Studies in plant competition

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STUDIES IN PLANT COMPETITION

by

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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.

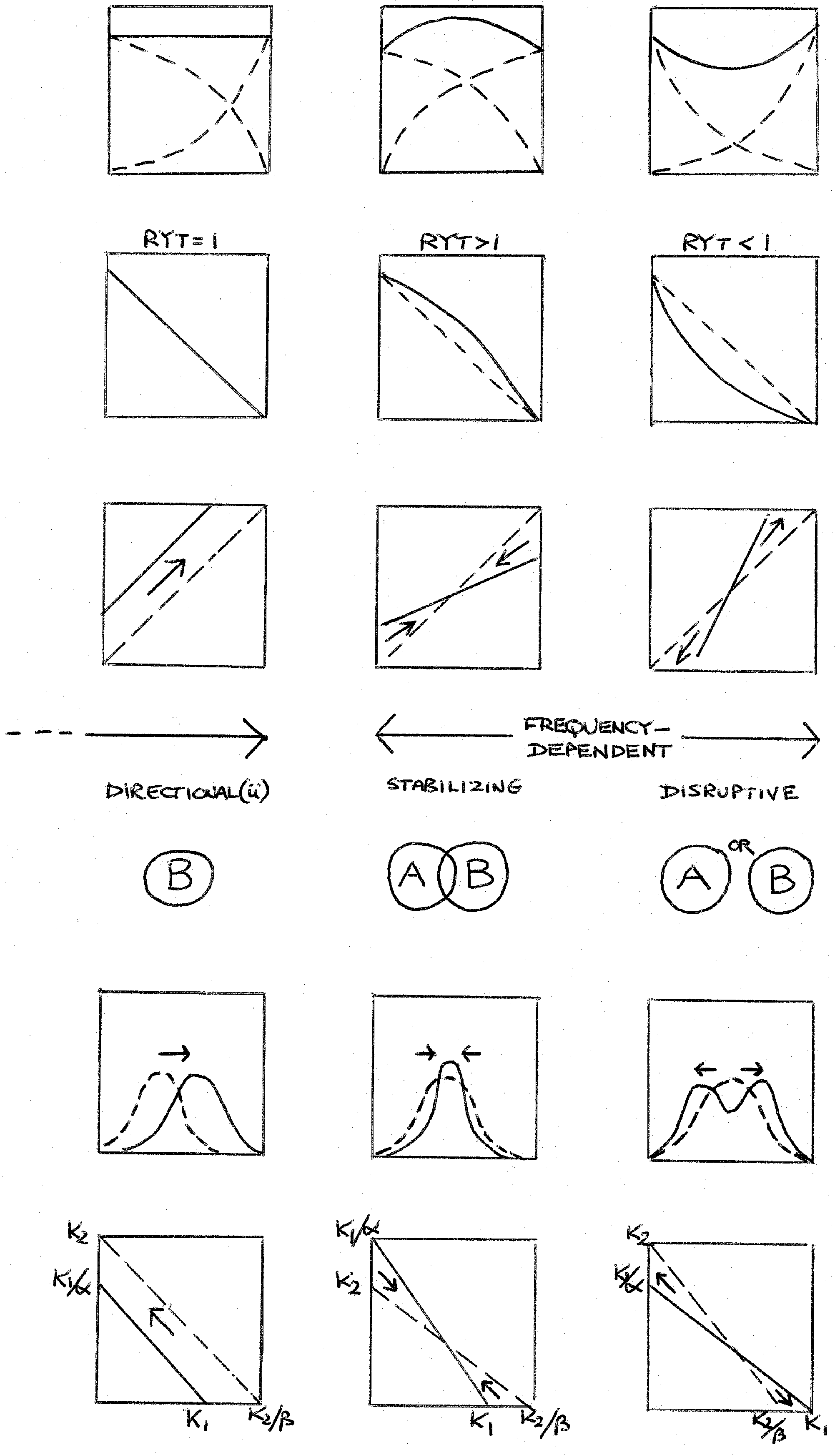
Huston (1979) has suggested that if competition occurs in a stable uniform environment for precisely the same limiting resource at the same time, for sufficiently long a period, then competitive exclusion is inevitable. Complete exclusion has been demonstrated in laboratory experiments (e.g. Gause 1934, 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 ?



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).

