. Movement of the population beyond the prevailing -3/2 line implies that conditions are good, either the population is more efficient at exploiting the resource (space) available to it, or the resource base is richer (in a sense these two possibilities are equivalent in terms of the effective availability of the resources). Seasonal wandering of the population trajectory along the -3/2 line also incorporates an increasing time lag as the fish get larger--not unexpected since larger body size should buffer the fish better as the environment changes.

The seasonality of response can be examined by looking at the departures from the -3/2 line as a function of time (Fig. 2.5b). What is plotted is the value of $\log k_3$ for the population at a given time (each point may be considered to lie on a line of slope -3/2 giving rise to a value of $\log k_3$ which becomes a measure of the efficiency with which a unit volume of environment has been converted into fish biomass). The actual values are not important here: Although the population itself is ill defined, being a record of censuses in a particular stream expressed as a cohort, and the area is ill defined, stream area, watershed area, or some other basis might be appropriate, the choice of definition is irrelevant to the given interpretations since the possibilities would only slide the curve along the $\log p$ axis without changing either its shape or the magnitude of the changes in $\log k_3$ for specific points.

The foregoing observations and interpretations suggest a new insight: The value of k, or its logarithm, may be interpreted as an index of the favorability of the site in which the population is growing.

The implication for plants is that the value of k may be an expression of soil fertility or inherent efficiency of exploitation of the environment by the organism.

Examination of a group of sexually reproducing experimental planaria populations (Boddington and Mettrick 1977) provides further insight. Populations were kept in aquaria of different sizes and fed tubificid worms in different amounts to compare food and space requirements. The populations were followed through several generations and biomass and numbers were measured. Fig. 2.6 is derived from data of one treatment having food and space provided in amounts comparable to those found in natural populations. The population clusters along a line of slope -1, looping down and back with each reproductive period. The slope of -1 suggests a two dimensional limiting resource for the population-- perhaps the tubificid worms on the substrate. In another population the food supply was doubled partway through the series of observations. The pattern was disrupted followed by a return to a thinning line displaced upward in response to the enhanced resource base (Fig. 2.7). The upward displacement, corresponding to a higher biomass per unit area, is another suggestion that the position of the thinning line may be a reflection of the quantity of the resource in the space being exploited. It is also interesting to note that the thinning line is displaced by about log 2 indicating a doubling of the population biomass following the doubling of the food supply. Mere examination of population density presents no such clear picture.

If, as observed above, a population falls away from the thinning line as reproduction begins, the question is raised of how efficiently

23
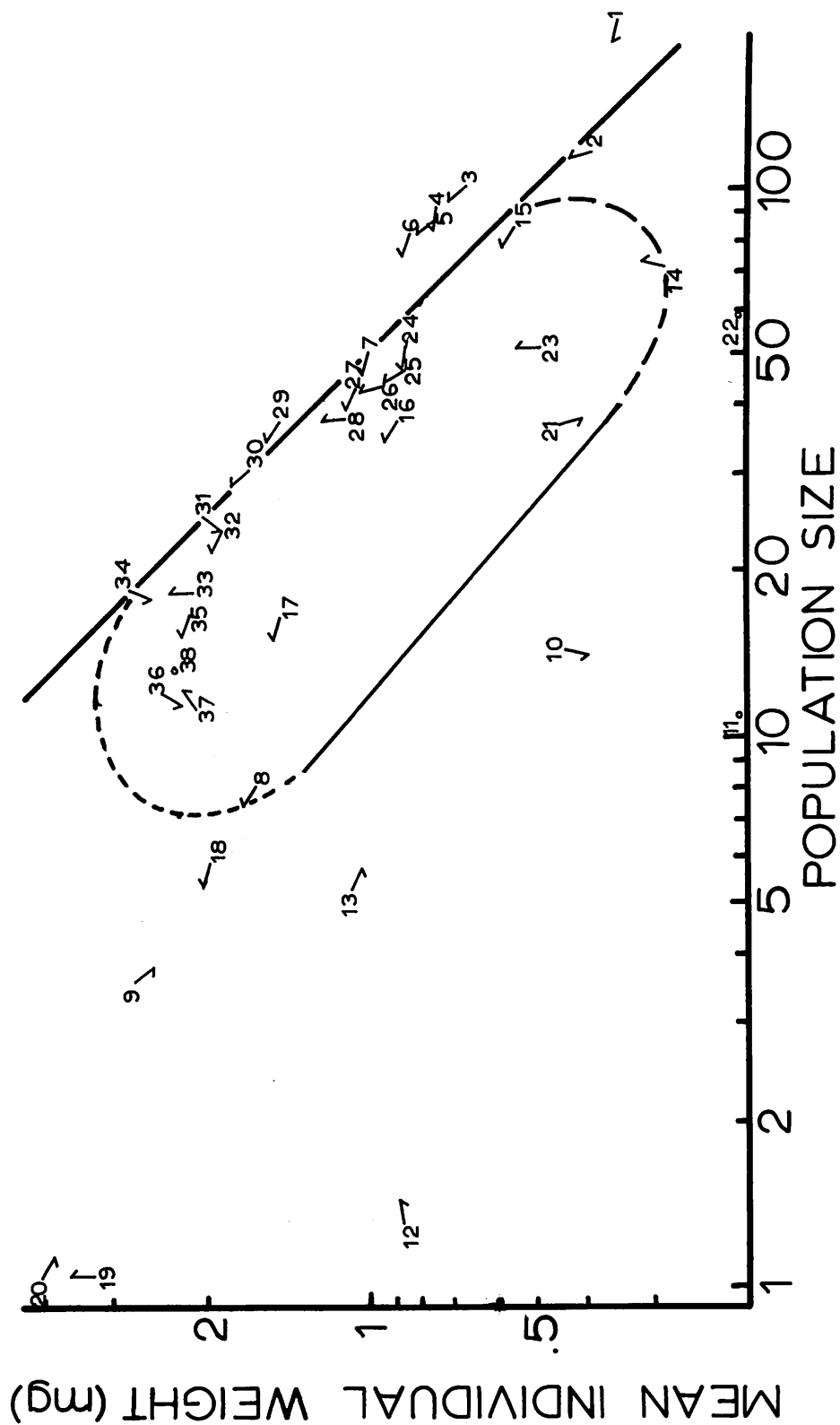
Fig. 2.6. The log-log relation between mean individual weight and population density for a planaria population. Numbers show population age in months, arrows show the direction the population moved in the subsequent sampling period. A line of slope -1 is shown. Also shown is a loop representing preparation to reproduce (---), reproduction (———); and return to the thinning line following reproduction (— —). (Data from Boddington and Mettrick 1977)
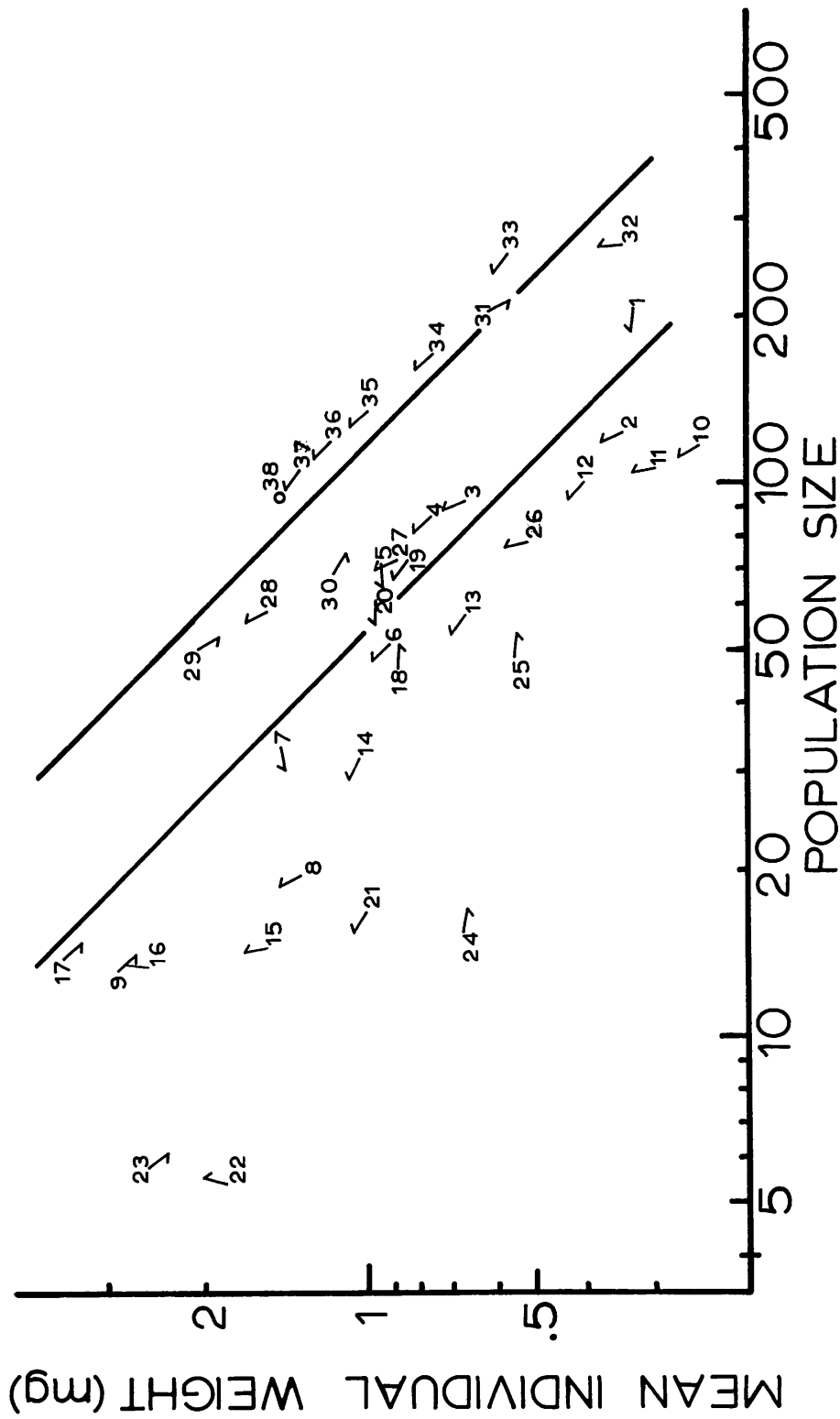
Fig. 2.7. The log-log relation between mean individual weight and population density for a planaria population in which the food supply was doubled midway through the experiment. Numbers show population age in months, arrows show the direction the population moved in the subsequent sampling period. Two lines of slope -1 are shown, displaced from each other by an amount corresponding to a doubling of the population biomass.

it may turn its resource into biomass. Throughout the period of observa-
tion, the resource base was being maintained at a fixed level so changes
in the resource base itself cannot account for the shift; rather it must
be a response by the organism, relating to its reproductive phase. Some-
how the planaria must be less efficient at converting food into biomass
at this time. This does not necessarily mean that their efficiency at
using resources has fallen. It is quite possible that they are using
nutrients to produce small units of biomass having disproportionately
high resource requirements--propagules. If biomass is no longer propor-
tional to the resource base we should expect to observe a substantial
but understandable departure from the simple thinning relation.

2.5. Exploitation Efficiency, Resource Richness and Dimensional Distribution

Critical to the present theory of thinning is the notion that
limiting resources are distributed either in a volume or over area. How
might that make a difference as plants exploit their environment? Con-
sider light. The placement of a leaf casts a shadow which reduces the
availability of light everywhere in the shadow. The total amount of
resource available is determined by the flux of light and the two-
dimensional area of exploitation. Roots exploiting nutrients in the soil
produce no such shadow effect. Although there may be a zone of depletion
immediately surrounding a root, the presence of a root does not reduce
the availability of nutrients by casting a shadow. The shadow effect is
a qualitative difference between exploitation of two- and three-
dimensional resources.

Some resources may be ambiguous in their dimensionality. Water rains down and typically enters the soil with a distinctly two-dimensional character, analogous to light. Unlike light, however, its availability does not vanish if unused immediately. Once the soil is charged with water, its exploitation in terms of the shadow effect is indistinguishable from that of nutrients. Water stress may thus be expected to produce -3/2 thinning with different values of k_3 for different degrees of water stress. An exception may occur, however, if the soil is never charged with water, as might be expected in some desert environments. Here a significant shadow may exist below the roots of plants with extensive rooting on the surface. Perhaps water can give rise to -1 thinning in such circumstances. The observation would be particularly interesting because light is surely not limiting in a direct way in such environments.

Nutrients, a three-dimensional resource, can be limiting, since it is common knowledge that adding fertilizer can increase yields. Yet changing the yield implies changing the constant yield relation which was earlier interpreted as a consequence of limitation by a two-dimensional resource. The apparent contradiction may be reconciled by observing that there are two distinct ways to raise the level at which a resource limits a population; either the absolute quantity of the limiting resource or the efficiency of its utilization may be increased. If fertilizer may be seen to increase the efficiency of light utilization, the contradiction is resolved. The validity of this interpretation could be corroborated with evidence from physiology, or indirectly with evidence that manipulation of fertilizer levels can change the intercept

but not the -3/2 slope of the thinning curve. The evidence that light can be strictly limiting in a two-dimensional fashion comes from -1 thinning at low light levels.

2.6 Density Convergence and Yield Convergence

After a period of growth, thinning reduces the ranks of populations to comparable densities ("Density Convergence," Mohler et al. 1978) and a maximum density is approached asymptotically as a function of initial growing density (Yoda et al. 1963). If the constant yield relationship were to hold absolutely, the densities should be identical and correspond to the density at which the -1 line of the constant yield relationship intersects the -3/2 line. This is not quite what Yoda et al. observed, however. They noted that higher initial densities did tend to lie along the -3/2 line but have densities somewhat higher than expected and hence somewhat lower yields. They described this phenomenon with the empirical relation:

$$1/p_t' = 1/p_0 + \varepsilon_t$$

in which p_t' is the observed density at time t in a population which has been thinning; p_0 is the initial population density before thinning; and ε_t the reciprocal of their "asymptotic maximum density."

A similar relation may be derived by considering the biology of the population yield. The empirical observations show the following basic pattern: At low densities the constant yield relation breaks down because plants are too widely spaced to use the available resources; the plants simply cannot grow fast enough. At intermediate densities the constant yield relation holds. At high densities, in populations which

have experienced mortality, the constant yield relation breaks down and total yields are again reduced.

A portion of the anticipated yield at high densities is missing. Was the missing yield never produced or is it merely no longer represented in the living population? If we make the approximation that the missing yield was indeed produced and is attributable to the individuals which have died out of the population the desired result is obtained: If the population has thinned from an initial growing density p_0 to its present growing density at time t, p_t', we may estimate the mass of the dying individuals by integrating along the -3/2 thinning line, since the line provides us with an estimate of their biomass (see Appendix A). Calculation, with an additional term to allow for the possibility that the dying individuals may tend to be smaller (a fraction f of average size) results in the following equation:

$$p_t'^{-\frac{1}{2}} = (p_t^{-\frac{1}{2}} + 2fp_0^{-\frac{1}{2}})/(1 + 2f)$$

or in terms of yield (Y) per unit area (since $kp^{-\frac{1}{2}} = Y$)

$$Y_t' = (Y_t + 2fY_0)/(1 + 2f)$$

which proves to be a weighted average of the yield to be expected without thinning (Y_t) at time t and the initial yield (Y_0) as thinning began. Using the first of these equations we may rearrange it (see also Appendix A) to make a comparison with the empirical expression of Yoda et al. It is equivalent to:

$$1/p_t' = (1/p_0 + \varepsilon_t)(1 + D_t)$$

in which D_t is a multiplicative error term showing the difference between the model of Yoda et al. and the present one. If the dying individuals are less than average size, D is less than $\frac{1}{2}$, giving at most a 50% difference between the present model and Yoda's. The large differences occur when Yoda's model breaks down, namely when the population has reached the thinning line but not yet begun to thin. In this situation $1/p_t' = 1/p_0$ and Yoda's predicted value for $1/p_t'$ is off by ϵ_t. The present model gives the answer which is correct by definition in this limiting case. In general for populations which have thinned to $\frac{1}{4}$ or less of their original population size and for which dying individuals are less than $\frac{1}{4}$ of average size, the two models differ by only about 10% and are asymptotically the same (see also Fig. 2.8).

We may conclude that the present derivation yields a relation comparable to Yoda's in its predictions for thinning populations. For populations which are about to start thinning, it gives a better approximation. The model of Yoda et al. would argue for an initial suppression of yield before thinning began or that thinning itself was not initially -3/2. In fact their graphs of actual data depart from their curves in the direction predicted by the present model (Fig. 2.9).

2.7. Interpretation of the Density Convergence Result

From the expression

$$Y_t' = (Y_t + 2fY_0)/(1 + 2f)$$

we may derive an expression for the maximum reduction in yield in a population undergoing self-thinning. This will occur when the yield at
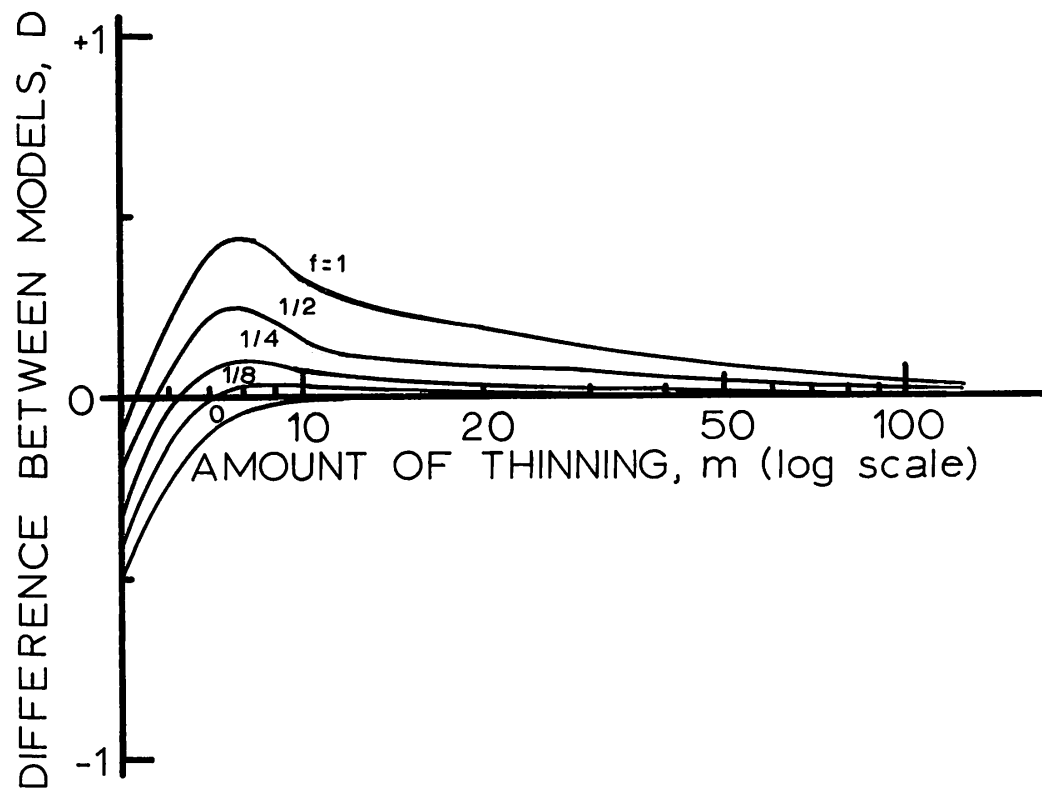
Fig. 2.8. The factor D, the difference between the model for asymptotic maximum density presented by Yoda et al. (1963) and the present biological model, as a function of the amount of thinning which has occurred m [= $(p_0/p_t)^{\frac{1}{2}}$] and the fraction f (= mean size of dying individuals/mean size of individuals in the population).
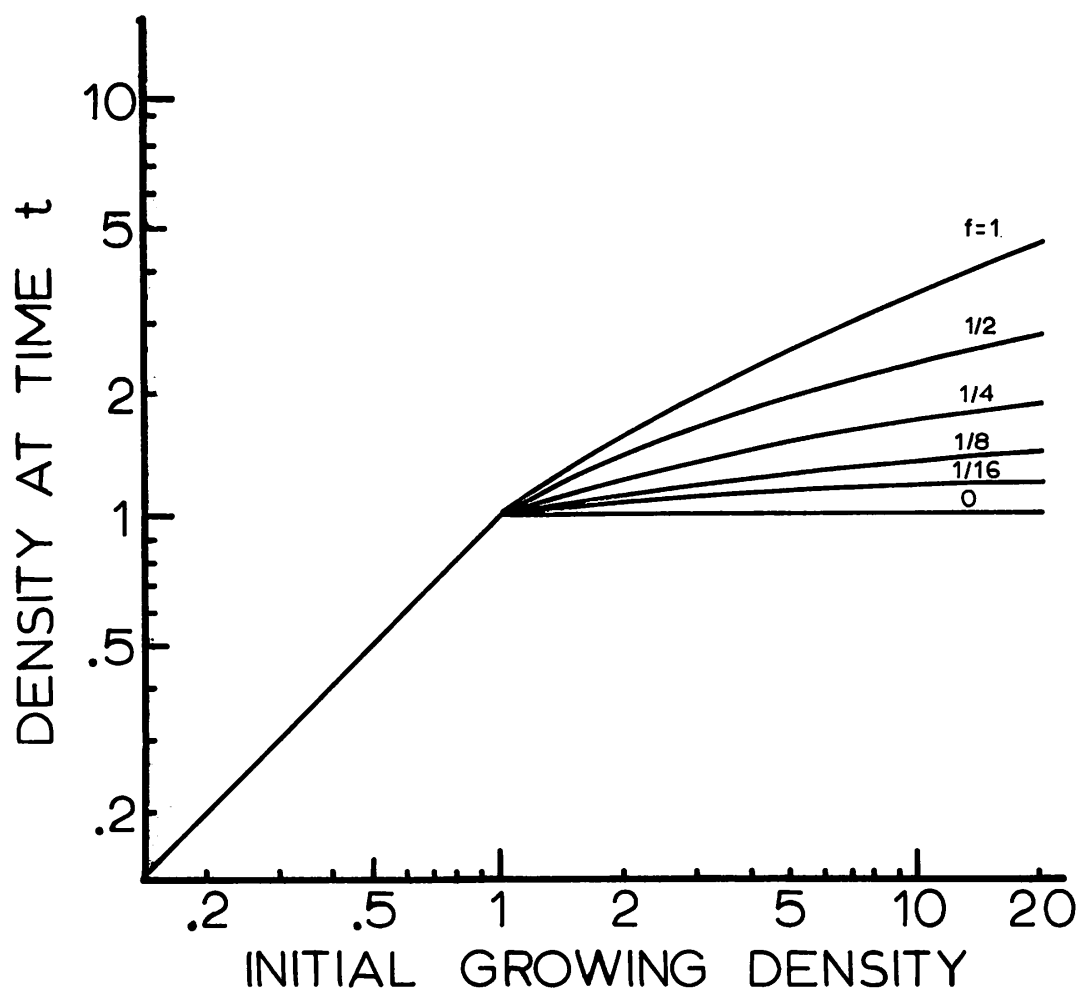
Fig. 2.9. The log-log relation between actual growing density at time t (p_t') and the initial growing density p_0 for various values of the fraction f (mean size of dying individuals/mean size of individuals in the population).

which thinning began (Y_0) is close to zero:

$$Y_t^{min} = Y_t/(1 + 2f)$$

which implies that yields should be no less than 1/3 of the yields (Y_t) to be expected from healthy full stands of low density which have not undergone self-thinning. If the population is such that the dying individuals are consistently a fraction (say 5%) of average size, the yield will be correspondingly closer to Y_t (in this case 90% of Y_t).

For populations which are managed this means that the yield need not be greatly reduced if mortality can be guaranteed to fall on a class of runt individuals. The result suggests a forestry practice of seeding an area with a mixture of wild type and vigorous hybrid strains. The saplings then grow in a crowded situation, producing straight trees of good form, but the process of self-thinning has been engineered into the growth of the stand by providing a less vigorous phenotype--the wild type strain. These die out leaving a nearly pure stand of the hybrid strain. The trees are of good form, yields have not been appreciably reduced, and the entire process takes place without much human intervention after the initial seeding.

