SYMPOSIA
OF THE SOCIETY FOR
EXPERIMENTAL BIOLOGY

NUMBER XV

MECHANISMS
IN BIOLOGICAL
COMPETITION

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PREFACE

The fourteenth Symposium of the Society for Experimental Biology was held at Southampton in September 1960 at the invitation of the University. Although no definition of the term 'competition' agreeable to all was suggested, members were unanimous in their desire to promote a spirit of *experimental* inquiry into those biological systems in which competition may be said to operate. This outlook is inherent in the papers presented and which are published here. They cover a range of systems, involving organisms as varied as marine invertebrates, crop plants, insect parasitoids and tadpoles, and analyse at various levels of detail the *mechanisms* concerned.

The Society is indebted to the University of Southampton for its hospitality and for the provision of facilities, as well as to members of the academic and technical staff for generous help in organizing the meeting and during its progress. It also records its appreciation to the Royal Society for a grant towards the travelling expenses of two speakers from overseas.

The programme was arranged and the meeting organized by Professor W. T. Williams with the assistance of Dr J. W. L. Beament. Professor G. Chapman acted as Symposium Secretary and Mr F. A. Barrett as Local Secretary. To these and to the Cambridge University Press for its assistance in the preparation of this volume, the Editor wishes to express his deep appreciation.

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F. L. MILTHORPE

Editor of the fifteenth Symposium of the
Society for Experimental Biology

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PROFESSOR ARRIEN G. WINTER

Professor Arrien G. Winter was only 50 years old when he died after a short illness at Bonn on 27 November 1960. Born in Hamburg, he studied biology, physics, chemistry and philosophy in his native city, in Munich and in Kiel, taking the degree of Doctor of Philosophy in Kiel in 1935. He was an assistant and then lecturer in the Institute for Plant Diseases of the University of Bonn and was appointed Professor of Plant Pathology and Soil Microbiology in that University in 1947. In 1952, he became head of the Botanical Institute in the firm of Dr Madaus and Co., Cologne, and was appointed Professor of Soil Microbiology in the University of Cologne. He held these positions until his death.

Professor Winter's early contributions were concerned with the assimilation of nitrogen by endophytic blue-green algae and whilst at Bonn he carried out his widely known basic investigations on the ecology of saprophytic and parasitic soil fungi. Impressed by the significance of antibiotic substances arising from the most varied sources he initiated the investigations on the effects of toxic substances in higher plants. His outstanding contributions in this field during the past decade established his reputation as one of the leading soil biologists. His interests and investigations ranged over a wide field and he will be remembered also for his outstanding ability in understanding the essential coherence of biological systems, for his lucid expositions, and for his warm-hearted and sympathetic human relationships.

The Society for Experimental Biology was delighted when Professor Winter agreed to contribute to this Symposium. His illness prevented him from attending the meeting and he prepared the paper, which we are proud to include in this volume (and which he did not see in proof), during a period of great pain and distress. This contribution embodies his wide vision and comprehension; it presents a refreshing approach to and a clear understanding of a very complex system.

We pay this humble tribute to the memory of a treasured colleague who will live in his many contributions to our knowledge of soil biology.

CONTENTS

APPROACHES TO THE STUDY OF PLANT COMPETITION

By JOHN L. HARPER

Department of Agriculture, University of Oxford*

There is some danger that a symposium on competition which begins with a section on definitions may so irritate later speakers that the whole meeting degenerates into a display of semantics. Controversy about the meanings of the word 'competition' might indeed be seen as a direct continuation of the mediaeval tradition of rhetoric in which 'some may make merry with that conceit of thousands of spirits dancing at once upon a needle's point'.

Much of the confusion in the use of the term 'competition' probably derives from the adoption into science of a word with so many special shades of meaning associated with its usage in sport, games and economics. At present the word is used in different senses in different fields of biology and indeed in the same field. It is not the aim of this paper to criticize the varied usage of the word, nor to suggest some one special desirable use, but rather to illustrate as if to a zoologist the sorts of experiments which plant scientists make in the name of 'studies on plant competition'.

