Durham E-Theses

Studies in plant competition

K. I. Alexander

How to cite:

Alexander, K. I. (1979) *Studies in plant competition.* Masters thesis, Durham University.

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a <https://etheses.durham.ac.uk/id/eprint/9242/> is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

STUDIES IN PLANT COMPETITION

by

K.I. ALEXANDER B.Sc.

M.Sc. DISSERTATION.

UNIVERSITY OF DURHAM

OCTOBER 1979

CONTENTS

GENERAL INTRODUCTION

Newbery & Newman (1978) set out to test whether shoot competition prevents different sized plants forming a stable mixture. They produced different sized plants by delaying the planting of one half of the plants (or one species), and then grew them together with either total competition or root competition alone (through the use of aerial partitions). The plants were clipped at intervals, to provide a measure of relative yield from which deductions were made about competitive ability. They conclude that competitive ability declines with increasing plant size, and cite Wilson (1970) as providing supporting evidence. In both these experiments the authors fail to appreciate the effect of clipping (disturbance) on competitive interactions. Thompson (1978) similarly criticized the interpretation of the experiment of Remison (1978), where an attempt to study the effect of planting density and mineral nutrient supply on root competition, was confounded by clipping on three occasions. Bergh (1968, 1969) and Bergh & Elberse (1970) attempted to follow competitive interactions over a long period through periodic clipping.

The term 'competition' needs to be carefully defined and employed, to avoid confusion (Milne 1961). The most appropriate definition is "the tendency of neighbouring plants to utilise the same quantum of light, ion of mineral nutrient, molecule of water or volume of space" (Grime 1977). The process is then defined by the basic mechanism of the relative abilities of plants to capture and utilise the available resources. A more competitive species will capture a disproportionate share of the resources, leading to differences in vegetative growth, seed production and mortality. Competition can take a variety of forms, which are not necessarily reciprocal, producing various, direct or indirect, deleterious results, making definition of the process through its effects difficult. Furthermore, similar effects can be produced through the selective action of stress or disturbance.

MAINTENANCE OF DIVERSITY.

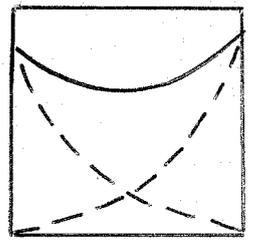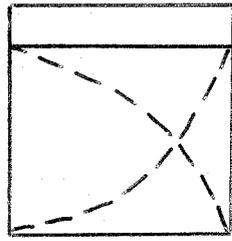Huston (1979) has suggested that if competition occurs in a stable uniform environment for precisely the same limiting resource at the same time, for sufficiently long a period, then competitive exclusion is inevitable. Complete exclusion has been demonstrated in laboratory experiments (e.g. Gause 1934, Crombie 1947), but the diversity of many natural communities indicates that complete exclusion rarely occurs in nature.

Competitive exclusion can be prevented by genetic changes in the competing populations. Frequency - dependent selection leads to a reduction in interspecific competition, so that competition is focused intraspecifically leading to an equilibrium, according to the Lotka-Volterra equations (e.g. Krebs 1972 p.217). Stabilizing selection (see Fig. 1) acts through increasing fitness with decreasing frequency; the high-frequency population suffering mainly intraspecific competition, whilst the low-frequency population suffers mainly interspecific competition (de Wit 1960, Harding et al 1966, Spiess 1968, Marshall & Jain 1969, Kojima & Huang 1972, Putwain & Harper 1972). Disruptive selection acts by reducing interspecific competition through niche differentiation, so that each population ceases to make such heavy demands on the resources needed by the other, either in space (Seaton & Autonovics 1967, Allard & Adams 1969, Ellern et al 1970) or in time (Hanes 1965, Khan et al 1975, Al-Mufti et al 1977).

Huston considers that species diversity is more often maintained by periodic population reductions (disturbance) within a heterogeneous environment, so that the equilibrium situation of competitive exclusion is never reached in some part of the environment. Consideration of the Lotka-Volterra equations shows that with no population reductions, low diversity arises through competitive exclusion. The addition of periodic population reductions leads to species diversity being maintained, although a high frequency of reductions causes low diversity through elimination of the slower-growing competitive species.

Whittaker & Goodman (1979) with a different theoretical approach using the logistic equation, demonstrate that disturbance and environmental heterogeneity are important in maintaining species diversity. However, they recognize three basic patterns of population behaviour corresponding to the three primary growth strategies of Grime (1977, 1979). The species diversity of communities is determined by the levels of stress and disturbance, with the highest species diversity being found under moderate levels of stress or disturbance (Grime 1973a).

Communities vary not only in species diversity but also in the genetic diversity of the constituent species. Electrophoresis can be used to estimate the genetic diversity of a population, and indicates that 23 - 81 % of loci are polymorphic in a range of organisms (Shorrocks 1978 p.119). Competitive exclusion has been shown to occur between genotypes (e.g. Merrell 1953), so how is the genetic diversity of a population maintained ?

RYT = 1   RYT > 1   RYT < 1
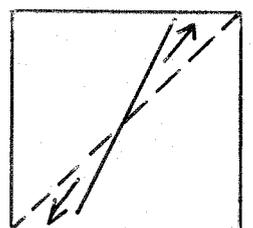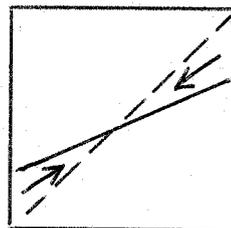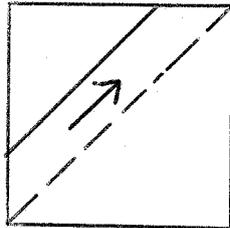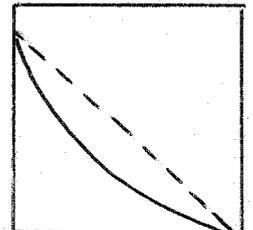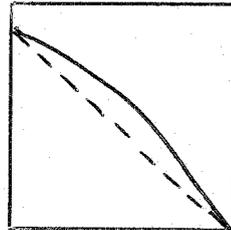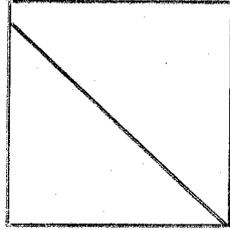
FREQUENCY—
DEPENDENT

DIRECTIONAL (ü)   STABILIZING   DISRUPTIVE

B A B A or B

K_2 K_1/α K_2
K_1/α K_2 K_1/α

K_1 K_2/β K_1 K_2/β K_2/β K_1

SOURCES   Harper (1977), Khan et al. (1975)
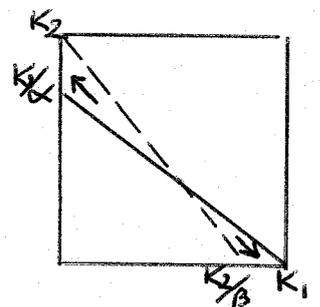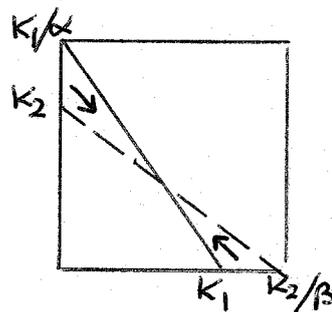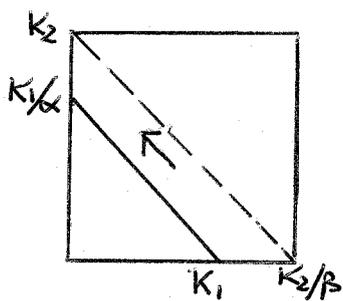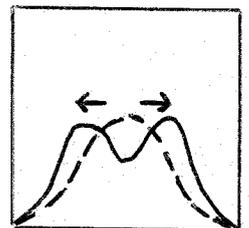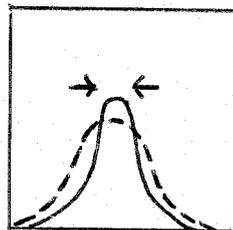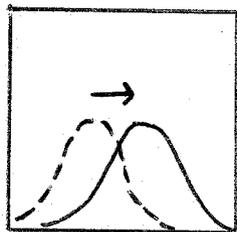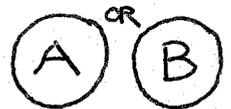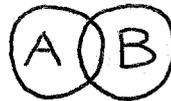
Disturbance and environmental heterogeneity have been shown to be important (Gadgill & Solbrig 1977, Warwick & Briggs 1978). A balanced polymorphism can be generated by directional selection operating against mutation and immigration (Goodenough & Levene 1975), or by selection alone. For outcrossing genotypes, there is also the possibility of heterozygote advantage (with consequent segregational load) in maintaining diversity.

HEIGHT AND COMPETITIVE ABILITY

Newbery & Newman (loc. cit.) concluded "that when two plants of different sizes interact, it is not necessarily the case that the larger one will gain at the expense of the smaller one" (p.377). They consider that the smaller plant was at a competitive advantage and the larger plant at a disadvantage. There is a very large body of published evidence indicating that a larger plant is at a competitive advantage over a smaller plant. The greater vertical and lateral spread of the larger plant will be able to intercept light and shade the smaller plant (Black 1958, Stern & Donald 1962, Harper & Clatworthy 1963, Stern 1965, Jennings & Aquino 1968). The more extensive root system of the larger plant will be able to utilise the available water and mineral nutrients before a smaller plant can extend its roots to the same lateral or vertical distance. Newman (1973) admitted that a slight difference in height can lead to the suppression of a smaller plant, but doubted whether any single root character could give such an advantage.

It cannot be absolutely demonstrated that any single character confers competitive ability, since the results may be due (at least in part) to unmeasured factors. Donald (1958) and Mahmoud & Grime (1976) have shown that the ability to compete for different resources (light, water, mineral nutrients, space) are interdependent, since a prerequisite of a high rate of production of above-ground biomass is a high rate of uptake of water and mineral nutrients.

The smaller plant must be at a competitive disadvantage and will suffer suppression through resource-stress from the larger plant. The smaller plant can only survive suppression if it is sufficiently more competitive to offset the size difference (the competitive strategy), or is adapted to tolerate the stress (the stress-tolerant strategy). The competitive strategy involves high relative growth rates to expand the root and shoot systems, requiring more efficient capture of resources than the larger plant in order to obtain resources from depleted areas. It would be expected that even small size differences would be insuperable, even by large differences in competitive ability.

The stress-tolerant strategy would involve adaptation to chronic low levels of resources rather than efficient uptake, leading to a low relative growth rate and requiring the avoidance of predators.

Newbery & Newman (loc. cit.) suggested that competitive ability decreases with increasing size, due to declining relative growth rates (p.377). The relative growth rate certainly declines with age (Hughes 1973), but growth rates are not good guides to competitive ability. They were originally included in the competitive index (now renamed the morphology index, Grime (1979)) of Grime (1973a), but were omitted from a revised index (Grime 1974) due to anomalous rates arising from secondary adaptations. It is also worth noting that in the revised index, height became of overriding importance.

The experimental evidence that large plants are at a competitive advantage is provided by experiments in which the planting of one species has been delayed. Sagar (1960) found that when Lolium perenne and Plantago lancedata were planted simultaneously, Lolium contributed 80% of the total dry weight. Delaying the planting of Plantago by three weeks led to the contribution of Lolium rising to 90%, but delaying the Lolium by three weeks led to its contribution falling to 6.4%. If the planting of Bromus rigidus with B.madritensis was delayed by three weeks, then the contribution of this species fell from 75% to 13%. of the total dry weight (Harper 1961). Chenopodium album reduced the yield of barley by 20%. when sown at the same time, but by delaying the sowing of the barley by seven weeks then the contribution of Chenopodium rose to 45%. (Williams 1962). Black & Wilkinson (1963) using Trifolium subterraneum delayed the planting of alternate seeds by variable periods. A five day delay reduced the final weight by 50%., and an eight or nine day delay by greater than 75%. Ross & Harper (1972) investigated the dry weight of seedlings of Dactylis glomerata emerging at different times. The mean weight was closely correlated to the time of emergence (95%. of the variance in weight); the later the emergence then the greater the divergence from the control line. In another experiment, plants were grown as a restricted population (neighbouring plants in the pot); the early emerging plants deviated from the unrestricted growth line only late in their growth, and deviated only slightly. As plants emerged later, they deviated earlier in their growth and the deviation became more marked. In general, the larger (earlier planted) plant gains in weight relative to the smaller (later planted) plant, even where the smaller plant is more competitive (e.g. Lolium/Plantago).

In an attempt to identify the mechanism of interaction, two forms of a single species differing in some well defined character, can be grown in a competition experiment. It must be assumed that they do not differ in other respects, although it is conceivable that measurement of some other character would provide an equally good correlation. Black (1958) grew together populations of Trifolium subterraneum from large and small seeds. Plants from the large seeds established a canopy rapidly with their larger reserve capital, and the mortality was concentrated on plants developing from small seeds. Black (1960) grew together mixtures of three varieties of T.subterraneum differing in petiole length. For each pair of varieties, the longer-petioled form was successful in dominating the canopy and yield of the mixture. Interspecific comparisons are less useful, since it is less easy to identify the important differences, though comparisons between closely-related species would be expected to be most useful. The experiment of Harper & Clatworthy (1963) is interesting in that the initial advantage of Trifolium repens through its earlier germination, was balanced by the larger seeds and capability of producing longer petioles by T.fragiferum. The long-term outcome cannot be predicted with accuracy, since much depends on the grazing regime, which would favour T.repens.

In a variety of experiments, competitive ability has been correlated with height (e.g. Aspinall 1960, Narasimha Rao & Rachie 1964, Jennings & Aquino 1968, Snaydon 1971). In agricultural science, the concept of 'critical period' has been advanced, to describe the period during which crops are susceptible to yield loss in competition with weed populations (e.g. Roberts et al 1976). If a summer cabbage crop was kept clean of weeds for the first two weeks, weeds that established after this did not affect yield. The changes in population structure further indicate the competitive advantage of larger plants, since the majority of mortality is concentrated in the smaller plants (Ford 1976, Naylor 1976). These changes can be summarised in the self-thinning law whereby the mean dry weight of the population is proportional to the - 3 / 2 root of the density (Yoda et al 1963, White & Harper 1970, Bazzaz & Harper 1976). As self-thinning proceeds, the density falls and mean dry weight increases through the mortality of the smaller plants.

DISTURBANCE AND COMPETITIVE INTERACTION

Disturbance is defined as "mechanisms which limit the plant biomass by causing its destruction" (Grime 1977). The effect of disturbance (e.g. clipping) is to reduce competitive interactions, as these depend upon the large size of the plant. Species of high competitive index are suppressed by clipping, whilst species of low competitive index are able to persist in mixed swards (Grime 1973c).

Burch & Andrews (1976) constructed a replacement series experiment (see later) using two varieties of _Trifolium subterraneum_. Under regular defoliation, the components of the sward remained stable, but if the sward was left undefoliated the proportion of the shorter-petiole form (Larissa) tended to decline. Species adapted to disturbance may possess characters positively disadvantageous in a competitive situation. For instance, Warwick & Briggs (1978) showed that under clipping, the prostrate genotypes of _Poa annua_ were at a selective advantage, growing and flowering more successfully than erect genotypes. The erect genotype of _Arrhenatherum elatius_ can be killed by clipping (Mahmoud et al 1977), an effect which could be mistaken for competition (Thompson 1978). Scarisbrick & Ivins (1970) grew three species together in mixed swards subject to clipping at intervals. They argue that a strong competitor in mixed swards should progressively monopolise resources, so that its yield should be higher than the control single-species swards. They observed that when the proportion of _Plantago_ increased, the yield of _Lolium_ did not decrease. They concluded that this change in botanical composition did not arise from competition, but rather from the individual reaction of each species to the clipping regime. This criticism can be levelled at all the experiments attempting to investigate competitive interactions using clipping to estimate relative yields.