A further comparison with the results of Yoda et al. may be made. Using the relationship $Y = k_3 p^{-\frac{1}{2}}$ for points on the -3/2 thinning line with constant k_3, we may derive an expression for the asymptotic maximum density solely in terms of the constants k_3 and f and the yield Y_t:

$$Y_t^{min} = Y_t/(1 + 2f)$$

$$k_3 p_{max}^{-\frac{1}{2}} = Y_t/(1 + 2f)$$

$$P_{max} = \left(\frac{1 + 2f}{k_3 Y_t}\right)^2$$

whose reciprocal is the constant ϵ_t in Yoda's formula. Consider the expression rewritten for comparison with Yoda's formula:

$$\frac{1}{P_t'} = (\frac{1}{P_0} + \epsilon_t)(1 + D)$$

Examination of the units involved shows that for small D the area per plant after thinning is approximately equal to the minimum required area per plant at that stage in the development of the population ϵ_t plus the area per plant present in the population when thinning began $1/P_0$. It is as though the individual plants on average had a certain area when thinning began and as time progressed acquired an additional area which is independent of the amount of thinning which has gone on. The interpretation, which would be exact under the formulation of Yoda et al., points out the peculiar properties of their expression as thinning begins. It implies that the area per plant as thinning first begins is equal to itself plus the area per plant at the "asymptotic maximum density" which is not possible since the area per plant at maximum density is not zero. In the present expression this relationship is only approximate for small values of D and the value of D is not small as thinning begins; it is relatively large and negative forcing the right hand side of the equation to equal $1/P_0$ as it must be.

2.8. Departures from -3/2 Thinning and Suggestions for Plant Allometry

We have now laid the foundation for interpreting a great deal from the log w vs. log p graphs. The basic patterns for populations

undergoing self-thinning proper have been described and we are in a posi-
tion to interpret departures from the basic pattern.

It is possible to seed populations at densities higher than the
weight-growing density relation of -3/2 thinning would allow (when seed
weight is taken as plant weight). Workers as early as Yoda et al. (1963)
noticed that such populations drop back to the -3/2 line because of in-
tense mortality after an initial bout of growth. We capitalize on pre-
cisely this initial growth in raising sprouts, with seed reserves used to
support the initial growth. Thinning mortality in such populations must
be more drastic than -3/2 or the population could not drop back to a
lower -3/2 line. Hickman (1979) grew populations at very high density
for a brief period on drastically reduced soil volumes. He observed not
-3/2 thinning but -1/2 thinning--massive mortality with little growth.
If his planting densities initiated populations far above the natural
-3/2 line, the early mortality would be an expression of exhaustion of
seed reserves, not the environmentally imposed limits of -3/2 thinning.

At the other end of the density spectrum a different pattern
occurs. If the population is not yet limited by a resource, the con-
straints implicit in -3/2 thinning do not apply. The individuals in
the population will grow and little or no mortality will occur. Such
populations will initially follow a line which is nearly vertical, giving
rise to a series of data points which lie substantially below the ulti-
mate thinning line. As Cormack (1979) points out, -3/2 thinning is not
the proper model to describe such populations.

White and Harper (1970) observed that trees seemed to be fairly
regular in their thinning pattern although there was a rather consistent

tendency for them to thin along a line steeper than -3/2. This observa-
tion may be rephrased: As thinning proceeds in large trees, the sur-
viving trees tend to be too large for the prediction of the -3/2 thinning
"law." Having examined planaria populations in which the organisms were
occasionally "too small" in comparison to their usual thinning pattern
and having interpreted it as a breakdown in the approximate proportion-
ality of biomass to resource base, we can ask whether such a breakdown
is occurring in the case of trees. The biomass of a tree requires
nutrients for its growth and maintenance yet a tree really has two kinds
of biomass: the living portion of the tree and the heartwood which is no
longer living. It is possible that the two kinds of biomass have dif-
ferent requirements, with the living portion of the tree being the
salient portion of the biomass for -3/2 thinning, and the heartwood a
biomass "cheap" to maintain once in place and therefore not relevant for
the relation between a resource base and the biomass of individuals.
Thus, the trees could be "too large" in terms of total biomass and yet
the basic constraint of -3/2 thinning as a reflection of a limiting
resource in space would still be the governing influence.

An Herculean dissection would be required to examine directly
whether the living portions of trees in a stand are indeed following -3/2
thinning, and such observations have not been made. There is another way
to examine the possibility, however, if individual trees are considered
to behave roughly as the population averages do. If an underlying -3/2
line governs the thinning process as described above, and the observed
line of slope -1.75 (= -3.5/2) (White and Harper 1970) is a consequence
of the increasing proportion of heartwood in large trees, a slope is

predicted for the allometric regression of sapwood weight (w_s, taken as proportional to the living portion of the tree) on the total tree weight, w:

$$w \propto p^{-3.5/2} \qquad w_s \propto p^{-3/2}$$

$$p \propto w^{-2/3.5} \qquad p \propto w_s^{-2/3}$$

$$w^{-2/3.5} \propto w_s^{-2/3}$$

$$w_s \propto w^{-2/3.5 \cdot -3/2}$$

$$w_s \propto w^{3/3.5}$$

Fig. 2.10 shows a graph of sapwood weight vs. total tree weight for a number of trees of several species (unpublished data of R. H. Whittaker from Hubbard Brook, New Hampshire). The slope of the line in the graph is predicted by the above method, not estimated from the points themselves. The fit, spanning three orders of magnitude, is extraordinarily good.

Several workers (White and Harper 1970, Mohler et al. 1978) have attempted to extend the observations about self-thinning and apply them to plant parts. Following an initial suggestion based upon the model of geometric similarity through development that plant parts should also follow the -3/2 thinning relation (White and Harper 1970), evidence has accumulated that it is not so simple. Westoby (1977a) attempted to relate self-thinning to leaf area rather than plant weight. However, in a subsequent exchange (1977b) with White (1977) he cedes major difficulties in the analysis and lack of generality of the result reported
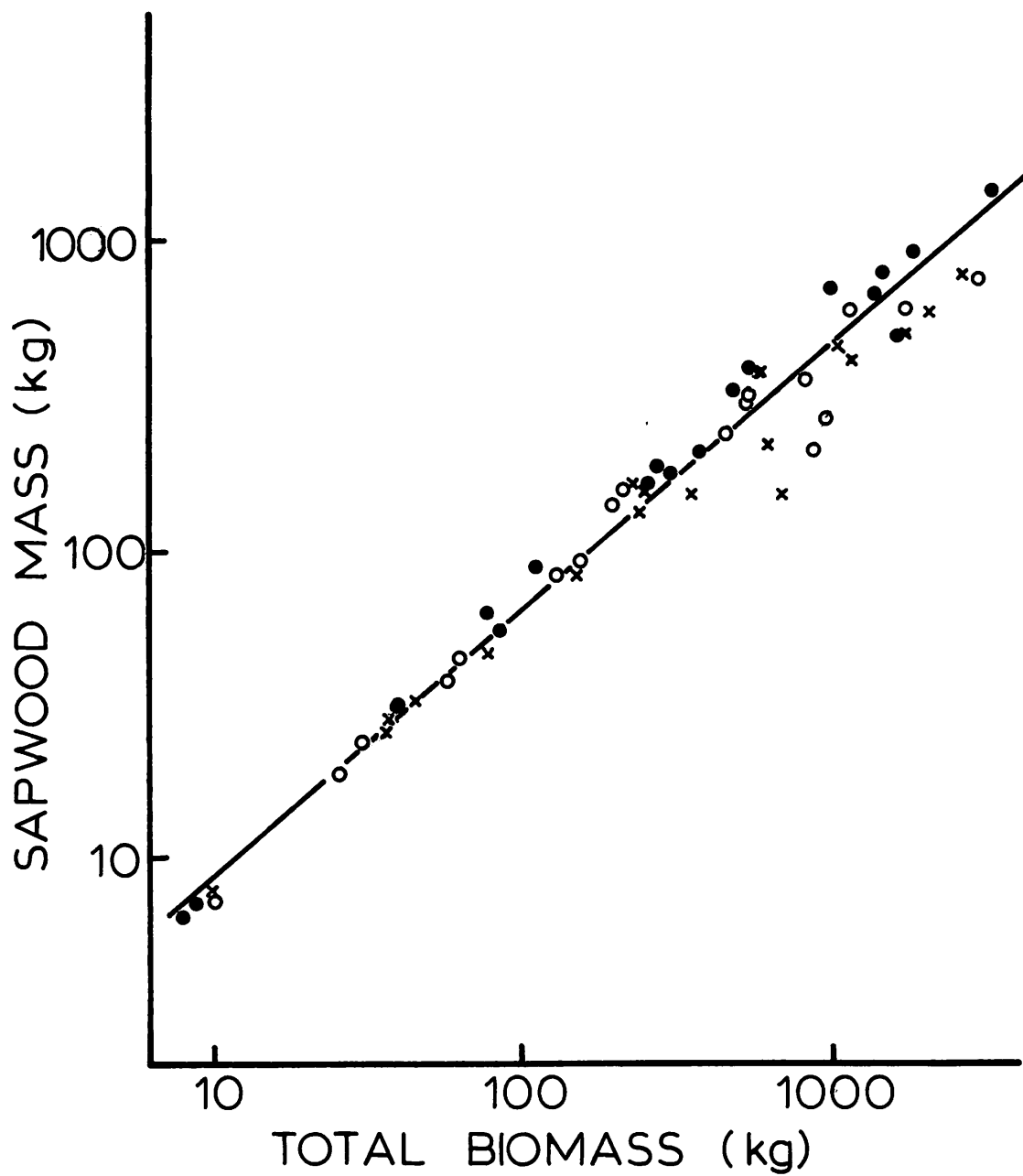
Fig. 2.10. The log-log allometric relation between sapwood mass and total tree biomass for Maple (●), Beech (o), and Birch (×) at Hubbard Brook, New Hampshire (unpublished data from Whittaker). A line of slope +1.17 predicted by the theory is shown.

earlier that year. White (1977) reported that leaves seemed to thin with a -1 slope and Mohler et al. (1978) reported that while a -3/2 relation did indeed seem to hold for roots, a -1 relation seemed to prevail for leaves and new twigs. Other plant parts are even less regular in their behavior. It is obvious, even without measurement, that stems, for example, can show no simple pattern on the log-log graphs since they may be entirely absent for some species, first appearing later in maturity.

The approach described above for examining thinning for sapwood rather than whole trees suggests that ideas about thinning for plant parts may be implicit in their allometric relations to whole plants (see also Kira et al. 1956). The argument about sapwood suggests that the living portion of the tree is exploiting the resource and the -3/2 relation should apply to it, not the whole plant. A view of plant parts as separate entities (White 1979) suggests in this context that the organs be viewed as exploiting a resource. Leaves exploit light--a resource distinctly two dimensional in terms of the return on investment of a unit mass of tissue. A leaf casts a shadow below it--some light has been removed from the projected area of the plant and another leaf placed below it cannot yield the return on an investment of tissue that the first one did. Thus, to the extent that leaves are only exploiting light, they should follow a -1 pattern of thinning since light is their limiting resource.

Similarly, roots are exploiting the soil volume by continuing to encounter regions from which nutrients and water may be withdrawn. We may conclude that roots, exploiting soil in three dimensions for water and nutrients, should tend to follow a -3/2 thinning pattern. The

relation should hold provided exploitation of the soil is the root's principal function, with such roles as support and storage being minor.

If whole plants follow -3/2 thinning and roots -3/2, there is a residual weight portion unaccounted for which is made possible by the leaves thinning with only -1 (Fig. 2.11). This surplus is the biomass from which storage, stems and reproduction can come. The pattern of thinning for roots and leaves produces a constraint on allocation to storage, stems, and reproduction arising from the theory. Note that no firm statement is made how the allocation should be partitioned among them or whether storage might take place in leaf or root tissue. Plants are very variable as to whether they produce stems, storage organs, reproduce vegetatively or sexually, and it would be suspicious if the theory were to favor some particular pattern of an allocation process which itself is known to be sensitive to density (Abulfatih et al. 1979, Beasleigh et al. 1974).

The thinning relations for rootweights w_r (thinning -3/2) and leafweights w_ℓ (thinning -1) imply corresponding allometric relations for these parts of the plants on the whole plants following the method of Kira et al. (1956):

$$\text{roots:} \qquad w_r \propto p^{-3/2} \qquad w \propto p^{-3/2}$$

$$w_r \propto w$$

so the log-log regression of roots on total weight should have a slope of 1.
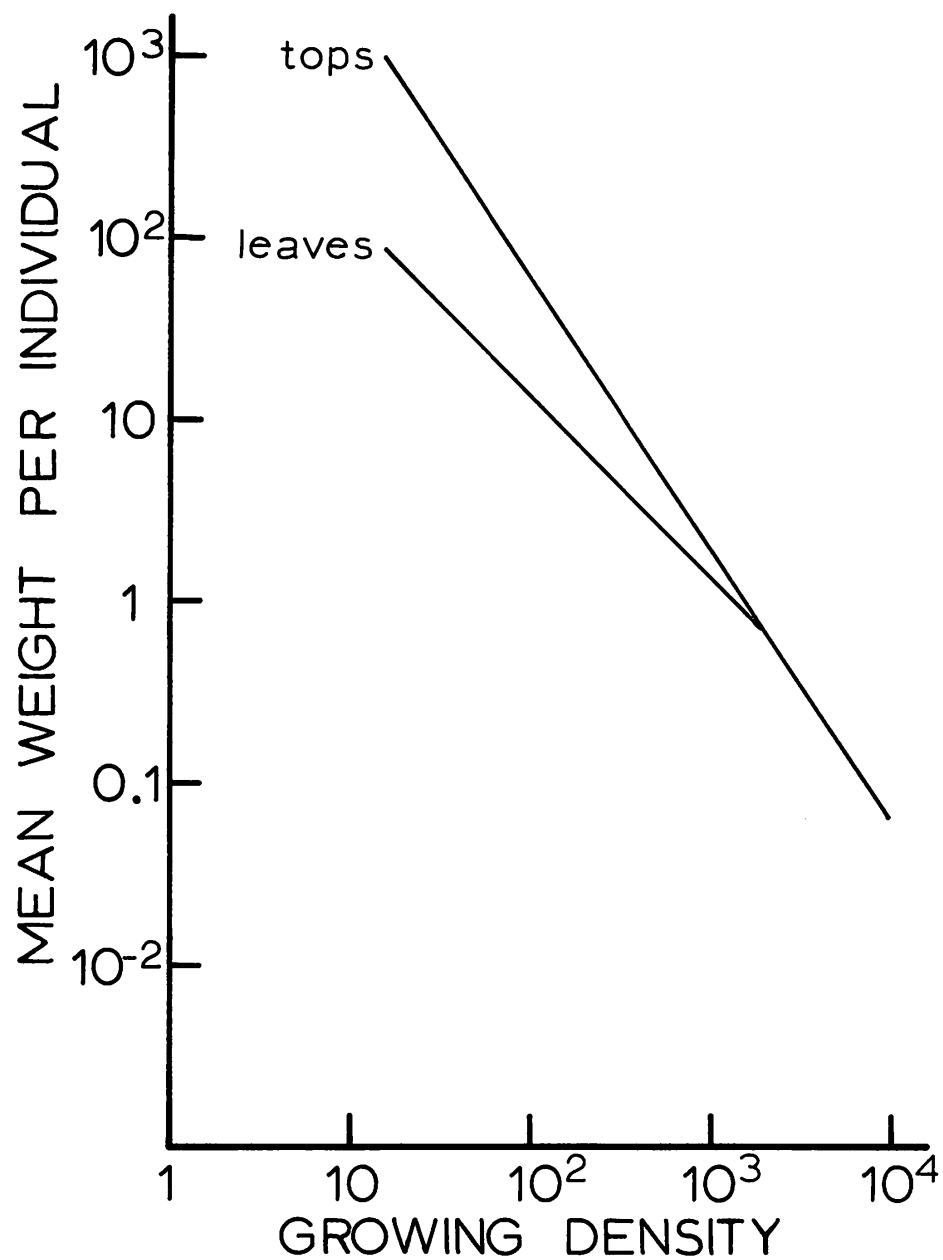
Fig. 2.11. The log-log relations with growing density p of the per individual mean weights of tops and leaves (simulated data).

leaves:
$$w_\ell \propto p^{-1} \qquad w \propto p^{-3/2}$$

$$w_\ell^{-1} \propto p \qquad w^{-2/3} \propto p$$

$$w_\ell^{-1} \propto w^{-2/3}$$

$$w_\ell \propto w^{2/3}$$

so the log-log regression of leaves on total weight should have slope of 2/3. Both predictions are readily measured and testable. It must be remembered that these results are contingent upon roots and leaves exploiting the soil (volume) and light (area) and not being used significantly for storage or other functions unrelated to their exploitation of those resources. Nevertheless, departures from the predicted patterns may be perfectly understandable in terms of known growth habits of the plants. Significant storage in leaves, for example, should steepen their allometric relation to the whole plant.

Plant roots are notoriously difficult to examine in biomass studies. From the above analysis of plant allometry we can now characterize those plants for which examination of tops should suffice to observe -3/2 thinning: plants whose roots are not major organs of support or storage. For other plants, tops (which always include leaves) may be expected to thin along lines at least as steep as -1, but the time course of movement of material in and out of storage is variable making more precise general predictions impossible. The confusing patterns observed for shoots in stands of perennials (Hutchings 1979, Ernst 1979, Hutchings and Barkham 1976, Hickman 1975, Schlesinger and Gill 1978) in which -3/2 thinning was not observed presumably are due to the substantial storage role of underground structures which (understandably) were not measured.

A problem related to plant parts is the interpretation of density effects in shoot production (Beasleigh et al. 1974) or tillering in grasses. Kays and Harper (1974) examined populations of Lolium perenne to determine the progress of thinning. Their observations suggest that -3/2 thinning is a good model for the description of genet populations, but is not very descriptive for ramets. The difficulty lies in the somewhat degenerate case presented by the ramets. By definition ramets in the population have a smaller range of sizes than genets and so resource limitation is expressed by a particular density of ramets of relatively uniform size. As a result there is a fixed point on the graph to which populations tend over a wide range of initial starting densities. It is nevertheless possible to see the vestiges of an underlying thinning relation even in their graphs (Fig. 2.12): The mortality in ramets does produce populations which lie below or on a thinning line defined by the point to which the populations converge, be it a -3/2 line (Fig. 2.12a) or a -1 line from thinning at low light levels (Fig. 2.12b). It is of further interest to note that the value of $\log k_3$ associated with this point must be higher than in the case of thinning among genets in the small population. The yield per unit area is the same from both points of view, yet when viewed in terms of ramets, p is larger, meaning that the point lies on a higher line of slope -3/2. Since it is the same group of plants, the resource base is the same and the higher value of k_3 implies that the efficiency of the stand at exploiting its resources is higher viewed from the standpoint of the ramets. The difference in the values of $\log k_3$ is an expression of the value of the shared exploitation enjoyed by the ramets which are part of a network of other ramets connected by the same rootstock.
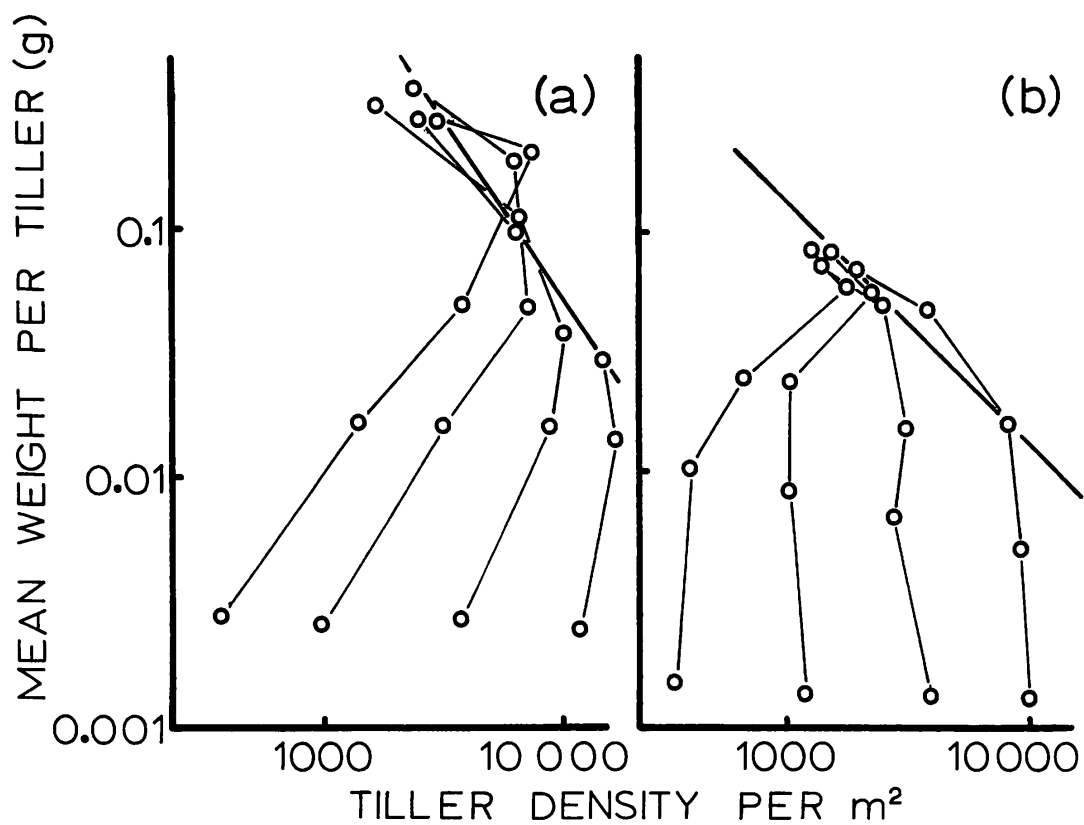
Fig. 2.12. The log-log relation between mean tiller weight and tiller density in populations of Lolium perenne sown at four densities, followed through five successive harvests in full daylight (a) and 30% light intensity (b). Lines of slope -3/2 (a) and -1 (b) are also shown. (After Kays and Harper 1974 with permission Blackwell Scientific Publications)

It can also be seen from the figure that for the stands grown at low light intensity, a -1 relation is a better descriptor of the ramet population's tendency to thin from high densities.

2.9. Fractals and Plant Shape

If as plants grow, the rooting volume being exploited by an individual increases as the -3/2 power of the area on the ground surface which a plant occupies, then the effective volume of exploitation by the population cannot be constant. Earlier models for -3/2 thinning postulated geometric similarity for the growth of the plants in order to derive the -3/2 exponent. With the present theory, we might postulate geometric similarity in exploitation of the environment in order to maintain the 3/2 relation to the area occupied per plant. In a sense the problem has only been shifted to the environment.

Careful analysis shows that while the maintenance of geometric similarity is a sufficient condition to achieve the desired value of the exponent, -3/2, it is by no means necessary. Imagine a lump of clay placed on a pedestal of unit area in such a way that the base of the lump covers the pedestal. Now imagine another lump with eight times as much clay on a pedestal having four times the area. This lump can have whatever shape we please. As long as its base covers the pedestal, it will retain the desired 3/2 power relation of weight to area in comparison to the first lump. Clearly the constraint of a particular base area per plant is not so demanding as to require that the plant maintain its shape throughout its growth in order to have the -3/2 relation exist. The appeal of assuming geometric similarity is that it insures the -3/2 relation in a very simple manner.

One might imagine that the exploitation of the soil by roots did achieve such a preservation of shape if roots continued to grow downward, filling out the soil at ever increasing depths. The volume is expanding downward, and we have pushed the question of geometric similarity underground into a realm of assured ignorance. What happens to rooting patterns of individual plants in thinning stands of high density is probably unobservable. One way to assess the average effects of such a process is to look at populations growing on shallow soils. If root growth into the soil is critical for maintaining the -3/2 exponent, then a shallow soil should limit that. If there are no greater depths for the roots to penetrate, there can be no compensatory growth in that direction to maintain the -3/2 exponent, and the population must revert back to the exponent of -1 since the available volume is filled.