In choosing experiments for discussion I have, as far as possible, avoided using those made by other speakers at this symposium and often I have deliberately chosen to describe experiments which are not published or of which descriptions are not readily available.

I have perhaps rashly interpreted the title of the symposium as indicating that the speakers are expected to talk about the mode of operation of the short- and long-term hardships which result to organisms from the proximity of neighbours; but I have taken it that the direct effect of parasites and predators upon their prey or hosts is not intended for discussion at this meeting. I propose, wherever possible, to use the word 'interference' as a blanket word to describe those hardships which are caused by the proximity of neighbours (usually other organisms feeding at the same trophic level). I hope that by using this less controversial word I may avoid judgement of what is or is not 'competition'.

* Now at the Department of Agricultural Botany, University College of North Wales, Bangor.

THE RELEVANCE OF STUDIES OF INTERFERENCE

There are perhaps seven major problems in biology which require informa-
tion on the manner and effects of interference between organisms for their
solution:

(1) What factors determine the efficiency of utilization of resources in a com-
munity? For example, what are the effects of increasing the density of crop
plants, livestock, fish, etc. on yield? What are the effects on the efficiency of
utilization of resources of mixing differently adapted organisms?

(2) In what ways are populations regulated? Does interference between
organisms regulate their numbers? Is such a self-regulating property merely a
mathematical concept, a property of controlled laboratory cultures, or is it part
of a regulating process occurring in nature?

(3) What are the mechanisms by which one flora and fauna becomes changed
into another with the passage of time? What is the role of interference between
organisms among the directing forces in ecological succession? What is the nature
of the forces which individuals exert upon each other such that one species
succeeds at the expense of another?

(4) A corollary of the concern in the role of interference in ecological succession
is an interest in the manner in which stable mixed populations may exist in
nature. We may ask the questions: What differences in the biology of indivi-
duals of species A and B determine that A ousts B? Or what differences in the
biology of A and B permit them to remain together without one succeeding at
the expense of the other?

(5) What is the role of interference between organisms in determining their
present abundance, distribution and range? To what extent is the ecologic and
geographic range of a species determined by present interference from others or
how much by interference which has occurred in the past and thereby has
selected populations with present innate tolerances?

(6) What is the role of interference between organisms as a force in natural
selection? What part does interference between individuals play in the course of
a plant or animal breeding programme? What, if anything, is meant by breeding
for competitive ability?

(7) What is the role of interference between organisms in determining the rate,
nature and extent of speciation?

The plant scientists who have been most concerned with interference
between plants have been agronomists, ecologists, geneticists and evolu-
tionists, and the usage of the word 'competition' has been coloured by
their various special interests.

THE AGRONOMIST'S APPROACH TO THE STUDY OF
PLANT COMPETITION

The agronomist is concerned with the ways in which the resources of an
environment may best be used in crop (or indirectly stock) production and
his concern with interference between organisms arises (a) in those

reactions of plants to density which determine crop yield in pure stands, and (b) in the mutual interference between species which may occur in mixed crops (e.g. grassland) or between weeds and crops. It is convenient to divide the agronomist's approach to plant competition into two phases: a description of effects (either on populations or on individuals); and, secondly, an analysis of causes, i.e. attempts to relate effects on the plant to changes in the environment created by increasing density.

Descriptive studies concerning total yield

The yield of a crop is not a linear function of the density of seed sown because over a wide range of densities further increase brings diminishing returns. A prime stimulus to the agronomist's interest in interference between organisms has therefore been the question—how many plants should be grown (and paid for) in order to obtain the most efficient use of land and capital? Perhaps the simplest of the agronomist's approaches involves sowing a crop at a range of densities and determining the relationship between density and yield. Selected examples from the results of such experiments are presented in Fig. 1. The characteristic features of the yield/density curve are that, over an initial increase in density, yield tends to increase at first linearly, that the rate of increase then declines to a plateau of more or less constant yield and that in some cases there may be a real loss in yield from further increases in density (see e.g. Holliday, 1960). In general the total yield of dry matter produced per unit area tends to increase to an asymptote or to a constant plateau with increasing density of plants (see Fig. 1). Table 1 shows the results of a series of experiments in which the yields from low and high densities were compared for a wide range of crop and other plants and except for situations in which some special irregularity occurred, such as the lodging of the crop, the yield at high density always exceeded or did not differ significantly from the yield at a lower density.