The clipping regime is used to provide a series of measures of relative rate of production, from which deductions are made about competitive ability. The clipping produces more subtle effects than just reducing competitive interaction. Clipping usually causes an overall reduction in yield (e.g. Rhodes 1968, Burch & Andrews 1976, Rossiter 1976, French & Humphries 1977); even twelve week intervals between clips causes a significant reduction in the yield of the grass _Danthonia_ (Hodkinson 1976). Furthermore, the frequency of clipping will affect the level of yield depression; usually the shorter the interval between clips, the greater the reduction (e.g. Mahmoud 1973, Hodkinson 1976, Rossiter 1976). The height of clipping can also affect the yield (Bogart & Beard 1973). Newbery & Newman (loc.cit.) altered the intervals between clips and the clipping height throughout their experiment, which may add further complications to the interpretation of their results. Clipping may affect the distribution of growth, in _Agrostis tenuis_ causing an increase in the rate of tillering (Mahmoud 1973), but in _Danthonia_ causing a decrease in the tillering rate (Hodkinson 1976). These changes in growth pattern will produce apparent changes in clip weight, which could be misinterpreted as due to competitive interaction.

In the case of the experiments designed to study root competition
(e.g. Remison 1978), clipping of the shoots has been shown to affect root
growth and metabolism (e.g. Davidson & Milthorpe 1966 a & b, Hodkinson & Baas
Becking 1977, Detling et al 1979).

The experiment of Newbery & Newman (loc.cit.) could be modified to overcome
these objections through the elimination of the clipping, and the use of
destructive sampling at various times during the experiment. As there will
then be no disturbance, competitive exclusion of the smaller plant would be
expected (Fig. 2).

THE RELATIVE IMPORTANCE OF ROOT AND SHOOT COMPETITION

The experiment of Newbery & Newman (loc.cit.) had been primarily designed to
demonstrate that "when root interactions alone were operative the ratios
(of large/small) would have converged faster than when there was total
interaction" (p.376). They detected no significant difference in plant growth
between the two competition modes; this lack of difference they attribute to
the lack of competition for light, because the shoots did not intermingle
sufficiently. They suggest that under intense soil competition and slight
competition for light, coexistence of species is promoted (p.379).

Newman (1973) made the same mistake in his criticism of the competitive
index of Grime (1973a), where he notes that the index is based solely on shoot
characters and apparently ignored root characters. He argues that only shoot
competition leads to competitive exclusion, since he is unable to conceive of
any single root character conferring such a significant advantage as a small
difference in height. As indicated earlier, the roots of the larger plant
would have been able to exploit a soil area first, leaving the roots of the
smaller plant to grow through depleted areas. Furthermore, he suggests that
there is more opportunity for niche differentiation in the soil, allowing
release from competition. It should be remembered that differentiation is
possible$_\wedge$through stratification of the leaf canopy (stress-tolerant plants
below competitive dominants), or through phenologic escape (Hanes 1965,
Al-Mufti et al 1977).

In his reply, Grime (1973b) concedes that on nutrient-deficient soils, root
competition will be more important than competition for light. The weakness
of Newman's arguement is implicit in the phrase "low nutrient supply leads to
intense soil competition" (Newbery & Newman p.379). Stress-tolerant plants
are adapted to survive low mineral nutrient availability not through increased
efficiency in uptake (the competitive strategy), but by the ability to survive

FIG. 2
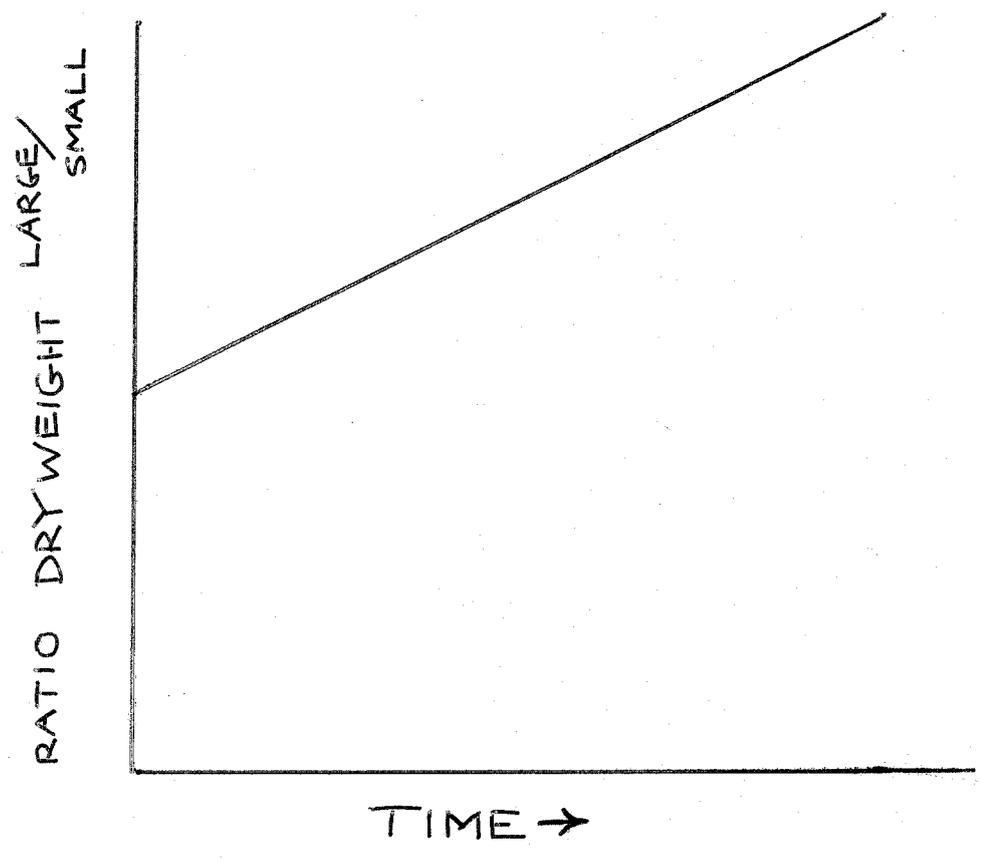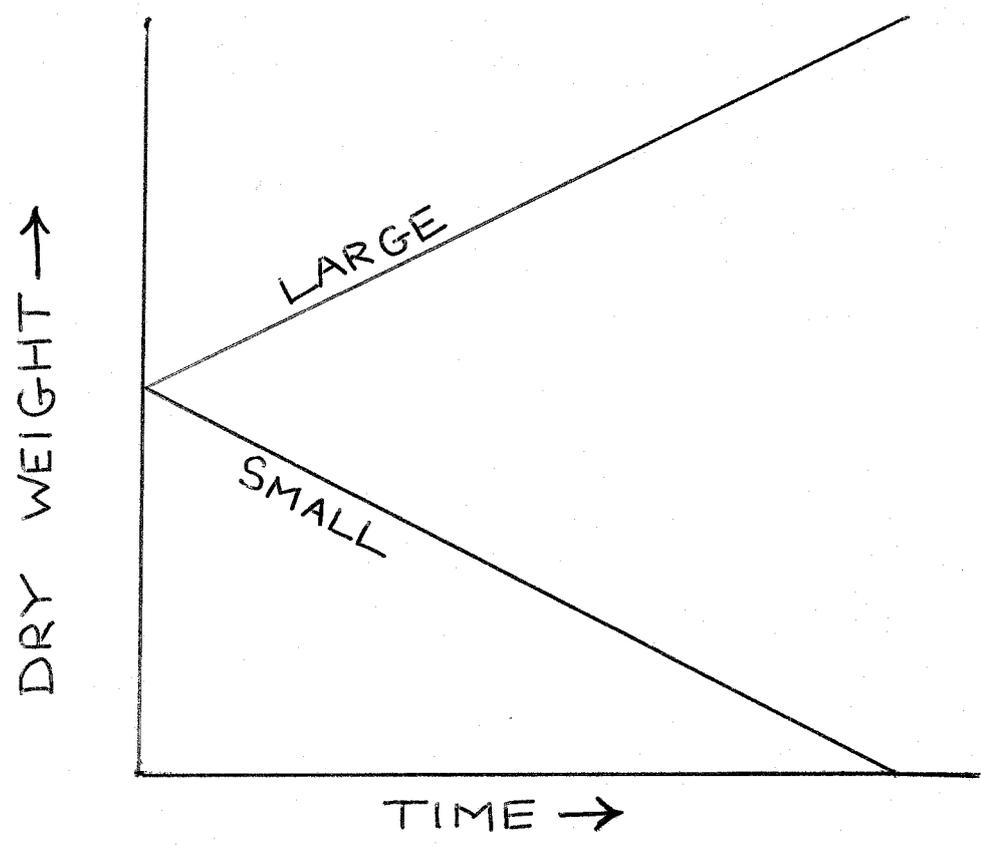
chronic deficiency and resist the impact of climatic stress and the attentions
of predators etc. (Bradshaw et al 1964, Mahmoud & Grime 1976). The high
species diversity of unproductive soils is the result of low competitive
interaction, rather than the shift in relative importance from shoot to root
competition.

Newbery & Newman (loc.cit.) cite Rhodes (1968), King (1971) and Eagles (1972)
as providing evidence of the higher competitive ability of one species' roots
leading to dominance over a species less able to compete (p.379). They
contradict their own statement about root competition promoting diversity,
through preventing dominance and competitive exclusion. The effects of
competition for light and in the soil can be separated through the use of
combinations of aerial and soil partitions, and it is possible to add the
experiments of Donald (1958), Aspinall (1960) and Snaydon (1971) into the
discussion. In general, root competition does appear to be more important, but
the fertility level must be considered, since shoot competition will become
important at high nutrient levels. In many of the experimental designs the
effects of root competition have been exaggerated because the soil partitions
reduce the potential rooting volume available to the competitive plants. It is
also important that the experiments are run for sufficiently long a period, as
shoot competition may occupy a terminal role, the outcome of which may have
been influenced or even decided by earlier competition below ground
(Aspinall 1960, Grime 1973a, 1977). Competition for light is the ultimate
controlling factor, but is modified by proximate factors such as nutrient
stress etc.

DESIGN OF COMPETITION EXPERIMENTS.

In studying the behaviour of two species grown in mixture, it is possible to
vary both density and proportion. Care has to be taken not to design
experiments in which the two are confounded so that interpretation is impossible.

In the additive type of experiment, species A is sown at a standard density
and species B at a range of densities. One special type (e.g. Donald 1958,
Aspinall, 1960, Mahmoud & Grime 1976) has species B added at the same density as
species A (see Fig.3). In the substitutive type the proportion of A and B are
varied while the overall density (A + B) is maintained constant (a replacement
series of de Wit 1960). The controls for both types show how the plants would
grow with only intra-specific competition, but they differ in density. For the
additive type the density in the controls is the same as in the experimental
pots, but in the substitutive type the density is greater in the controls than
in the experimental pots.

FIG. 3

ADDITIVE

Experimental
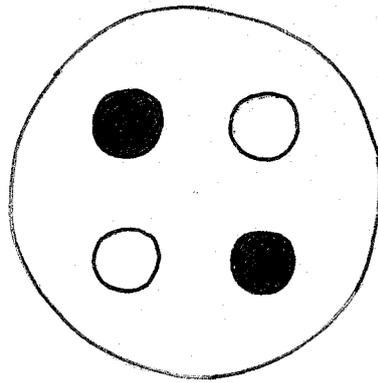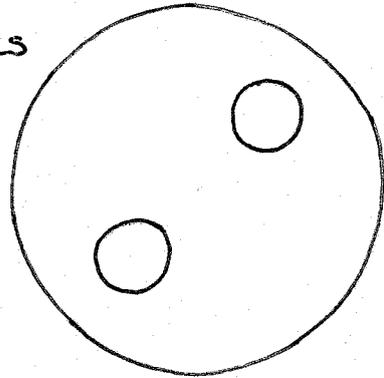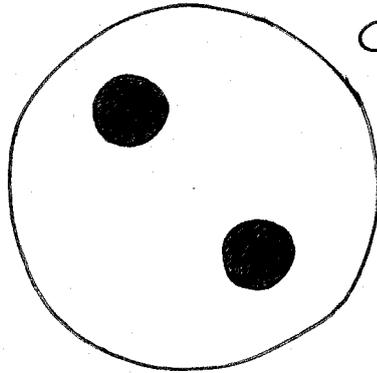
Controls

SUBSTITUTIVE

Experimental
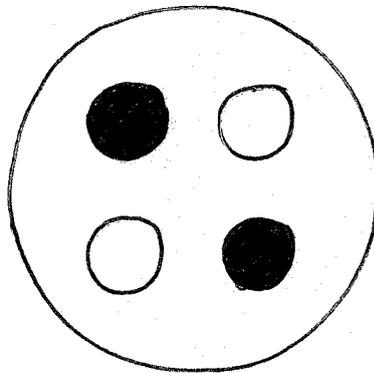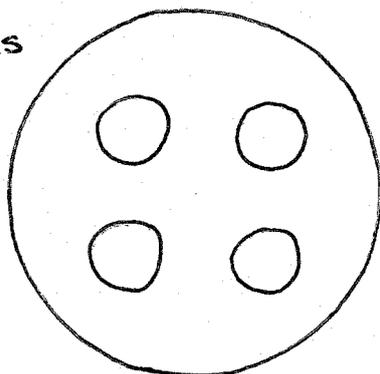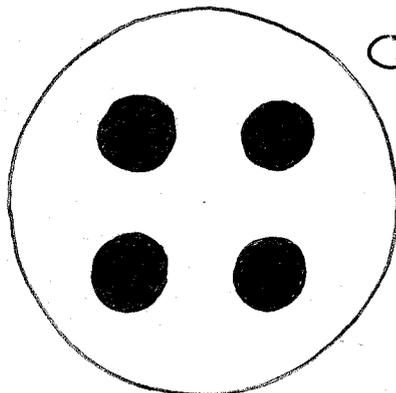
Controls

In the additive type, the controls enable the effect of one species upon the other to be calculated by comparing yields in mixture and monoculture. The additive experiment measures the competitive ability of A relative to competition against nothing, but substitutive experiments measure competitive ability of A relative to competition against itself. The additive experiment provides an <u>absolute</u> measure of competitive ability, but substitute experiments provide a <u>relative</u> measure.

EXPERIMENT   ONE

THE   EFFECT   OF   SIZE   DIFFERENCES   ON   THE

COMPETITIVE   INTERACTION   OF   HOLCUS LANATUS L.

AND   AGROSTIS TENUIS Sibth.

INTRODUCTION

The previous experiments designed to explore the effects of differences in size on competitive ability, have mainly used large differences to produce clearly appreciable results (e.g. Sagar 1960, Harper 1961, Williams 1962). Ross & Harper (1972) utilised the variability in time of emergence of Dactylis seed to produce a wide range of different sized plants. They found that the time of emergence (and hence size) was of overriding importance in determining the plant weight. A delay of about 30 days would be enough to prevent growth of seedling beyond that provided by the seed capital. It would be of interest to analyse a two-species interaction, and determine what size difference is necessary to offset the difference in competitive ability. If the two species were planted at the same time, the more competitive species would be expected to eventually exclude the less competitive species. So, if the more competitive species were planted at increasingly later times, there would come a point at which the greater competitive ability would not be capable of offsetting the size difference, and the more competitive species will eventually be excluded. The greater the difference in initial sizes of the two species, then the more rapid should be the competitive exclusion.