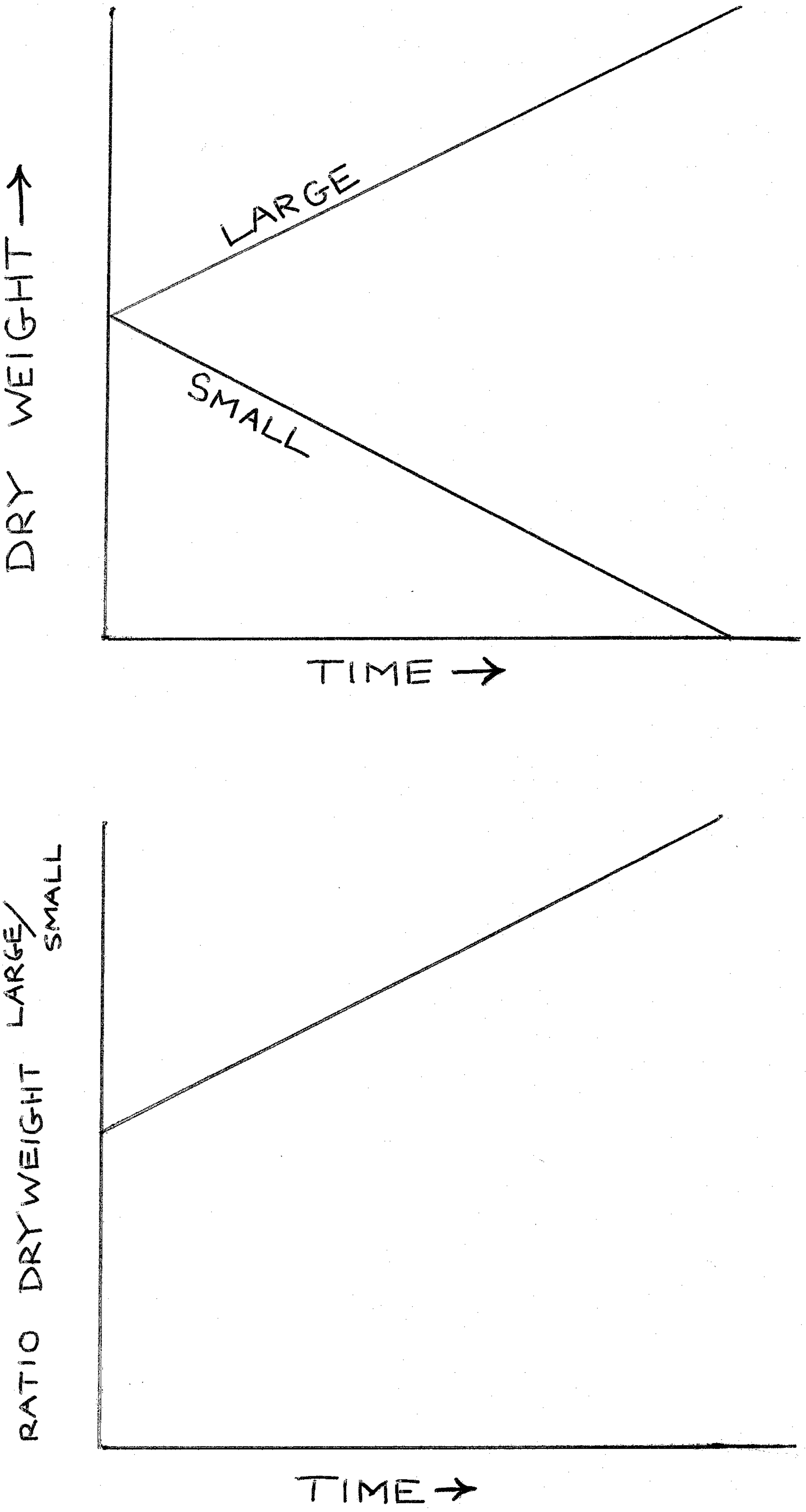
THE RELATIVE IMPORTANCE OF ROOT AND SHOOT COMPETITION

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 above ground 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


DRY WEIGHT →
LARGE
SMALL
TIME →
RATIO DRYWEIGHT LARGE/SMALL
TIME →

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.

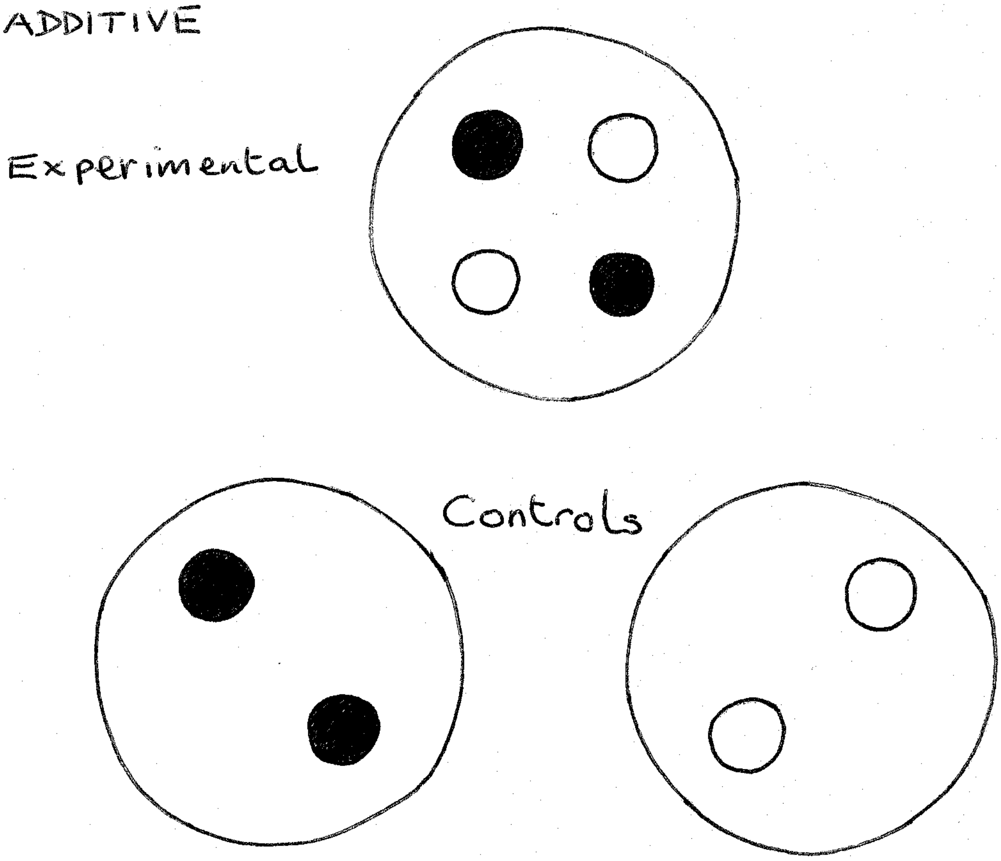
DESIGN OF COMPETITION EXPERIMENTS.

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.

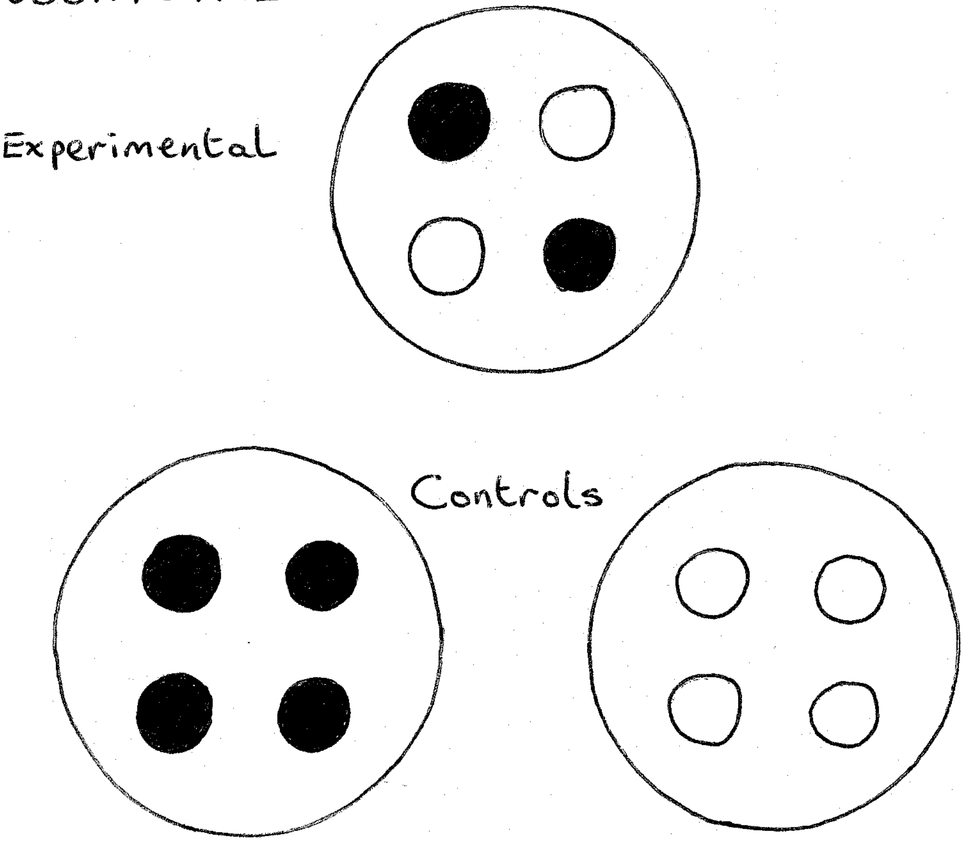
In the additive type of experiment, species A is sown at a standard density and species B at a range of densities. One special type (e.g. Donald 1958, Aspinall, 1960, Mahmoud & Grime 1976) has species B added at the same density as species A (see Fig.3). In the substitutive type the proportion of A and 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