However, the relationship between density and some special component of yield, such as grain production, may show a decline in yield with very high densities. Fig. 1c illustrates such a situation for sunflowers and Fig. 1a shows the changes in total dry weight per unit area for maize at various densities and the comparable data for cob production. Although the dry weight of above-ground parts of these crops increases with density, the yield of cobs (or seed in the sunflower) declines above an intermediate density. The reaction of crops to density is such that the weight of the individual plant at high densities almost exactly compensates for the increased number of plants per unit area. However, as the density is increased so the proportional allocation of assimilatory products to the
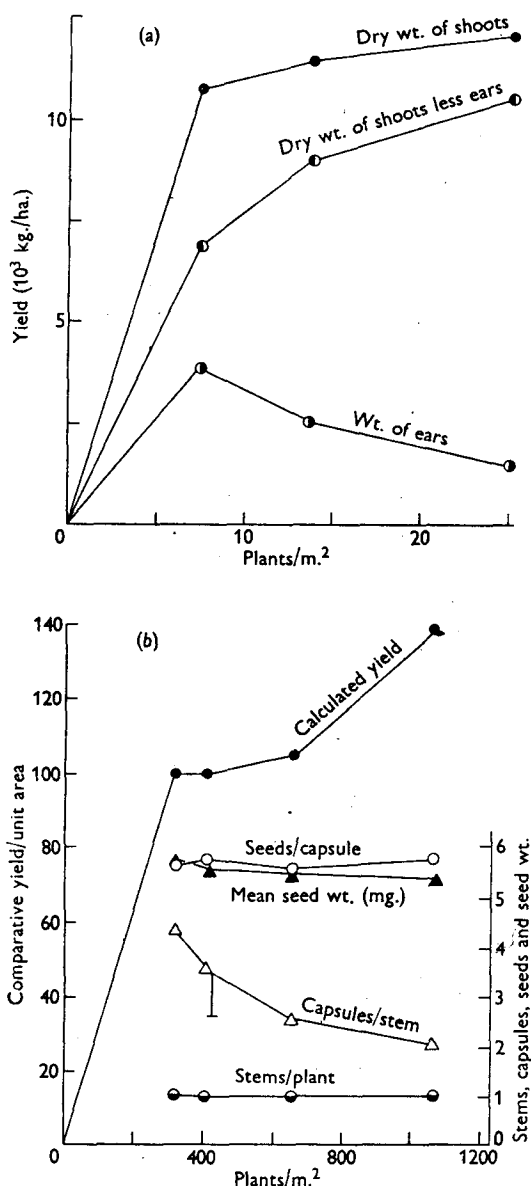