METHODS

It was decided to use Holcus Lanatus and Agrostis tenuis, because of the ready availability of seed. Arrhenatherum elatius had initially been considered instead of Holcus, but was found to give too low a germination rate. Nevertheless, Holcus and Agrostis make a good contrast; the larger seed, higher relative growth rate, greater maximum height and more competitive growth form giving Holcus an overall competitive advantage (see Table 1).

The seed of the two species were collected from wild populations growing in the Science Site at Durham during 1978, and were stored dry over winter. Initial germination tests on moist filter paper indicated that 93%. germination within a week could be expected from the Holcus, and greater than 99%. from the Agrostis. Tarred paper pots (3 inch diameter) were filled with potting compost (500 cm^3) and watered to field capacity. The seeds were separated from the remains of the inflorescences simply by gentle rubbing together. In order to improve the rate of germination, the seeds were soaked for 24 hours in tap water on filter paper. Using a moist brush, the seeds were then placed out in a fixed pattern (Fig 20c) on the moist compost surface. Two seeds were placed at each position, which after one week were thinned to one seedling per position. This procedure ensured that at least one plant was established at each position without requiring transplanting rooted plants

TABLE ONE

	HOLCUS LANATUS	AGROSTIS TENUIS	LOLIUM PERENNE
R_{MAX}	2·01 (SE = 0·13)	1·36 (SE = 0·12)	1·30 (SE = 0.06)
MAXIMUM HEIGHT (cm)	>100	26–50	50–75
MORPHOLOGY	Perennials attaining a diameter of 10–25 cm.		
MAXIMUM ACCUMULATION PERSISTENT LITTER	Thin Continuous	Up to 1 cm depth	Thin Continuous
COMPETITIVE (Morphology) INDEX	5·0	4.0	4·0
MEAN SEED WEIGHT (mg)	1·13		

SOURCES

Grime & Hunt (1975)

Hubbard (1968)

Grime (1973a, 1974, 1979)

(with danger of damage etc.), and further allows a degree of selection to produce an even-sized stand of plants. For the first week, the pots were covered by a sheet of clear polythene to maintain a high moisture level, and produce rapid and even germination. It is important that there is no bias in the germination of one species, so that any subsequent differences in the plants will be due to inherent differences in competitive ability. Care must be taken during hot weather, as the plants can overheat and be killed beneath the plastic sheeting.

In order to produce plants of various sizes, Holcus seeds were planted in their respective positions on each successive week, as shown in Table 2. Since the Holcus plants will all grow for different lengths of time, it is necessary to plant a control set of pots each week. As explained in the general introduction (p.9), the control used will be of the additive type where the species (here, Holcus) is planted at the same density as in the experimental pots, and the second species (here, Agrostis) is not planted. As it would not be possible to cover established plants with plastic sheeting, the method was modified after the first week, whereby the seeds were soaked for four days until the radicle began to appear. No size difference in the seedlings was apparent between the two methods. Allowing the seeds to germinate before planting removes the possibility of the Agrostis cover affecting the germination of Holcus (Fenner 1978).

Eight replicates were used for each treatment, as many as practically feasible in an attempt to reduce the standard error estimates. Newbery & Newman (loc.cit) used only four replicates and found that their results suffered from undue variation. The pots were arranged 2 cm. apart in a single block and randomised weekly, so that when complete it consisted of 23 x 6 pots. After three weeks, all pots were fitted with clear polythene sleeves (30 cm. high) to prevent lateral spread and interference with neighbouring pots. The pots were watered to field capacity every 2 - 3 days, and once a week were given nutrient solution (2.2 ml. Maxicrop liquified seaweed concentrate per litre of tap water). The nutrient solution allows high growth rates to be maintained throughout the experiment, so that the later planted plants do not suffer from lower nutrient levels. The experiment was harvested after 15 weeks, all above-ground biomass being removed and dried at 105°C for 24 hours, then weighed to an accuracy of 0.1 mg.

TABLE TWO

DIFFERENCE IN PLANTING DATES (Weeks delay of Holcus)	DATE OF PLANTING		DATE OF HARVEST
	Holcus	Agrostis	
−1	15th May	22nd May	29/30th Aug.
0	15th May	15th May	"
+1	22nd May	15th May	"
2	29th May	15th May	"
3	6th June	15th May	"
4	13th June	15th May	"
5	20th June	15th May	"
6	27th June	15th May	"

RESULTS

The actual dry weight data is summarised in Appendix 1, and is visually presented in Fig. 4. The 95%. confidence limits were calculated by the method for small samples (Parker 1973 p.18). For testing the significance of differences between sample means, a standard t-test was employed in which the population variances were not assumed to be equal.

DISCUSSION OF THE RESULTS

The results confirm the overriding importance of plant size in competitive interactions (see Fig.4). When the two species were planted together, the yield of Holcus does not differ significantly ($P > 0.1$) from the controls, whereas the yield of Agrostis does differ significantly ($P < 0.001$) from its controls. The more competitive Holcus is able to partially suppress Agrostis in 12 weeks, whereas the Agrostis is incapable of reducing the yield of Holcus. It would be expected that Holcus will eventually exclude the Agrostis, provided that the experiment is not subject to disturbance. Indeed, if the Holcus is planted a week earlier than the Agrostis then the yield of Agrostis is further depressed, and should be excluded more rapidly. The Holcus plants form a taller and denser canopy which shades the shorter and slower-growing Agrostis leading to yield depression. If the planting of Holcus is delayed by one week, then the yield of Agrostis is significantly increased ($P < 0.05$) and the yield of Holcus significantly decreased ($P < 0.001$). A three week delay in the planting of Holcus is sufficient to allow almost complete suppression by the Agrostis, whereas it shows a yield insignificantly different ($P > 0.05$) from the controls. Holcus is common in competitive situations (e.g. ungrazed grassland) where Agrostis will be competitively excluded. However, the two species are found together in moderately stressed habitats (e.g. moorland), where the lower rate of production prevents competitive exclusion. In disturbed environments Holcus tends to be eliminated as it is not capable of withstanding frequent moderate disturbance, (e.g. grazed grasslands),(Beddows 1961, Hubbard 1968, Grime & Lloyd 1973).

FIG. 4
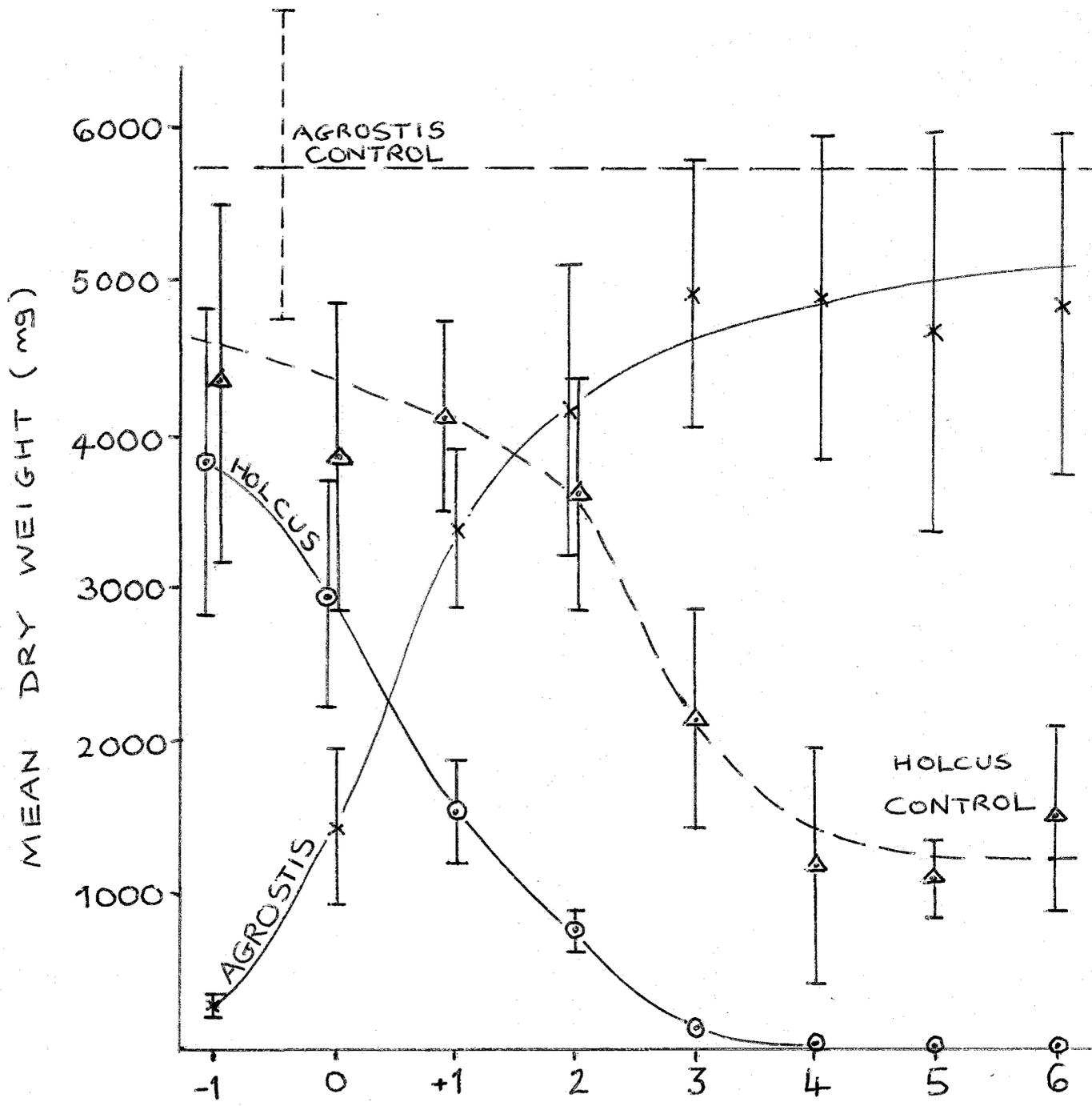
EXPERIMENT TWO

INTRODUCTION

Disturbance has clearly been shown to reduce competitive interactions, and the frequency of disturbance is important in determining the relative reduction (Mahmoud 1973,Hodkinson 1976,Rossiter 1976). Only in _Danthonia_ has clipping frequency been systematically studied, using intervals of 4, 8 and 12 weeks (Hodkinson 1976). It was decided to investigate the effects of a wider range of clipping frequencies on competition between species differing in competitive ability and in reaction to clipping.

METHODS

Lolium perenne and _Agrostis tenuis_ were the species chosen, because seed was readily available. _Lolium_ is the more competitive species, and their reaction to clipping was known to differ significantly (Mahmoud 1973). In germination tests, _Lolium_ was found to give 93%. germination within a week. The seeds were separated from the remains of the inflorescences by rubbing, and soaked on moist filter paper for 24 hours. The seeds were then placed out on moist compost (in 4.5 inch plastic pots containing 650 cm^3 compost) using a moist brush. The same pattern as experiment one was used (Fig.20c), with initially two seeds at each position, which were thinned to one per position after one week. All the pots were covered by clear polythene sheeting for the first week, to promote germination. After two weeks (on 5th.June) the plants had grown sufficiently for the clipping regime to commence. An overall time period of twelve weeks was selected, since this allows four clipping frequencies (every 1, 2, 3 and 6 weeks) to be run simultaneously and to all finish on the same day. The control treatment of unclipped plants was also run. After two weeks, it was felt that the clipping might not be sufficiently frequent to produce clear results, so using available spare pots (planted at the same time as the others), clipping was carried out every four days.

Ten replicates for each treatment were established, and watered every 2 - 3 days. The pots were organised into a single block (6 x 10) 3 cm. apart. The pots were randomised weekly and also given nutrient solution (2.2 ml. Maxicrop per litre tap water) weekly. The clipping was by scissors at a height of 4 cm., the clippings being dried for 24 hours at $105^{o}C$. before being weighed to an accuracy of 0.1 mg. At the end of the experiment, the above-ground biomass was harvested and dried at $105^{o}C$. for 24 hours.

RESULTS

The clip dry weights and total dry weights at the final harvest are summarised in Appendices 2 and 3, and visually displayed in Figs. 5 - 19. Data analysis was as for experiment one.

DISCUSSION OF THE RESULTS

For all the clipping frequencies, the plots of clip dry weight against time show a similar pattern (Figs. 5 - 9). The clip dry weight initially increases rapidly to a maximum and then declines following an exponential-type course, so that the clip weights gradually approaches zero over a long period of time. This decline might be produced through exhaustion of reserves available for regrowth. It is interesting that the decline is still very marked with a clip interval of six weeks, when it might be expected that there would have been sufficient time for the recovery of the reserves. The two species show a notable correlation of their respective clip weights, especially the coincidence of the peaks, which tends to suggest that the pattern for each clipping frequency is controlled by the clipping. The decline in clip weight might then be produced through declining growth rates with age. It should be remembered that the clipping regime will produce different effects on the two species (Mahmoud 1973).

Lolium maintained a significantly greater ($P < 0.01$) clip dry weight production over Agrostis for all clipping frequencies. Lolium was clearly capable of faster regrowth after clipping (see Fig.10) which might not have been expected, since most of the remaining plant biomass of Lolium was a brown stubble compared with the green (and presumably photosynthetically more active) stubble of Agrostis. Nevertheless, Lolium achieves the greater regrowth, possibly through a greater ability for storage.

The more infrequent the clipping, then the greater the yield of the clip dry weights, which can clearly be seen from the plot of cumulative clip dry weights (Fig. 11 and 12). This would be expected, since the longer the period between clips, the greater the production of new leaf material and capability for photosynthesis. The irregular course taken by the cumulative clip weight of the plants clipped every four days (marked 'half' on Figs. 11 & 12) was probably due to the initial two week delay before commencing clipping. In this time the plants would be able to develop larger root systems and reserves for regrowth than would have been possible under clipping.

The more frequent the clipping, then the closer the convergence of the total dry weights at harvest of the two species (Figs. 13 and 14).

One unexpected feature was the low _Lolium_ / _Agrostis_ ratio of the unclipped controls. The _Agrostis_ performance was better than expected, due to the production of long stolons, which because of the plastic supporting sleeves were able to grow upwards in a competitive manner, avoiding shading by _Lolium_.

In the natural environment, such support would not be present, and the stolons may represent the attempt by _Agrostis_ to move laterally away from competition (cf. _Trifolium repens_ Turkington & Harper 1979). In the clipped treatments, the stolons were prevented from growing to the same height as the faster regrowing _Lolium_, leading to shading and yield reductions in _Agrostis_. This situation was envisaged by Grime (1979 p.13) where infrequent disturbance can enhance rather than prevent competitive exclusion, by allowing the faster-regenerating species to dominate slower-regenerating species. It was noted by Jones (1933) that the most species rich communities were maintained by continuous grazing rather than by intense grazing in only one season. Scarisbrick & Ivins (1970) found that under close cutting (2.5 cm. height) the yield of _Plantago lanceolata_ was reduced by the rapid regrowth of _Trifolium repens_ and _Lolium perenne_. Thomas (1970) demonstrated that lax grazing allowed greater competitive interaction than close grazing. The increasing frequency of clipping allows the _Lolium_ to regrow to successively lower heights, with consequently less shading and yield reduction in _Agrostis_.

The effect of clipping differs for the two species leading to changes in the pattern of growth. _Lolium_ does not significantly alter the number of tillers formed per plant, whereas in _Agrostis_ tiller number increases with increasing clipping frequency (Fig.15). This is reflected in the dry weight below 4 cm., the ratio of _Lolium_ / _Agrostis_ decreasing with increasing clipping frequency (Figs. 17 and 18). The distribution of dry weight above 4 cm. (the cumulative clip dry weights) and the weight below 4 cm. can be seen in Fig.19. When clipped at six week intervals, this ratio is similar for both species. With more frequent clipping, the ratio for _Agrostis_ falls below that of _Lolium_, due to the lower clip production and greater production of tillers (initially below 4 cm.) of _Agrostis_.