SUBSTITUTIVE



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.8), 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	"

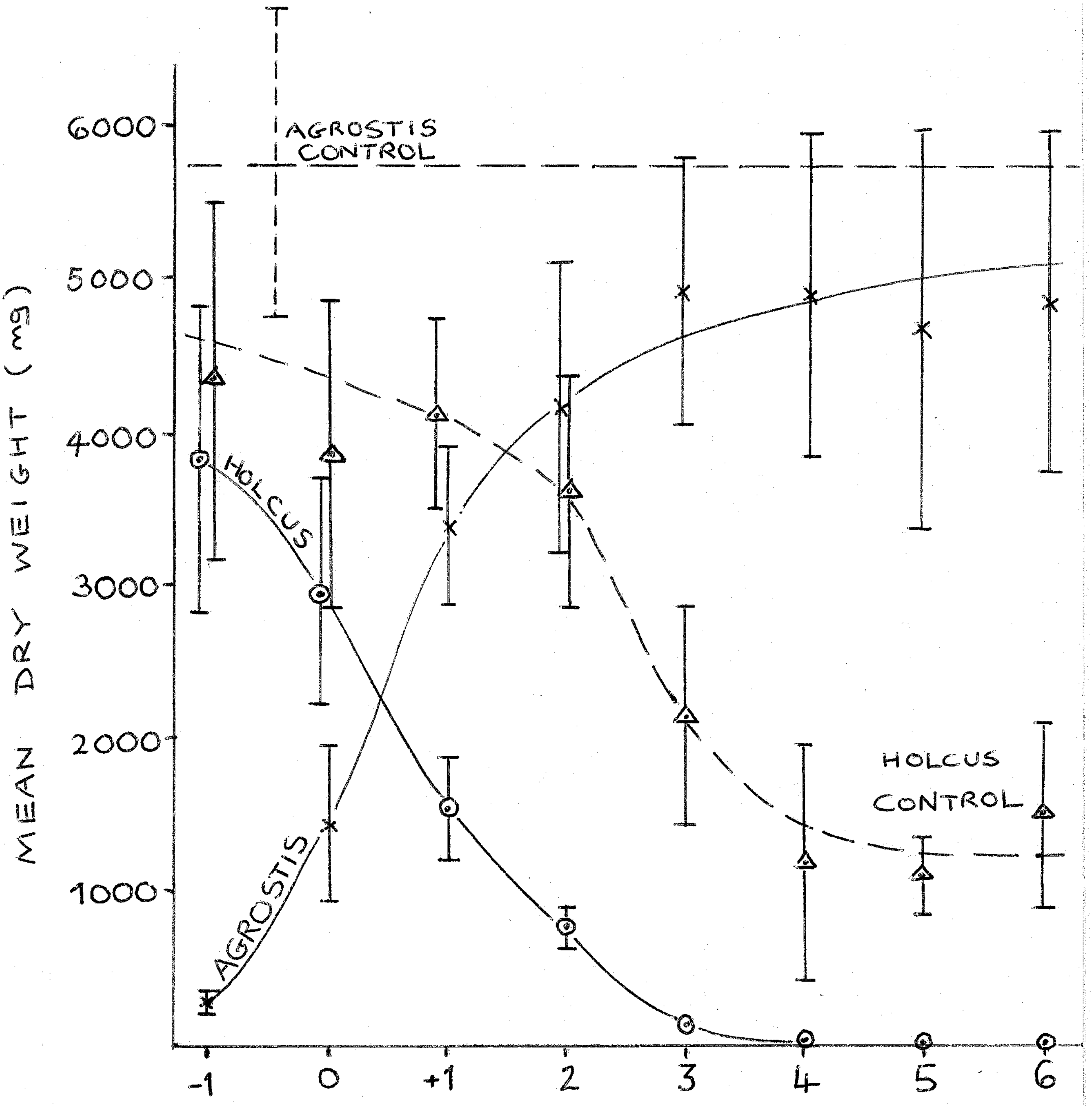
RESULTS

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



MEAN DRY WEIGHT (mg)
6000
5000
4000
3000
2000
1000
AGROSTIS CONTROL
HOLCUS
AGROSTIS
HOLCUS CONTROL
-1
0
+1
2
3
4
5
6

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°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°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~~ 16). 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