Fig. 1. The influence of plant density on yield and the components of yield. (a) Total yield of above-ground parts and the weight of ears of maize grown for silage (var. Pioneer 395). Data kindly provided by E. S. Bunting. (b) Linseed (*Limum usitatissimum*). After Blackman and Bunting (1954).
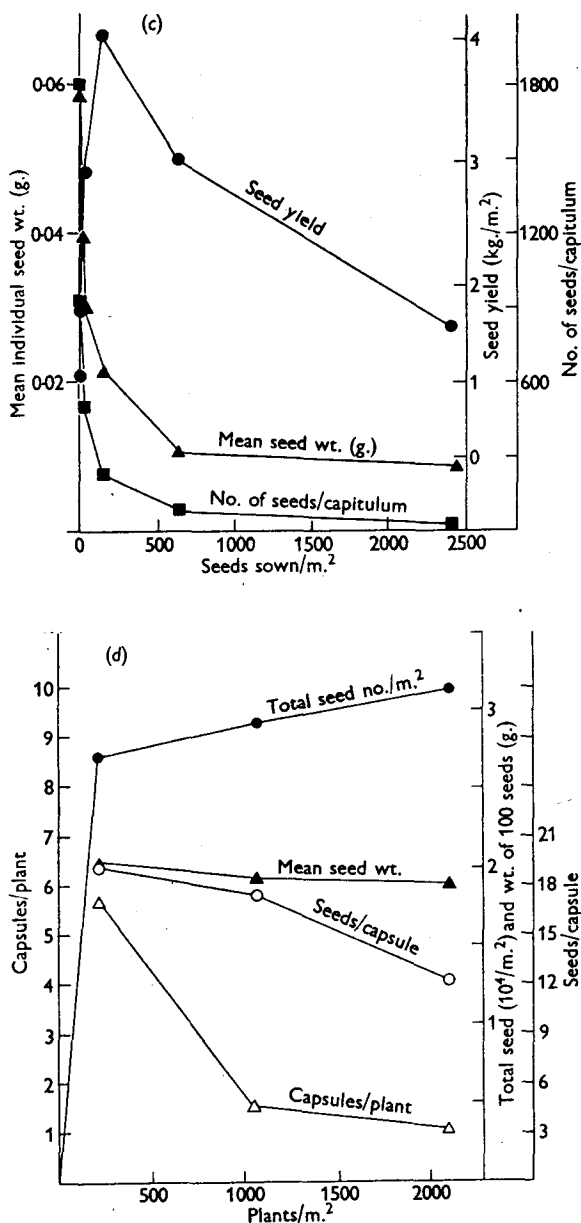
Fig. 1 *continued.* (*c*) Sunflower (*Helianthus annuus*). After Clements, Weaver & Hanson (1929). (There is some indication in Clements' data that a degree of self-thinning had occurred at high densities and so the number of plants per unit area was probably not directly proportionate to density of seeds sown.) (*d*) Corncockle (*Agrostemma githago*). Original data.
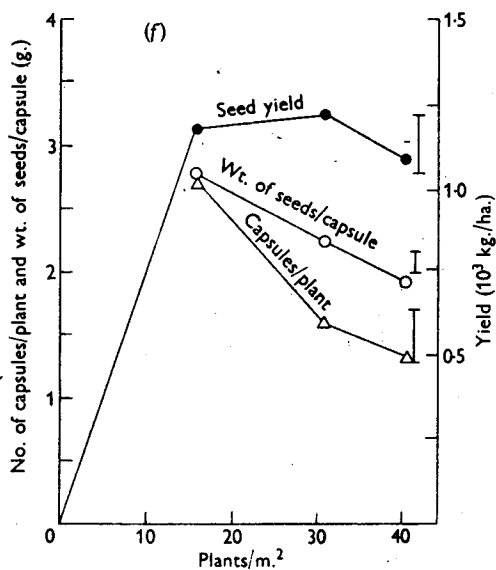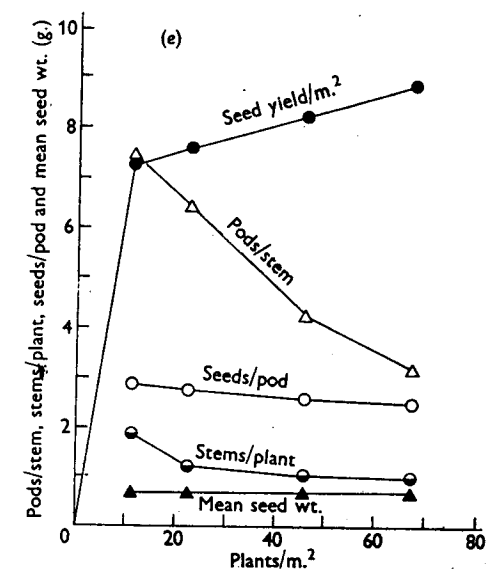
Fig. 1 *continued.* (e) Field bean (*Vicia faba*). After Hodgson & Blackman (1956). (f) Oil-seed poppy (*Papaver somniferum*). After Bunting (1956).