The total yield (cumulative clip dry weight + dry weight below 4 cm.) demonstrates further differences between the two species (Fig.19). _Lolium_ maintains its total yield when clipped at six week intervals, but thereafter the yield decreases rapidly with increasing clipping frequency. _Agrostis_ produces a much smaller total yield, but is relatively little affected by clipping frequency.

These growth responses represent two different strategies, Agrostis adapted to frequent close-grazing through its low compact sward (disturbance-tolerant strategy). Lolium is adapted to infrequent-grazing where its competitive regrowth enables it to dominate the sward (competitive-disturbance strategy, Grime 1977).

These experimental findings can be related to the field distributions of the two species. Lolium is found in competitive environments (e.g. low-stress ungrazed grasslands) where Agrostis will be competitively excluded. However, with disturbance the two species can coexist, the more frequent the clipping then the better the performance of Agrostis (Beddows 1967, Hubbard 1968, Grime & Lloyd 1973). In stressed environments, Agrostis is able to survive when Lolium cannot, probably through the lower growth rate of Agrostis.

The results confirm that larger plants are more competitive than smaller plants, and competition experiments using clipping are only valid for the actual intensity and frequency of clipping used, and have no wider application.

FIG. 5

MEAN CLIP DRY WEIGHT (mg)

CLIP NUMBER (CLIPS AT 4 DAY INTERVALS)

FIG. 6

MEAN CLIP DRY WEIGHT (mg)

TIME (weeks)

FIG. 7

MEAN CLIP DRY WEIGHT (mg)

1000

800

600

400

200

0

TIME (weeks)

0 1 2 3 4 5 6 7 8 9 10 11 12

FIG. 8

MEAN
CLIP
DRY
WEIGHT
(mg)

TIME (Weeks)
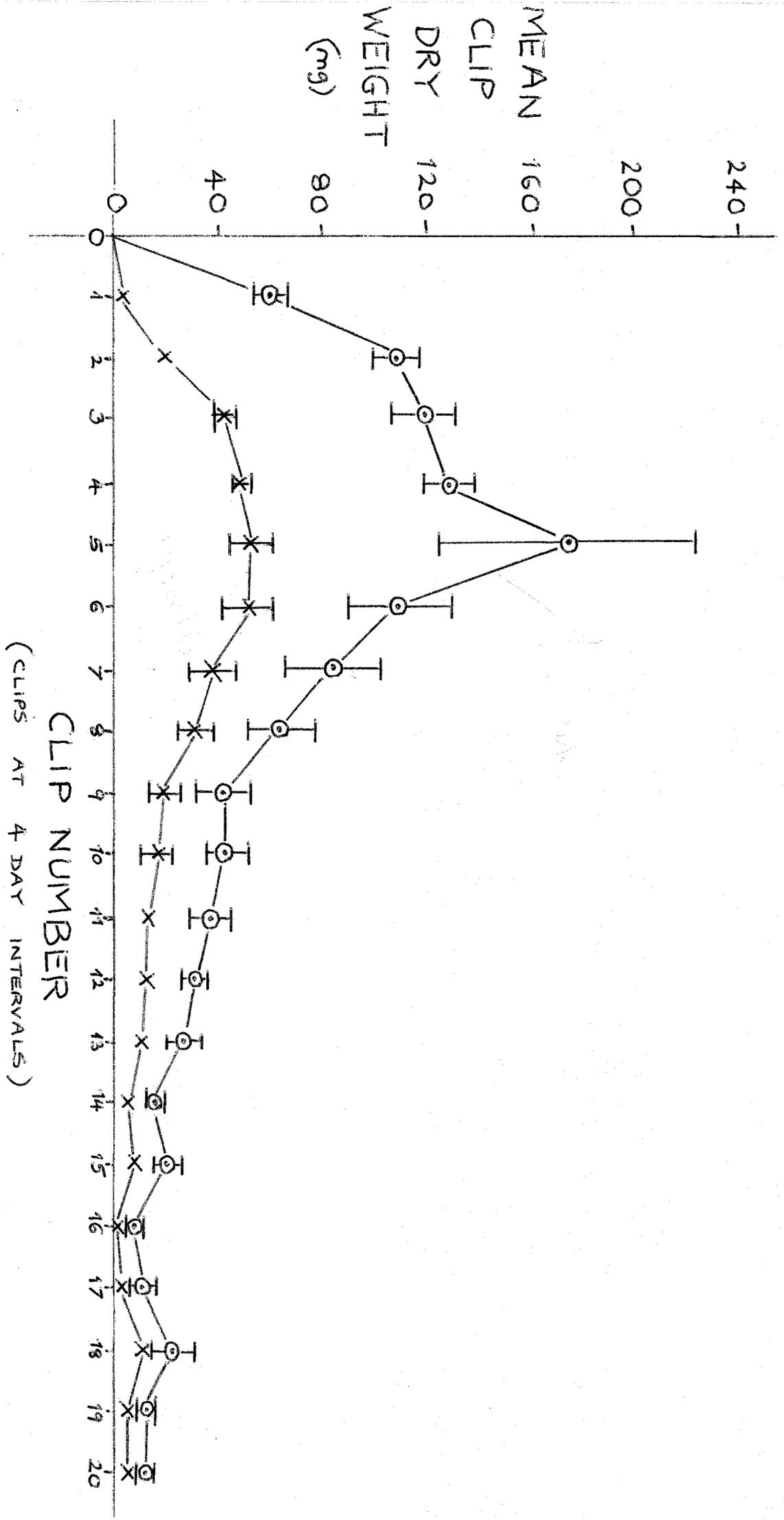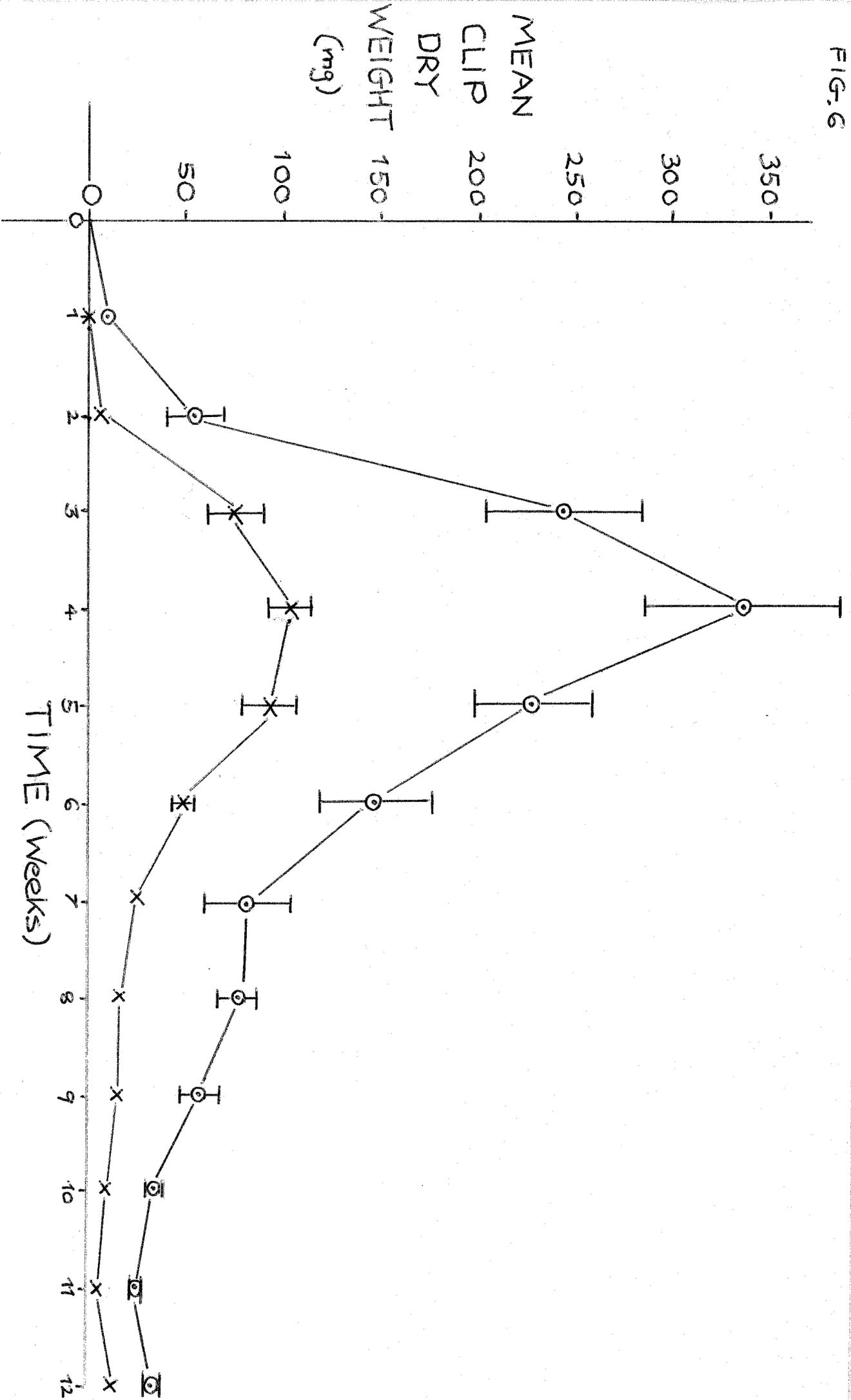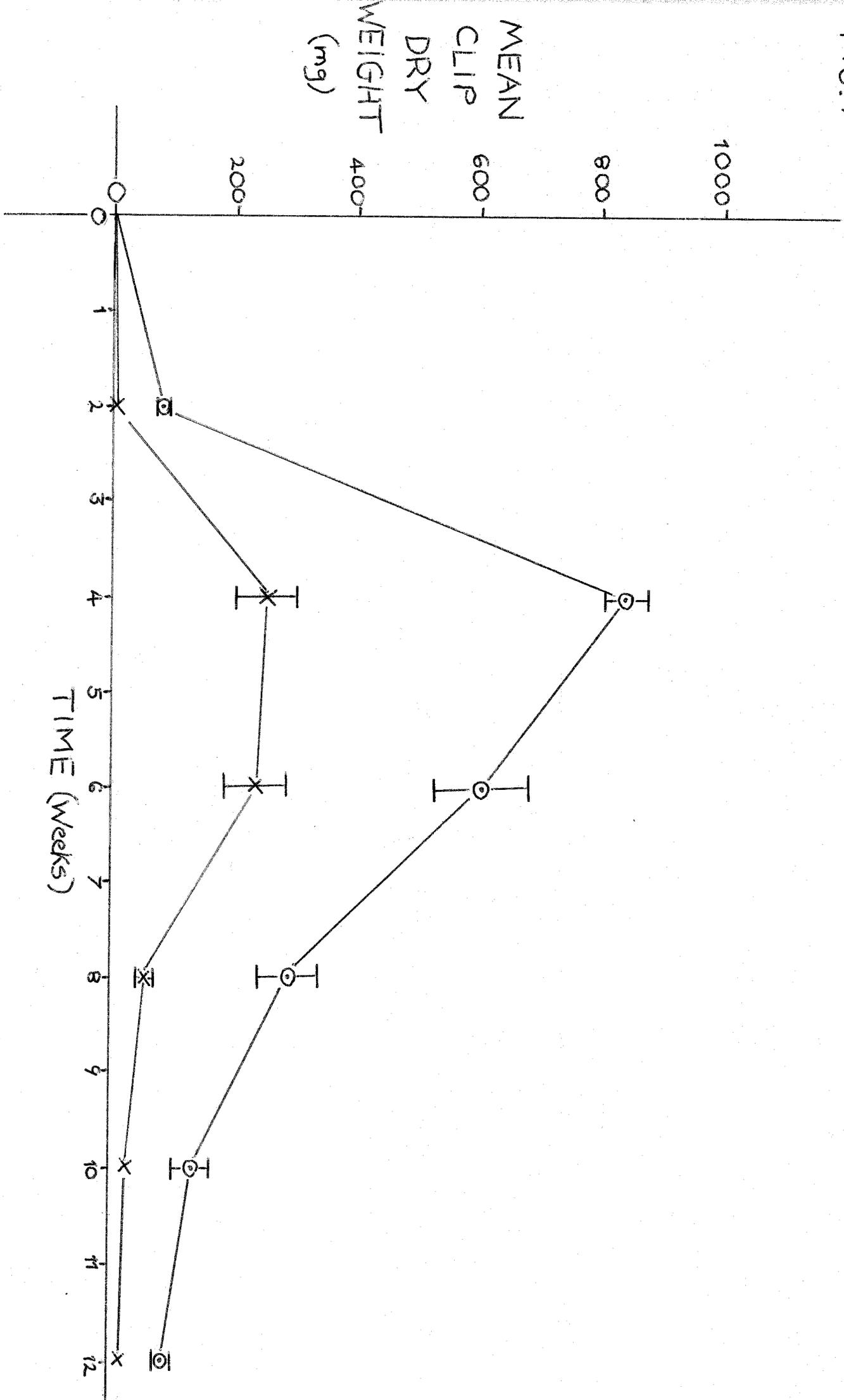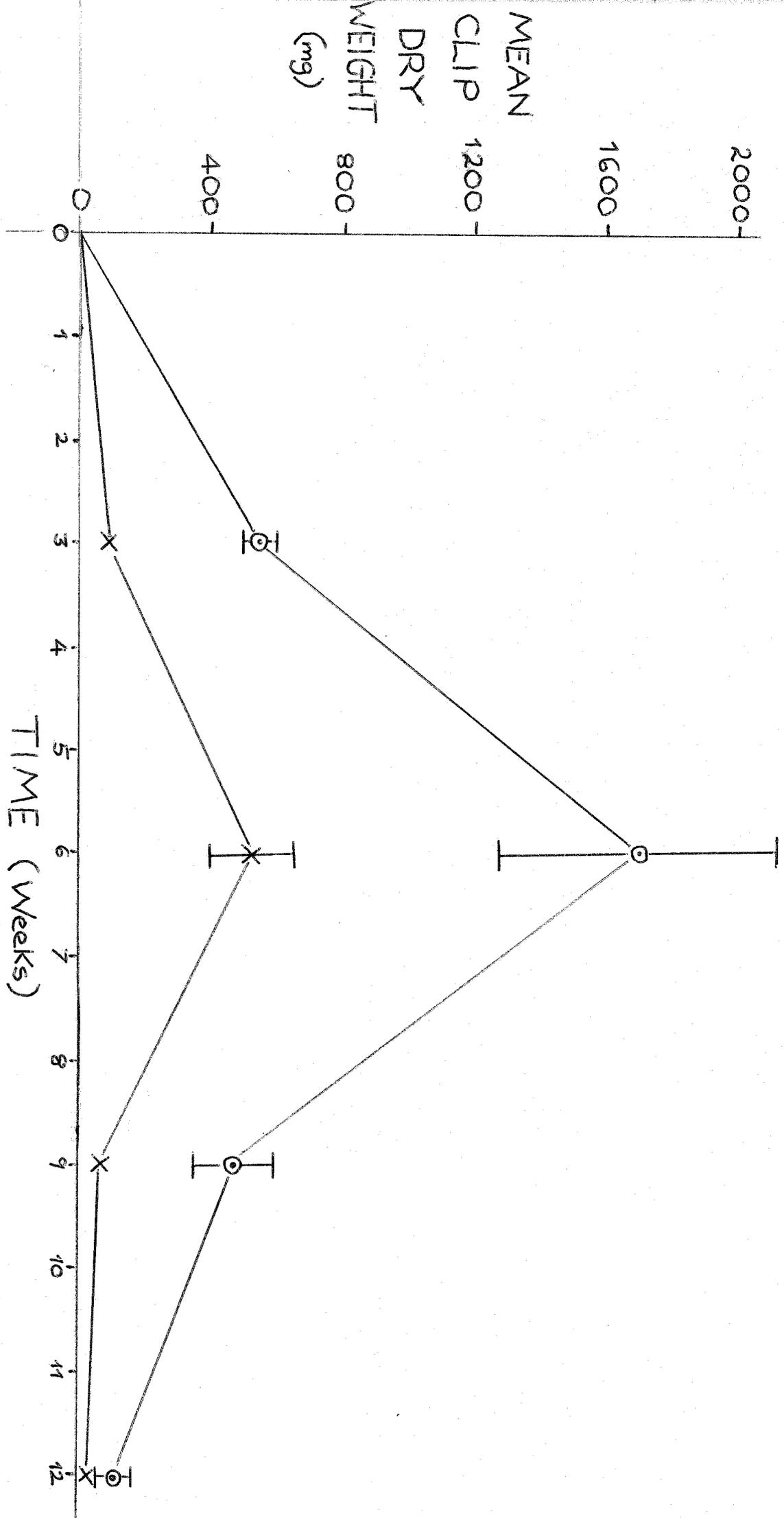
FIG. 10

Photographs of representative pots from Expt. 2 at time of final harvest. The clipping interval is marked on the stakes (in weeks).