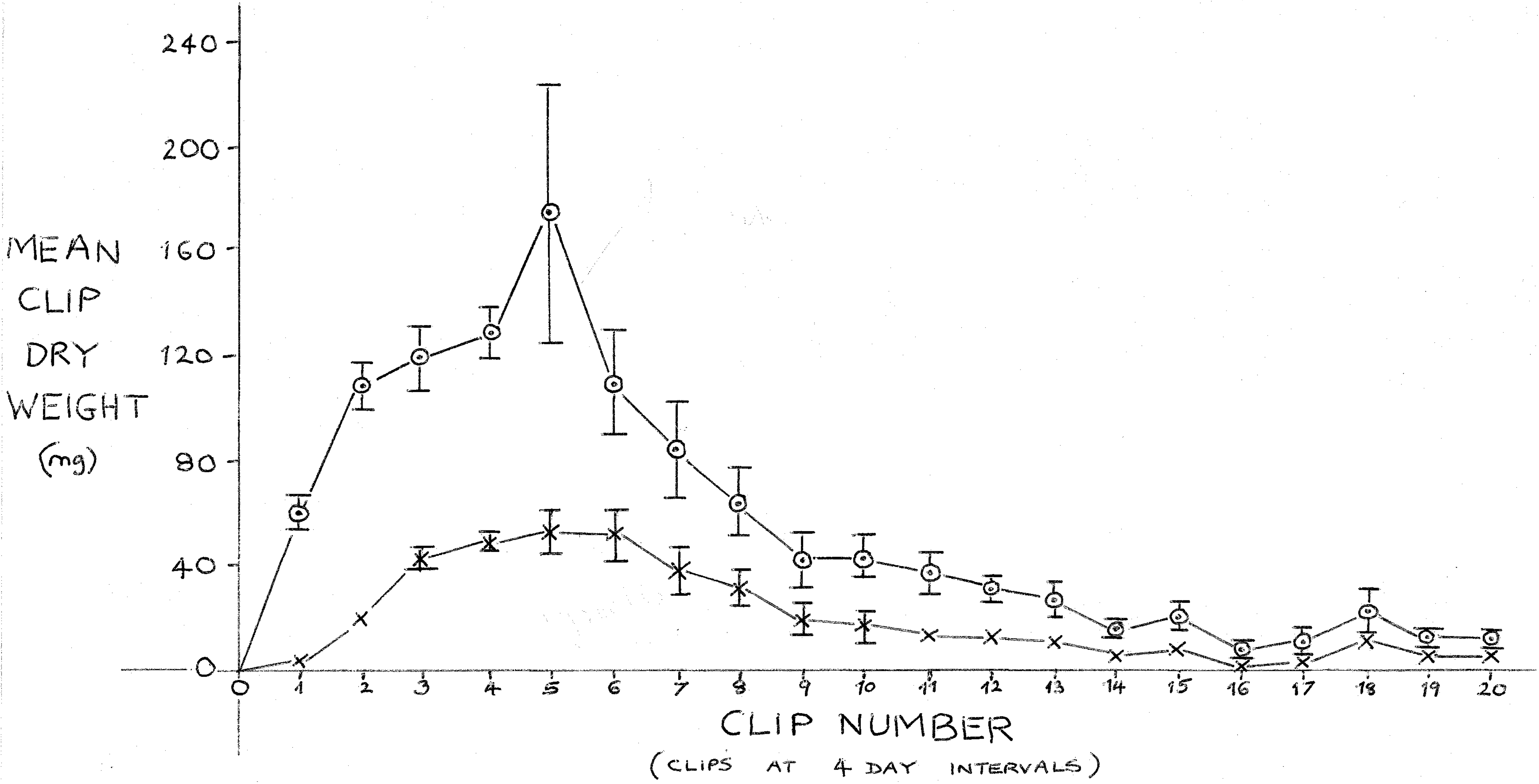

MEAN CLIP DRY WEIGHT (mg)
240
200
160
120
80
40
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
CLIP NUMBER
(CLIPS AT 4 DAY INTERVALS)

FIG. 6

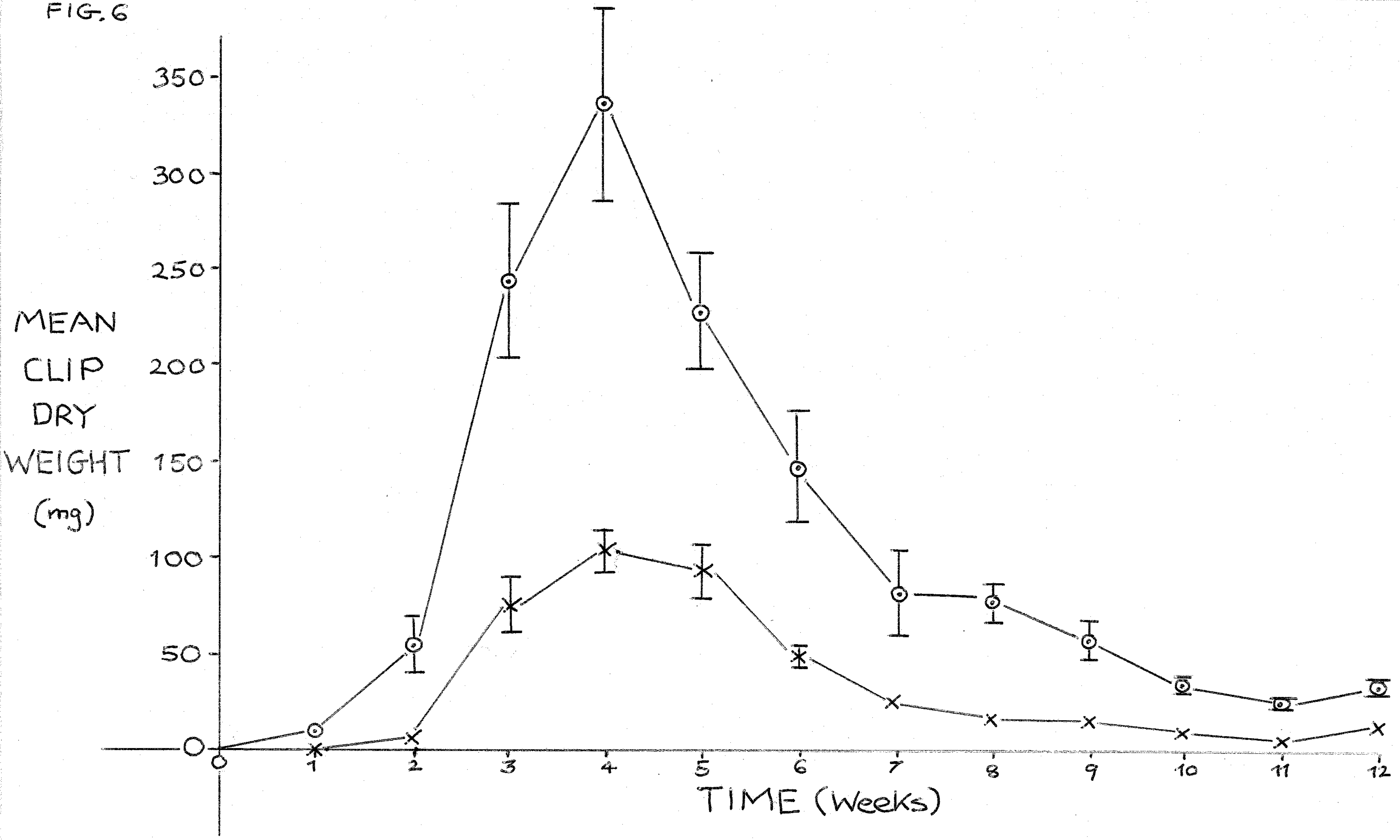

MEAN CLIP DRY WEIGHT (mg)
350
300
250
200
150
100
50
0
0
1
2
3
4
5
6
7
8
9
10
11
12
TIME (Weeks)