I have been speaking of area and volume as having two and three dimensions. To the extent that exploitation of a limiting resource is governed by whether it is distributed over area or in a volume, it seems natural that these geometric properties should find their expression in the populations dependent on that resource. A dendritic drainage pattern, though one dimensional in the classical sense since it is a network of lines--the streams--has a dimension of two in another sense because every point on the surface of the landscape is drained by the drainage system. Mandelbrot (1977) refers to this other notion of dimension as fractal dimension and the objects which display it as fractals. In an analogous fashion to the drainage pattern, he considers the role of veins and arteries in the body, which are one dimensional in being filamentous and yet each system has a fractal dimension of three since each services

every point in the body's tissues--a three dimensional corpus. Fractals present another class of geometrical objects which have properties of filling space in one sense and yet not filling it up: blood vessels may reach every point in the body's tissues yet they leave room for the tissues themselves. Plant roots may usefully be considered in a similar light. They should reach all portions of the local soil to extract nutrients and yet not completely displace the soil.

Mandelbrot examines numerous examples of processes of growth through the elaboration of branches which bear startling resemblance to structures and developmental pathways in plants (Fig. 2.13). Plants typically are connected structures which grow by the elaboration of branches, be they runners, petioles, stems, twigs, or roots. Many of Mandelbrot's fractals also exhibit these properties. These similarities suggest the use of fractals as a descriptive tool for understanding the development and functions of plant form.

It may be that the progressive elaboration of root hairs provides an aspect of plant growth which is naturally related as -3/2 with the growing density. In a sense the model of earlier investigators is deficient, not because it makes a false general observation about plants as they thin; to the extent that plant tissues have comparable specific gravities, the existence of -3/2 thinning implies that they do have displacements (volumes) which follow a -3/2 relation as they grow. The difficulty of the earlier model lies in the overzealous and unnecessarily restrictive assumption of geometrically similar plant growth which yields the right answer but does not provide useful predictions of how the -3/2 relation might break down.
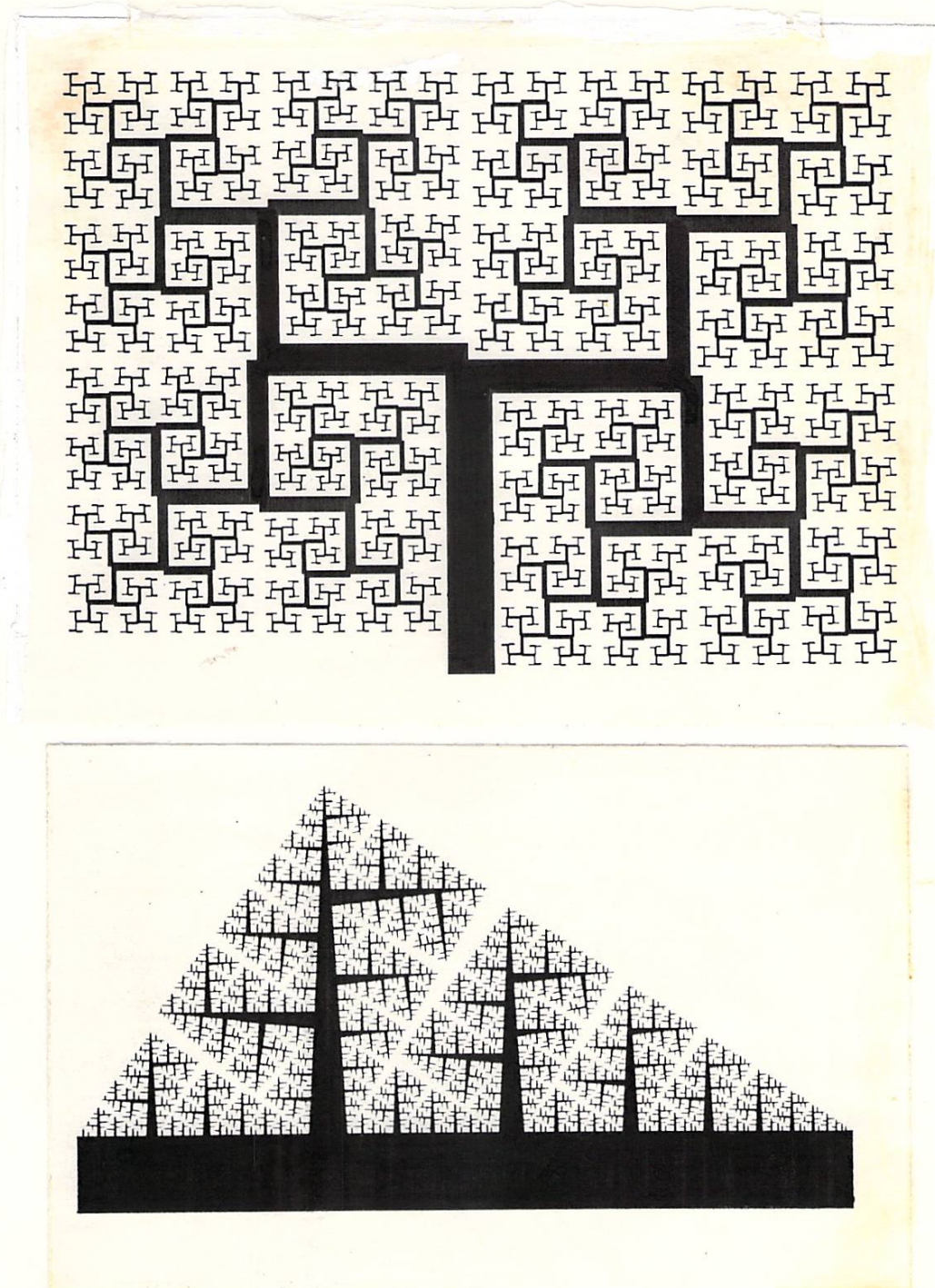
Fig. 2.13. Fractal curves (from Fractals by Benoit B. Mandelbrot,
W. H. Freeman & Co. © 1977)

The notion of fractal dimension may allow the examination not only of growth form in plant populations but also of the environment. Can the environment, the "space" from which the resources come, have a fractal dimension? If indeed the soil can behave as a two-dimensional resource when sufficiently shallow, then what of a soil over a cracked and fissured subsurface? Such surfaces are shown by Mandelbrot to have fractal dimensions between 2 and 3. In this context, the notion of fractal dimension is intimately associated with intuitive notions of roughness. Perhaps populations which thin with an exponent strictly between -1 and -3/2 are experiencing a fractal dimensionality of the space they are exploiting.

Fractals may provide us with a more versatile model of form which comes closer to meeting the demands of the diversity of plant forms found in nature. By shifting the emphasis to the environment, I have maintained a more classical and intuitive view that resources limit populations. I have described their growth as literally constrained by an obvious property of the resource--its dimensionality. In a sense, growing plants can adopt whatever strategy works to take advantage of that property. Geometrically similar growth would do it but it is only one possibility and it is hardly the rule in plant growth. Fractals may provide a more versatile perspective, allowing discussion of varied forms of growth and statistical properties of the elaboration of structures.

2.10. Multiple Species Stands

Bazzaz and Harper (1976) experimented with thinning in two species stands. They found that -3/2 thinning seemed to provide a good

description for the stand as a whole--without regard to the identity of the individual species. It is clear from qualitative observation that the regularity of -3/2 thinning cannot apply to single species in a mixed stand since species commonly become very rare or die out of a stand without individuals of the species growing large. If, as suggested here, the -3/2 thinning relation is a consequence of partitioning a volume among the survivors in a population, as long as access to the associated resources is similarly partitioned, the -3/2 relation should apply to individuals in a stand without regard to their species identities.

If species in a stand vary substantially in their ability to convert resources to biomass, the -3/2 thinning for all individuals in the stand may still be a fair approximation although consistent biases as thinning progresses could result in significant but interpretable departures from the simple pattern of thinning.

2.11. Significance of the Present Theory

As a purely empirical relation -3/2 thinning has already begun to see application in various contexts. Drew and Flewelling (1977) describe its use in forestry to predict ultimate yields based on the parameters of the initial thinning curve. Barkham (1978) has used the presence of a -3/2 relation to infer natural self-thinning in an oak woodland, while Schlesinger (1978) working on cyprus in Okefenokee Swamp used the absence of such a relation to infer the converse. Hickman (1979) has suggested the application of the -3/2 relation to natural mixed populations even when thinning was not apparent under the assumption of full use up to the -3/2 constraint.

The foundation of the theory offered here differs from that of previous workers (Yoda et al. 1963, White and Harper 1970, White 1979, Mohler et al. 1978) in one primary detail. Rather than emphasizing the displacement volume of the plants themselves, it attributes the 3 in the -3/2 thinning "law" to the three dimensional volume in which a limiting resource is distributed. This seemingly minor shift in perspective has important implications. The earlier theories have relied heavily upon a certain geometry of plants. While beguilingly simple, the assumed geometry is not observed, even approximately, and as a result, few predictions, none of them successful, have arisen from the theory beyond the original observation of -3/2 thinning itself. No credible basis was provided from which departures from -3/2 thinning could be interpreted.

The foregoing discussion of the present theory has included numerous testable predictions. Some of them have already been corroborated with data in the literature. Some exceptions to -3/2 thinning have been interpretable and, based on the theory, suggestions have been made as to the source of confusion in some patterns as yet unexplained. The umbrella of the theory has also been extended to cover two important groups of ideas not before directly related to -3/2 thinning, though often discussed in the same papers (e.g., Yoda et al. 1963, White and Harper 1970, Mohler et al. 1978): the constant yield relation and plant allometry. The experimental portion of the thesis provides further corroborative evidence for predictions of the theory.

3. EXPERIMENTS/METHODS

--I love fools' experiments
I am always making them.

--Charles Darwin

3.1. Summer 1977: Field Populations of Leaf Mustard

In the summer of 1977 a battery of experiments was undertaken to
investigate many of the predictions of the theory. Since the present
derivation for -3/2 thinning suggests that plants in a population are
subdividing their resource base, it made most sense to follow single
populations undergoing thinning, sampling them at successive points in
time to determine mean plant weight and growing density. This method is
in contrast to that used by most investigators--replicate plots which are
destructively harvested for biomass measurements. Non-destructive bio-
mass estimation was accomplished by allometric estimation of biomass from
measurements of randomly selected individuals from the populations.
Likewise, counts were made of plants present in a plot. The necessary
measurements could thus be obtained from populations without sacrificing
them.

For the present experiments leaf mustard, Brassica juncea, and
Swiss Chard, Beta vulgaris var. cicla, were grown. The two species were
selected for their relatively short and comparable growing seasons
($\sim$20 days) and similar growth form (rosette) to allow examination of two
species interactions. With much of the biomass aboveground, I had a

51

reasonable expectation of estimating biomass by allometry. The measurements used for biomass estimation were number of leaves and the length of the longest leaf.

Populations were seeded on 23 June 1977 by hand scattering seed into plots 2m on a side on the lacustrine soil of Thompson Research Farm of the Cornell University Department of Vegetable Crops (space there was kindly made available to me by the late Dr. Phillip A. Minges). Following seeding, the plots, in a field which had been plowed, harrowed, and fitted, were raked to cover the seed which was then left to germinate. A ten day sampling cycle was used. Plots which were most likely to be directly compared were sampled on the same day or on days close together. There were two sets of control plots, one set was sampled at the start, the other halfway through the sampling cycle.

In order to sample without damaging the plants, I devised a portable rack which could be placed on sawhorses spanning a plot. By lying on the rack, suspended over the plants, I could reach down into the middle of the population wherever necessary without damaging or crushing any plants.

All samples were from the central portion of a plot, a quadrat 0.9 m on a side, thus allowing a .53 m border around the sampled populations. Each central quadrat was delimited by placing a balsa wood square into the middle of the plot at the time of sampling. The square had a grid of threads on it with 0.1 m spacing. The grid was then used as a basis for locating plants and areas within the plot for the actual measurements of growing density and biomass.

Growing density was measured either by direct count of all individuals in plots of low growing density or by estimation from subsamples.

A stack of cards was made containing all 2-digit numbers which do not contain zeros. The stack of 81 cards was shuffled and used to index access to individual squares in the 9 x 9 square balsa wood grid. All individuals were counted in the subplot and then another square was selected by the same method and the individuals counted in it. To control the variance of the estimates of density, I counted a minimum of five subplots and continued to count until the standard error of the estimate of mean growing density was less than 10% of the observed density. Thus the sample size depended upon the amount of local variation in growing density. Such sampling could be accomplished in real time by using a calculator (HP-97) to compute the statistics as each count was made. The calculator was also used to print the observed values. The stack of shuffled cards insured that sampling from the population was random and that no subplot was counted more than once.

A similar scheme was used to measure leaf length and count number of leaves. Plants were located approximately at random with respect to the intersection points of the string grid. A pointer was lowered vertically past an intersection chosen at random (the lower right-hand corner of a square chosen as above using the stack of cards). The rosette whose center was closest to where the pointer hit the ground became the chosen plant from which measurements were taken. The center of the rosette was used to avoid a size-dependent bias which would arise from taking the "closest." It was quite possible, for example, to have the pointer land on a large plant but the chosen plant be a tiny one whose center was closer to the pointer than the center of the large plant. Once the plant was chosen, the longest leaf was measured, and a count made of the leaves which were unfurled. Both of these values were entered on the calculator

and the sampling continued. As with growing density, an effort was made to control the variance of estimates made by this procedure. A minimum of ten plants was always measured and sampling continued until the standard error of the mean of each of the measured quantities was less than 10%.

At the end of sampling from each plot, the calculator printed the values of the sums, sums of squares, and cross products of the measurements taken. These proved valuable later as checksums for determining whether data from the calculator printout had been correctly keypunched. The calculator printout was taken up on a homemade rubber-band powered spool which permitted the calculator, operating on batteries, to be entirely enclosed in a zip-lock bag, protecting it against dust and rain. A shelf was built into the rack to support the calculator at a convenient level somewhat below me and a sun shield fastened over it to keep it from exceeding its rated temperature and to improve readability of its LED display.

The primary experimental species for the summer of 1977 was leaf mustard with swiss chard being used only to examine two species interactions. Initial growing densities were established by seeding at different rates. There were seven principal questions addressed experimentally:

1) 77-Variance. Does the variance of the size of individuals in the population influence the rate of thinning? This set of experiments also included the control for the other experiments.

2) 77-Shade cloth. Does shade cloth change the slope of the thinning line?

3) 77-Fertilizer. Does an elevated fertilization level change the intercept of the thinning line?

4) 77-Water. Does an elevated watering regime change the intercept of the thinning line?

5) 77-Pseudo-leaves. Do "pseudo-leaves," aboveground structures to provide shade simulating plants' aboveground structures, change the constant yield relation?

6) 77-Chard. Does competition with a second species, swiss chard, change either parameter of the thinning line for the individual species or for the two species taken together?

7) 77-Roots. Does increasing root competition by removing about 1/3 of the soil volume from access to the plants reduce the intercept of the thinning line? Swiss chard was used for this experiment and it was not begun until 20 July 1977.

The densities at which seeds were sown were 20; 200; 2,000; and 20,000 per m^2. A schematic of the experimental investigations is in Fig. 3.1.

3.1.1. Size Variance (Experimental Series 77-Variance)

One series of experiments manipulated the variance of individual size in the population. By mixing several varieties of leaf mustard together, I achieved a variability in individual size which could be manipulated. Seed from three varieties of leaf mustard were used: (1) Florida Broad Leaf; (2) Southern Giant curled, long standing; and (3) Tendergreen or Spinach Mustard. The three treatments represented attempts to achieve three levels of variability in the populations:

MANIPULATION	TREATMENT	PLANTING DENSITY

SUMMER 1977

MANIPULATION	TREATMENT	1	2	3	4
VARIANCE	77-VARIANCE 1	O	X	X	X
	VARIANCE 2	O	X	X	X
	VARIANCE 3a	X	X	X	X
	3b	X	X	X	X
SOIL	77-FERTILIZER	O	X	X	X
	WATER	O	X	X	X
	ROOTS - EXP.	O	O	X	O
	- CONT.	O	O	X	O
LIGHT	77-SHADE CLOTH	X	X	X	X
	PSEUDO-LEAVES	O	X	X	O

SUMMER 1978

MANIPULATION	TREATMENT	1	2	3	4
THINNING	78-FERTILIZER	O	O	O	X
	ABOVEGROUND	O	O	O	X
	- -CONTROL	O	O	O	X
	SHALLOW SOIL15cm	O	O	O	X
	- - 25cm	O	O	O	X
	BELOWGROUND	O	O	O	X
CONSTANT YIELD	78-CONTROL	X	X	X	X
	FERTILIZER	X	X	X	O
	"LEAVES" black	X	X	X	O
	clear	X	X	X	O

SUMMER 1979

MANIPULATION	TREATMENT	1	2	3	4	5	6
THINNING	79-YODA	X	X	X	X	X	X
	FERTILIZER	X	X	X	X	X	X
	- -, CHANGE IN	X	X	X	X	X	X
	SHALLOW SOIL	O	X	X	X	X	X
	0.1 HOAGLAND'S	X	X	X	X	X	X
	0.5 HOAGLAND'S	X	X	X	X	X	X
REPRODUCTION	79-OATS	X	X	X	X	X	X

Fig. 3.1. The conceptual framework of the experimental manipulations.
O marks a density in the experiment but not in the treatment
x marks a density in the experiment and also in the treatment

Variance 1 consisted of seeds of just one variety, the Tendergreen Spinach Mustard, thereby striving for the greatest uni- formity in the stand.

Variance 2 was seeded as a mixture of the other two varieties attempting to achieve a different level of variability from either Variance 1 or Variance 3.

Variance 3 was a mixture of all three varieties.

Since the primary interest in these populations was their behavior under thinning, Variance 1 and Variance 2 were sown at the three highest densities. Variance 3, as control for other experiments as well, was sown at all four densities.

The mixture of all three varieties was used as the standard seeding for all the other experiments. This mixture was chosen to avoid the relative stagnation implicit in the analysis of density convergence and its relation to the fraction f: the ratio of the size of the dying indi- viduals to the mean size of the individuals in the population.

3.1.2. Shade Cloth (Experimental Series 77-Shade cloth)

In an effort to examine the nature of thinning under reduced light levels, I planted mustard in plots under shade cloth. The shade cloth was erected as a tent over a set of four adjacent plots at the NW end of the experimental area. Light levels under the shade cloth were reduced to about 15% of ambient. Seed was planted at all four densities.

3.1.3. Fertilizer (Experimental Series 77-Fertilizer)

To provide an enriched soil volume, and thereby test the prediction of the theory that the value of the intercept of the thinning line should

be raised, a set of plots was fertilized with 15-15-15 NPK fertilizer at the rate of 100 g/m^2. Seed was sown only at the three highest densities.

3.1.4. Water (Experimental Series 77-Water)

Extra water was provided to these plots. Additional water totalling 7.9 cm was provided by hand watering from a watering can during five dry periods. This experiment was done to test whether water could operate as a limiting resource in the soil volume, and its addition thereby raise the -3/2 line.

3.1.5. Pseudo-Leaves (Experimental Series 77-Pseudo-leaves)

A pilot experiment was done to produce shade analogous to plant leaves but which lacked the belowground influence of roots. Initially, small triangles of aluminum flashing were randomly stuck in the ground in an effort to simulate shading effects of plant leaves. This proved awkward as time progressed since the growing plants overtopped the pieces of flashing and soon sufficiently large pieces of flashing would not support themselves upright. Another tack was taken and bamboo stakes were stuck in the ground on a 0.1 m grid and dark brown returnable beer bottles inverted on the poles. These cast distinct shadows and could be adjusted both in size, by switching from 12 to 32 oz. bottles as the season progressed, and in height by pulling up on the bamboo stakes. The plots were seeded only at the two intermediate densities.

3.1.6. Competition with Swiss Chard (Experimental Series 77-Chard)

An experiment was designed to examine thinning in a stand of two species. The second control, needed for this experiment, Chard 3, was a

pure stand of swiss chard sown at all four densities. The two experimental treatments were Chard 1/3 and Chard 2/3 composed of mixtures of 1/3 and 2/3 swiss chard respectively. The balance was sown as mustard (fractions reckoned as fraction of number of seeds sown). The two treatments were sown at the three highest densities.

3.1.7. Increased Root Competition
(Experimental Series 77-Roots)

Another pair of plots was used to manipulate the soil volume accessible to the plants. The experiment was begun later in the summer due to problems in designing a suitable manipulation and obtaining the necessary materials. Plots were dug out and in the control plot the soil was merely returned to the hole. In the experimental plot roughly 1/3 of the soil volume was excluded from access to the plants' roots.

Rejected beer cans without tops were obtained from a cannery. These were taped together in pairs end to end with duct tape to make a cylinder closed at both ends. One of the closed ends was then sawed off with a band saw. These were filled with soil and stood upright, closed end up, on 0.1 m centers in the excavated plot, and soil filled in around the array of cans. The cans had concave bottoms and holes were punched in the bottom of each can to allow water to drain. The two plots (each half of the same standard 2 x 2 m plot) were then seeded with swiss chard at 2,000 seeds per m^2. Seeds falling on the cans were brushed into the adjacent interstices between the cans and the surfaces of the plots strewn with a thin layer of soil to cover the seed. To prevent roots from climbing over into the cans and going down into the drainage holes, the exposed portions of the cans were brushed clean.

3.1.8. Biomass Regressions

To estimate biomass from the measurements of leaf length and number of leaves, plants were collected periodically to establish the necessary regressions. Sample plants included the range of sizes found in the population, with independent collections made for each of the following treatments: Variance 1, Variance 2, Variance 3, Shade cloth, Fertilizer, Water, and Chard. Plants were collected at roughly two week intervals with a minimum of ten, usually 15, plants in each collection. Plants were pulled up with roots from the borders of plots growing at high densities, assigned a number and placed in a folded sheet of newspaper after recording leaf length and the number of leaves. Swiss chard plants were weighed as whole plants and tops (allowing root weights to be determined by difference). Mustard plants were weighed as whole plants, tops, stems plus reproductive structures, and reproductive structures alone (allowing root weight, leaf weight, and stem weight to be separately determined by difference). The intention was to be able to examine directly the thinning relationships for plant parts as well as whole plants using the empirical allometric relationships on leaf length and number of leaves. The data were also, however, a source of information about the allometric relations between the various plant parts themselves. Individuals were chosen to span the observed size range in thinning populations. More than 600 plants were measured for the purpose of establishing the allometric relations.

The regression model used was a multiple linear regression of log biomass on the logarithms of leaf length and the number of leaves. Since I was very concerned about the precision of the estimates of biomass, I calculated the regression parameters, and in addition to computing the

value of R^2, the value of the root mean squared (RMS) deviation of the actual log biomass of the measured plants from the values predicted by the regressions was also computed.

As will be discussed in the results section, a time dependence of the regression parameters in swiss chard is pronounced and seems to be roughly linear. Estimates of plant weight were made on the basis of regression parameters chosen to vary linearly with time. In mustard, the pattern, if any, was unclear since any initial consistent tendency shifted as the populations were not sampled often enough to judge a more complex pattern. Consequently, constant values of the regression parameters were used.

3.2. Summer 1978: Field Populations of Swiss Chard

In the summer of 1978 another series of experiments was performed, designed primarily to manipulate values of the intercepts, the constants k_2 in the constant yield situation and k_3 in the case of -3/2 thinning. Since swiss chard is a biennial, it was used for all experiments to avoid complications with the shift into the reproductive phase. Biomass was measured directly by harvest in replicate plots. Plants, including roots, were excavated, placed in paper bags en masse from a plot (after counting), and oven dried at 80 C to constant weight.

In contrast to the broadcast seeding of the previous year, seeds were sown in rows $\frac{1}{2}$ m apart since some of the experimental treatments restricting volume naturally gave rise to row planting formations. Seed was again sown at four densities: 1,400; 320; 100; and 32 seeds per m^2 (or equivalently per two meters of row).

Controls were planted at each of the same densities. Only the highest density was used to examine the thinning relationship. The three lowest densities alone were used to explore effects on the constant yield relation.

Plots were on the same land as the previous year. As before the field had been plowed, harrowed, and fitted. Plots were worked with a hand cultivator, rows marked and scored into the earth, seeds planted in the rows and covered.

The constant yield experiment plots were planted 23 June 1978. The plots themselves were 3 m on a side, each with seven rows of plants. Plots to be harvested were sections of row $\frac{1}{2}$ m in length. A row was left between each row from which a harvest would be taken. There were thus 9 harvest plots in each treatment plot (see Fig. 3.2a). These were harvested in groups of three yielding data in triplicate for any particular nominal harvest date. There were three such nominal harvest dates: 12 August; 26 August; and 9 September. In fact, because of limited space in the drying oven, the three replicates for any particular harvest date were harvested on three successive days. To minimize variability due to possible position or illuminance effects, for any given harvest all plots came from the same tier in the array (see Fig. 3.2a).