W2 = Clipped every four days

12 = Unclipped controls.

FIG. 9

MEAN CLIP DRY WEIGHT (mg)

3000
2500
2000
1500
1000
500
0

TIME (Weeks)

0 1 2 3 4 5 6 7 8 9 10 11 12

FIG. 11

LOLIUM

CUMULATIVE CLIP DRY WEIGHT (mg)

TIME (weeks)

CLIPPING FREQUENCY (Clip intervals in weeks)

HALF

ONE

TWO

THREE

SIX

FIG. 12

AGROSTIS

CUMULATIVE CLIP DRY WEIGHT (mg)

TIME (weeks)

SIX

THREE

TWO

ONE HALF

FIG.13

TOTAL DRY WT. AT HARVEST

6000 –
5000 –
2000 –
1000 –

½   1   2   3   6

CLIPPING FREQUENCY

(Clip intervals – in weeks)

LOLIUM AGROSTIS

UNCLIPPED
CONTROLS

FIG. 14

FIG. 15

⊙ LOLIUM
× AGROSTIS

MEAN TILLER No. PER PLANT

15·0
13·0
11·0
9·0
7·0
5·0

½   1   2   3   6   12

CLIPPING FREQUENCY
(Clip intervals — in weeks)

FIG. 16

AGROSTIS

LOLIUM

MEAN DRY WT. BELOW 4 CM. (mg)

FIG.17

FIG. 18

FIG. 19

TOTAL YIELD (mg)

5000

4000

3000

2000

1000

0

CLIPPING   FREQUENCY

(Clip intervals – in weeks)

½   1   2   3   6   12

EXPERIMENT THREE

INTRODUCTION

Taraxacum officinale is an apomictic species with a low frequency of
sexual outcrossing. These sexual forms can be recognized as they are diploid;
all polyploids (except plants containing 3n - 1 chromosomes) being
completely apomictic (Darlington & Wylie 1955, Valentine & Richards 1967).
The apomictic forms produce a large number of genetically identical seeds,
which provides an opportunity to analyse competitive interactions between
genotypes. In sexually outcrossing forms, all the progeny differ
genetically, and it is not possible to separate differences in competitive
ability from the random genetic variation. Competitive analysis enables
conclusions to be made on relative competitive ability, and by the use of a
replacement series (de Wit 1960), it is possible to investigate the dynamic
properties of the interaction.

METHODS

Close inspection of individuals of *Taraxacum* reveals a wide variation in
morphology, notably in the red colour of the leaves and stems and in the
hairiness of leaves. The amount of red colouring of the leaves (due to
leuco-anthocyanin) was chosen because of clear differences and the use as a
population marker in other studies. The Science site was then investigated
for plants differing in pigment content growing adjacent to each other.
The seed from these plants was collected (9 - 30th June) only from mature
heads which could be recognized by their dark colour and ease of separation.
Some seeds were germinated on moist filter paper, and the root tips used to
make chromosome counts. They were fixed in 3 ‡ 1 ethanol / glacial acetic acid
for 24 hours and stained using Feulgens reagent (Darlington & La Cour 1976).
The counts varied from 30 - 34, and are clearly in the apomictic range.

The seeds were separated from their pappi by vigorous rubbing, and then
soaked for 48 hours on moist filter paper. The seeds were then planted out
(on 4th July) on moist compost (650 cm^3) in 4.5 inch plastic pots. The patterns
are shown in Fig.20 and they allow each seed type to occupy the same
proportion of location type (corner, edge or centre) as it does overall.
For instance, in Fig.20d, the red seeds occupy 25%. of each of the location
types. Two seeds were initially placed at each position, but were thinned to
one seedling per position after one week. In the case of the green seeds,
94%. germination was achieved, but for the red seeds many failed to produce good
root growth and had to be replaced by spare seedlings germinated on filter paper.

FIG. 20

A.

100% R

B.

75% R : 25% G

C.

KEY

● RED
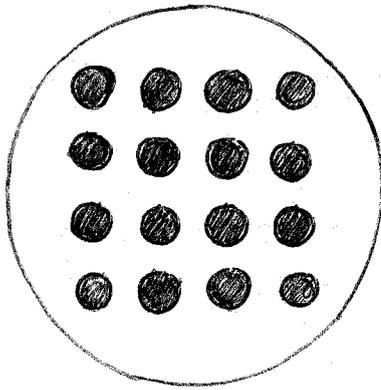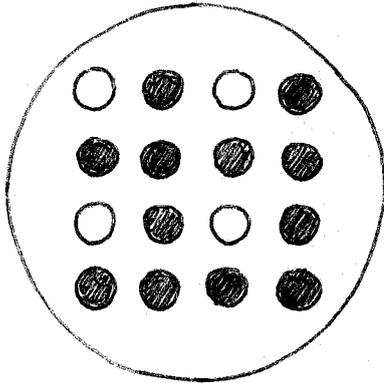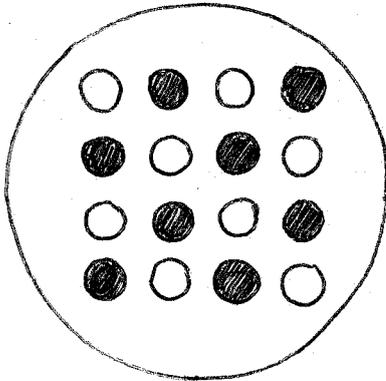
○ GREEN

50% R : 50% G

D.
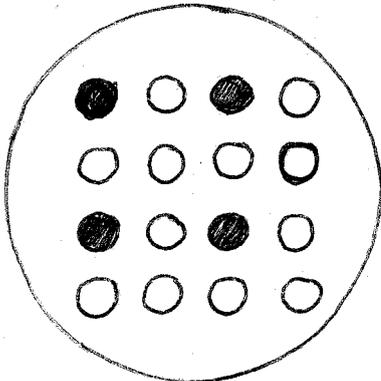
25% R : 75% G

E.
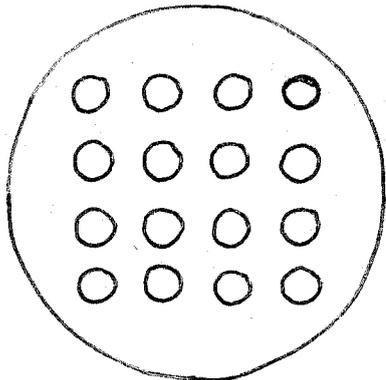
100% G

The pots were arranged into a single block (6 x 13), but after seven weeks growth the plants were beginning to overlap. They were rearranged into five blocks of fifteen (5 x 3 pots, each 18 cm. apart). The plants were watered every two days, with nutrient solution once a week after the blocks had been randomised.

After two weeks growth, the heights of a sample of 64 plants were measured, to determine whether the subjective impression of the greater size of the green plants was correct. The plants were remeasured at the end of the experiment, to determine whether there was still a significant difference. After eight weeks, a purple mildew infection developed which was treated by spraying with a general fungicide. Though this halted the development of the mildew, even a second spraying failed to produce any clearing of the leaves. After 12 weeks growth the above-ground biomass was harvested, dried at 105°C. for 24 hours before being weighed to an accuracy of 0.1 mg.

RESULTS

The dry weight data are summarised in Appendix 4, and presented visually in Figs. 21 +22 . Data analysis was as in experiment one. The t-test results on the mean heights at weeks two and twelve are presented in Table 3.

DISCUSSION OF THE RESULTS

The initial aims of the experiment were defeated by the late germination of the red-leaved seedlings, which allowed the faster germinating green-leaved seedlings to become significantly ($P < 0.001$) taller after two weeks. They managed to maintain this significant advantage throughout the course of the experiment. The replacement series diagram (Fig.21) shows that the Relative Yield Total probably does not differ from 1.0 (so the plants are competing for common limiting resources). From the ratio diagram (Fig.22), it can be inferred that directional selection will occur leading to the red-leaved plants being eventually excluded. This is most probably due to the size differences, and as such provides confirmatory evidence of the competitive advantage of larger plants.

FIG. 21

FIG. 22

$y = -0.601x + 2.416$

R = -0.8830
P = 0.0001
DF = 62

OUTPUT $\frac{RED}{GREEN}$

INPUT $\frac{RED}{GREEN}$
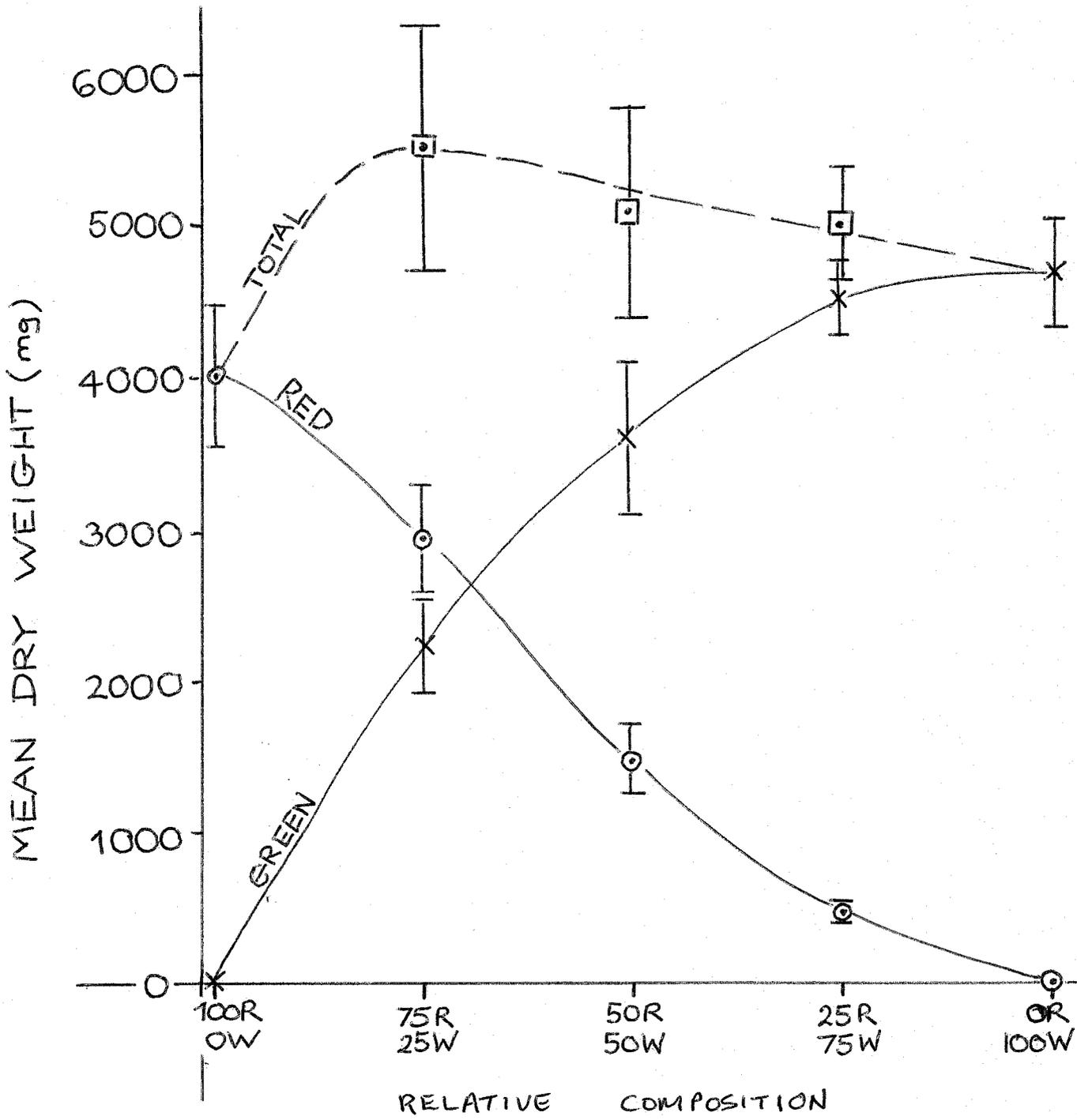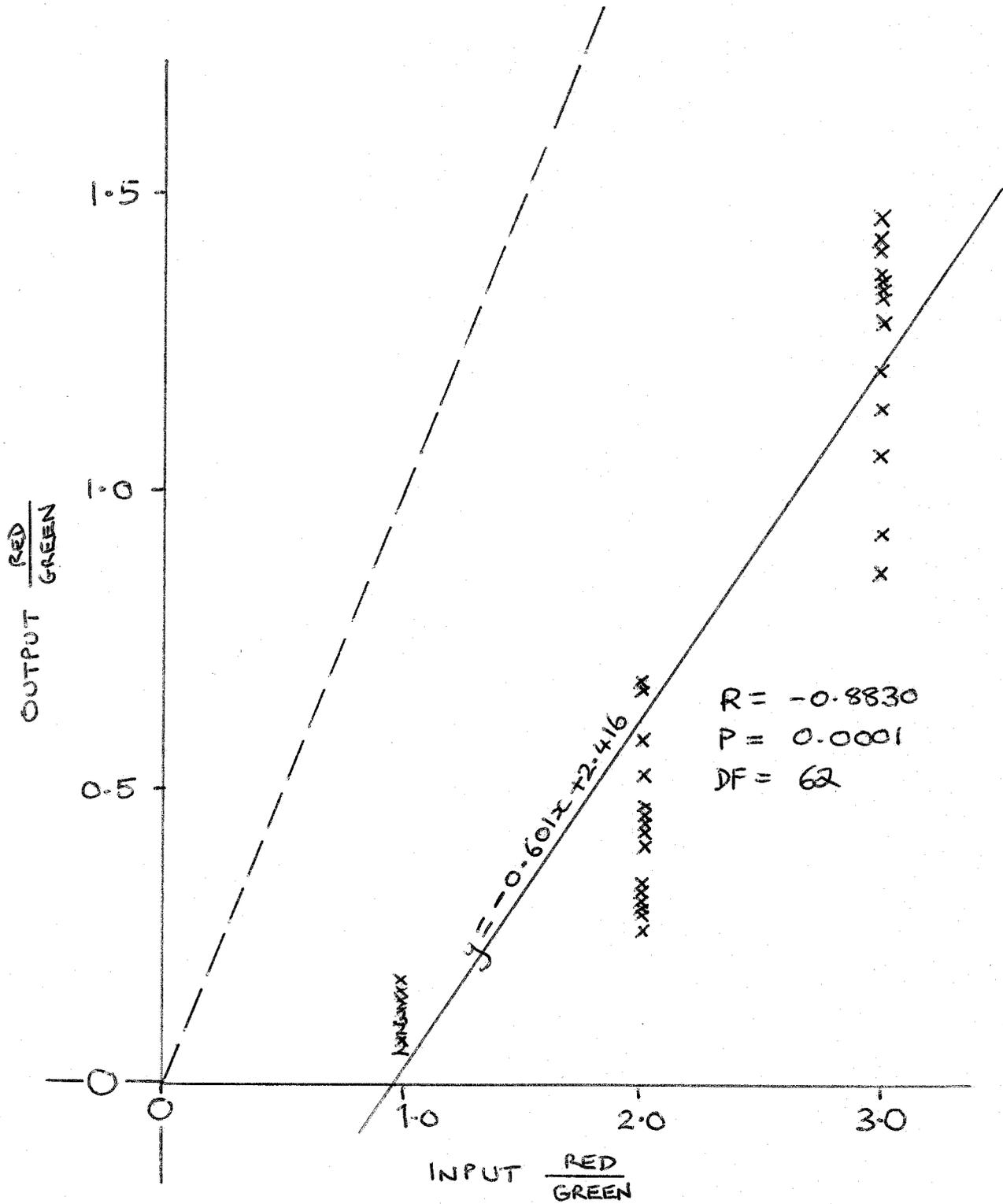
SUMMARY

The use of clipping as a measure of relative production in competition experiments was criticized, and in particular the interpretation of the experiment of Newbery & Newman (1978). They concluded that competitive ability decreased with increasing size; an effect produced by the reduction in competitive interaction through disturbance (clipping). An experiment was designed to test a prediction that a small advantage in height (of Agrostis tenuis) would be insuperable for a smaller but otherwise more competitive plant (Holcus lanatus). Height was found to be of overriding importance, a delay of one week leading to a reduction in yield of Holcus, and probable eventual exclusion.