Table 1. *The dry matter production by pure stands of various species of plants at low and high densities*

(Unpublished data kindly provided by Professor G. E. Blackman and Dr E. G. Brittain. Plants were grown from seed unless otherwise stated.)

Species	Low density Plants/m.^{2}	Dry matter production g./m.^{2} (a)	High density Plants/m.^{2}	Dry matter production g./m.^{2} (b)	Level of significance, of difference between (a) and (b) (%)
Galanthus nivalis (from bulbs)	172	317	688	1086	0·1
Galanthus nivalis (from bulbs)	688	446	2750	1449	0·1
Endymion non-scriptus (from bulbs)	172	992	387	1991	0·1
Helianthus annuus	14·4	1076	28·7	1147	N.S.
Raphanus sativus	387	737	1548	822	0·1
Raphanus sativus	97	117	1547	451	0·1
Brassica oleracea (Broccoli)	387	1689	1547	1600	N.S.
Helianthus annuus	14·4	520	28·7	570	N.S.
Helianthus annuus	172	411	387	756	0·1
Agrostemma githago	387	740	1548	683	N.S.
Phaseolus multiflorus	172	755	387	975	1·0
Tropaeolum majus	172	90	387	157	0·1
Brassica arvensis	387	722	1548	667*	0·1
Raphanus sativus	387	737	1548	549*	0·1

* These two values are aberrant in that the yield from high density was significantly less than from low density. With *B. arvensis* severe lodging occurred at the high densities. Comparison of densities for *R. sativus* was unfair because the controlled densities were obtained by thinning after considerable interference had already occurred between individuals and they had become strongly etiolated.

various organs of the plant may change and there are indications that seed output often suffers in this reallocation.

A number of attempts have been made to give mathematical expression to the relationship between yield and density. Two which may serve as examples are those proposed by Mitscherlich and by Kira and his associates. [See also the paper by de Wit in this volume, p. 314.] Mitscherlich (1919) suggested the relationship

$$W = (1 - e^{-cx}),$$

where W = plant weight in absence of interference from neighbours, and x = space available for each plant.

Kira, Ogawa & Sakazaki (1953) have shown that a more accurate fit to experimental data is often obtained from the relationship

$$W = Ks^a,$$

where W is the plant weight, s the mean area available for each plant, and a indicates changes in the degree of utilization of space with the stage of

growth. A convenient way of testing the validity of Kira's equation is to plot the logarithm of individual plant weight against the log of the reciprocal of plant density—that is, the area available per plant. This has been done by Kira *et al.* (1953) for some data of Donald (1951) on the development of swards of *Trifolium subterraneum* at various densities (Fig. 2). The figure illustrates clearly the development with time of a linear relationship
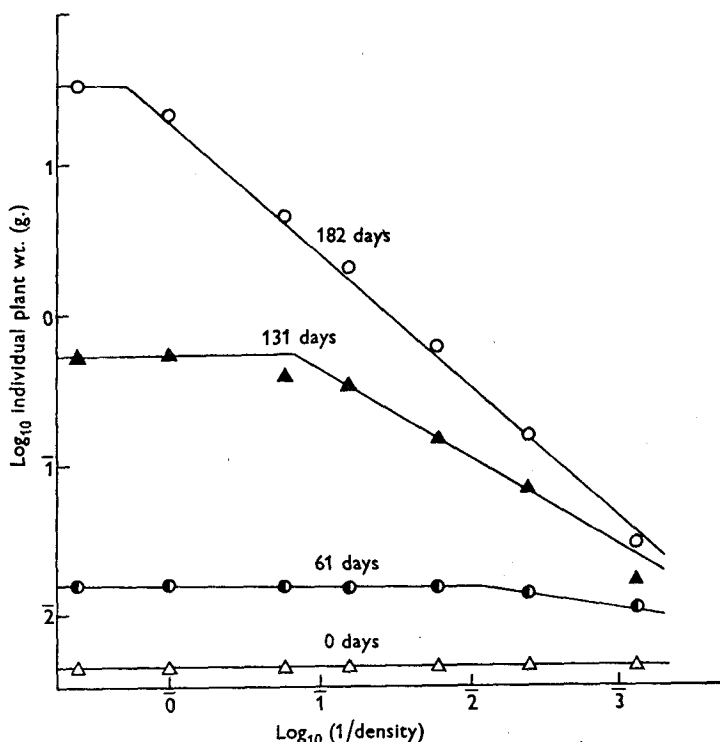