FIG. 7

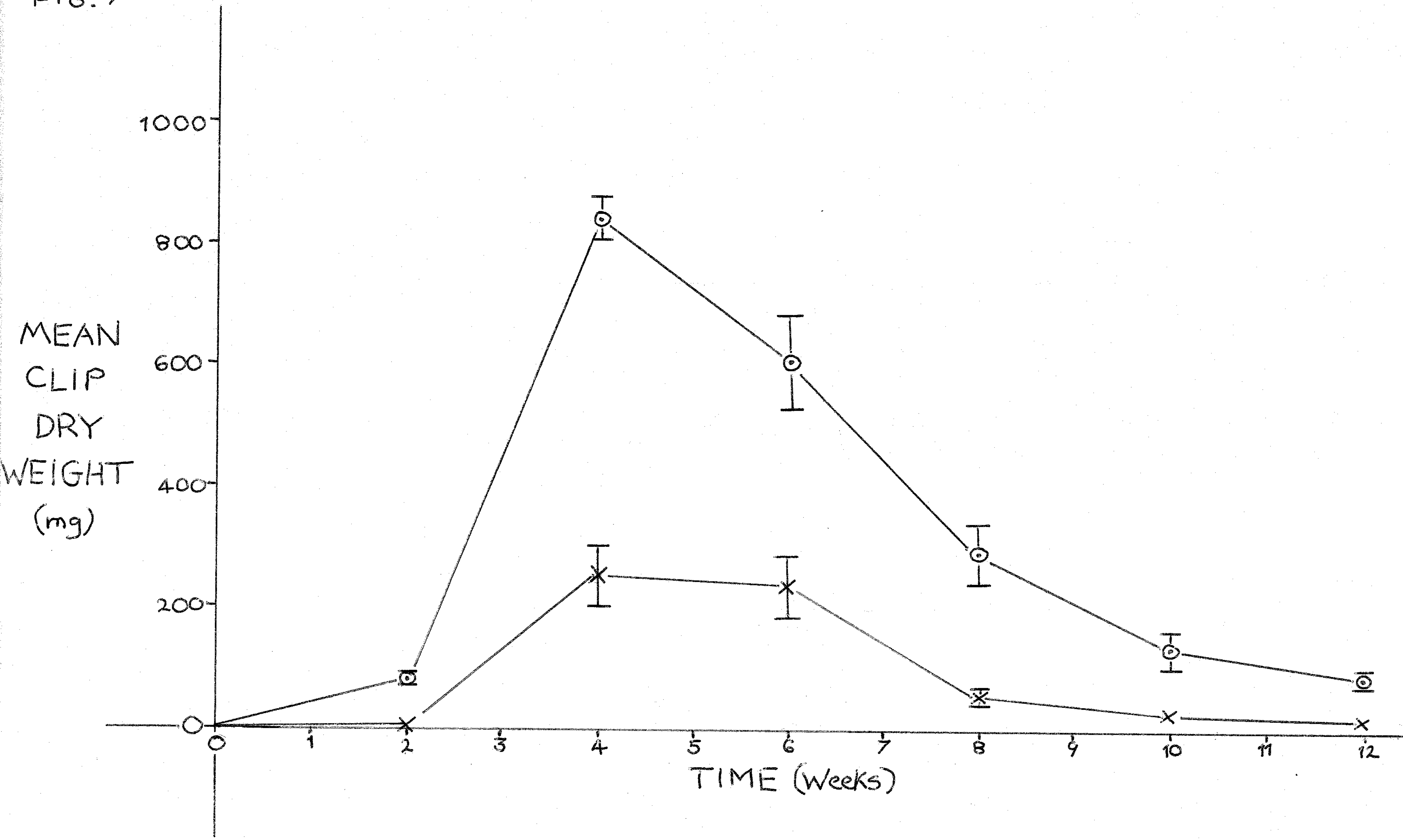

MEAN
CLIP
DRY
WEIGHT
(mg)
1000
800
600
400
200
0
1
2
3
4
5
6
7
8
9
10
11
12
TIME (Weeks)