A second experiment was designed to investigate the effects of clipping frequency on competitive interaction. Lolium perenne was capable of more rapid regrowth leading to increasing competitive suppression of Agrostis tenuis with decreasing frequency of clipping. In the unclipped controls, stolon production enabled Agrostis to grow upwards and compete more effectively. The two species differ in their response to clipping, Lolium producing vertical regrowth of the cut leaves whereas Agrostis produces new tillers; these differing strategies were related to their field distributions.

In a third experiment, it was intended to investigate the competitive interaction of two genotypes of the apomict Taraxacum officinale. Unfortunately, the germination was biased leading to a height advantage of one genotype suppressing the second genotype.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. K. Thompson for suggesting the project and for advice throughout the course of the experiments and writing of this dissertation. He also kindly carried out several of the clips in my temporary absence.

REFERENCES

Allard, R.W. & Adams, J. (1969)

Population studies in predominately self-pollinating species 8.
Intergenotypic competition and population structure in barley
and wheat.
Amer. Nat. 103, 621-645

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. (1977)

A quantitative analysis of shoot phenology and dominance in
herbaceous vegetation.
J. Ecol. 65, 759-791

Aspinall, D. (1960)

An analysis of competition between barley and white persicaria.
II Factors determining the course of competition.
Ann. Appl. Biol. 48, 637-654

Bazzaz, F.A. & Harper, J.L. (1976)

Relationship between plant weight and numbers in mixed
populations of Sinapsis alba and Lepidium sativum.
J. Appl. Ecol. 13, 211-216

Beddows, A.R. (1961)

Biological flora of the British Isles. Holcus Lanatus.
J. Ecol. 49, 421-430

Beddows, A.R. (1967)

Biological flora of the British Isles. Lolium perenne.
J. Ecol. 55, 567-587

Bergh, J.B. van den (1968)

An analysis of yields of grasses in mixed and pure stands.
Versl. Landbouwk. Onderz. Ned. 714, 1-71

Bergh, J.B. van den (1969)

Distribution of pasture plants in relation to chemical
properties of the soil.
Symp. Brit. Ecol. Soc. 9, 11-23

Bergh, J.B. van den & Elberse, W.T. (1970)

Competition between Lolium perenne and Anthoxanthum adoratum
at two levels of phosphate and potash.
J. Ecol. 50, 87-95

Black, J.N. (1958)

Competition between plants of different initial seed sizes
in swards of subterranean clover (Trifolium subterraneum)
with particular reference to leaf area and the light microclimate.
Aust. J. Agric. Res. 9, 299-318

Black, J.N. (1960)

The significance of petiole length, leaf area and light
interception in competition between strains of subterranean
clover (Trifolium subterraneum) grown in swards.
Aust. J. Agric. Res. 11, 277-291

Black, J.N. & Wilkinson, G.N. (1963)

> The role of time of emergence in determining the rate of dry matter production of swards of subterranean clover (Trifolium subterraneum).
>> Aust. J. Agric. Res. 14, 628-638

Bogart, J.R. & Beard, J.B. (1973)

> Cutting height effects on the competitive ability of annual bluegrass (Poa annua).
>> Agron. J. 65, 513-522

Bradshaw, A.D. Chadwick, M.J., Jowett, D. & Snaydon, R.W. (1964)

> Experimental investigations into the mineral nutrition of several grass species 4. Nitrogen level.
>> J. Ecol. 52,665-676

Burch, G.J. & Andrews, P. (1976)

> Replacement of cv. Yarloop in swards by new genotypes of Trifolium subterraneum subsp. yanninicum and the effects of defoliation.
>> Aust. J. Agric. Res. 27, 217-226

Crombie, A.C. (1947)

> On competition between different species of graminivorous insects.
>> Proc. R. Soc. London B 132,362-395

Darlington, C.D. & La Cour, L.F. (1976)

> The handling of chromosomes 6th Edition
> George Allen & Unwin Ltd., London.

Darlington, C.D. & Wylie, A.P. (1955)

> Chromosome atlas of flowering plants. 2nd Edition
> George Allen & Unwin Ltd., London.

Davidson, J.L. & Milthorpe, F.L. (1966a)

> Leaf growth in Dactylis glomerata following defoliation.
>> Ann. Bot. 30, 173-184

Davidson, J.L. & Milthorpe, F.L. (1966b)

> The effect of defoliation on the carbon balance in D. glomerata.
>> Ann. Bot. 30, 186-198

Detling, J.K., Dyer, M.I. & Winn, D.T. (1979)

> Net photosynthesis, root respiration and regrowth of Boutcloua gracilis following simulated grazing.
>> Oecologia 41,127-134

Donald, C.M. (1958)

> Interaction of competition for light and for nutrients.
>> Aust. J. Agric. Res. 9, 421-435

Eagles, C.F. (1972)

    Competition for light and nutrients between natural
    populations of Dactylis glomerata.
                        J. Appl, Ecol. 9, 141-151

Ellern, S.J. Harper, J.L. & Sagar, G.R. (1970)

    A comparative study of the distribution of Avena fatua
    and A. strigosa in mixed stands using a ^{14}C - labelling
    technique.
                    J. Ecol. 58, 865-868

Fenner, M. (1978)

    A comparison of the abilites of colonizers and closed-turf
    species to establish from seeds in artificial swards.
               J. Ecol. 66, 953-964

Ford, E.D. (1965)

    Competition and stand structure in some even-aged monocultures.
               J. Ecol. 63, 311-333

French, S.A.W. & Humphries, E.C. (1977)

    The effect of partial defoliation on yield of sugar beet.
               Ann. Appl. Biol. 87,201-212

Gadgill, M. & Solbrig, O.T. (1972)

    The concept of r- and k- selection; evidence from wild flowers
    and some theoretical considerations.
               Amer. Nat. 106, 14-31

Gause, G.F. (1934)

    The struggle for existence.   Hafner, New York.

Goodenough, U. & Levine, R.P. (1974)

    Genetics.   Holt, Rinehart and Winston, London.

Grime, J.P. (1973a)

    Competitive exclusion in herbaceous vegetation.

               Nature 242, 344-347

Grime, J.P. (1973b)

    Competition and diversity in herbaceous vegetation - a reply.

               Nature 224, 311

Grime, J.P. (1973c)

    Control of species diversity in herbaceous vegetation.
               J. environ. Mmgt. 1, 151-167

Grime, J.P. (1974)

    Vegetation classification by reference to strategies.

               Nature 250, 26-31

Grime, J.P. (1977)

Evidence for the existence of three primary strategies in
plants and its relevance to ecological and evolutionary theory.
Amer. Nat. 111, 1169-1194

Grime, J.P. (1979)

Plant strategies and vegetation processes.
John Wiley & Sons, Chichester.

Grime, J.P. & Hunt, R. (1975)

Relative growth rate : its range and adaptive significance
in a local flora.
J. Ecol. 63, 393-422

Grime, J.P. & Lloyd, P.S. (1973)

An ecological atlas of grassland plants.
Edward Arnold, London.

Hanes, T.L. (1965)

Ecological studies on two closely related chaparral shrubs
in southern California.
Ecol. Monog. 35, 213-235

Harding, J., Allard, R.W. & Smeltzer, D.G. (1966)

Population studies in predominately self-pollinated species.
9. Frequency-dependent selection in Phaseolus lunatus.
Proc. Natn. Acad. Sci. U.S.A. 56, 99-104

Harper, J.L. (1961)

Approaches to the study of plant competition.
In Mechanisms of Biological Competition (ed F.L. Milthorpe).
Symp. Soc. Exp. Biol. 15, 1 - 39

Harper, J.L. (1967)

A Darwinian approach to plant ecology.
J. Ecol. 55, 247-270

Harper, J.L. (1969)

The role of predation in vegetational diversity.
Brookhaven Symp. Biol. 22, 48-62

Harper, J.L. (1977)

Population biology of plants.
Academic Press, London.

Harper, J.L. & Clatworthy, J.N. (1963)

The comparative biology of closely related species.
6. Analysis of the growth of Trifolium repens and
T. fragiferum in pure and mixed populations.
J. exp. Bot. 14, 172-190

Hodkinson, K.C. (1976)

    The effects of frequency and extent of defoliation,
    summer irrigation and fertilizer on the production
    and survival of the grass Danthonia caespitosa Gand.
                Aust. J. Agric. Res. 27, 755-767

Hodkinson, K.C. & Baas Becking, H.G. (1977)

    Effect of defoliation on root growth of some arid
    zone perennial plants.
                Aust. J. Agric. Res. 29, 31-42

Hubbard, C.E. (1968)

    Grasses.   Penguin, England.

Hughes, A.P. (1973)

    A comparison of the effects of light intensity and
    duration on Chrysanthemum in controlled environments.
                Ann. Bot. 37, 267-274

Huston, M. (1979)

    A general hypothesis of species diversity.
                Amer. Nat. 113, 81-101

Jennings, P.R. & Aquino, R.C. (1968)

    Studies on competition in rice. 3. The mechanism of
    competition among phenotypes.
                Evolution 22, 529-542

Jones, M. (1933)

    See Harper (1969).

Khan, M.A., Putwain, P.D. & Bradshaw, A.D. (1975)

    Population interrelationships 2.
    Frequency-dependent fitness in Linum.
                Heredity 34, 145-163

King, J. (1971)

    Competition between established and newly sown grass species.
                J. Br. Grassland Soc. 26, 221-229

Kojima, K. & Huang, S.L. (1972)

    Effects of population density on the frequency-dependent
    selection in the esterase - 6 locus of Drosophila melanogaster
                Evolution 26, 313-321

Krebs, C.J. (1972)

    Ecology.   Harper & Row, New York.

Mahmoud, A. (1973)

    A laboratory approach to ecological studies of the grasses,
    Arrhenatheum elatius, Agrostis tenuis and Festuca ovina.
                Ph.D. thesis, University of Sheffield.

Mahmoud, A., Grime, J.P. & Furness, S.B. (1975)

    Polymorphism in Arrhenatherum elatius (L.)
    Heauv. ex J. & C. Presl.
                New Phytol. 75, 269-276

Mahmoud, A. & Grime, J.P. (1976)

    An analysis of competitive ability in three perennial grasses.
                New Phytol. 77, 431 - 435

Marshall, D.R. & Jain, S.K. (1969)

    Interference in pure and mixed populations
    of Avena fatua and A. barbata.
                J. Ecol. 57, 251-270

Merrell, D.J. (1953)

    Selective mating as a cause of gene frequency changes in
    laboratory populations of Drosophila melanogaster.
                Evolution 7, 287-298

Milne, A. (1961)

    Definition of competition among animals. In Mechanisms of
    biological competition. (ed F.L. Milthorpe).
                Symp. Soc. Exp. Biol. 15, 40-62

Narasimha Rao, D.V. & Rachie, K.O. (1964)

    Survival of genotypes in a mixture of fourteen sorghum varieties.
                Indian J. Genet. Pl. Breed. 24, 22-26

Naylor, R.E.L. (1976)

    Changes in the structure of plant populations.
                J. Appl. Ecol. 13, 513-521

Newbery, D. McC. & Newman, E.I. (1978)

    Competition between grassland plants of different initial sizes.
                Oecologia 33, 361-380

Newman, E.I. (1973)

    Competition and diversity in herbaceous vegetation.
                Nature 224, 310

Parker, R.E. (1973)

    Introductory statistics for biology.
    Studies in Biology No.43.   Edward Arnold, London.

Putwain, P.D. & Harper, J.L. (1972)

    Studies in the dynamics of plant populations 5. Mechanisms
    governing the sex ratio in Rumex acetosa and R. acetosella.
                J. Ecol. 60, 113-129

Remison, S.U. (1978)

    The effect of mineral nutrition and density on root
    interactions in three grass species.
                Ann. Bot. 42, 277-83

Rhodes, I. (1968)

> The growth and development of some grass species under
> competitive stress 3. The nature of competitive stress
> and characters associated with competitive ability
> during seedling growth.
> > J. Br. Grassland Soc. 23, 330-335

Roberts, H.A., Bond, W. & Hewson, R.T. (1976)

> Weed competition in drilled summer cabbage.
> > Ann. Appl. Biol. 84, 91-95

Ross, M.& Harper, J.L. (1972)

> Occupation of biological space during seedling establishment.
> > J. Ecol. 60, 77-88

Rossiter, R.C. (1976)

> The influence of defoliation on vegetation growth in
> swards of three strains of subterranean clover.
> > Aust. J. Agric. Res. 27, 197-206

Sagar, G.R. (1959)

> Quoted in Ross & Harper (1972)

Scarisbrick, D.H. & Ivins, J.D. (1970)

> Some aspects of competition between pasture species:
> the effect of environment and defoliation.
>
> > J. Appl. Ecol. 7, 417-428

Seaton, A.P.C. & Antonovics, J. (1967)

> Population interrelationships 1. Evolution in
> mixtures of Drosophila mutants.
> > Heredity. 22, 19-33

Shorrocks, B. (1978)

> The genesis of diversity.   Hodder & Stoughton, London.

Snaydon, R.W. (1971)

> An analysis of competition between plants of Trifolium repens
> L. populations collected from contrasting soils.
> > J. Appl. Ecol. 8, 687-697

Spiess, E.B. (1968)

> Low frequency advantage in mating of Drosophila
> pseudo-obscura Karyotypes.
> > Amer. Nat. 102, 363-380

Stern, W.R. (1965)

> The effect of density on the performance of individual
> plants in subterranean clover swards.
> > Aust. J. Agric. Res. 16, 541-555

Stern, W.R. & Donald, C.M. (1962)

    Light relationships in grass-clover swards.
                Aust. J. Agric. Res. 13, 599-614

Thomas, V.J. (1970)

    A mathematical approach to fitting parameters in a competition
    model.
                J. Appl. Ecol. 7, 487-496

Thompson, K. (1978)

    On the interpretation of competition experiments.
                Ann. Bot. 42, 1231-1232

Turkington, R. & Harper, J.L. (1979)

    The growth, distribution and neighbour relationships of _Trifolium_
    repens in a permanent pasture 2. Inter- and intra- specific contact.
                J. Ecol.   219-230

Valentine, D. & Richards, A.J. (1967)

    Sexuality and apomixis in _Taraxacum_.
                Nature 214, 114

Warwick, S.I. & Briggs, D. (1978)

    The genecology of lawn weeds.
                New Phytol. 81, 711-737

White, J. & Harper, J.L. (1970)

    Correlated changes in plant size and number in plant populations.
                J. Ecol. 58, 467-485

Whittaker, R.H. & Goodman, D. (1979)

    Classifying species according to their demographic strategy 1.
    Population fluctuations and environmental heterogeneity.
                Amer. Nat. 113, 185-200

Williams, J.T. (1962)

    Quoted in Ross & Harper (1972).