Fig. 2. The influence of density (plants/sq.link, where 1 sq.link = 0·041 m.²) on the weight of plants of *Trifolium subterraneum* at successive dates from sowing. Data obtained from Donald (1951) and presented according to the log/log transformation of Kira, Ogawa & Sakazaki (1953).

between log plant weight and log reciprocal density. At the time of sowing, individual plant weight is, of course, uninfluenced by density. As the plants develop, those at a high density interfere with each other and individual plant weight is reduced. The graph of log plant weight plotted against log reciprocal density is linear and sloping within the range of densities at which interference is occurring. This slope becomes steeper with the passage of time and extends to lower and lower densities until it reaches a slope of 45° and extends over the whole of range of densities; at

this time a constant final yield, irrespective of plant number, has been obtained.

I have adopted this same method of analysis for the results of an experiment on the relationship between yield and density of two species of the genus *Bromus*, *B. rigidus* and *B. madritensis*. These two species are invaders from Europe into the flora of California. They were chosen for experimental study in California because they are closely related taxonomically, of comparable growth form, and because they commonly form mixed stands in their Californian rangeland habitats. Both species are annuals, so that a complete life-cycle may be studied in less than a year. The grains of both species carry awns which may be used as 'planting handles' making it easy to sow individual grains in accurately determined positions. In this experiment plants were grown from seed to maturity in 9-in. flower pots. Seeds were sown by hand at densities of 1, 2, 10, 30 and 100 per pot and arranged within each pot on a hexagon pattern, so that each individual except those at the edges of the pots and those at low densities was surrounded by six equidistant neighbours. Both species were sown in pure stands and also in mixed stands in which half the seeds were of one species and half of the other. In these mixed stands the seeds of the two species were again sown in a hexagonal pattern, but arranged so that each individual was surrounded by three neighbours of one species and three of the other (arrangement (*a*) in Fig. 8).

Sufficient replicate sowings were made to permit three independent harvests to be made, to allow a contrast in soil fertility to be introduced into the experiment and to provide two independent replicate pots for each combination of species × density × harvest-time × fertility level. The experiment was sown on 25–26 September 1959 and 97 % of the seed sown germinated and produced vigorous seedlings. The 3 % of 'missing plants' were replaced with transplants of even age, but at harvest the transplants were removed and discarded, correction being made for the missing plants in the estimates of total yield per pot. The three harvests were made on 26 November 1959, 14 December 1959 and 18 July 1960. The total dry weight of above-ground parts was determined for the contents of each pot and in mixed stands each species was weighed separately. Some of the results of this experiment are summarized in Figs. 3, 4 and 5 (a more detailed analysis will be published elsewhere). At the time of the first harvest the weight of individual plants had not been influenced by increasing the density from one to ten plants per pot, but further increases had resulted in a decline in individual plant weight (Fig. 3). At this time, *B. rigidus* had produced a greater weight of growth than *B. madritensis* and the mixed population had a mean plant weight intermediate between that