The treatments examining the effects on -3/2 thinning were sown in plots measuring 2 x 3 m. These plots also had seven rows at $\frac{1}{2}$ m spacings and sampling also came from $\frac{1}{2}$ m segments of the internal rows. All plots were set up in duplicate with the control in quadruplicate. Harvests were made 8 times (see Fig. 3.2b for placement of harvest plots) with the harvested plot initially chosen at random from the six principal sections

63
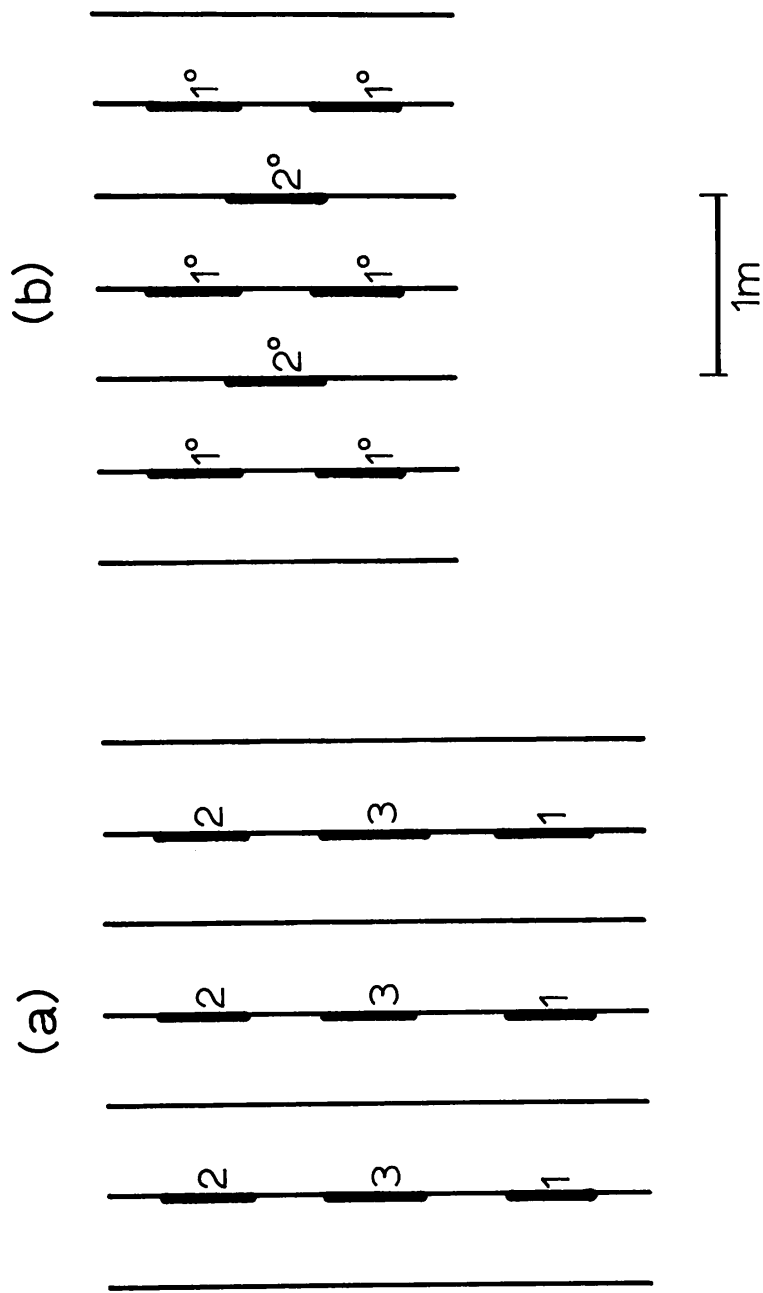
Fig. 3.2. The physical plan of the plots for the 1978 experiments. a) three harvests in the constant yield experiments; b) primary subplots sampled randomly for the first six harvests (1°), secondary suplots sampled randomly for the last two harvests (2°).

of row and the last two harvests chosen from the pair of secondary sections of row.

Questions addressed by the experimental treatments were as follows:

1) 78-Control. Control plots.

2) 78-Fertilizer. Does fertilizer change the intercept of the thinning line, k_3?

3) 78-Black plastic leaves. Do plots with reduced light intensity due to black plastic "pseudo-leaves" still show the constant yield relation?

4) 78-Clear plastic. A control version of 78-Black plastic leaves using clear plastic.

5) 78-Aboveground restriction. Does restricting the aboveground volume laterally accessible to the plants' tops change the value of k_3?

6) 78-Aboveground control. Control for 78-Aboveground restriction.

7) 78-Underground restriction. Does restricting the belowground volume laterally accessible to plant roots change the value of k_3?

8) 78-Shallow soil. Does a shallow soil change the parameters of the thinning line?

3.2.1. Control (Experimental Treatment 78-Control)

Planted as controls for the experimental treatments, the 78-Control plots received no further treatment beyond planting and weeding.

3.2.2. Fertilizer (Experimental Treatment 78-Fertilizer)

5-10-5 NPK fertilizer was added to these plots at the rate of 150 g/m^2, by hand spreading on the surface of the soil two days after planting.

3.2.3. Black Plastic "Leaves" (Experimental Treatment 78-Black plastic "leaves")

As an outgrowth of the experiments with the bittles (77-Pseudo-leaves) the previous summer, an attempt was made to simulate leaves in the canopy which would reduce light levels and yet have no competing underground structures. According to the theory, reducing light levels should maintain the constant yield relation but lower the yield. Strips of 4 mil black polyethylene 3.7 cm wide and 56 cm long were folded in half and placed over the intersections of 2" mesh chicken wire in an hexagonal array with 4" centers (Fig. 3.3). The pieces of plastic were stapled in place and the chicken wire was stretched over a frame 3 x 3 m made of 2 x 2 construction lumber. This frame was then supported over the plot by iron fence posts. Wire loops suspended the frame so that its height could be adjusted as the plants grew. The black plastic strips yielded a much different shade from the shade cloth of the previous summer since on clear days small patches of full sunlight penetrated to the plant canopy below. The average reduction in light intensity was comparable and the arrangement did not restrict air flow nearly as much as the shade cloth tent of the previous year.

3.2.4. Clear Plastic "Leaves" (Experimental Treatment 78-Clear plastic "leaves")

In this control for 78-Black plastic "leaves," plots were arranged identically to the plots with the black plastic except that clear, 4 mil polyethylene was used.
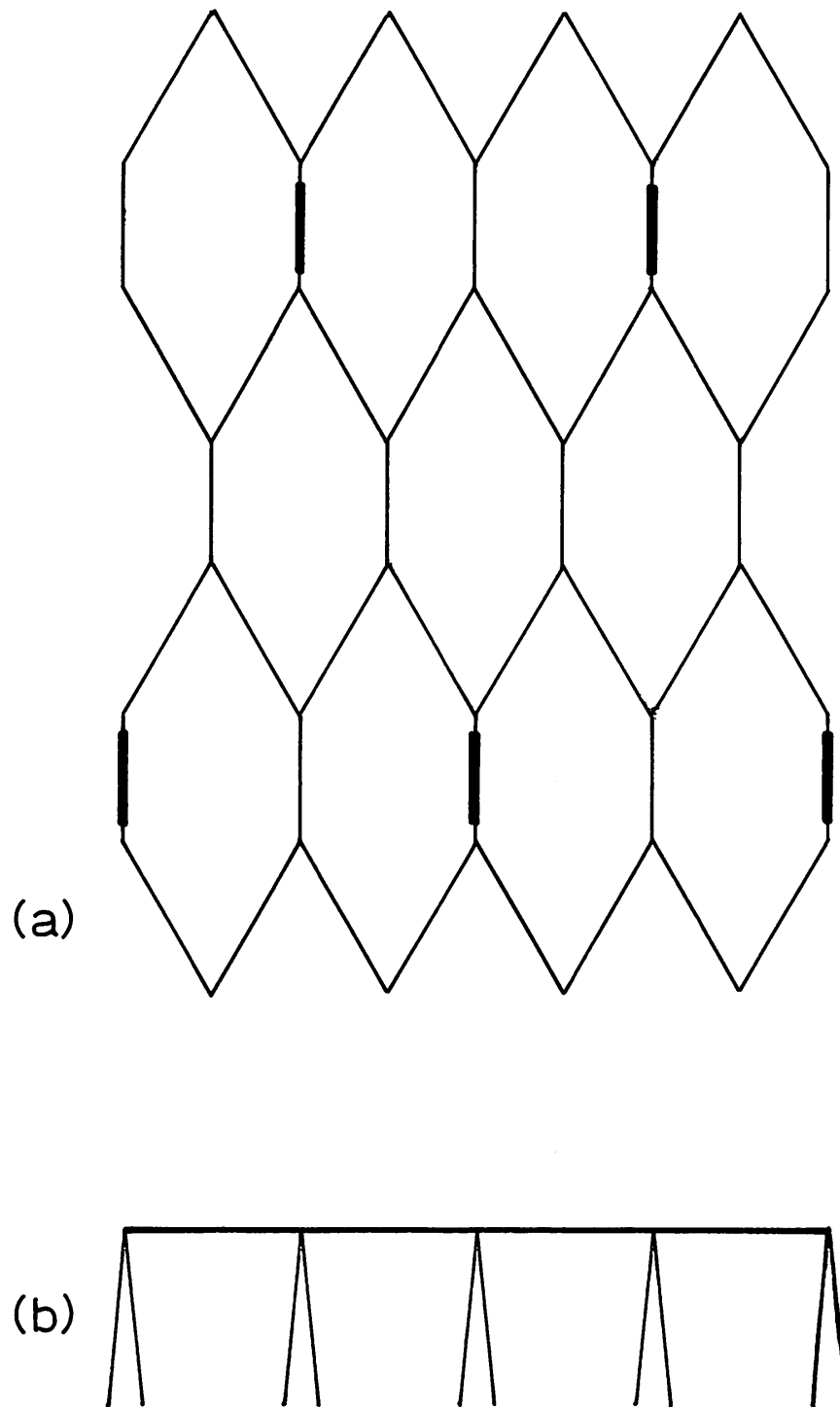
Fig. 3.3. Plan view (a) and side view (b) of the arrangement of plastic strips stapled onto chicken wire to simulate leaves.

3.2.5. Aboveground Volume Restriction (Experimental Treatment 78-Aboveground restriction)

Rather than allowing the plants to spread out in the rows, the tops of the plants were mechanically restrained to explore the possible reduction of the intercept of the thinning line by limiting the accessible space above ground. Pairs of stakes were placed at each end of a row. These stakes had attached pieces of tackless carpeting--a fierce array of tack points protruding at an angle (designed to hold down wall to wall carpeting). Pieces of 3/4" mesh black polypropylene netting, such as is used to keep birds off fruit trees, were then stretched between the posts and pulled taut, the tackless capret holding the stretched net in place. One such fence 60 tm high was placed on either side of the row with a 12 cm row space allowance. In this fashion, with only 12 cm instead of the possible 50 cm average per row, the aboveground volume accessible to the plants was reduced to roughly ¼ of controls.

3.2.6. Control for Aboveground Volume Restriction (Experimental Treatment 78-Aboveground control)

As a control for the possible shading effects of the two layers of mesh per row, a pair of stakes was placed back to back midway between the rows and the mesh stretched between them. No space was taken up by the arrangement since the two layers of mesh were tight against one another.

3.2.7. Underground Volume Restriction (Experimental Treatment 78-Underground restriction)

In a fashion analogous to the 78-Aboveground restriction experiments, the restraint of access to belowground volume was achieved. For each row a trench was dug 12 cm wide and about 40 cm deep. The trench was then lined with 4 mil polyethylene sheeting. The bottom of the

sheeting was slashed to allow drainage and the trench was filled again
and planted down the center of the trench.

3.2.8. Shallow Soil (Experimental Treatment 78-Shallow soil)

Two pairs of plots were manipulated to produce a shallow soil under
otherwise similar field conditions. The two treatments coming under this
heading differ only in the depth of the soil accessible to the plants.
Plots were excavated to depths of about 40 and 30 cm. The bottom of the
pit was leveled off, ditched slightly around the perimeter, and a sheet
of 4 mil polyethylene used to line the pit. The plastic was slashed to
allow drainage around the perimeter. On the top of the polyethylene,
pieces of perforated 4" PVC drainage tile were laid running the 3 m
length of the plots. Above the drainage tile came another layer of
polyethylene which was slashed in the depressions between the curved
surface of the drainage tile. The soil which had been removed was
returned to the pits and the remaining piles of earth (displaced by the
drainage tile) were leveled so as not to shade the plots or substantially
reduce the amount of visible sky. The soil in the resulting plots
averaged 15 and 25 cm. Following leveling of the surface, the plots
were planted.

3.3. Summer 1979: Greenhouse Populations of Buckwheat and Oats

In 1979 a series of experiments was undertaken in the greenhouse
to allow better control of the environment in which the plants were
growing. The experiments were aimed primarily at manipulation of the
value of k_3 in the thinning populations. The experimental species was

buckwheat, the species used by Yoda et al. (1963) in their most compre-
hensive experiment; one experiment used oats. Chard was not used again
because of its deep tap root which could not be accommodated well in a
relatively shallow pot. Oats were selected for their ability to tiller
and relatively synchronous flowering and fruiting. Plants were grown in
perlite in 10" diameter circular bulb pans. Perlite is a light weight
aggregate which for manipulation of non-trace mineral nutrients is com-
parable to sand (Hewitt 1952). It comes from a volcanic rock which has
been heated causing it to expand into particles having a specific gravity
somewhat less than one due to entrapped air bubbles.

Part of the reason for the choice of perlite was a desire to
measure root masses. Perlite has a relatively large particle size and
the pores are generally smaller than the rootlets so penetration is
minimal. Thus perlite can be separated from the roots. Another major
advantage of perlite is its light weight. This property makes it easy to
handle, reduces tearing of the roots when first removing plants from the
medium, and allowed development of a gravimetric technique for the
determination of root masses. Following harvest the perlite and roots
were dried and weighed together. The difference between this value and
the weight of perlite initially present was taken and the resulting
weight changes of blanks (pots without plants) used to estimate root
weight. Since perlite is of such low density, the mass of perlite could
readily be ascertained with a precision allowing detection of the weight
change due to root growth. The gravimetric method of estimation was only
attempted on pots grown at high densities or with mature plants so that
a reasonable mass of roots could be expected to be present.

To prevent loss of perlite through the drainage holes in the bottom of a pot a square of fine nylon bridal veil was placed in the bottom of the pot. Perlite was then put in the pot, filling it to the shoulder (about 3 ℓ). Seed was sprinkled onto the perlite and an additional half liter of perlite added to cover the seed. To improve germination, each pot was watered with a misting nozzle and a piece of thin polyethylene (actually a 1 gal plastic BAGGIE TM) placed against the surface of the perlite to maintain the humidity in the upper layers of the aggregate. The buckwheat was planted 30 June 1979 and the oats 22 June 1979.

Measurement of growing density and biomass was accomplished by direct counting, following harvest at the "soil" surface, drying, and weighing the tops. At low initial densities, root masses were estimated by rinsing the roots free of perlite, drying and weighing them. I found serendipitously that roots washed cleaner if harvested pots were allowed to stand at room temperature for several days before rinsing. The tiniest rootlets would start to decompose and the perlite would have still less tendency to cling, making the rinsing operation more consistent and less exasperating. Perlite has the delightful property of being highly visible on the roots. What mass remains is bound to be small because of the low density of the perlite. The result is a peculiar psychological contrast with the use of sand, however. Sand also has a tendency to cling, but because of the fine particle size, and its invisibility when wet, one is quickly satisfied that the sand is rinsed off. A comparable amount (volume) of perlite remains visible and though far less massive than the sand would be, remains a source of concern because it is still visible. By allowing the pots to stand for about a week, the tendency

of the perlite to cling virtually disappears and with it the frustration of the rinsing process for pots having low-density populations.

At high densities no attempt was made to separate roots from perlite. Instead, the gravimetric technique described above was used. Although initially pots and contents were oven dried, it was found that the drying rate was very slow in the plastic pots and so pot contents were transferred to paper shopping bags ($\frac{1}{4}$ bbl) before drying. Drying times to constant weight remained quite long, however, requiring ten days to two weeks to lose the last couple of grams. Some difficulty was experienced achieving constant weight because of a tendency of the dry paper bags to absorb water from the air. This problem was substantially reduced by allowing bags with contents to cool a standard $1\frac{1}{2}$ hours before weighing, and by emptying the bags and weighing them (as tare weights) within $\frac{1}{2}$ hour from the initial weighing with their contents. The dust produced by emptying the dry perlite from the bags precluded weighing a bag and contents, immediately emptying it, and weighing it again, since weighing and emptying had to take place in different rooms.

After an initial week to germinate under the plastic, pots were watered on Monday and Friday with Hoagland's Solution (Hoagland 1950, Solution II) and with tap water on Wednesday (and Saturday in the hottest part of the summer as needed).

The experiment with oats was designed to examine tillering and a possible departure from the -3/2 thinning line as seed set occurred. The observation in planaria that just prior to reproduction, the population dropped away from its "thinning line" motivated the experiment. The departure from the thinning line suggested that propagule biomass is not

proportional to the resource base, in violation of an important approximation in the derivation of the thinning relation. Propagules are apt to be rich in resources per unit biomass.

Six planting densities of the oats were used: 14; 44; 140; 440; 1,400; 4,400 seeds per pot or equivalently 280; 880; 2,800; 8,800; 28,000; and 88,000 seeds per m^2. Harvests were made at two week intervals starting 10 July 1979, for a total of 7 harvests. Each treatment and density was represented by three replicates.

On 16 July 1979 the beginning of an infestation of army worms was noted, and on 20 July 1979 and again on 3 August 1979 the plants were sprayed with Malathion 25. This successfully controlled the outbreak.

The oats were watered and fertilized on the standard regimen with full strength Hoagland's solution applied from a beaker. The initial growth of these populations was in the weed control greenhouse #3 at Guterman Bioclimatic Laboratories, space made available to me by Dr. Peter Minotti of the Department of Vegetable Crops. On 15 August 1979 the remaining pots were removed from that greenhouse and taken to the greenhouse at Langmuir Laboratory where the Buckwheat experiments were underway.

Two sets of experiments were performed with buckwheat. The first was begun on 30 June 1979 and consisted of four parts addressing the following questions:

1) 79-Yoda. Can the results of Yoda et al. (1963) with buckwheat be reproduced in a greenhouse setting?

2) 79-Shallow soil. Does a shallow soil change the parameters of thinning?

3) 79-Fertilizer. Does a much reduced fertilizer level (0.2 vs. 1.0

Hoagland's Solution) reduce the value of k_3?

4) 79-Change in fertilizer. Can the value of k_3 be shifted partway

through a population's development by shifting the fertilization

regime?

3.3.1. Replication of Experiments of Yoda et al. (1963) (Experimental Series 79-Yoda)

In an effort to create a data set similar to that used by Yoda et

al. in their 1963 paper, seed was sowed at six densities: 12; 38; 120;

1,200; 3,800 seeds per pot. Each density was represented in triplicate

and there were 5 harvests at two week intervals starting 20 July 1979.

3.3.2. Shallow Soil (Experimental Series 79-Shallow soil)

This treatment used 1/3 the perlite as the standard pot (1 ℓ) under

the seed making a total depth in the pot about $\frac{1}{2}$ that in the controls

since the seed was buried under the usual $\frac{1}{2}$ liter of perlite to insure

comparable germination. This amounted to reducing the soil volume to

half that of controls; it also was an attempt to investigate whether a

very shallow soil might behave as a two dimensional resource rather than

a three dimensional resource. The lowest density and first harvest were

omitted.

3.3.3. Low Fertilizer (Experimental Series 79-Fertilizer)

Designed to shift the -3/2 line downward by reducing the resource

base, these pots were watered with 0.2 Hoagland's solution. All harvests

and densities were represented.

3.3.4. Change in Fertilizer (Experimental Series 79-Change in fertilizer)

This experiment was specifically designed to test the response of a population to a shift in the resource base. These pots were initially grown with 0.2 Hoagland's. One week before the third harvest they began to receive full strength Hoagland's solution and they were harvested at the fourth and fifth harvests. The lowest growing density was omitted.

The second set of experiments with buckwheat was another attempt to examine different fertilizer treatments. It was nearly identical to the Yoda, Fertilizer pair of experiments described above. They were planted on 14 September 1979, and received half the nutrient supply (0.5 and 0.1 Hoagland's solution). Extending into early December, these experiments were confounded by the effects of reduced light, day length, fertilizer, and temperatures. The same six densities as in the previous set of experiments were used and the harvests were again at two week intervals starting 15 October 1979. Because of the lowered temperatures, watering was cut back to Monday only with fertilizer solution.

3.4. Methods of Data Analysis

Because I am operating from an axiomatic theoretical foundation which predicts certain outcomes to experiments, I have departed rather significantly from the style of curve fitting of previous workers. A model has been presented which is understandable both in terms of its basic conception and in terms of the approximations involved in the predictions it makes. Consequently, data have been examined not in terms of what regression line (White and Harper 1970; Yoda et al. 1963) or

principal axis (Mohler et al. 1978) from a Principal Components Analysis best describes the data, but rather what line of slope -3/2 or -1 best describes the data. The values of k_3 and k_2 which thereby arise may be directly interpreted within the context of the theory and any tendencies toward systematic departures from either of the slopes may be seen from inspection of the graphs. Departures of observation from prediction do not require scrapping the theory altogether, but suggest a careful re-evaluation of the underlying approximations and a search for the circumstances which may make the approximation poor.

Data analysis has been largely graphical. Graphs communicate well, and experience in replicability and precision of measurement in this area convinces one that graphs have more than adequate precision to represent the relationships to be emphasized. Furthermore, they preserve information about peculiarities of the data which can yield important insights impossible to obtain from numerical summaries.

Some controversy may arise as to how to treat replicates. The standard temptation is to take some kind of average, but what kind? Arithmetic, Geometric and Harmonic means could each be used with some justification. Here again the theory provides an answer and an unexpected one. Since the theory is describing constraints on populations, replicates are repeated attempts to observe where those constraints lie. Since counting and dry weight measurements are both precise measurements having low variance in comparison to the variable influences on observed yields of mold infestations, insect damage, or lodging of tops, an appropriate estimate of where a constraint lies comes from that replicate which is farthest in the direction in which the constraint must lie; the

non-parametric maximum likelihood estimator of the highest value of k possible is the largest value of k observed among the replicates. No numerical averages were taken among replicates; rather a comparison of magnitudes of k_2 or k_3 is made and the replicate having the largest value is selected. Figure 3.4 shows a simulated data set graphed in its entirety and then graphed using this estimation technique to extract the most salient information from the replication performed in that experiment.