FIG. 8

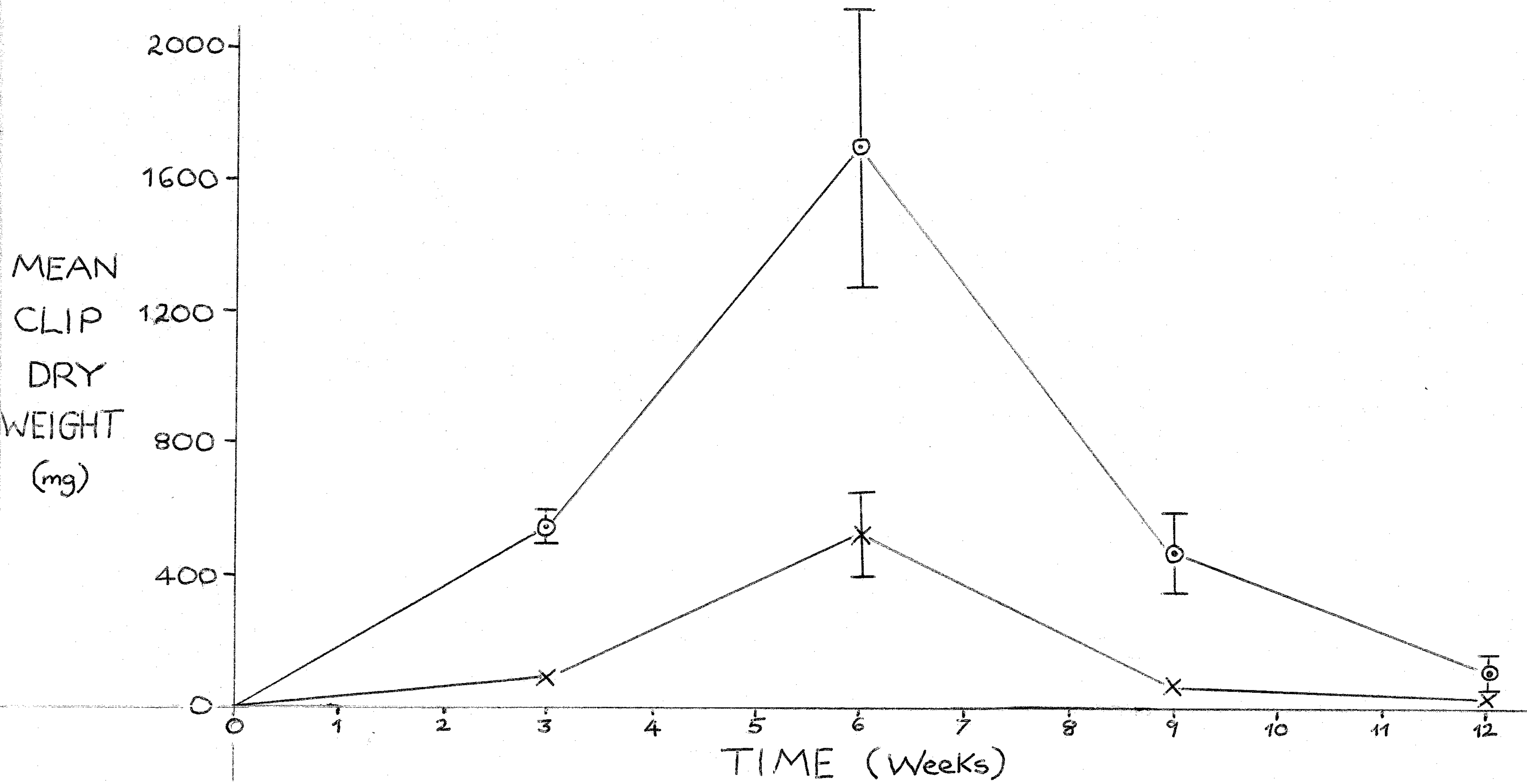

MEAN
CLIP
DRY
WEIGHT
(mg)
2000
1600
1200
800
400
0
0
1
2
3
4
5
6
7
8
9
10
11
12
TIME (Weeks)

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.


2


3

FIG. 9

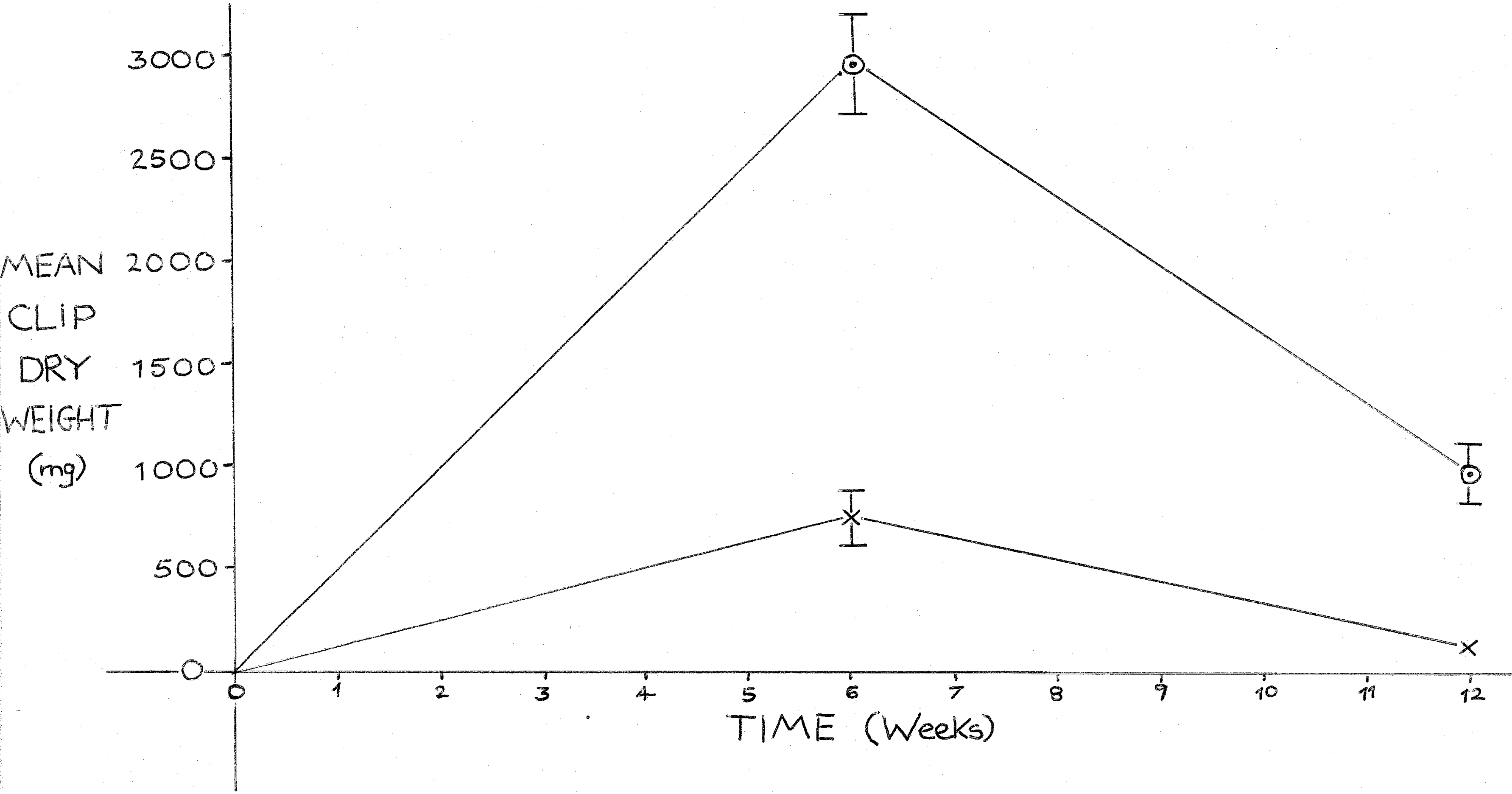

MEAN CLIP DRY WEIGHT (mg)
3000
2500
2000
1500
1000
500
0
1
2
3
4
5
6
7
8
9
10
11
12
TIME (Weeks)