Wilson, (1970)

    Quoted in Newbery & Newman, (1978).

Wit, C.T. de (1960)

    On competition.
                Versl. Landbouwk. Onderz. Rijksl-and bproestfn.
                        66 (8), 8-82

Yoda, K., Kira, T., Ogawa, H. & Hozumi, K. (1963)

    Self-thinning in overcrowded pure stands under cultivated
    and natural conditions.
                J. Biol. Osaka Cy. Univ. 14, 107-129

APPENDIX ONE

TOTAL DRY WEIGHT AT HARVEST (mg)

(Experiment One)

t = Difference in planting dates (weeks delay of _Holcus_).

R = Replicate

S = Standard deviation

HOLCUS (Experimental)

				R				MEAN	S
i	2	3	4	5	6	7	8		
1	2739.8	5700.4	5045.1	4418.9	3228.1	3925.5	3393.3	2215.4	3870.8	1223.9
2	3163.5	2097.6	2099.3	3567.9	3177.8	4597.3	1911.3	3232.1	2980.9	929.7
3	2486.8	1617.5	1499.7	1204.6	1481.3	1612.2	1150.3	1491.3	1568.0	409.4
4	732.6	1058.5	738.4	862.9	449.9	800.5	769.4	797.6	776.2	158.2
5	114.9	209.2	132.8	137.0	142.7	91.7	164.9	114.1	138.4	36.0
6	19.3	57.0	76.1	18.1	37.0	35.9	43.0	32.8	39.9	19.2
7	17.8	28.0	15.5	20.8	28.5	21.6	10.6	17.3	20.0	6.1
8	9.4	18.2	17.0	5.5	8.7	9.3	4.7	7.0	10.0	5.0

(left margin label: t)

TOTAL DRY WEIGHT (mg)
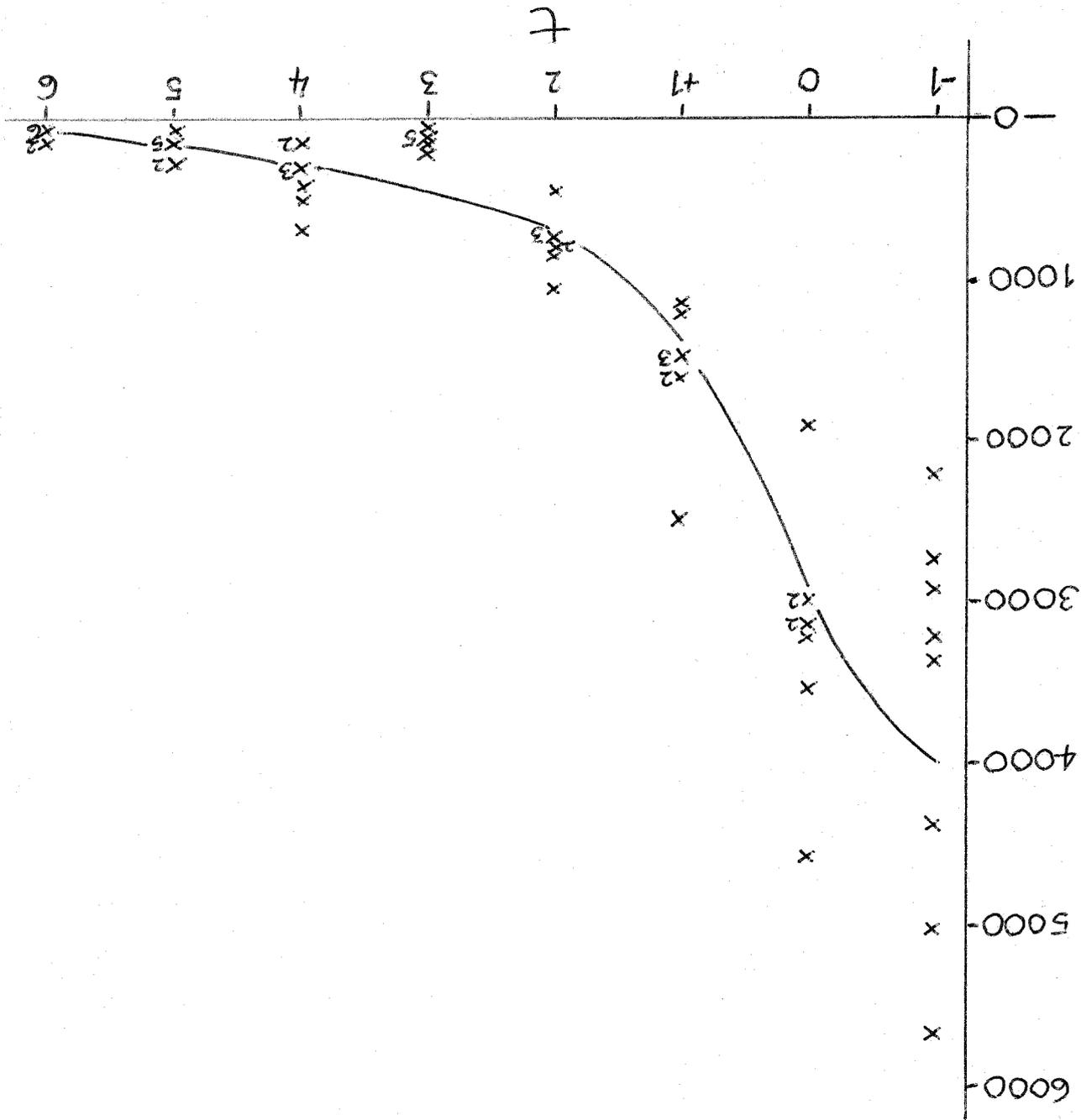
HOLCUS (CONTROL)

				R					MEAN	S
	1	2	3	4	5	6	7	8		
1	3105.2	3069.0	4014.1	3097.1	7275.3	3319.1	3500.7		4042.7	1455.7
2	5102.6	1977.9	4734.8	2629.8	4486.0	3834.1	5293.1	3079.3	3892.2	1219.6
3	5375.9	3690.2	3925.5	4842.6	4201.1	4227.1	4047.1		4148.1	745.4
4	3925.0	5515.2	3267.4	4229.6	2568.1	2889.5	3261.5	3565.1	3652.7	921.5
5	2436.6	1532.9	1344.4	1790.6	3987.4	2667.4	1546.0	1899.6	2150.6	871.2
6	3664.0	1075.4	1474.6	1184.2	2371.1	691.9	2031.7		1204.9	959.8
7	1205.8	1047.6	1805.0	994.9	1255.4	1033.8	1007.2	662.1	1125.5	326.3
8	1890.4	1486.0	2501.2	541.6	1278.1	1670.5	2392.6	542.9	1537.9	741.9
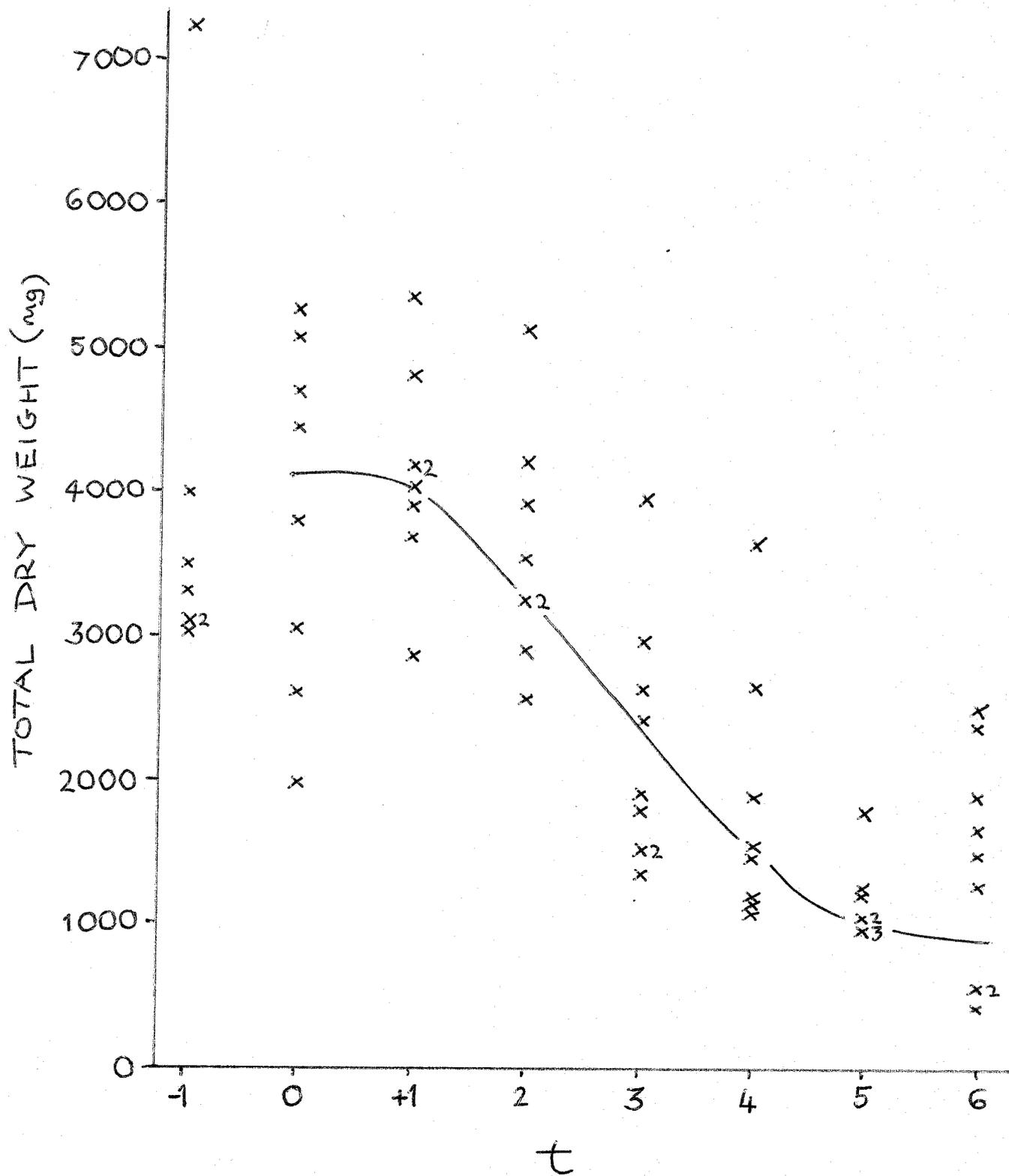
AGROSTIS

				R					MEAN	S
	1	2	3	4	5	6	7	8		
1	226.8	395.5	341.3	191.4	237.1	301.6	412.4	178.7	285.6	90.7
2	1555.0	1306.0	864.6	1565.0	1237.4	1988.6	831.9	1163.3	1439.0	587.5
3	4129.0	3268.0	3322.5	2303.6	3174.6	4336.2	3408.0	3700.6	3455.4	626.8
4	3218.0	5888.6	4611.2	5887.5	3208.9	3311.6	3680.4	4631.1	4188.4	1141.6
5	4825.4	6222.7	3511.7	4938.6	4958.6	3613.4	6375.4	5111.2	4944.4	1038.4
6	5569.3	6269.2	7028.6	3818.5	3773.3	4855.0	4478.1	3459.8	4906.5	1284.3
7	3896.5	4038.3	4946.3	7976.1	5044.1	3762.0	5231.5	2749.7	4710.6	1548.5
8	3852.8	5358.0	5417.3	6610.2	5593.0	5270.2	4357.7	2301.3	4845.1	1316.9
CONTROL	5517.3	6685.9	5071.3	8115.4	4515.2	6560.1	4943.2	4846.7	5781.9	1732.0

t

*

✳ Two plants flowered.
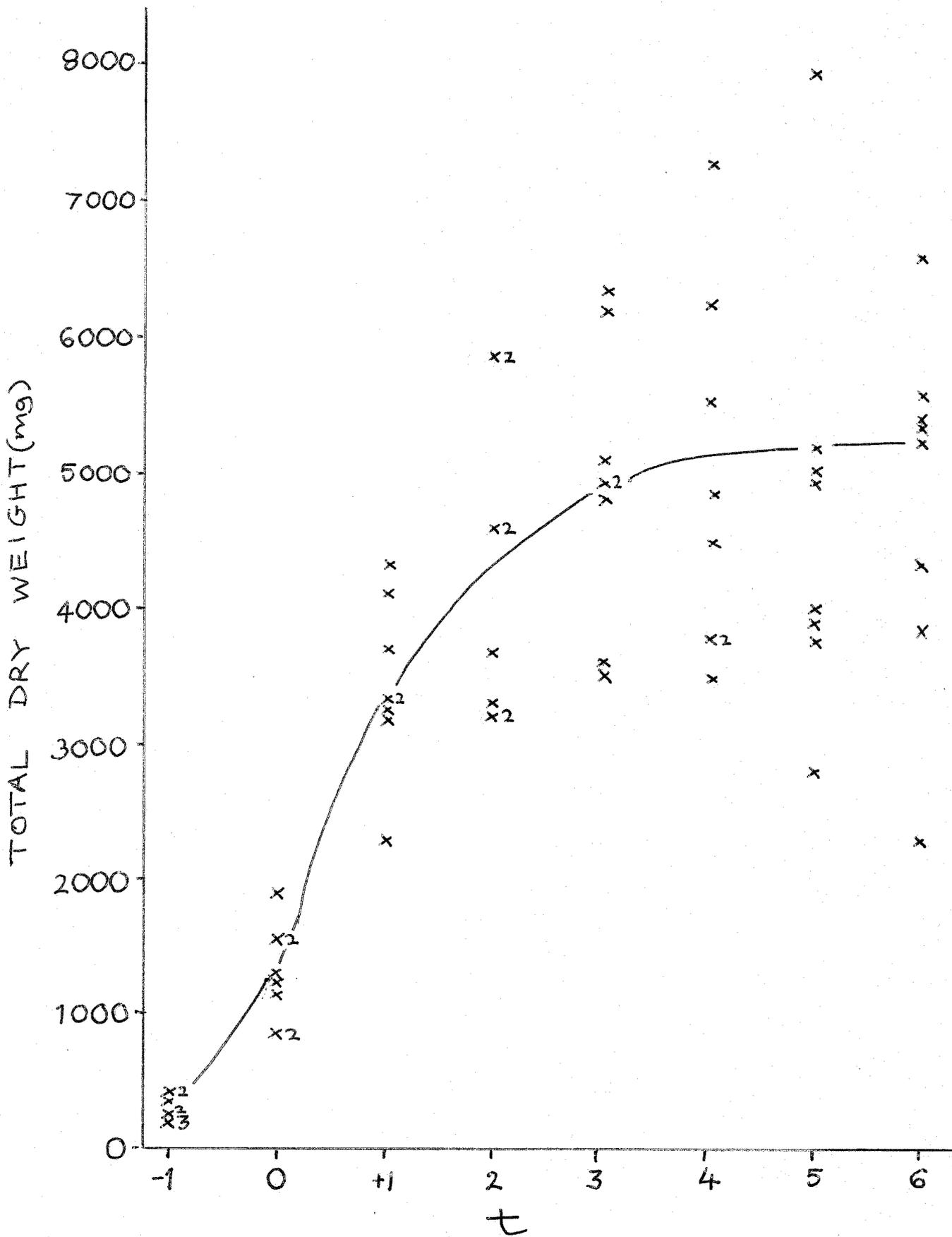
CLIP DRY WEIGHTS (mg)