1000

100

10

1

0.1

0.001

0.0001

MEAN INDIVIDUAL WEIGHT

1   10   100   1000

GROWING DENSITY

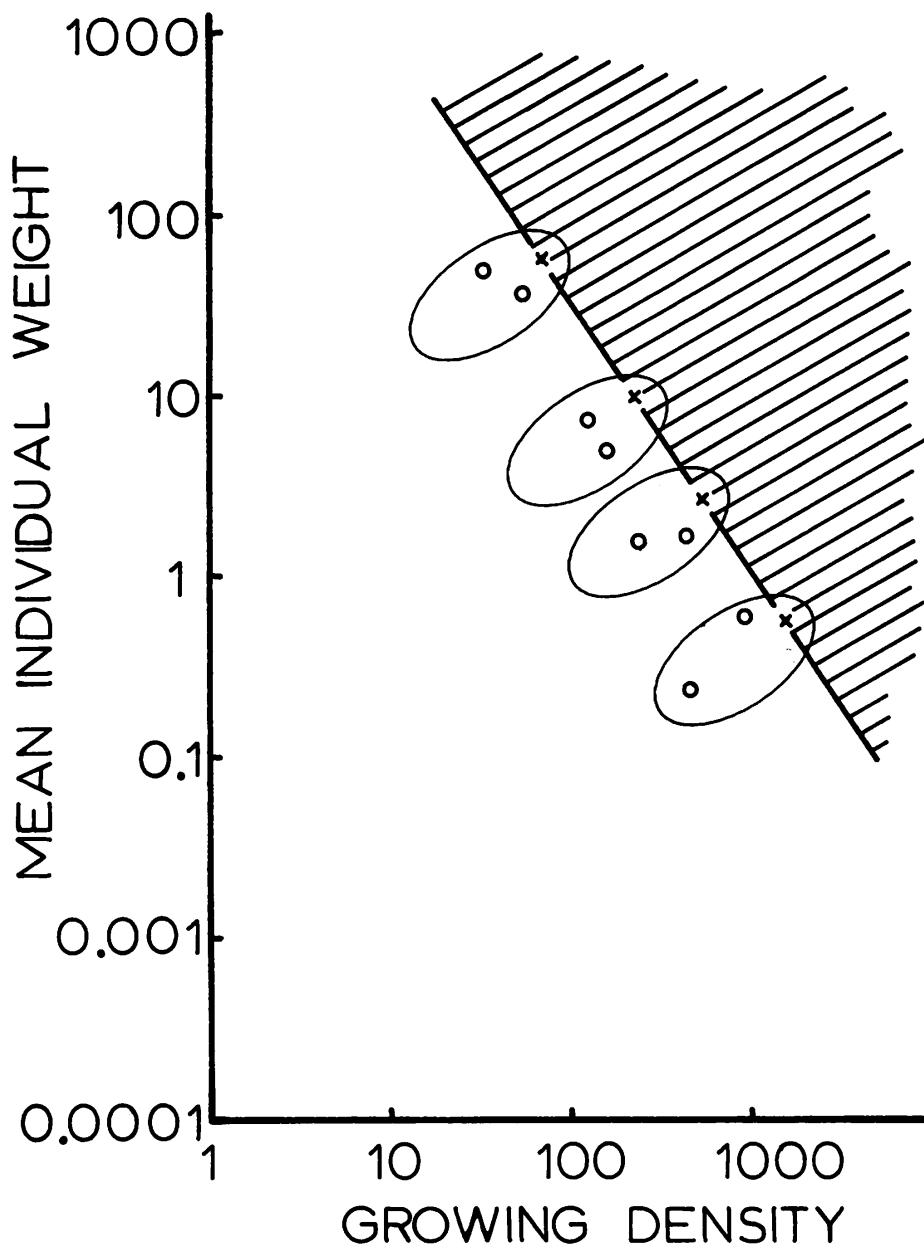Fig. 3.4. Treatment of replicate samples (circled) from a thinning experiment having four sampling dates. The position of the -3/2 constraint above which a population may not lie (shaded region bounded by a line of slope -3/2) is estimated by selecting the replicate farthest in the direction of the constraint (x) (simulated data). This is the nonparametric maximum likelihood estimate of the position of the constraint.

4. RESULTS/DISCUSSION

--There is something fascinating about science.
One gets such wholesale returns of conjecture
out of such a trifling investment of fact.

--Mark Twain, Life on the Mississippi

Discussion of the experimental results is divided into seven principal areas of inquiry:

1) Does changing the richness of the exploited volume change the value of k_3?

2) Does changing the size of the volume exploited by the population change the values of k_3, and the slope of the thinning line?

3) Does the variation in size in a population presage the amount of thinning?

4) How does a two-species population behave during thinning?

5) Does growth under shade cloth change the slope of the thinning line to -1?

6) Does changing the light level change the value of k_2 in the constant yield relation?

7) Does the allometry of plant parts, particularly roots and leaves, follow patterns predictable from the dimensionality of the resources the parts exploit?

Technical problems rendered the results of some experiments inconclusive. These experiments are discussed briefly in Appendix B. The

78

section concludes with a discussion of the significance of the experimental results.

4.1. Richness of the Exploited Volume

One group of thinning experiments attempted to manipulate the value of k_3 by changing the richness of the exploited volume. The -3/2 thinning relation was produced from the theory by considering the individuals to be partitioning the available volume, and thus, the available resources. The derivation also predicts a change in the intercept of the thinning line following a change in the richness of the volume being partitioned. The effects of fertilization have been examined by several workers (Yoda et al. 1963, Harper 1976, White and Harper 1970), who have stressed (1) that the regression lines maintain a slope very close to -3/2 for all the fertilizer treatments, and (2) that thinning is faster (there is a higher rate of mortality) in populations with abundant fertilizer. In their reanalysis of data from Yoda (1963), White and Harper (1970) present a graph which shows these two observations particularly well. A closer look at their graph suggests a further observation which they did not make: points on the graph derived from low fertilization levels tended to lie below the regression line whereas data from the high fertilizer treatments tended to be consistently above it. This tendency is to be expected from the present theoretical analysis, since the physical volumes accessible to the plants are comparable but differ in their richness. Although between populations the resource bases may differ, within a population, the partitioning of the volume from which resources come implies a comparable access per unit volume to the available resources.

In 1979 I set up the greenhouse experiments to allow for emphatic differences in the fertilization levels in the populations. By using perlite, I was starting with a virtually inert growing medium, and by watering with nutrient solution of different concentrations I was able to assure that the available nutrients in the soil volume were well regulated. The two nutrient concentrations used differed by a factor of five.

The gravimetric estimates of root weight for buckwheat were unsatisfactory because the root masses involved were small compared to the variability of accumulated weight in the pots "raised as blanks" having no plants in them. Evidence from weighing plants directly and from the pots from which roots were rinsed free of perlite suggested that the root weights in the buckwheat seldom exceeded 10% of total plant weight. Furthermore, the log-log regression of root weight on total plant weight is well described by a line of slope 1, so the approximation of plant weight by aboveground parts is justified and only aboveground parts are considered here.

Fig. 4.1 shows data from populations grown with full strength and 0.2 strength Hoagland's solution. The graphed points come from both treatments showing the highest yielding replicates in populations which have undergone thinning. This experiment shows the effect of a severe limitation of nutrients--the depletion of the richness of the soil volume. The line of slope -3/2 continues to describe the data well and the reduction of the value of log k_3 from 4.837 ± .048 S.E. to 4.622 ± .035 S.E. is substantial.
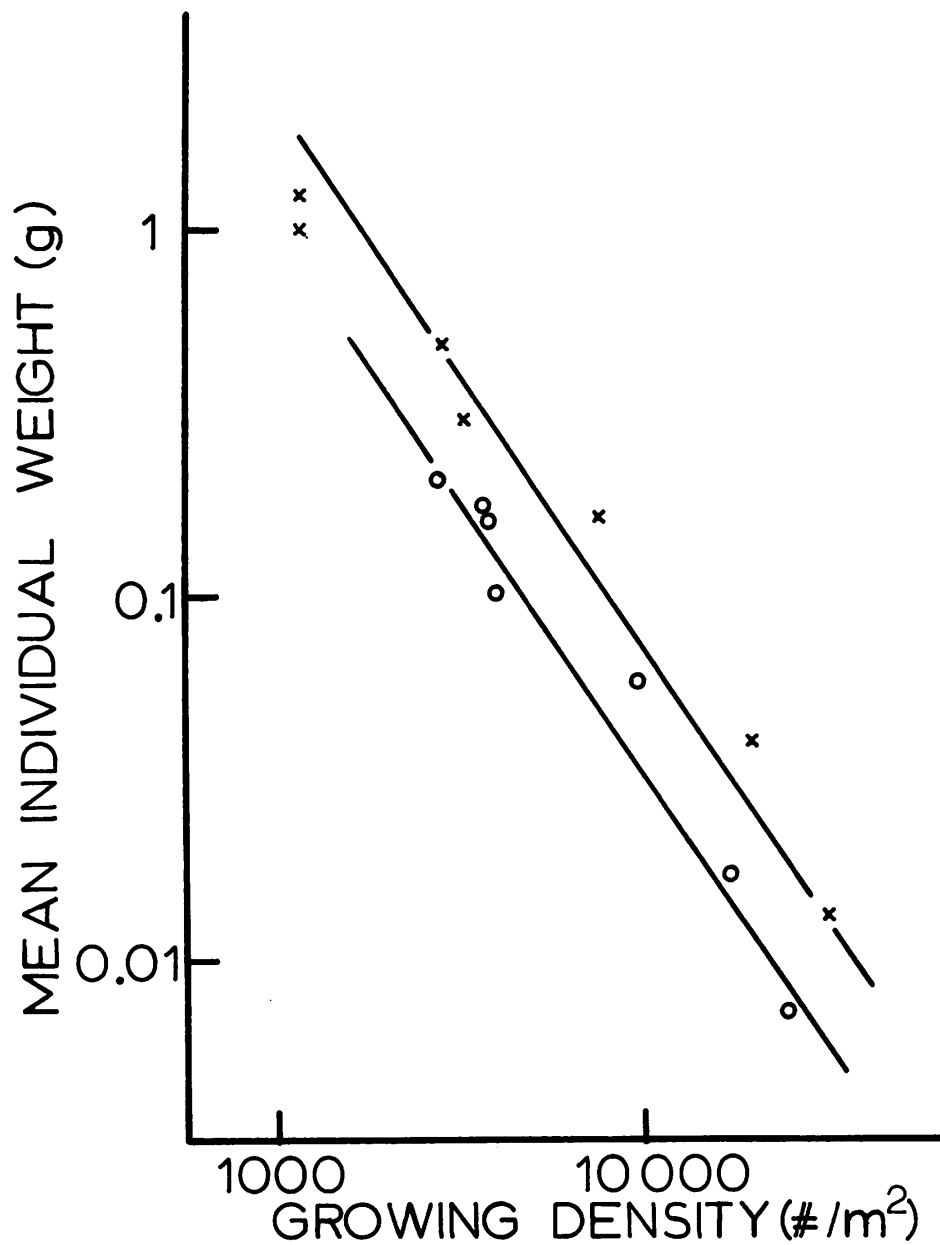
Fig. 4.1. The log-log relation between mean individual weight w
and growing density p for self thinning buckwheat populations grown in
perlite with full strength (x) and 1/5 strength (o) Hoagland's solution.
Best fit lines of slope -3/2 are shown for each treatment.

4.2. <u>Volume of Exploitation</u>

Several experiments were performed to influence the volume of the environment available for exploitation by the plants. The experiments address three questions:

1) Does reduction of the accessible volume above ground reduce log k_3, the intercept of the -3/2 thinning line? (78-Aboveground limitation, 78-Aboveground control)

2) Does reduction of the laterally accessible volume in the soil reduce log k_3? (77-Roots)

3) Does reduction of the vertically accessible volume in the soil reduce log k_3 or perhaps even the steepness of the thinning line? (78-Shallow soil, 79-Shallow soil)

4.2.1. <u>Above Ground</u>

The mesh used to restrain the plants above ground was successful in keeping the plants confined to the intended space, roughly 25% of the space available to the control populations. An examination of the graph (Fig. 4.2) shows that the experimental and control populations behaved very similarly with a slight tendency for the experimental populations (78-Aboveground limitation) to lie below the control (78-Aboveground control). The mean values of $\log_{10} k_3$ for the two populations once they were well into thinning (the last five of the eight harvests) were 4.07 ± .04 S.E. and 4.14 ± .04 S.E. for 78-Aboveground limitation and 78-Aboveground control, respectively, suggesting that while k_3 may be reduced by restraining growth in this fashion, the effect is small.

One complication in this and the other experiments in 1978 is the extent to which the populations could fully exploit the aboveground

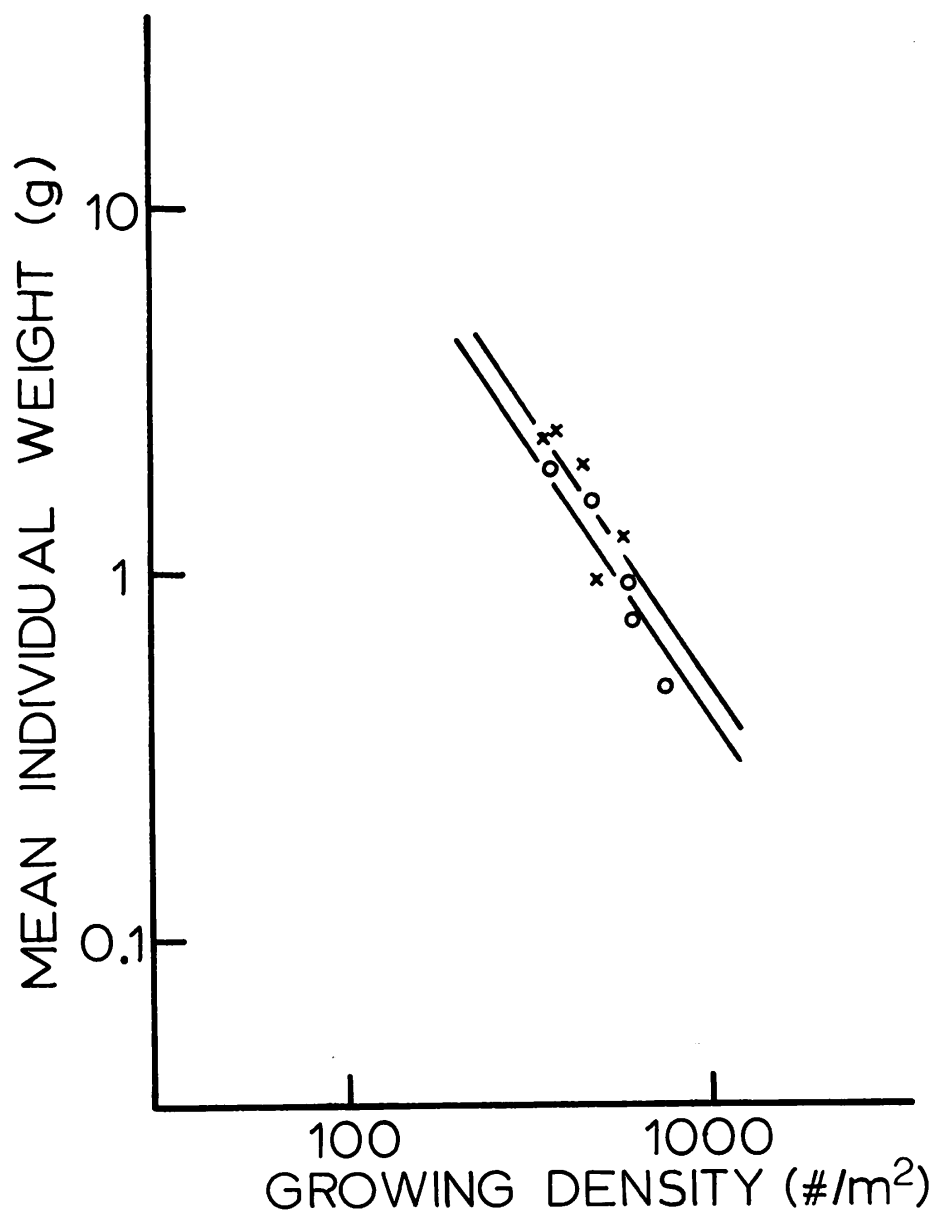Fig. 4.2. The log-log relation between mean individual weight w and growing density p for self thinning swiss chard populations grown in the field. Treatment populations had the accessible aboveground volume restricted to ∿25% of controls by plastic netting (o). Controls had netting arranged to provide comparable shading but not restrict the volume (x). Best fit lines of slope -3/2 are shown for each treatment.

space. Since the growth form of swiss chard is an erect rosette, there
was much bare ground between the rows which was not occupied until late
in the season in the control plots while in the experimental plots, full
coverage of the ground, in plots where that was intended, often was not
achieved. Moreover, thinning, in terms of population reduction, was
somewhat less pronounced this year than in the broadcast seeded plots of
the year before. As mentioned earlier, the -3/2 thinning constraint
need not be viewed as a direct cause of mortality in the population,
rather it may be seen as a limitation on the growth of the survivors,
with mortality falling on individuals for whatever proximate reasons.
One conspicuous difference between the broadcast seeded plots of 1977 and
the row plantings of 1978 was the apparent vigor of the small individuals
in the population. Whereas the suppressed plants of 1977 were often
spindly and flaccid, even under good moisture conditions, those of 1978,
growing in rows, were much more robust. The combination of the growth
form of the swiss chard with the row planting pattern allowed small indi-
viduals to persist. Doubtless light from the side was not being filtered
out as effectively by the taller plants. The effect was reminiscent of
larger trees in a hedgerow and a lush growth of shrubs and herbs at their
bases, in contrast to the relatively sparse understory in an extensive
closed forest.

The pattern of plant placement plays an important role in refining
the descriptions afforded by models of plant growth which deal only with
average growing density. Wiley and Heath (1969) warn of its general
importance in models of plant populations while Mack and Harper (1977)
examine the effects on growth in the context of neighbor effects. Mead

(1966) describes a relation between individual plant growth and the eccentricity of the polygon of space surrounding an individual. It should be possible to refine predictions based on -3/2 thinning and the constant yield relation by taking such aspects of pattern into account.

Caveat in Interpreting Results from 1977

In 1977 plant weights were estimated by regression of total plant weight on number of leaves and length of the longest leaf. Although the values of R^2 were consistently high, the Root Mean Square (RMS) error of the estimates was found to imply a factor of two as the average error for the estimation of the biomass of an individual plant, a rather grim record and a rude awakening to the imprecision of such methods (Fig. 4.3). This implied that the efforts to control the precision of the size estimates by controlling the variance of the estimates of leaf length and number of leaves in the population were largely futile since a far more important contribution to the variance comes from the looseness of the allometric relations themselves. Estimation problems as described above would cause more scatter in the graphs yet not necessarily jeopardize estimates of the slopes and positions of lines. Another problem arose, however, which compounded the difficulties but did raise some interesting observations about allometric relationships. The values of the regression parameters can change with time (see also Hutchings 1975). While most pronounced in the swiss chard, the mustard showed some variation in its regression parameters whose significance cannot be ruled out because the necessary subdivisions of the sample for determination of the parameters result in minute sample sizes. The case of swiss, however, is
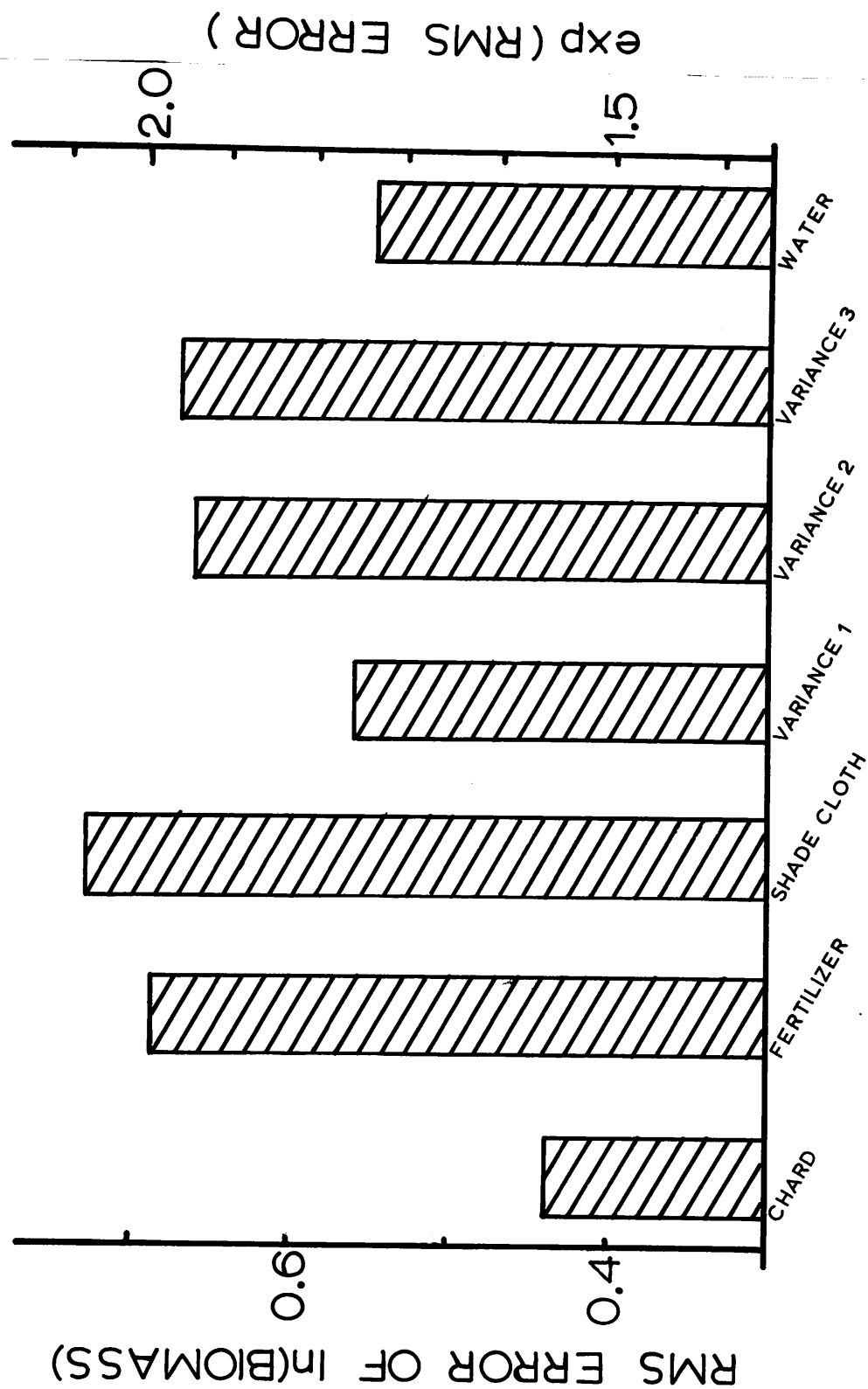
Fig. 4.3. Root Mean Squared (RMS) errors in the allometric estimation of biomass from leaf length and number of leaves for swiss chard and various treatments of leaf mustard (arranged alphabetically).

clear (Fig. 4.4), showing strong secular changes in all three regression parameters. Since points along the thinning line are produced sequentially in time, a time-dependent bias can seriously distort the apparent slope of the line passing through the points. Results from the summer of 1977 therefore must be interpreted cautiously; the relative positions of lines and relative slopes should remain useful indices of relationships, but exact values are questionable.

The problem of time dependence of the values of regression parameters is understandable in retrospect since shape relations within plants are shifting as they mature; the petiole of swiss chard thickens considerably as it matures and leaf length understandably changes its importance as a predictor of plant weight. Such shifts in plant allometric relations are another manifestation of the shortcomings of the earlier thinning models; plant shape does change during development. Unfortunately there is no reason to suspect that "it should all come out in the wash" with the allometric relations. The -3/2 thinning process is empirically more robust than the earlier theory could predict. This robustness does not extend to the allometry of swiss chard, is questionable in mustard, and raises important questions about the ease with which the method of allometric biomass estimation may be applied in other species.