of the two species in pure stands but closer to the higher-yielding *B. rigidus*. At the second harvest there were indications that interference between individuals had occurred at densities as low as two plants per pot and the relationship between log individual plant weight and log reciprocal density had become approximately linear over the range 10–100 plants per pot.
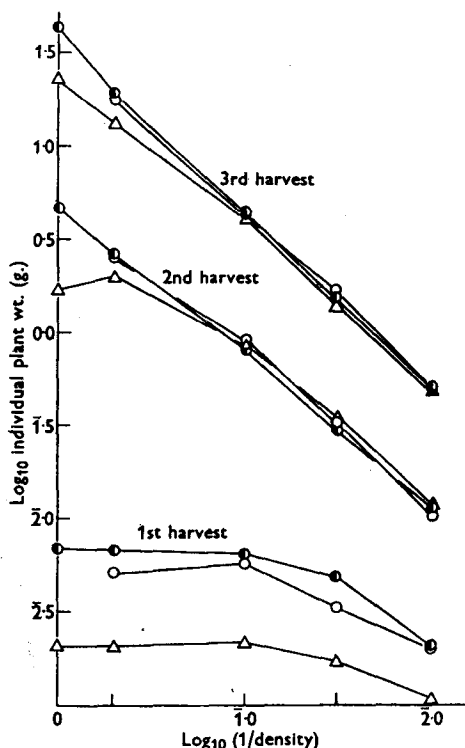

Fig. 3. The relationship between mean individual plant weight and the density of stands (plants per pot) of *Bromus rigidus* and *B. madritensis* and a mixture composed of equal numbers of the two species to give the same total density as in pure stands. Seed sown 25–6 September 1959. 1st harvest: 26 November 1959; 2nd harvest: 14 December 1959; 3rd harvest: 18 July 1960. ◐, *B. rigidus*; △, *B. madritensis*; ○, average weight of individuals in the mixture of the two species.

However, at this second harvest there was no significant difference between the yield of plants of the two species in pure stand over the range 10–100 plants per pot. The effect of intraspecific interference had been to force the populations into a limiting mould in which the two species made comparable growth. This effect had become even more apparent at the third harvest.

In Fig. 4 experimental results are presented to show the effect of density on the response of plants to nutrient status. The low nutrient status was

obtained by using a standard soil-mix of three parts of fine washed sand and one part of Yolo silty loam. A corresponding high nutrient status was obtained using the same soil-mix but applying a commercial high-nitrogen fertilizer in liquid form at intervals of 10 days throughout the growing period. At the time of the first harvest the differences between fertility treatments were insignificant, but these differences became marked at the
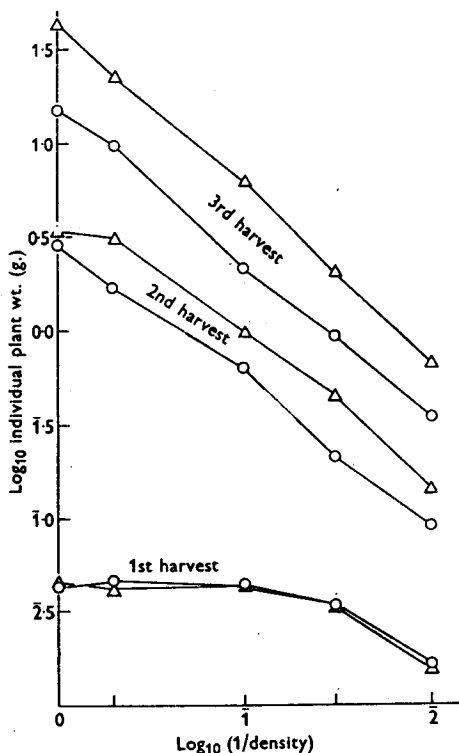

Fig. 4. The relationship between mean individual plant weight and the density of stands (plants per pot) of *Bromus* spp. Data are summarized over the two species and the mixture for two levels of nutrition. Dates of harvest as in Fig. 4. △, high level of fertilizer; O, low level of fertilizer.

later harvests. We may perhaps take the slope of the log/log regression as a measure of the intensity of interference. The application of fertilizer has not changed this slope, and has not affected the intensity of interference so measured—it has simply increased the size of the plants which are interfering with one another.

Fig. 5 illustrates the relationship between the weight of individuals of each species when grown in pure and in mixed stands. The data are summarized over fertility levels and are presented for only the second harvest.