(Experiment Two)

F = Clipping frequency (clip intervals - in weeks).

t = Clip number

R = Replicate

S = Standard deviation

LOLIUM

F	t	1	2	3	4	5	6	7	8	9	10	MEAN	S
						R							
HALF F	1	52.3	76.0	69.4	59.4	48.5	53.8	61.6	54.7	54.1	62.7	59.25	8.45
	2	132.0	93.2	114.8	108.6	93.0	104.4	108.0	117.6	107.6	—	109.17	11.89
	3	119.8	104.5	119.8	104.8	104.8	95.5	116.8	150.5	133.8	—	120.63	15.66
	4	141.5	148.3	141.8	114.6	126.4	103.1	126.4	126.4	—	—	129.60	12.71
	5	122.8	274.0	121.3	251.0	125.7	201.6	124.4	133.5	241.1	—	175.34	65.87
	6	102.8	126.3	120.2	165.3	99.7	102.4	70.9	97.2	105.4	—	110.02	25.88
	7	75.7	64.8	128.3	85.9	108.9	70.0	84.4	83.6	—	—	83.60	23.24
	8	52.8	50.2	97.2	55.3	71.0	53.8	46.4	69.6	71.6	—	63.10	15.96
	9	33.3	32.4	69.6	44.1	34.6	49.8	45.1	50.5	—	—	43.36	12.45
	10	33.3	30.8	30.8	37.4	38.2	45.6	46.5	47.3	—	—	43.18	9.61
	11	32.3	37.6	65.2	37.4	38.2	43.1	41.7	—	—	—	37.82	10.29
	12	19.2	31.0	60.7	28.2	29.7	32.2	38.7	31.5	—	—	31.59	9.74
	13	27.3	29.6	50.0	33.3	25.5	36.9	38.7	23.1	—	—	27.21	8.34
	14	15.3	33.5	19.8	18.0	19.6	30.0	29.2	19.7	23.1	—	15.83	3.77
	15	13.0	16.5	22.5	18.7	17.4	16.1	9.3	13.5	17.7	—	19.55	6.47
	16	7.3	31.1	12.1	15.4	23.4	19.5	24.5	—	—	—	8.63	2.86
	17	4.1	5.5	12.9	9.1	10.3	11.9	6.1	—	—	—	10.03	5.97
	18	20.0	8.1	23.5	5.9	9.1	6.1	5.7	—	—	—	22.64	8.48
	19	12.2	11.7	31.9	12.4	9.0	8.9	13.4	—	—	—	12.04	3.28
	20	20.0	16.6	8.9	32.8	19.7	8.5	34.0	16.9	—	—	22.64	8.48
	19	12.2	16.6	11.6	8.9	9.2	12.4	8.5	16.9	—	—	12.04	3.28
	20	10.8	11.2	13.6	17.9	9.9	12.0	9.3	9.3	—	—	11.75	2.88

LOLIUM

Columns 1–10 are headed **R** (replicates).

F	t	1	2	3	4	5	6	7	8	9	10	MEAN	S
ONE	1	12.5	7.8	7.1	11.7	5.5	7.9	8.2	8.2	6.8	9.1	8.5	2.15
	2	59.1	54.4	47.4	54.8	39.7	56.6	59.2	71.6	70.5		54.3	17.12
	3	101.8	275.0	295.9	255.3	259.0	281.6	242.1	238.4	243.3		244.6	53.51
	4	455.7	316.9	369.3	272.1	330.5	306.1	335.6	214.1	359.1		337.8	69.05
	5	228.3	305.6	269.6	231.9	147.5	182.6	223.9	230.7	217.8		228.6	43.27
	6	202.0	181.6	204.0	138.0	135.0	123.0	86.5	169.7	112.0		147.7	39.64
	7	86.2	109.6	105.2	93.7	108.3	91.3	93.6	84.0	68.0		81.5	29.78
	8	53.5	61.6	63.6	50.2	81.0	61.0	63.8	86.8	74.6		67.9	12.58
	9	59.0	63.6	55.0	45.5	90.4	45.2	55.9	58.8	62.0		58.3	13.29
	10	33.7	34.7	56.0	26.2	32.0	36.8	37.9	32.7	38.1		35.7	8.12
	11	25.8	22.2	20.4	20.5	25.8	26.3	26.4	19.5	27.8		24.0	3.05
	12	29.0	29.2	34.8	23.2	27.4	35.7	25.0	45.2	53.6		32.9	9.74
TWO	1	61.4	59.3	53.3	93.0	91.3	82.7	103.3	88.7	86.1	89.5	80.9	16.77
	2	577.2	919.4	804.9	794.7	829.5	874.7	840.5	899.5	898.7	799.7	843.5	51.53
	3	583.1	583.6	537.2	456.5	482.5	633.3	674.6	684.8	829.8	592.2	605.8	108.2
	4	258.8	209.8	382.9	298.4	226.6	416.4	293.8	202.1	309.1	300.0	289.9	70.18
	5	119.5	121.4	136.4	117.2	148.2	105.6	169.8	158.2	115.0	167.8	136.2	23.29
	6	74.0	92.4	90.6	90.6	104.1	75.8	76.1	97.2	75.1	77.1	83.2	11.84
THREE	1	521.5	564.7	529.5	485.9	632.0	419.4	580.3	573.7	624.2		547.9	67.32
	2	1761.8	1074.9	1500.7	1630.1	1730.5	2965.0	1758.7	1753.4	1103.4		1697.6	548.0
	3	332.9	346.2	560.5	530.7	597.9	703.6	463.4	235.2	509.9		474.5	148.5
	4	270.7	261.1	203.8	159.0	122.7	203.1	203.1	149.1	307.2		217.6	65.53
SIX	1	3280.0	2783.5	2485.9	2665.8	2433.1	2307.1	2374.1	2814.0	2818.1	3080.8	2968.2	316.6
	2	1360.7	1029.1	990.3	855.4	814.6	818.6	739.1	947.8			962.8	190.3

AGROSTIS

F	t	1	2	3	4	R 5	6	7	8	9	10	MEAN	S
1	3·7	3·4	2·1	1·1	3·6	1·1	2·9	1·8	1·9	4·1	—	2·47	1·23
2	20·0	19·3	15·9	21·4	16·0	20·1	18·2	22·0	15·9	—	—	18·87	2·54
3	41·6	48·2	35·4	44·7	45·1	47·6	41·4	37·8	—	—	—	41·98	4·80
4	51·8	49·6	45·3	49·6	40·5	51·2	47·0	52·4	—	—	—	48·28	3·77
5	42·7	65·6	52·0	52·0	45·5	58·1	65·4	52·4	—	—	—	52·87	9·79
6	31·9	52·0	48·4	52·7	32·0	49·1	59·1	68·6	—	—	—	51·41	13·39
7	24·7	40·5	46·6	45·0	30·0	39·5	55·4	—	—	—	—	36·97	11·06
8	18·8	27·6	41·0	17·6	30·5	33·8	29·2	31·6	46·5	—	—	30·73	9·30
9	7·6	8·0	24·3	25·1	22·2	14·8	16·8	19·1	28·1	—	—	18·44	7·32
10	8·7	11·0	20·4	7·8	26·9	15·3	19·1	13·4	26·4	—	—	16·56	7·12
11	3·4	7·9	22·3	10·4	19·7	14·6	16·2	15·3	17·9	—	—	14·19	5·98
12	8·5	5·3	17·9	15·1	11·5	18·1	11·8	16·2	17·9	—	—	13·59	4·59
13	15·4	10·9	5·7	15·1	4·7	13·8	10·7	11·4	13·2	—	—	11·21	3·82
14	5·9	6·7	10·3	7·6	2·6	0·8	3·0	7·6	4·3	—	—	5·42	2·75
15	11·3	8·8	10·6	3·7	3·7	7·4	11·8	9·5	—	—	—	8·36	3·17
16	0·4	0·6	0·6	1·6	1·1	3·2	4·6	0·5	1·0	—	—	3·26	1·62
17	1·3	2·0	5·0	3·7	4·2	3·8	1·0	2·7	—	—	—	1·58	1·53
18	18·3	6·8	9·9	17·7	4·4	9·7	11·7	7·1	—	—	—	11·88	4·41
19	9·2	8·4	7·2	4·4	6·1	2·1	2·7	—	—	—	—	5·34	2·78
20	2·4	6·0	3·1	5·7	6·7	5·9	8·2	—	—	—	—	5·68	2·00

HALF

AGROSTIS

F	t	1	2	3	4	5	6	7	8	9	10	MEAN	S
						R							
ONE	1	3.7	5.1	3.7	5.3	3.5	5.3	7.0	6.9	4.3	5.8	5.1	1.27
	2	0	0	0	0	0	0	0	0	0	0	0	—
	3	35.3	71.5	86.0	69.7	60.5	81.7	88.3	67.7	75.6	106.2	74.3	18.83
	4	106.7	102.8	71.7	100.5	117.2	128.2	97.3	105.1	118.4	101.7	105.0	15.18
	5	84.8	128.2	113.4	110.0	66.4	101.2	78.0	83.5	84.6	93.4	93.4	19.02
	6	65.4	53.3	46.0	41.3	46.2	44.6	42.9	54.3	44.5	48.4	48.4	7.29
	7	32.9	31.5	25.6	24.0	30.6	25.8	24.0	21.0	17.4	27.5	25.04	4.45
	8	12.2	17.6	16.2	16.0	21.4	18.0	16.3	21.5	19.0	23.4	18.2	3.29
	9	12.6	13.8	20.9	15.4	18.7	16.0	15.9	21.4	21.4	15.8	15.8	3.63
	10	10.7	10.2	11.7	11.5	7.1	9.5	10.7	7.3	9.1	10.2	10.2	2.20
	11	4.2	4.5	2.2	4.6	7.7	7.9	5.0	9.3	6.1	6.1	6.1	2.41
	12	12.4	16.8	15.2	4.8	11.2	16.0	12.8	17.0	10.1	12.9	12.5	3.49
TWO	1	0.5	1.6	2.8	4.8	6.2	3.6	4.9	4.6	6.0	5.4	4.0	1.89
	2	171.3	151.8	287.6	294.5	304.9	201.7	237.0	353.9	286.3	190.5	247.9	66.94
	3	174.0	170.8	227.8	148.0	229.3	200.8	263.2	334.9	334.2	283.0	236.6	66.30
	4	36.8	39.7	86.5	63.0	43.4	60.7	40.3	39.8	56.0	86.4	55.3	18.92
	5	28.0	26.6	24.4	19.8	26.1	25.9	25.6	27.8	33.2	41.4	28.3	5.78
	6	17.6	12.5	19.7	19.2	12.7	22.2	9.5	14.1	32.0	12.9	17.2	6.53
THREE	1	80.4	74.0	77.1	84.7	103.9	115.7	71.8	123.7	92.7	—	92.3	11.15
	2	354.7	329.5	539.0	446.5	655.0	705.7	376.0	745.0	582.4	—	525.9	156.9
	3	68.5	74.7	106.3	64.5	88.3	107.0	66.7	65.7	51.5	—	77.0	19.38
	4	53.2	49.3	40.1	39.5	39.3	32.0	21.3	44.0	46.0	—	40.5	13.11
SIX	1	682.6	801.2	770.8	807.8	847.3	955.8	847.6	829.5	919.2	594.2	754.6	173.4
	2	128.5	147.0	162.8	94.8	156.7	127.0	103.5	103.9	175.3	—	127.5	34.90

APPENDIX THREE

TOTAL DRY WEIGHTS AT HARVEST (mg)

(Experiment Two)

t = Replicate number

F = Clipping frequency (clip intervals - in weeks).

S = Standard deviation

LOLIUM

	t											
F	1	2	3	4	5	6	7	8	9	10	MEAN	S
1/2	533.2	744.5	617.4	755.5	602.3	677.7	597.9	659.7	—	—	648.5	76.2
1	528.4	504.2	546.4	568.6	727.3	590.1	660.9	735.4	670.0	725.0	625.6	88.5
2	847.7	796.8	844.2	798.7	998.2	782.7	841.0	918.3	769.1	812.3	840.9	69.8
3	1510.2	1483.5	2125.5	1022.3	909.1	1329.9	1598.1	956.1	1322.6	—	1361.9	381.3
6	2387.1	2712.8	2351.0	2221.2	1963.5	1871.0	2237.8	2569.4	2192.1	2411.2	2291.7	254.7
12	5720.7	3878.0	4792.8	3919.3	8284.5	6251.6	7823.0	5010.0	4746.0	—	5391.3	1295.8

AGROSTIS

	t										MEAN	S
	1	2	3	4	5	6	7	8	9	10		
HALF	615.2	476.6	478.7	450.7	431.7	380.9	470.3	621.1	—	—	490.7	84.85
ONE	312.6	472.2	494.6	310.7	319.5	458.4	276.6	352.7	388.0	317.3	370.3	78.36
TWO	394.4	302.2	408.0	278.4	448.3	343.2	303.4	279.5	350.2	292.1	340.0	59.58
THREE	439.8	440.4	354.3	369.2	398.2	468.4	281.2	545.5	347.0	—	404.9	78.11
SIX	2387.1	2712.8	2351.0	2221.2	1963.5	1871.0	2237.8	2569.4	2193.1	2411.2	469.9	89.12
TWELVE	2515.4	1602.0	2021.8	2492.8	1844.4	2455.8	1165.9	1788.9	1833.9	—	1968.9	455.3

F

APPENDIX FOUR

TOTAL DRY WEIGHTS AT HARVEST (mg)

(Experiment Three)

R = Red-leaved plants

W = Green-leaved plants

S = Standard deviation

REPLICATE	100% R	75% R : 25% W		50% R : 50% W		25% R : 75% W		100% W
	R	R	W	R	W	R	W	W
1	3899.9	2724.1	1932.7	948.7	3689.7	334.3	4809.7	4961.7
2	3556.6	1822.3	1953.9	1916.3	2655.1	416.7	5162.4	4873.1
3	4582.3	2469.1	1834.4	1520.2	5161.2	423.9	4388.9	4098.7
4	4398.7	2243.3	1980.1	1181.3	3484.5	490.8	3633.0	5787.0
5	3946.8	3038.0	2869.7	1824.7	3128.2	338.7	5108.5	4319.1
6	5769.6	3699.9	2714.5	1309.1	3274.8	439.1	4678.7	3885.9
7	3569.7	2224.6	2627.7	1546.3	5004.5	728.6	4469.7	4625.1
8	2422.2	3557.5	2445.0	1413.5	3100.2	488.4	4643.4	3646.7
9	3159.7	3549.4	2953.5	2229.1	3320.9	327.2	4133.7	5260.1
10	4825.9	3204.9	2386.6	1578.8	3715.8	394.1	3950.9	4286.3
11	3632.6	2781.0	1131.1	1187.7	3567.8	590.8	4437.3	4283.9
12	4516.4	4032.6	3116.9	2085.9	4876.9	330.8	5139.5	4568.7
13	5204.3	2802.5	2450.9	861.4	1671.0	604.1	4575.4	5460.6
14	3567.9	3128.2	2192.3	904.8	3131.9	535.7	4806.7	4971.4
15	4050.0	—	1583.3	1750.0	3890.1	716.3	4269.2	5659.8
MEAN	4037.4	2948.7	2278.17	1477.2	3628.7	477.6	4547.1	4712.5
S	838.6	632.4	548.2	418.6	906.4	134.4	438.4	644.2