4.2.2. Below Ground--Laterally Accessible Volume

The experiment limiting belowground volume by planting between cans suggests that k_3, the intercept of the -3/2 thinning line may be manipulated by explicitly changing the volume accessible to roots. Fig. 4.5 shows that the thinning lines in both the experimental and control
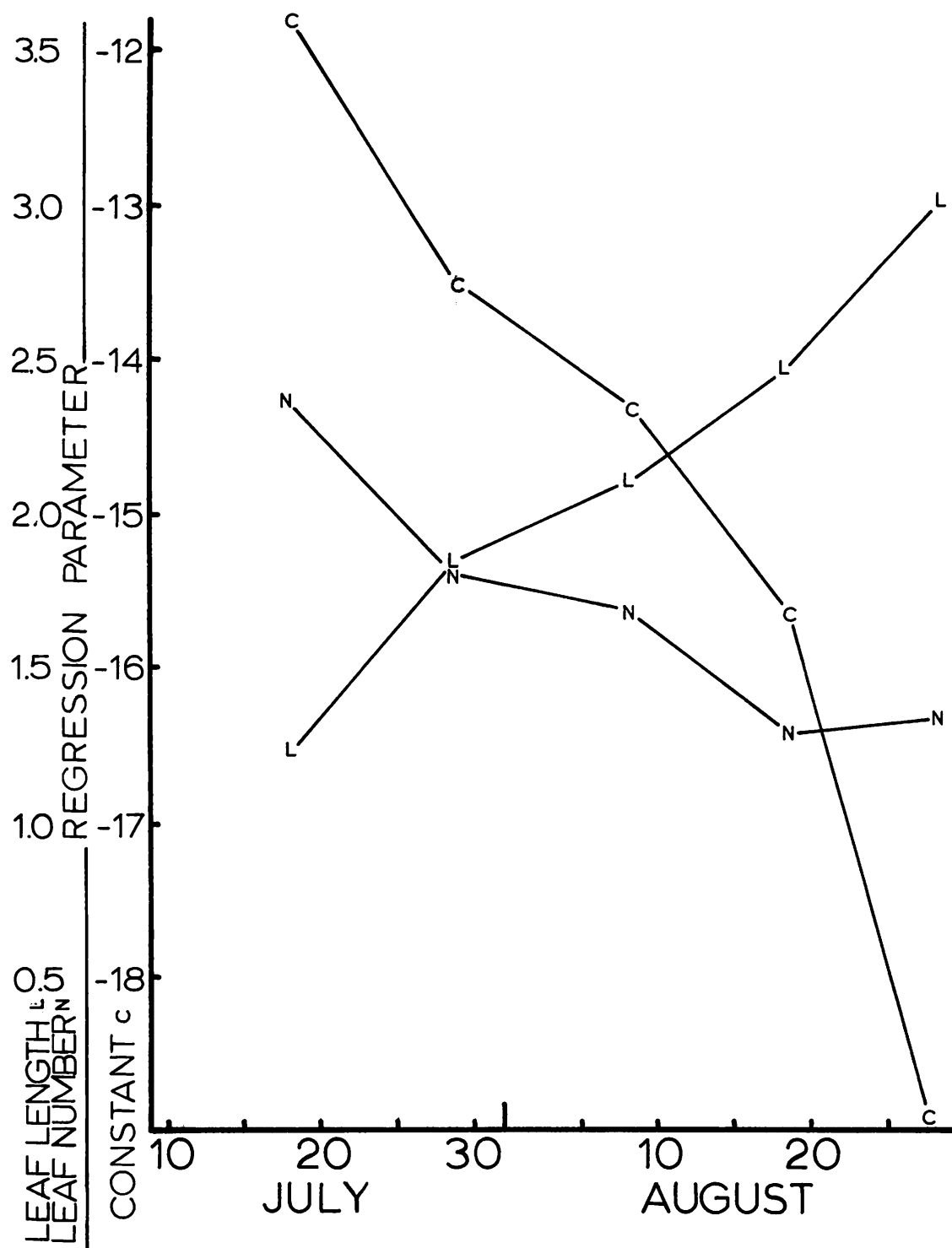
Fig. 4.4. Relation to time of regression parameters for the allo-
metric estimation of biomass of swiss chard. Regressions were log-
transformed multiple regressions based on leaf length (L), number of
leaves (N), and a constant term (C).
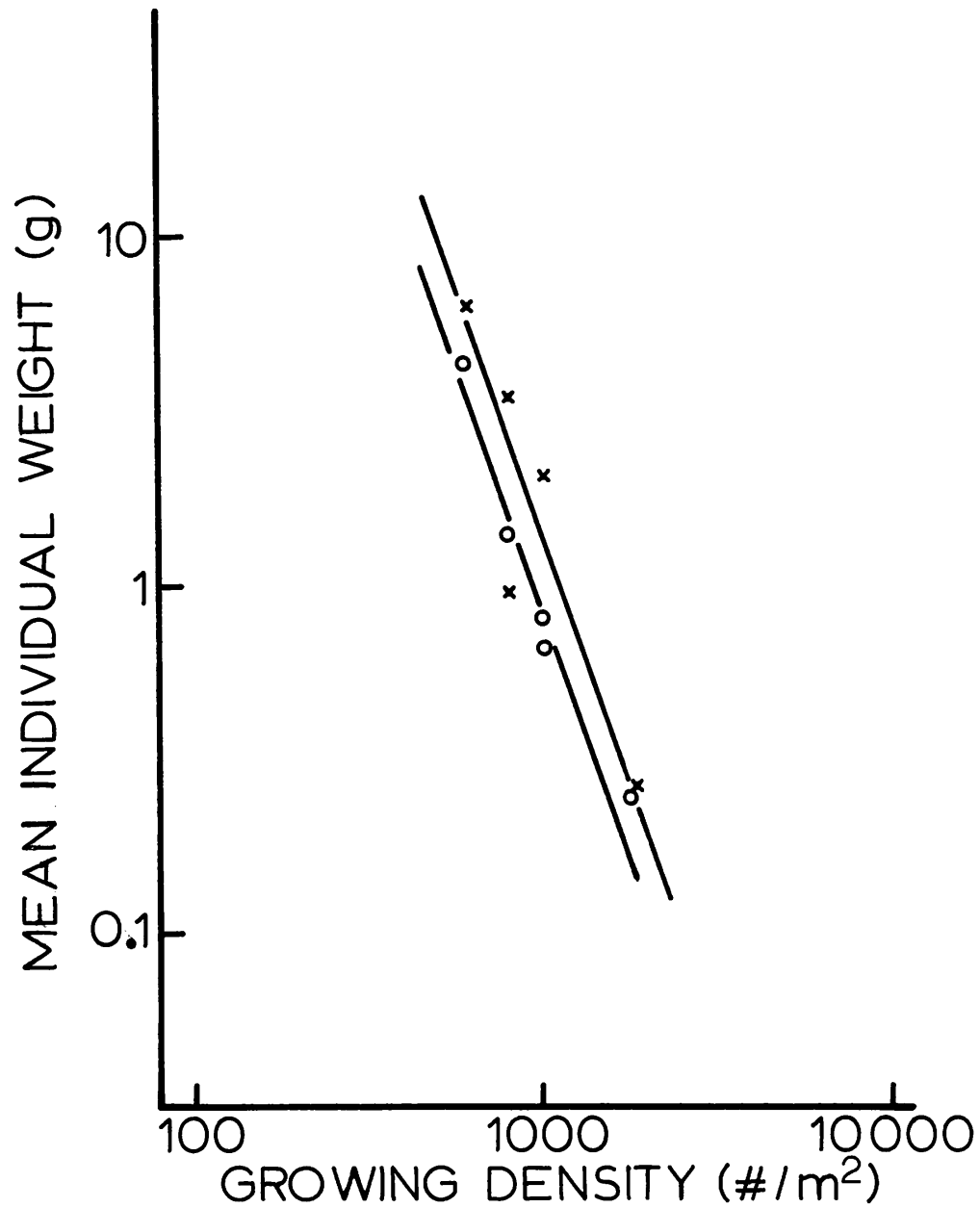
Fig. 4.5. The log-log relation between the estimated mean individual weight w and the growing density p for self-thinning populations of swiss chard grown in the field. The treatment population had the rooting volume laterally restricted by planting between cans placed in the soil (o). The control population had unrestricted rooting volume (x).

populations were quite regular and that there is a tendency for the experimental population to thin along a line lying below that of the control. The lines on the graph are regression lines of common slope, derived from the data from sampling dates two through six. Although the mean vertical displacement on this graph is small, so was the volume of soil displaced by the cans, which left about 2/3 of the soil volume accessible to the plants. The mean values of log k for the populations with and without cans are 7.27 ± .05 S.E. and 7.40 ± .07 S.E. for a mean displacement of .13. This is a separation greater than the sum of the standard errors for k of the two treatments, suggesting that k can be manipulated by restricting the laterally accessible volume below ground. If the displacement of the lines were to follow the volume fraction precisely, accessibility of 2/3 of the soil volume would correspond to a displacement of .18 = $|\log 2/3|$ units in the value of k_3. Although the meaning of k_3 itself is tenuous given the problems of bias in the estimation of the biomass, the mean values of log k_3 for harvests 2 through 6 were 3.427 ± .101 S.E. and 3.588 ± .132 S.E. for a mean displacement of .161, close to the predicted value of .18.

4.2.3. Below Ground--Vertically Accessible Volume (Shallow Soil)

The final group of experiments attempting to manipulate the soil volume directly examined the effect of a shallow soil. The motivation for this treatment was twofold. Firstly, a shallow soil is another relatively straightforward way to change the soil volume. Secondly, a sufficiently shallow soil might shift the exploitation by the plants from a response showing a three dimensionality of the soil to one in which the exploitation was effectively two dimensional.

In 1978 I arranged plots with shallow soils. These populations did
not exhibit anything like the normal pattern of thinning, perhaps because
of row arrangement of the resulting stunted plants, or disruption of the
water regime. The populations grew up and stagnated completely. Highest
yields occurred weeks before the last harvest and all densities were in a
very narrow range of values compared with the controls. The populations
displayed a totally unexpected lack of dynamic, thinning neither accord-
ing to the -3/2 litany nor with any other regularity. The scatter of
points indicates populations in stagnation. Yields were suppressed in
both the shallowest and deeper-soiled populations. The greatest suppres-
sion occurred in the shallowest soil where yields were 69% and 55% of
yields in the controls. The mean values of log k_3 for the last five
harvests were also significantly (at the 5% level) less than those in the
control, with values of 4.009 ± .036 S.E. and 4.075 ± .045 S.E. in the
shallowest and deeper soils in contrast to a value of 4.162 ± .045 S.E.
in controls.

The buckwheat populations grown in pots (79-Shallow soil) with half
the depth of perlite showed pronounced thinning presumably because the
watering regime was regular and the plants were not planted in rows.
While the regression line for all points derived from populations which
had thinned is not significantly different at the 5% level from a line
of slope -3/2, the pattern of thinning for the more mature populations
(ignoring the two lowest points on the graph) is significantly different
from -3/2 (Fig. 4.6). These populations, however, are described well by
a line of slope -1, the hypothesis of equality not being rejectable until
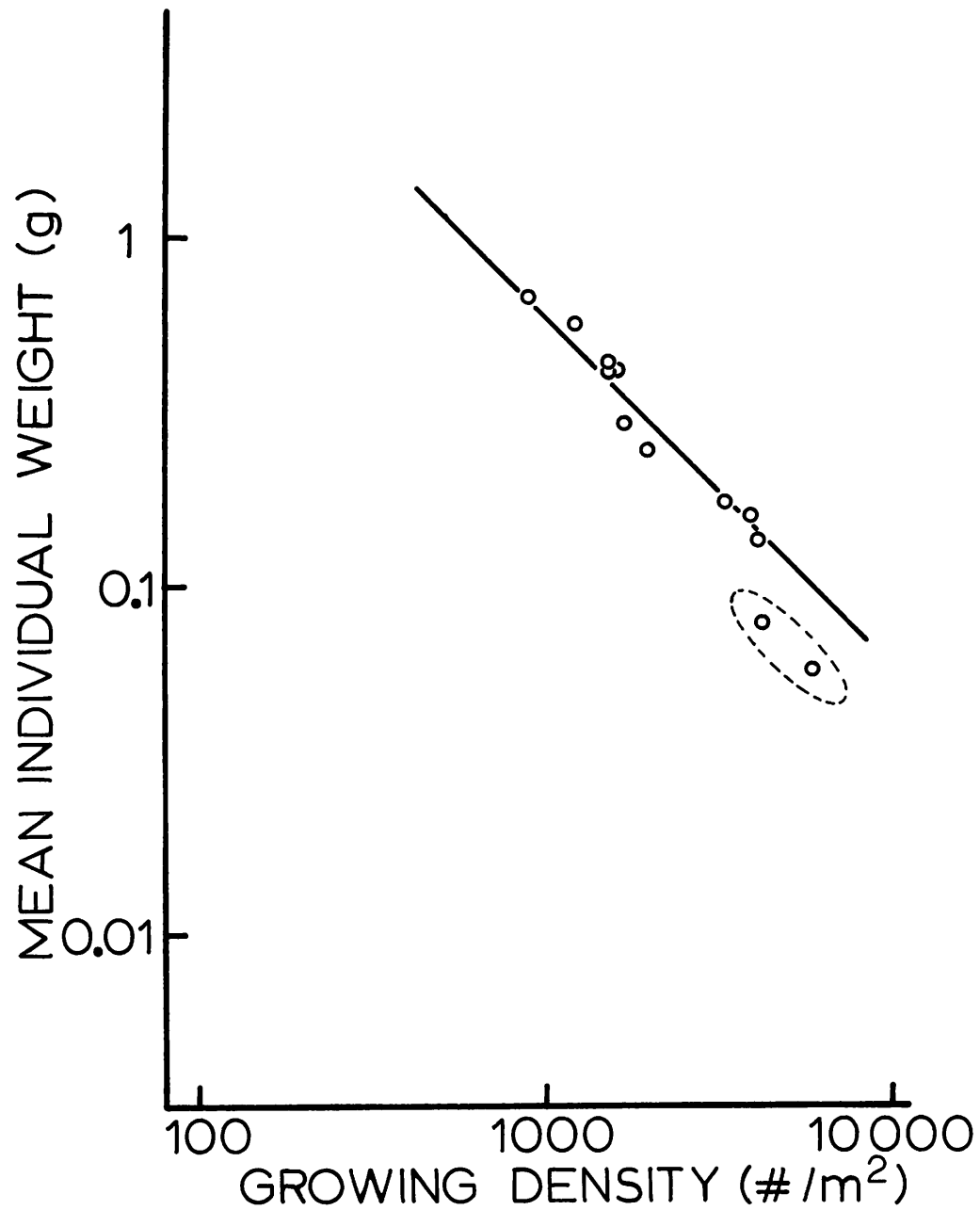about the 18% level of significance. In any case, the value of log k_3

Fig. 4.6. The log-log relation between mean individual weight w and growing density p in self thinning populations of buckwheat grown in shallow perlite. The youngest populations are circled and the best fit line of slope -1 for the remaining points is shown.

for the 79-Shallow soil experiment is substantially lower (4.436 + .026 S.E. vs. 4.837 + .048 S.E.) than that of the control populations receiving otherwise identical treatment.

A shallow soil unquestionably alters the pattern of thinning. The data from the present experiments attest to this but do not provide a clear picture of the overall effect.

4.3. The Variance of Size

The subject of skewed size distributions has been widely addressed (Yoda et al. 1963; White and Harper 1970; Ford 1975; Bazzaz and Harper 1976; Mohler et al. 1978). The attractive idea is often suggested that as the size distribution skews, the mortality in the population would naturally fall on smaller individuals. It is further suggested that an initial imbalance in size (skewness) gives rise to mortality and that as thinning proceeds, the amount of skewness stabilizes. Obeid et al. (1967) found an increased skewness of the size distribution with increasing planting density, a pattern which could readily give way to the initial mortality as suggested by White and Harper (1970). The source of the skewed size distribution has been addressed by several workers. Gottlieb (1977) found that genetic variation did not contribute significantly to the variation in the case of Stephanomeria exigua, an observation consistent with that of Ross and Harper (1972) working with Dactylis glomerata who attributed the establishment of a dominance hierarchy of individuals to differences in early emergence. Reader (1978) reports skew size distributions in natural mixed stands, but finds they are not lognormal. His conclusions may be suspect, however, if he actually used the

arithmetic mean as stated in the paper rather than the geometric mean when analyzing the skewness. Hozumi et al. (1968) also examined size-frequency distributions. Their analysis claims to be quite robust although the regularity they observe may be a product of the powerful smoothing effect of the cumulative distributions and averages used. Skewness of the simple probability density function is not readily observable in their approach.

A recurring theme in the analysis of size distributions is the presence of bimodality (Ford 1975; Mohler et al. 1978; Rabinowitz 1979). These descriptive observations have also given rise to mathematical models which produce bimodality from competitive interactions based on size, which influence growth rates in neighboring individuals (Diggle 1976; Gates 1978). All of these investigations are severely handicapped by the lack of good analytical methods to describe distributions having more than one mode.

In the present experiments, I attempted to manipulate the amount of variability in the size distribution by seeding a mixture of varieties of mustard. Aside from the desired differences in size, however, the varieties had different tolerances for low light levels; the Southern Giant Curled showed a consistent tendency to tolerate reduced light as evidenced by disproportionately greater representation among survivors in the populations growing under shade cloth and the suppressed individuals in the high density stands.

Estimates of size variability come from two sources; (1) the sample size at the time of sampling was chosen on the basis of one index of size variability; and (2) the measured variance of the logarithm of the

estimated biomass, derived from the biomass estimates of the measured
plants. Although these indices are correlated, the correspondence is
weak (r^2 = .314) and by either criterion the attempt to manipulate size
variability was not very successful (mean values for Variance 1, Variance
2, and Variance 3 were .846 ± .336; 1.185 ± .536; and 1.152 ± .409 for
s(log biomass) and 21.56 ± 13.81; 20.61 ± 14.52; and 24.56 ± 10.39 for
sample size).

It was clear from early in the experiment that different planting
densities favored different varieties. Although not quantified, the
effect was pronounced and mortality fell initially on individuals of the
suppressed variety or varieties. Thus, despite having seeded a mixture
of varieties, I had relatively pure stands within the first few weeks,
particularly at the highest density. The later pattern of thinning was
determined largely by the variety which survived. The initial mixture of
seeds was irrelevant.

Although thinning in more mature populations showed no detectable
pattern with variation in the size distribution of individuals, it is
interesting to note that virtually no thinning occurred at the highest
density in 77-Variance 2 between the first two sampling dates; s(log bio-
mass) went from .46 to 2.27, and by the third sampling period the popula-
tion had dropped to 1/9 of its previous value. Although most pronounced
in 77-Variance 2, a skewing of the size distribution followed by mor-
tality was generally observable in the initial stages of thinning at the
highest density in all four populations observed (Fig. 4.7) corroborating
the earlier suggestions that thinning may follow an initial development
of a strongly skewed (= large variance of log (biomass)) size distribution.
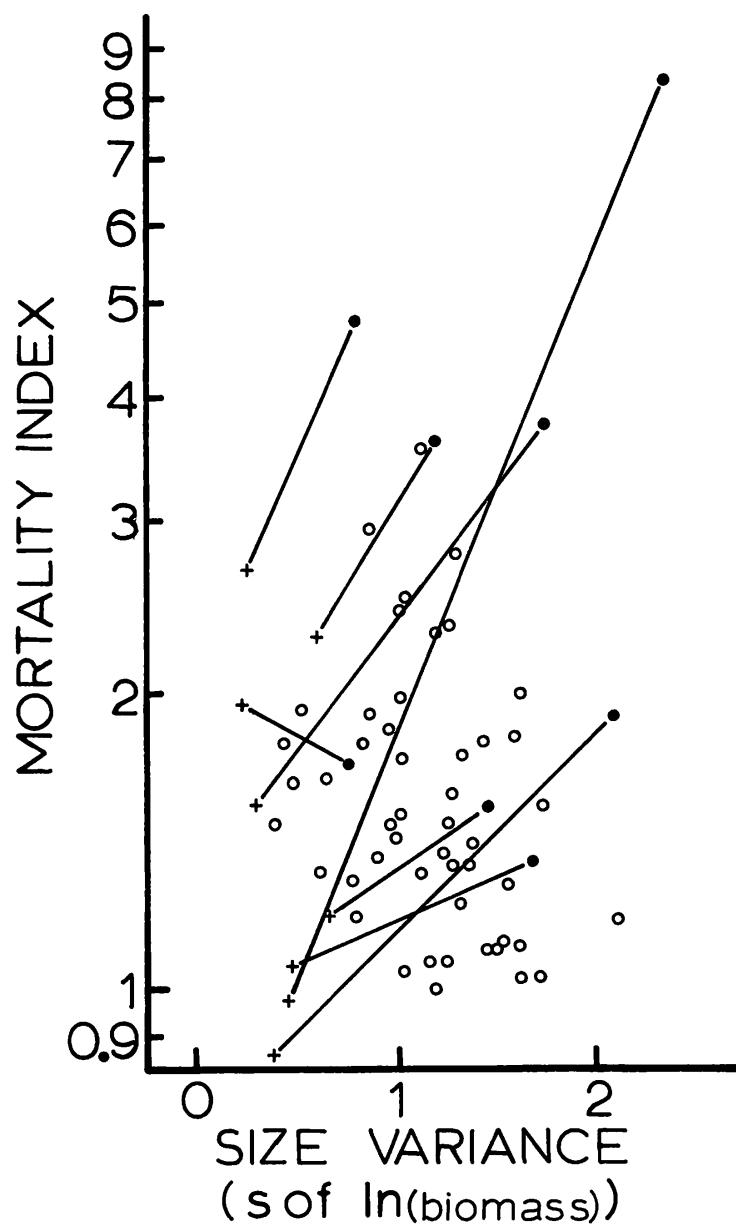
Fig. 4.7. The relation between the amount of mortality in leaf mustard (expressed as the ratio of the growing density in the population at time i, to the growing density at time i+1) and the amount of variation in the size of individuals (measured as the standard deviation of the natural logarithm of individual weight in the population at time i). Line segments connect the first + and second ● points from the same plot. A positive slope for such lines indicates development of a more skewed size distribution followed by greater thinning.

The subsequent pattern of the relation between the standard deviation of the log (biomass) distribution (s_i) at a particular time i, and the amount of mortality by a later time (p_i/p_{i+1}) is confused (Fig. 4.7). The confusion may be a result of measurement difficulties, for a population may thin in a fashion dependent upon the variability within it and yet the particular times of measurement prohibit its detection:

> Suppose a population were to be sampled and found to have a particular s_i. If there is considerable growth between sampling periods, the population could undergo a tremendous change in s_i in the interim with its (by hypothesis) associated thinning. The observed values of s_i, however, would be unrelated to the amount of thinning.

Growth rates in the present populations resulted in order of magnitude increases in average size between sampling periods, and the postulated pattern could thus easily have escaped detection. In the initial growth of the populations, however, all the individuals are forced to start with comparable sizes due to comparable seed reserves, and as they grow the skewed distribution develops. Results from the initial growth in the populations are therefore least subject to such measurement artifacts and are consistent with the prediction.

4.4. Two Species Interactions

As with all the experiments from 1977, little can be said in detail about slopes of the thinning lines arising from the plots sown with mixtures of mustard and swiss chard. Nevertheless, several patterns are

clear. Thinning for individual species in a mixed stand cannot conform to the regularities of -3/2 thinning. Bazzaz and Harper (1976) reported irregularities when species were examined separately and it would seem that such irregularities must occur: species die out of mixed stands. In doing so, they do not continuously increase their yield per unit area by having fewer, larger individuals as the -3/2 relation would predict, but by having a decreasing yield consisting of small plants, ever fewer in number. In many of the populations examined, the initial mortality was high in one of the two species and the subsequent thinning was virtually that of a pure stand of the surviving species. To the extent that one species or the other dominated the stand as thinning began, the pattern is as though the other species were not there. Not surprisingly, mustard was strongly favored at the highest density, with swiss chard almost completely suppressed, even when started with numerical superiority. At the middle density shifting from 1/3 mustard and 2/3 swiss chard to the reverse influenced the outcome of the competitive interaction. Whereas the chard substantially died out when starting in the minority, those which did survive grew quite well, and in the plot in which it started out in the majority, it held its own. At the lowest density mustard all but died out when started with the numerical disadvantage, holding its own when given the initial advantage.

With all the trading back and forth between species, the pattern of thinning for the individual species is seen to be quite intricate. A regularity emerges when the data are amalgamated to ignore the identity of individual species and merely individuals and their biomasses are considered. Bazzaz and Harper (1976) found a similar result and my

results corroborate it well (Figs. 4.8, 4.9). Given the range of inter-
actions observed in the populations, several further observations suggest
themselves. In populations in which thinning had decimated one or the
other species, the remaining population thinned in a fashion similar to
the controls for that species. It is fortunate that the control popula-
tions of mustard and swiss chard showed somewhat different tendencies--in
swiss chard the individuals seem to have been more efficient at producing
biomass (averaged larger at a given density) than the mustard. A direct
comparison may therefore be made of the differential tendencies of thin-
ning in the mixed stands. When mustard dominated, the population
followed the pattern for the control mustards and likewise for the swiss
chard. Of particular interest are the populations which maintained
reasonable densities of both species. Both such populations (C1 at low,
and C2 at middle density) follow closely the pattern of the more effi-
cient swiss chard, despite the presence of both species at comparable
densities and sizes (within a factor of two).

The results suggest the use of the value of k_3 under comparable
conditions as an index of the efficiency of a species at exploiting its
available space and furthermore that a stand may have an efficiency
higher than might be expected from the species composition and the beha-
vior of the pure stands.