FIG. 11

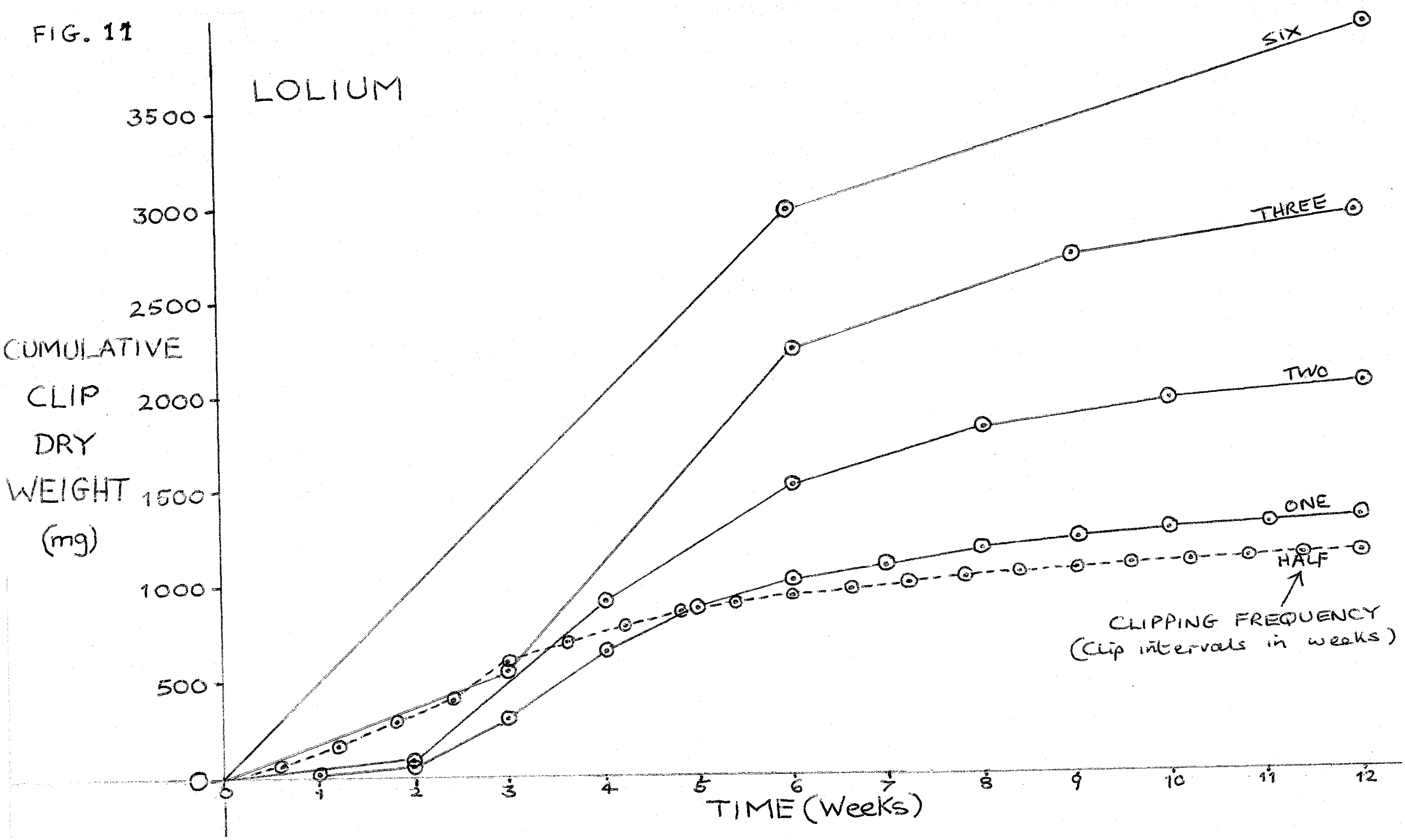

LOLIUM
CUMULATIVE CLIP DRY WEIGHT (mg)
3500
3000
2500
2000
1500
1000
500
0
TIME (Weeks)
0
1
2
3
4
5
6
7
8
9
10
11
12
SIX
THREE
TWO
ONE
HALF
CLIPPING FREQUENCY
(Clip intervals in weeks)