The patterns of thinning for the mustard and chard are understand-
able given the rapid start which mustard makes in contrast to chard. The
basic regularity of the thinning relationship holds sway so that a
species making a rapid start at high density may be seen to gain hold of
the available space and prevent encroachment by a more "efficient"
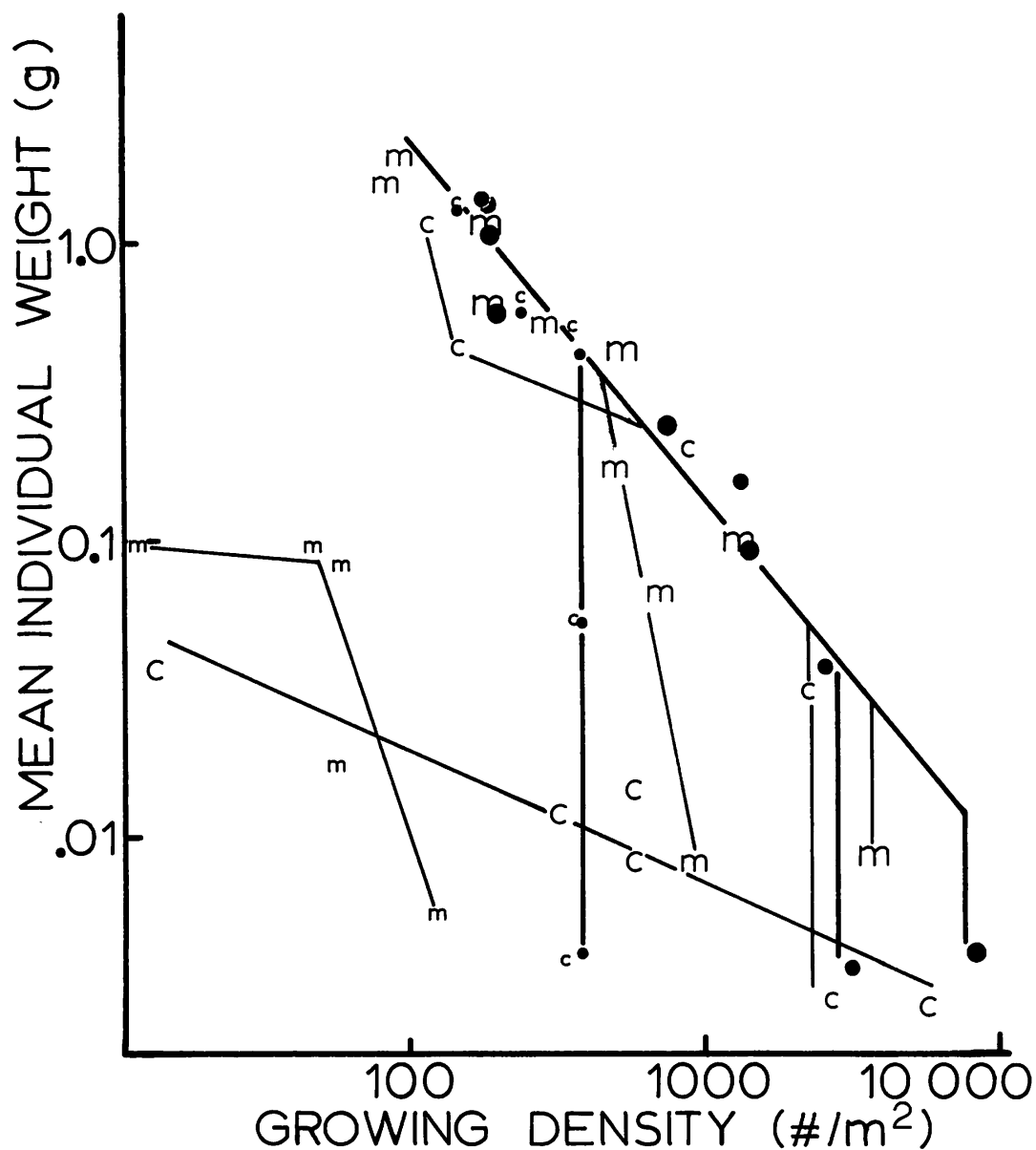
Fig. 4.8. The log-log relation between mean individual weight w and growing density p in mixed populations of swiss chard (c) and mustard (m) initially sown at three seeding densities. Points ignoring the identity of individual species are also shown (●). Heavy lines show the path of the composite population and lighter lines show the path of subpopulations of the individual species. Populations were initiated with 2/3 chard and 1/3 mustard (by number of seed planted).
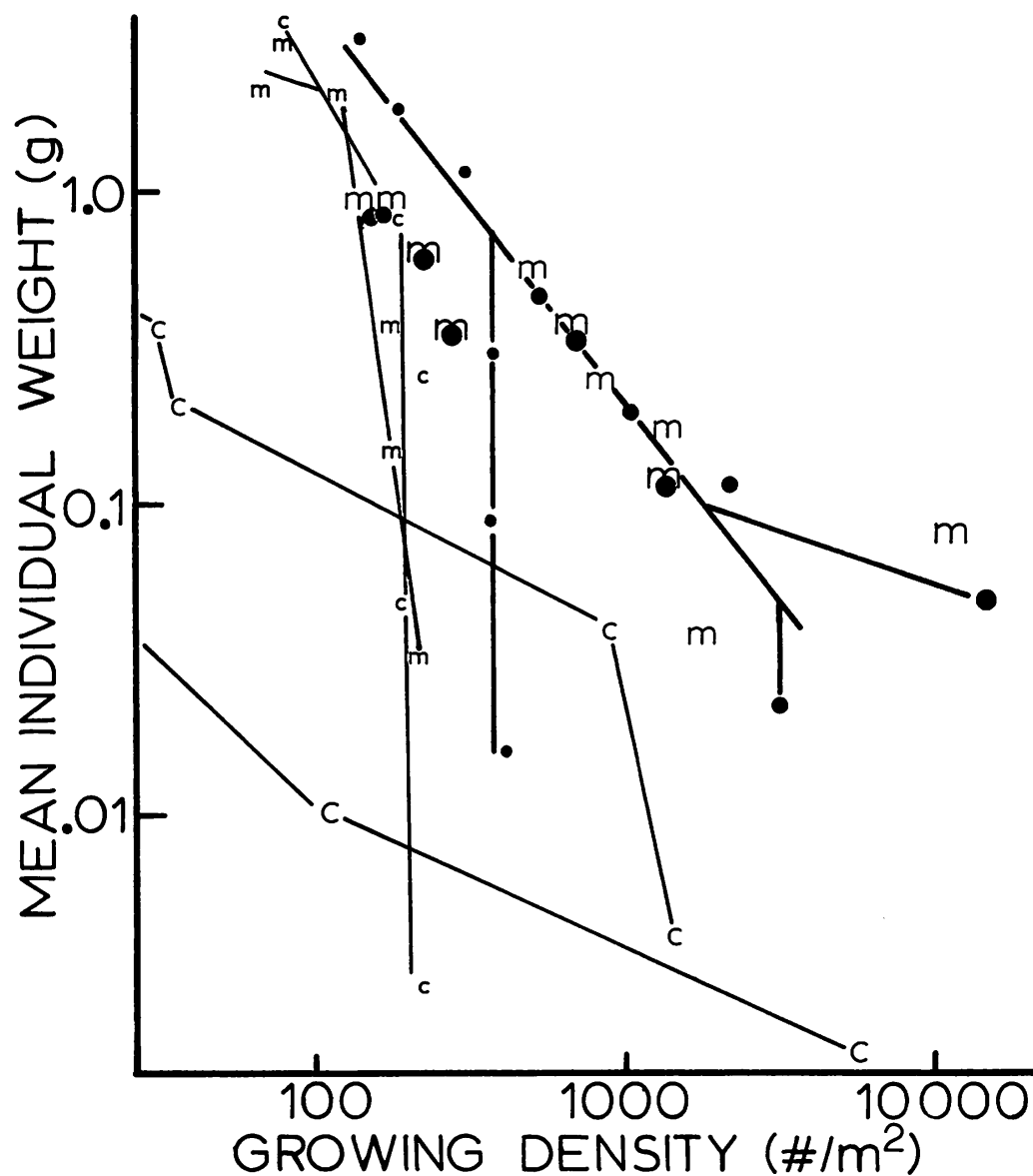
Fig. 4.9. The log-log relation between mean individual weight w and growing density p in mixed populations of swiss chard (c) and mustard (m) initially sown at three seeding densities. Points ignoring the identity of individual species are also shown (●). Heavy lines show the path of the composite population and lighter lines show the path of subpopulations of the individual species. Populations were initiated with 1/3 chard and 2/3 mustard (by number of seeds planted).

competitor. The initial advantage does not hold if initial growth is at lower densities. It may be possible to make specific predictions combining the basic constraints imposed by "available space" with the time course of exploitation and the ultimate efficiencies of the species as measured by the value of k_3 in pure stands. The techniques developed by de Wit (1960) for examining reproduction may be readily adaptable to the investigation of biomass relations and their interactions within the constraints presented by the constant yield relation and -3/2 thinning. While the present sojourn into the interpretation of this particular data set may be somewhat tenuous given the lack of replication and the difficulties of biomass estimation, it is important to consider the interpretive and even strong predictive power which may lie in a careful analysis of thinning in multi-species stands.

4.5. Shade Cloth and -1 Thinning

The plots of mustard grown under shade cloth (77-Shade cloth) in 1977 showed extremely suppressed growth and substantial thinning. Although precise values of the resulting slopes cannot be considered because of the problems with the allometric relations, the slope of the best-fit regression line for 77-Shade cloth is substantially less than that of the controls. 77-Variance 3 (the controls for the 1977 experiments using mustard) had a slope of -.916, significantly steeper than -.690 at the 1% level (Fig. 4.10). It is clear that the shade cloth reduced the slope of the thinning line although it cannot be concluded from the present data that it was shifted specifically from -3/2 to -1. Reduction of the slope of the thinning line is consistent with earlier
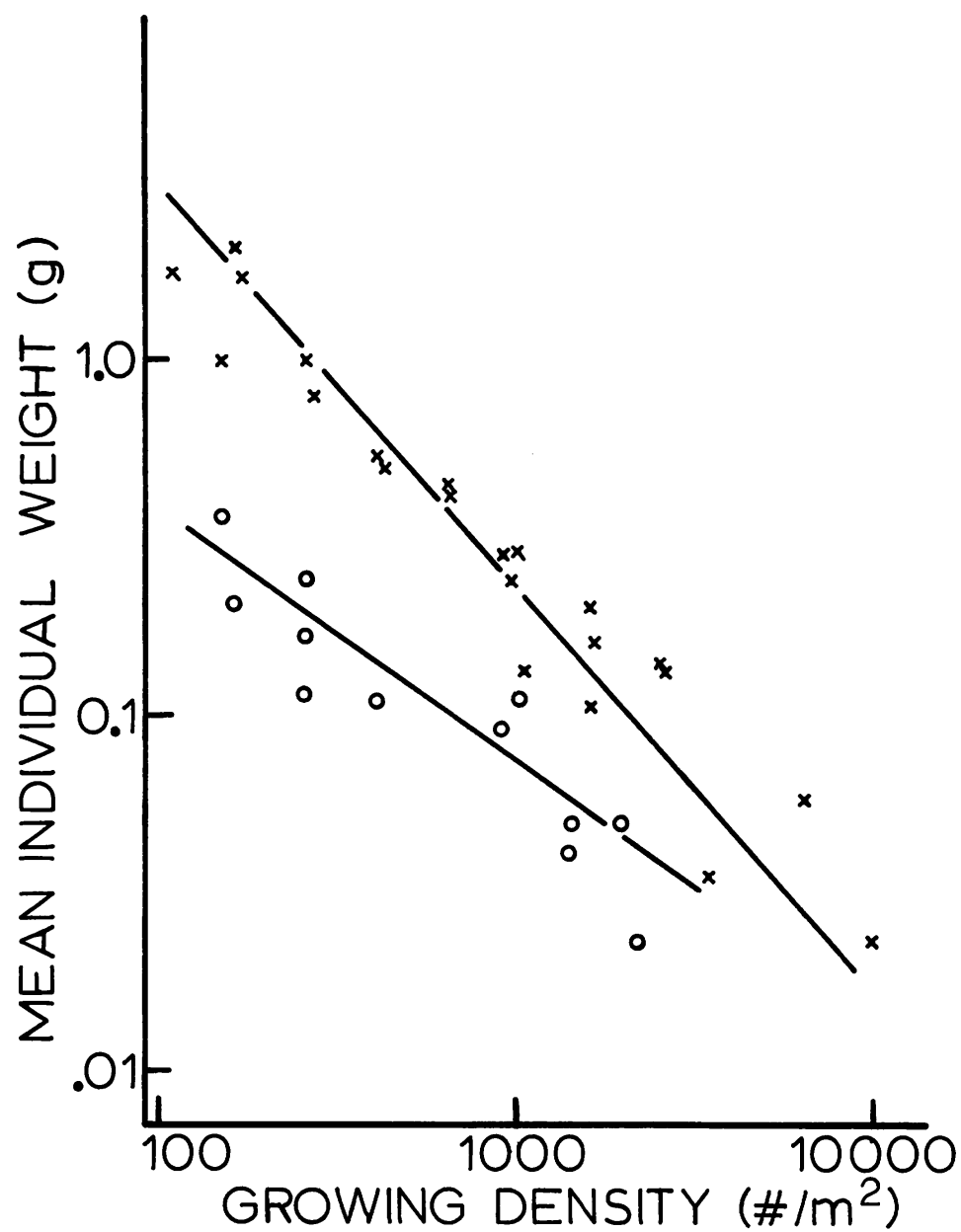
Fig. 4.10. The log-log relation between estimated mean individual weight w and growing density p for self-thinning populations of leaf mustard grown in the open (x) and under shade cloth (o).

work (White and Harper 1970; Hiroi and Monsi 1966) although the reduction of the slope from -3/2 to -1, as found by earlier workers and predicted by the present theory, cannot be addressed with these data.

4.6. The Constant Yield Relation

The present theory has been extended to populations which are not thinning by considering the constant yield relation. In its basic form the constant yield relation states that yield per unit area is constant over a wide range of densities for populations growing under similar conditions and of the same age. When graphed as mean weight per individual vs. growing density, this relation implies a line of slope -1 on the log-log graph of mean plant weight vs. growing density. Such lines may be interpreted under the theory as implying a constraint on growth in the population by a resource having a two dimensional character (e.g., light).

In 1978 experiments were performed which reduced the light levels for populations of low density (non-thinning). If light is the important two dimensional resource which limits individual plant growth resulting in the constant yield relation, reduction of the light level should reduce the yield yet allow it to remain constant across densities; lines of slope -1 should result, having a lower intercept than controls. Fig. 4.11 shows the results of this experiment with swiss chard (78-Black plastic leaves, 78-Clear plastic leaves). Visible light was reduced to 16% of controls in the experimental treatment, and yields were suppressed. For the range of densities represented, the constant yield relation holds. The points along the upper line are for control populations
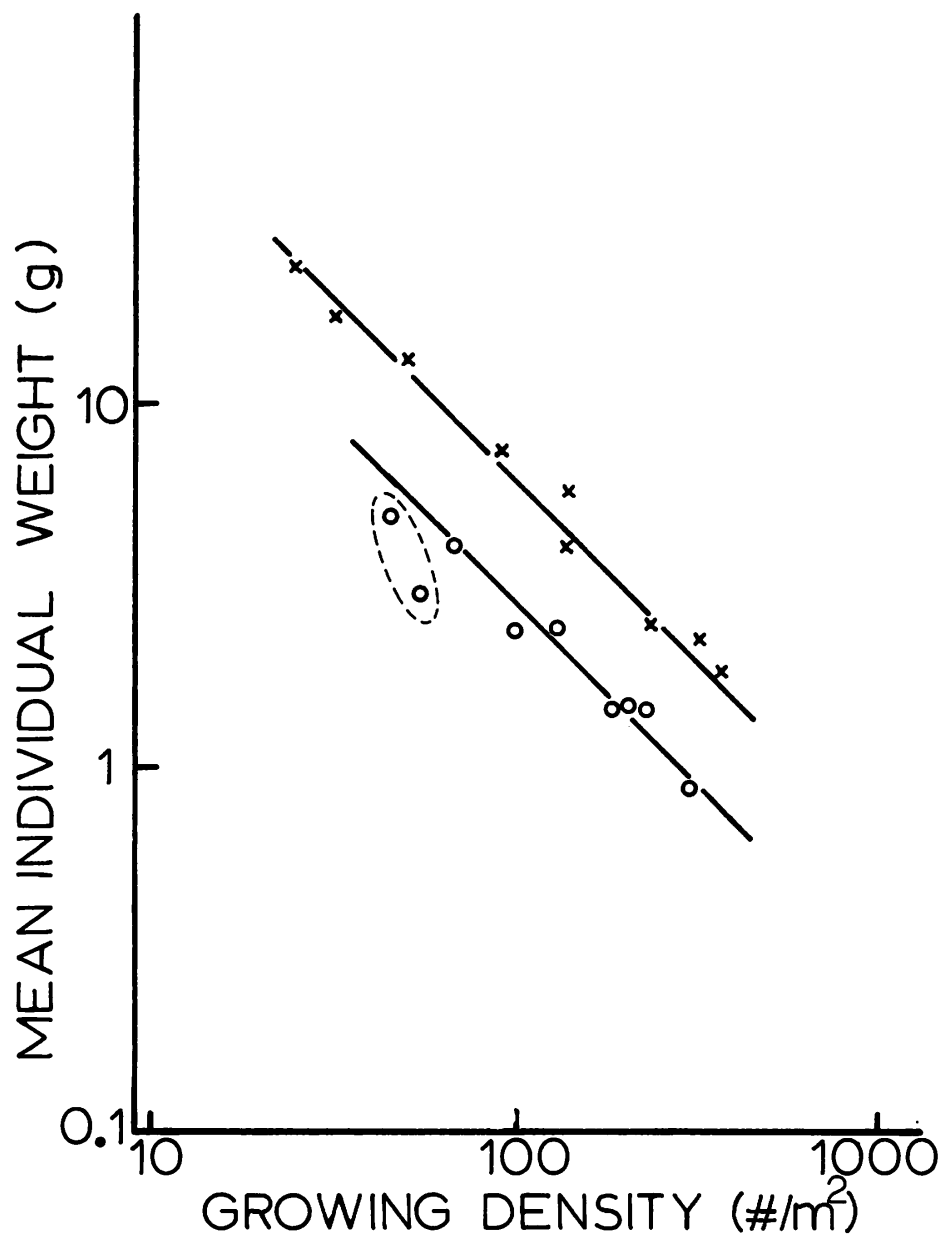
Fig. 4.11. The log-log relation between mean individual weight w and growing density p for same-aged populations of swiss chard grown in the shade of black plastic strips arranged to simulate leaves (o). Control treatments used clear plastic (x). Best fit lines of constant yield (slope equals -1) are shown. Circled points show populations which had not yet achieved full cover.

growing under clear plastic "pseudo-leaves" while those along the lower line are for populations of the same age growing under "pseudo-leaves" made of black plastic. Results conform exactly to the pattern predicted by the theory.

As discussed in the development of the theory, light presents a peculiar property as a resource. Although limiting, it streams in on a regular basis. Time for growth is often considered of great importance to yields but the amount of growth which can be achieved by a plant will be constrained in many circumstances by the amount of light received in that time (viz., short growing season and huge cabbages grown in Fairbanks, Alaska). Because light is continually coming in on a daily basis, the plants can continue to grow in response. Light may be limiting in the sense of dictating growth rates of individuals in the population without constraining growth so much that mortality ensues. Since a line of slope -1 is less steep than a line of slope -3/2, the constant yield relation may be seen as a driving force which brings populations along until they begin to encounter another type of limitation at larger sizes or higher densities--the -3/2 line. At still lower densities or smaller sizes, yet another limitation takes over--the physiological limits to growth rate. Physiological limits are largely a function of individual size and hence at very low densities populations lie along a line of slope 0 indicating a constant weight per individual.

The standard graphs of yield vs. growing density may be seen readily in the graph of weight per individual vs. growing density. Since lines of slope -1 are lines of constant yield, we may take such a line as a new horizontal axis. By rotating the graph 45° we produce from the

graph of weight vs. growing density, another graph directly showing yield as a function of growing density, the more usual view when population yields are being examined (Fig. 4.12).

4.7. The Allometry of Plant Parts

The analysis of the allometric relation for trees showed a predictable relationship between sapwood weight and total tree weight. Several other constraints on biomass allocations arise in the form of allometric relations. The principal predictions outlined in the description of the theory are that roots should have a slope of 1 for the allometric regression of root weight on total plant biomass, and that leaves should have a slope of 2/3. The predictions are based on the argument that roots, as exploiters of soil volume (3 dimensions), should have a slope for the log-log allometric relation to total plant weight (which in a thinning population is also being limited by a volume-based (3 dimensional) resource) given by the ratio 3/3 = 1. Leaves, as exploiters of light, and hence area (2 dimensions), should have a slope for the log-log allometric relation to total plant weight (limited by a volume-based (3-dimensional) resource) given by the ratio 2/3. The predicted relations should hold in populations which are thinning and for species which are not using roots or leaves as significant storage organs. The last criterion may be particularly difficult for leaves to meet generally, but in any case 1 and 2/3 may be regarded as minimal slopes for the allometric relations of roots and leaves since any consistent use of an organ for storage would steepen the slope.

Fig. 4.13 shows the graph of leaf weight on total plant weight for mustard. The principal line has a slope of 1 corresponding to -3/2

(a)

(b)
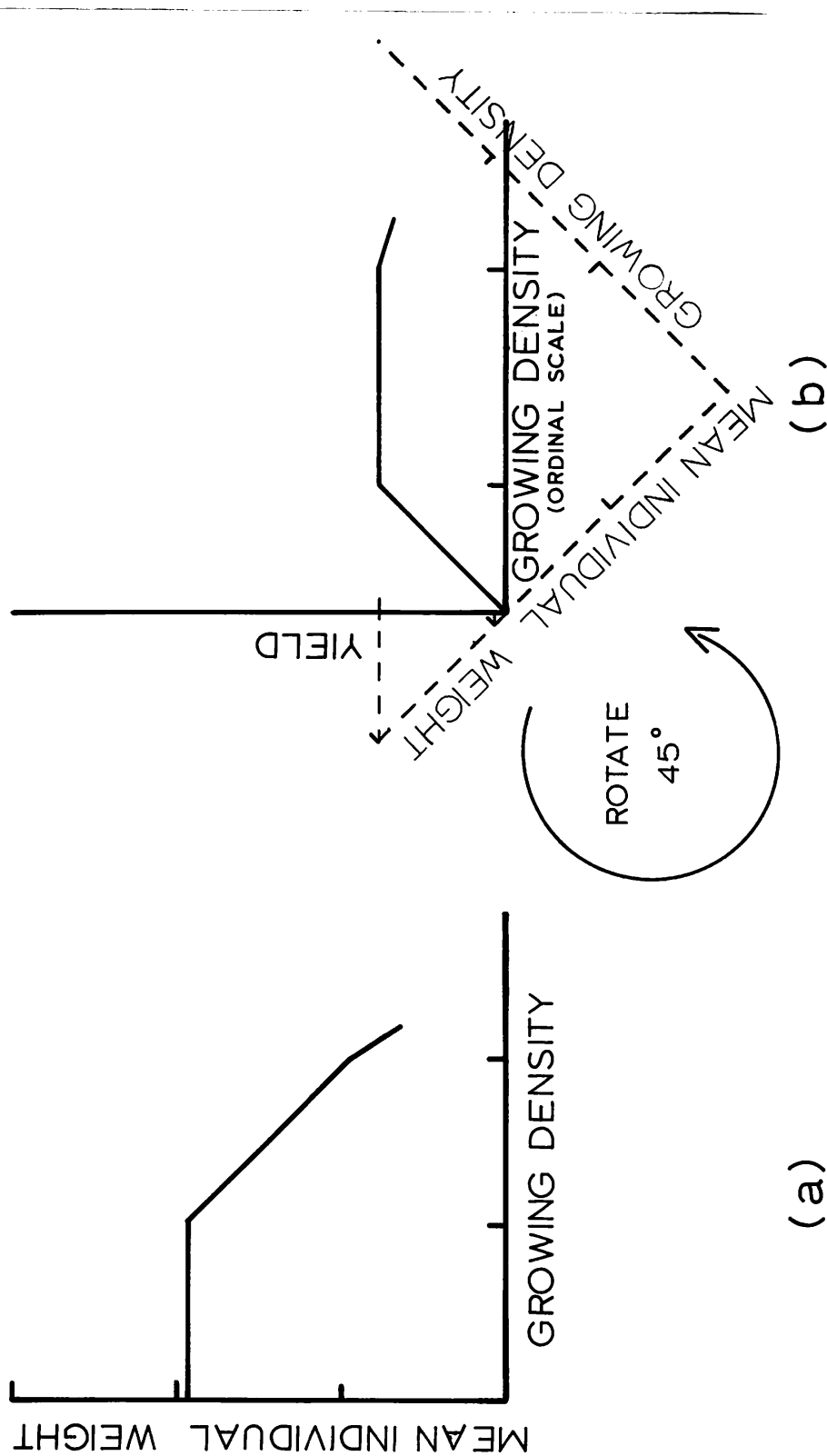
ROTATE
45°

Fig. 4.12. The log-log relation between mean individual weight w and growing density p for same-aged populations (a). Rotated 45% the log-log relation between yield Y and growing density emerges (b).
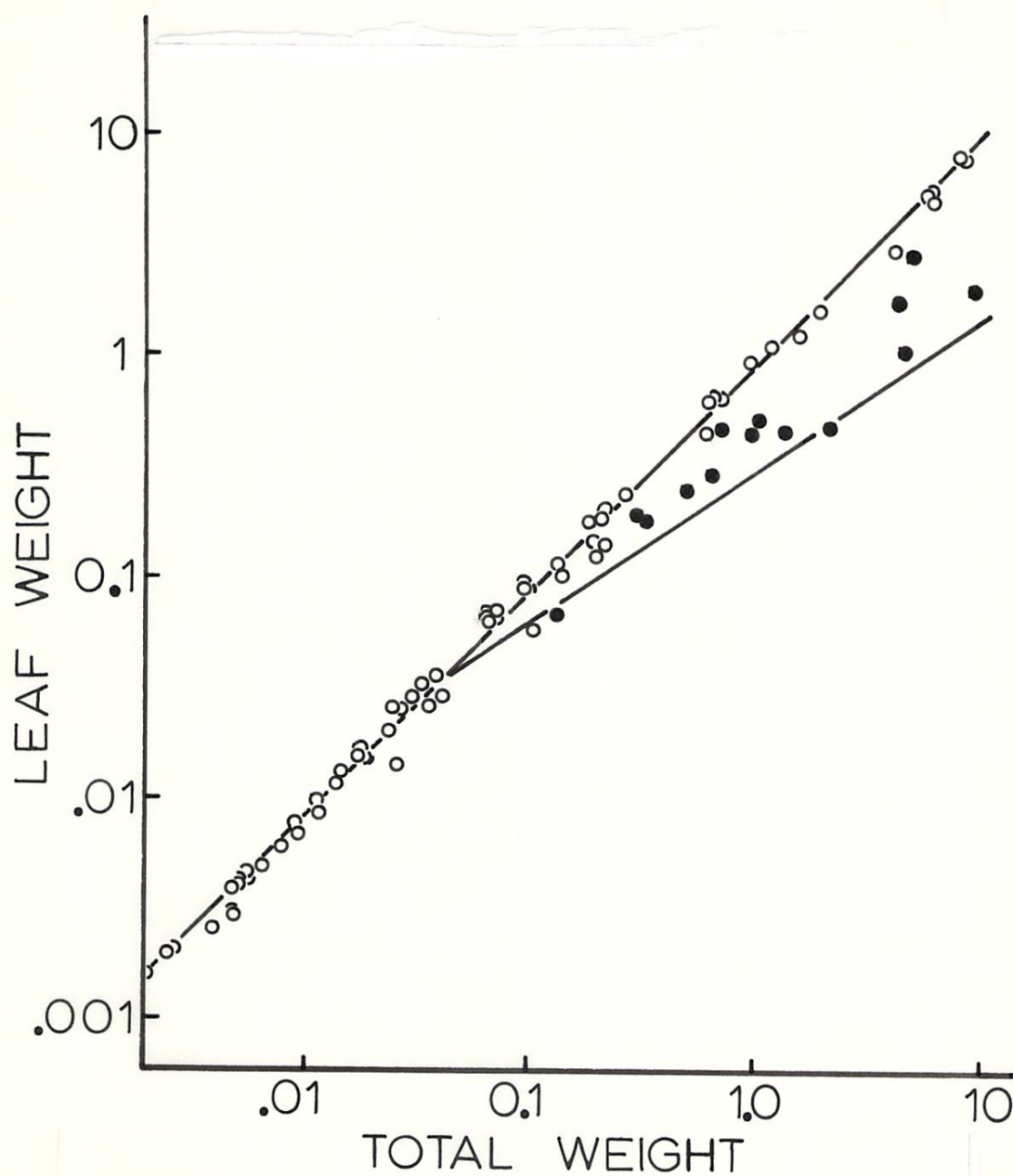
Fig. 4.13. The log-log allometric relation between leaf weight and total plant weight in sterile (o) and reproducing (x) leaf mustard. Lines of the predicted slopes of 1 (for leaves used initially for storage) and 2/3 (for leaves used solely for light gathering) are shown. The line of slope 2/3 originates at the plant size at which thinning began in this population.

thinning of leaves in the mustard. Substantial storage may be expected

in the leaves since the rosette growth form allows little other place

for it. Particularly telling however is the second line of slope 2/3.

The line in the figure originates at the size at which plants in the popu-

lation began to thin. The points which lie substantially below the line

of slope 1 are all plants which have begun to reproduce. They have lost

the rosette growth form, moving material out of storage to produce stems

and reproductive structures. Reproductive individuals are stripping the

leaves back to the minimal amounts to be found in leaf tissue and they

all lie above the "boundary" defined by the line of slope 2/3. An alter-

nate formulation of the prediction based on the theory is also clear from

the figure: larger plants can afford to move proportionately more from

their leaves than smaller plants (as evidenced by a greater displacement

from the line of slope 1).

Fig. 4.14 shows the graph of root weight on total plant weight,

again for mustard. Here the scatter is greater than in leaf weight, but

the predicted slope holds over more than 4 orders of magnitude. Note

that what tendency does exist to depart from the predicted slope is in

the direction of a steeper slope (points toward the lower left tend to

lie more consistently below the line and those toward the upper right

above the line)--the anticipated form for the departure from prediction

if the root is being used for storage.

Although merely a beginning in examining these relations, the

marked agreement between prediction and observation is evidence in sup-

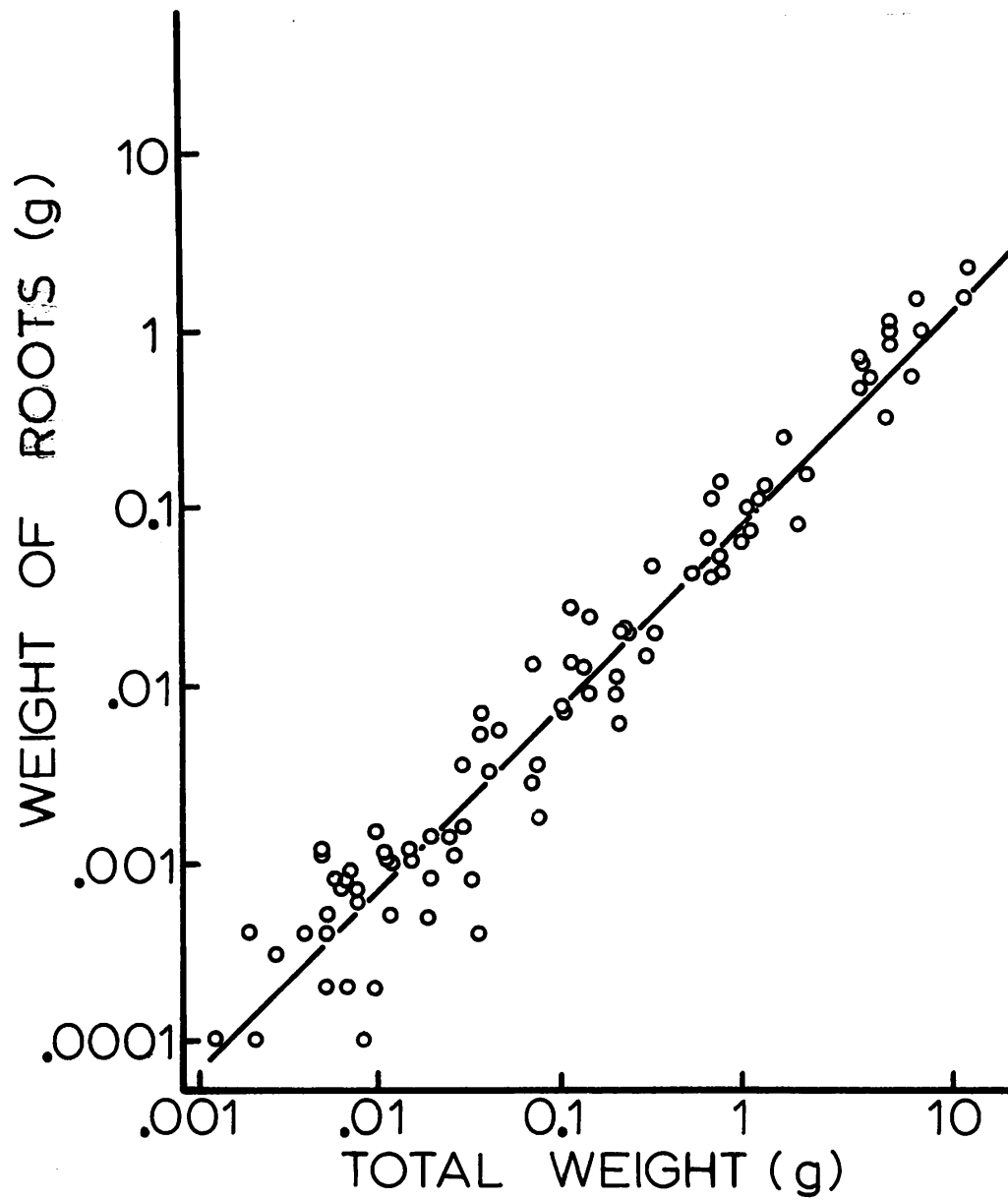port of a much different approach to the problems of resource allocation

in plants.

Fig. 4.14. The log-log allometric relation between root weight and total plant weight in leaf mustard. A line of slope 1, as predicted by the theory, is shown.

4.8. Significance of the Experimental Results

Many experiments relating to -3/2 thinning have been performed and reported in the literature (see White 1975, 1979 for summaries). The results reported here are more than a series of separate contributions to that literature, broadening the range of manipulations reported upon. The added importance of the present experiments stems from the theoretical framework in which they were developed, performed, and their results interpreted.

New approaches to the analysis of data were suggested by the theory, tested experimentally, and the predictions of the theory corroborated. Although the effects of fertilizer had been examined in the past (e.g., White and Harper 1970) the effect on the intercept of thinning lines of slope -3/2 had never been addressed. The effect of a reduced light level on yields was also not before examined as a -1 relation separate from, but related to, the constraints of -3/2 thinning. Though plant allometric relations and resource allocation have been examined before, a new perspective based on constraints related to the dimensionality of the exploited resource has been developed here and corroborated.

Altogether new manipulations arose from the theory and were attempted here. The reduction of accessible volume above or below ground and its influence on the pattern of thinning have not been examined before. Likewise the distinctions between a shallow soil and a soil of reduced laterally accessible volume had not been made.

Several experiments were also performed to corroborate the results of earlier workers. These experiments ranged from examination of

variation in the size distribution to the observation of two-species interactions during thinning. No results contradictory to the theory arose.

As with any group of experimental results, some experiments produce clearer statements than others about the hypotheses being tested. Some experiments reported here have produced strongly corroborative evidence in support of the theory, others less so. However, all the predictions made by the theory and critically tested here were supported in some measure.

5. CONCLUSIONS

Only on the edge of the grave
can man conclude anything.

—H. B. Adams

In this thesis I propose a theory which brings together the -3/2 thinning law, the constant yield relation, and some basic constraints on resource allocation in certain plant parts. All of these phenomena are seen as limitations imposed by a geometrical property of the limiting resource. In particular, whether a resource is distributed in volume or over area is seen as a property of paramount importance. Individuals in a population quantitatively express this property of their limiting resource in the readily observable tradeoff between individual size and growing density.

Corroboration for these ideas comes from several sources. The basic ideas and initial support come from published literature from which good evidence exists attesting to:

1) The generality of the phenomenon of -3/2 thinning in a wide variety of plant species and morphologies.

2) The utility of applying these methods to certain animal populations.

3) The derivability from the present theory of the asymptotic maximum density of Yoda et al. (1963), a documented empirical relationship about plant density and maturity.

114

4) The confirmation of a predicted allometric relation between sapwood
   weight and total tree weight [done here with data from Whittaker
   (unpublished)].

5) The generality of the constant yield relation.

6) The observation of -1 thinning in plant populations grown at low
   light intensities.

   Arising from the theory are several predictions which were tested
directly through experiment and observation. From these experiments,
strongly corroborative evidence exists for the following predictions of
the theory:

1) Reducing the level of fertilization lowers the intercept but not the
   slope of the -3/2 thinning line.

2) Reducing the light level at low densities (impoverishing the area as
   regards light) maintains the constant yield relation and shifts the
   position of the -1 line of constant yield downward.

3) A strongly reduced light level causes thinning at high densities to
   take place on a line which is less steep than controls.

4) Allometry of plant parts--specifically leaves and roots--on total
   plant weight is constrained by geometrical properties of the resources
   they exploit.

5) A shallow soil--and hence reduced soil volume--can shift the pattern
   of thinning. The -3/2 line is at least shifted downward and a change
   in slope may also occur.

6) The pattern of thinning in mixed stands of two species is much more
   regular when the species identity of individuals is ignored.

Less strongly supported but still suggestive are the following:

7) While reduction of belowground volume accessible to roots does shift the position of the thinning line, manipulation of aboveground volume does not.

8) The amount of variability in the population may presage the amount of mortality the population will experience as thinning progresses. Good evidence is presented here that this is so initially.

9) The regularity of -3/2 thinning may provide a useful framework for orchestrating life history strategies into quantitative constraints on population growth in multiple species populations.

A number of challenging questions arise from this work:

1) To what extent can these ideas be applied in the examination of animal populations?

   a) Is the value of k_2 or k_3 a better index of carrying capacity than the traditional "number of individuals, K" in such models as the logistic?

   b) Do allocations to certain body parts in animals (e.g., combs in filter feeders) shows a similarly predictable allometric relationship to the resource being exploited?

2) The phenomenon of the runt in a litter is a familiar example of how the size of offspring may be manipulated to minimize losses if resources are limiting. Is there an analogous variability in seeds of species in which one plant spawns a large population of offspring which are apt to be competing at the same place and time?

3) Is it always possible to distinguish between efficiency of exploitation as expressed by the value of k, and the inherent richness of the resource? Is this a philosophical question?

4) Can a rigorous relation be established between the distribution of sizes among individuals in a population, and the population's tendency to thin?

5) Can the dimensionality of a resource be experimentally manipulated in a manner that plants can successfully exploit? (E.g., perhaps growing on the surface of a porous block could shift nutrients to being a 2-dimensional resource.)

6) Can the notion of fractal dimension provide useful insight into plant geometry and the exploitation of resources?

7) How widespread is time or age-dependence of regression parameters in allometric estimation?

I hope that with this thesis I have opened up a new perspective on the interactions between populations and the resources on which they depend.

6. LITERATURE CITED

For out of olde Feldes, as men seyth,
Cometh al this newe corn fro yer to yere;
And out of olde bokes, in good feyth,
Cometh al this new science that men lere

--Chaucer, The Parlement of Foules

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118

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DENSITY CONVERGENCE/YIELD CONVERGENCE

w = mean weight per individual

p = # plants/area, the growing density

wp = biomass per unit area in a stand = Y

Suppose that the yield in a thinning stand, Y_t' at time t is equal to the yield in a full stand which has not yet begun to thin at time t, Y_t, diminished by the yield lost due to mortality of individuals of weight fw (small individuals a fraction f of the average weight w)

$$\int_{p_t'}^{p_0} fw \, dp :$$

$$Y_t' = Y_t - \int_{p_t'}^{p_0} fw \, dp \qquad \text{but if the population follows the}$$

thinning relation, $w = kp^{-3/2}$

so

$$Y_t' = Y_t - \int_{p_t'}^{p_0} fkp^{-3/2} dp$$

$$= Y_t - fk(-2p^{-\frac{1}{2}}) \Big|_{p_t'}^{p_0}$$

$$= Y_t + 2fkp_0^{-\frac{1}{2}} - 2fk(p_t')^{-\frac{1}{2}} \quad \text{but } Y = kp^{-\frac{1}{2}}$$

so

$$Y_t' = Y_t + 2fY_0 - 2fY_t'$$

123

$$Y'_t(1+2f) = Y_t + 2fY_0$$

$$Y'_t = \frac{Y_t + 2fY_0}{1 + 2f}$$

we now put the equation in a form to compare with Yoda's

$$\frac{1}{p'_t} = \frac{1}{p_0} + \varepsilon$$
(my version of symbols since I am making a distinction p_t vs. p'_t which he does not)

since $Y = kp^{-\frac{1}{2}}$

we may rewrite

$$Y'_t = \frac{Y_t + 2fY_0}{1 + 2f}$$

as

$$(p'_t)^{-\frac{1}{2}} = (p_t^{-\frac{1}{2}} + 2fp_0^{-\frac{1}{2}})/(1+2f)$$

$$\frac{1}{p'_t} = \left(\frac{1}{p_t} + \frac{4f}{\sqrt{p_t p_0}} + 4f^2 \cdot \frac{1}{p_0} \right) \cdot \frac{1}{(1+2f)^2}$$

Note here: $\dfrac{1}{p'_t} = \dfrac{1}{p_t (1+2f)^2} = \varepsilon$

$\lim p_0 \to \infty$

$$= \frac{p_0 + 4f\sqrt{p_0 p_t} + 4f^2 p_t}{(1+2f)^2 p_0 p_t}$$

$$= \frac{p_0}{p_0 p_t (1+2f)^2} + \frac{p_t(4f^2+1+4f) - p_t(1+4f)}{(1+2f)^2 p_t p_0} + \frac{4f\sqrt{p_0 p_t}}{(1+2f)^2 p_0 p_t}$$

$$= \varepsilon + \frac{1}{p_0} + \frac{4f\sqrt{p_0 p_t} - p_t(1+4f)}{p_0 p_t (1+2f)^2}$$

$$\frac{1}{P_t'} = \epsilon + \frac{1}{P_0} + \frac{4f\sqrt{P_0}}{\sqrt{P_0}\sqrt{P_t}\sqrt{P_0}\ (1+2f)^2} - \frac{1+4f}{P_0(1+2f)^2}$$

$$\text{let } m^2 = \frac{P_0}{P_t} \quad \text{so } m = \sqrt{\frac{P_0}{P_t}} = \frac{Y_t}{Y_0}$$

$$= \epsilon + \frac{1}{P_0} + \frac{4fm}{P_0(1+2f)^2} + \frac{1+4f}{P_0(1+2f)^2}$$

$$= \frac{1+\epsilon P_0}{P_0} + \frac{4fm - 1 - 4f}{P_0(1+2f)^2}$$

$$= \frac{1+\epsilon P_0}{P_0} + \frac{1}{P_0}\ \frac{4fm - 1 - 4f}{(1+2f)^2}$$

$$= \frac{1+\epsilon P_0}{P_0} + \frac{1}{P_0} \cdot \frac{1+\epsilon P_0}{1+\epsilon P_0} \cdot \frac{4f(m-1) - 1}{(1+2f)^2}$$

(see below for expres-
tion equivalent to
$1+\epsilon P_0$ to be used here)

$$= \frac{1+\epsilon P_0}{P_0} + \frac{1+\epsilon p}{P_0} \cdot \frac{4f(m-1) - 1}{(1+2f)^2} \cdot \frac{(1+2f)^2}{(1+2f)^2 + m^2}$$

$$= \frac{1+\epsilon P_0}{P_0}\left(1 + \frac{4f(m-1) - 1}{(1+2f)^2 + m^2}\right)$$

$$= \frac{1}{P_0} + \epsilon(1 + D)$$

$$1+\epsilon P_0 = 1 + \frac{P_0}{P_t(1+2f)^2} = 1 + \frac{m^2}{(1+2f)^2} = \frac{(1+2f)^2 + m^2}{(1+2f)^2}$$

APPENDIX B

EXPERIMENTS WITH SERIOUS TECHNICAL PROBLEMS

Various technical problems rendered the results of some experiments inconclusive. The difficulties which arose are of some inherent interest and yet do not shed light on the theory or its experimental verification in any direct way. These experimental results are described here with brief annotations.

The Resource Enrichment Experiments 77-Water, 77-Fertilizer, 78-Fertilizer, 79-Change in fertilizer

In 1977 I provided one set of plots with extra water. This was done during drier periods and a total of 7.9 cm additional water was supplied. Neither this treatment nor the treatments of some plots with additional fertilizer provided substantial deviation from control plots receiving no such additional resources. The field plots these years were all provided with adequate fertilizer in the process of fitting the land for planting. The plots were also irrigated when signs of severe water stress seemed to threaten the welfare of the experiments. It seems therefore that conditions were quite ample for the populations and the plants were largely unable to respond to the additional resources provided.

The attempt to shift the thinning line midway through the experiment (79-Change in fertilizer) suggests that the plants were not able to respond to the addition of fertilizer so late in their development. The

126

value of log k_3 was shifted upward from that of treatment 79-Fertilizer, from 4.620 ± .035 S.E. to 4.658 ± .074 S.E., a shift in the predicted direction but hardly dramatic.

The water, temperature, and nutrient problems associated with the second set of experiments in 1979 were described in the experiments section.

The Volume Reduction Experiment
78-Underground restriction

There were two experiments designed to restrict the volume of soil available to laterally growing roots: the 1978 experiment using a plastic-lined trench (78-Underground restriction) and the 1977 experiment using cans (77-Roots). Although rooting depth was observed in 1977 and used as a basis for establishing the depth of the trenches in 1978, the plastic-lined trench was not successful at restraining the roots. Above-ground growth was conspicuously suppressed initially but the length of excavated roots made it clear that they were penetrating through the slashes in the plastic. Yield per unit area in these populations was initially severely suppressed to as little as 40% of the yield in the controls. By the fourth of the eight harvests, however, the roots were starting to reach through the plastic and yields were up to 81% of the controls. The mean value of log k_3 for the last five harvests was 4.15 ± .07 S.E., not significantly different from the 4.16 ± .06 S.E. of the controls. Because the roots grew through the trench lining, no conclusion can be drawn about the influence of restricting rooting volume in this manner.

Constant Yield Experiment 77-Pseudo-leaves

The "pseudo leaf" experiment of 1977 was a pilot which was con-
founded many-fold. The treatment changed several times during the
season, from aluminum triangles to 12 oz beer bottles to 32 oz bottles in
an effort to simulate the shading effect of leaves. The bottles damaged
the plants mechanically, occasionally crushing leaves and stems between
one another. The above difficulties coupled with the problems of biomass
estimation for 1977 rendered the results of 77-Pseudo-leaves useless.
The 78-Pseudo-leaves experiments using the plastic strips hung on chicken
wire were an outgrowth of the 77-Pseudo-leaves experiments and were a
successful manipulation of the light environment.

Oats

Several difficulties arose in the experiments with oats which made
cogent use of the data difficult. Initial growth in the highest density
populations resulted in leaves spreading into adjacent pots. In an
effort to control the sprawling, the populations having the two highest
planting densities were tied up with string. The resulting abrupt change
in the light environment in these populations apparently was intolerable
to the plants and the populations died out almost completely. Thus data
from the high density populations, so necessary for documentation of the
placement of the thinning line, were not available. These populations
also provided insight into a shortcoming of the gravimetric method for
root estimation. Substantial root masses were measurable in pots having
no remaining living plants. Measured root masses obviously could not be
assigned to living plants in these pots since there were none and the

general problem for other populations is clear: some of the added weight in the root zone is dead tissue which has not yet decayed.

Lodging was also a problem. At the intermediate densities some populations remained erect while others lodged. Great differences in tillering arose as a result of the differential lodging (lodging resulted in much more extensive tillering) making "replicates" difficult to compare sensibly, especially from one harvest to the next.

Although sampling was stratified to distinguish parent ramets, and tillers, and whether they were reproducing, the poor replicability due to the variation in degree of tillering and mortality at the highest densities did not even allow observation of patterns similar to those of Kays and Harper (1974) and detection of a departure from the initial -3/2 thinning line due to reproduction could not be attempted.