FIG. 12

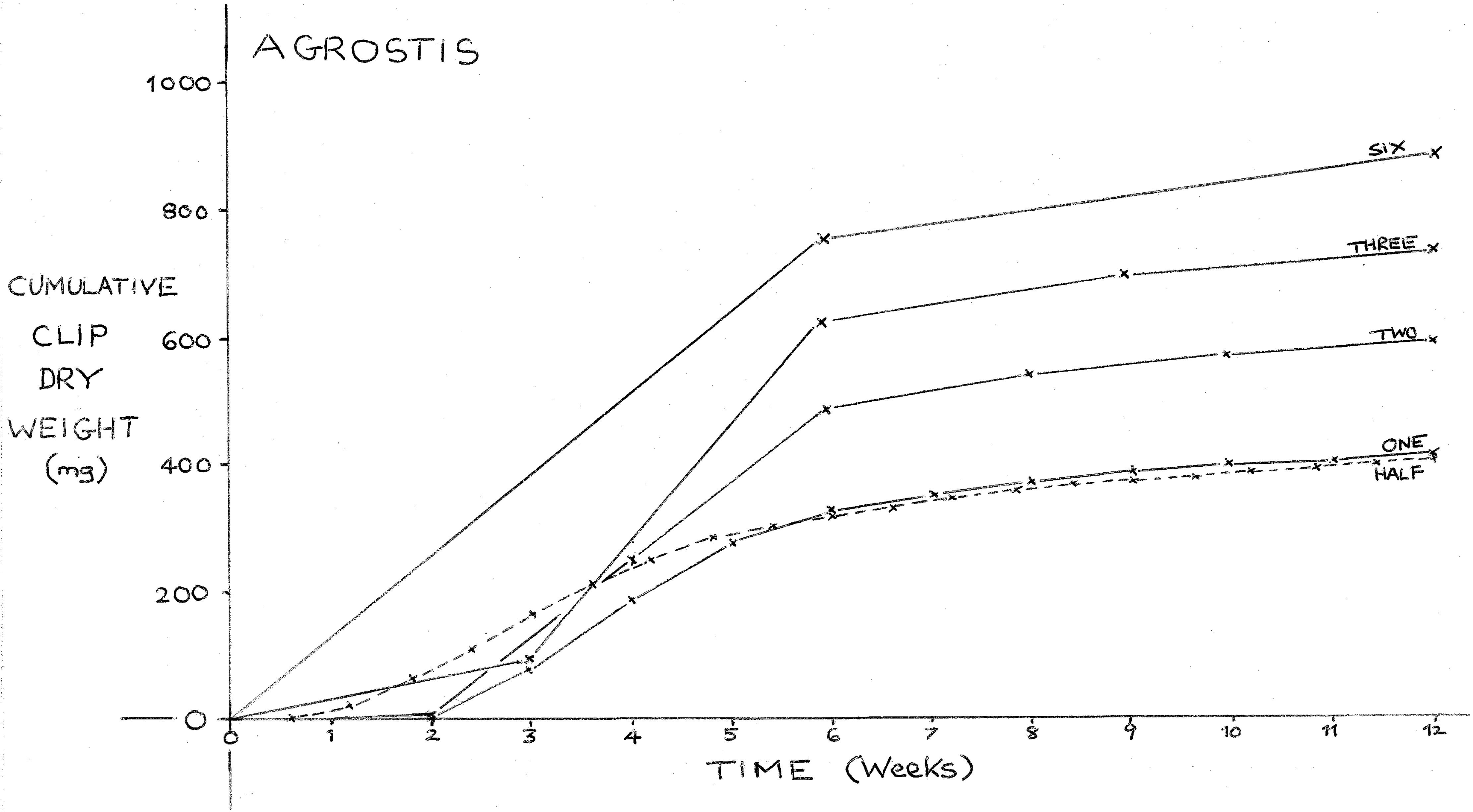

AGROSTIS
CUMULATIVE CLIP DRY WEIGHT (mg)
0
200
400
600
800
1000
TIME (Weeks)
0
1
2
3
4
5
6
7
8
9
10
11
12
SIX
THREE
TWO
ONE
HALF

FIG. 13

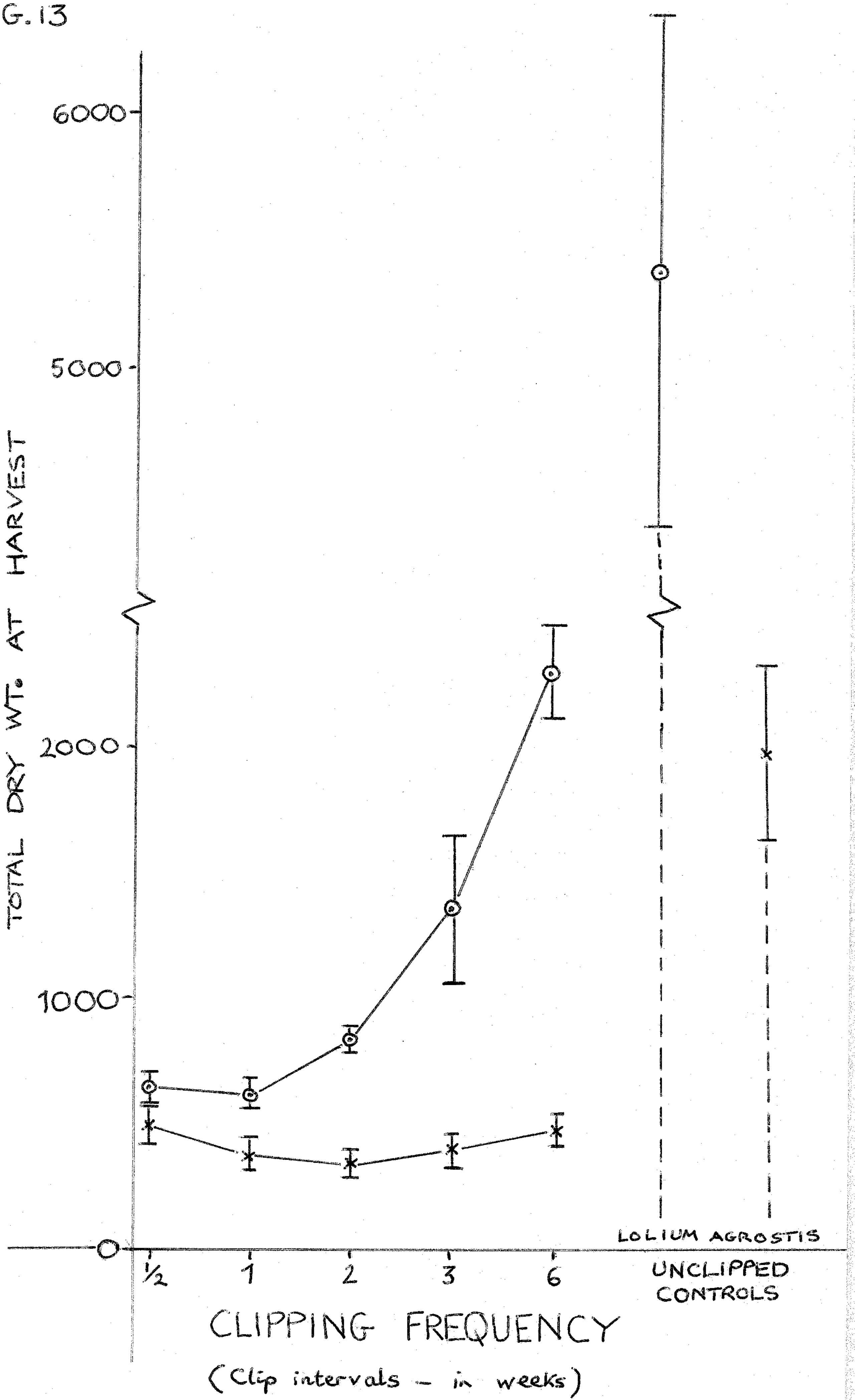

6000
5000
2000
1000
0
TOTAL DRY WT. AT HARVEST
½
1
2
3
6
LOLIUM
AGROSTIS
UNCLIPPED CONTROLS
CLIPPING FREQUENCY
(Clip intervals – in weeks)

FIG. 14

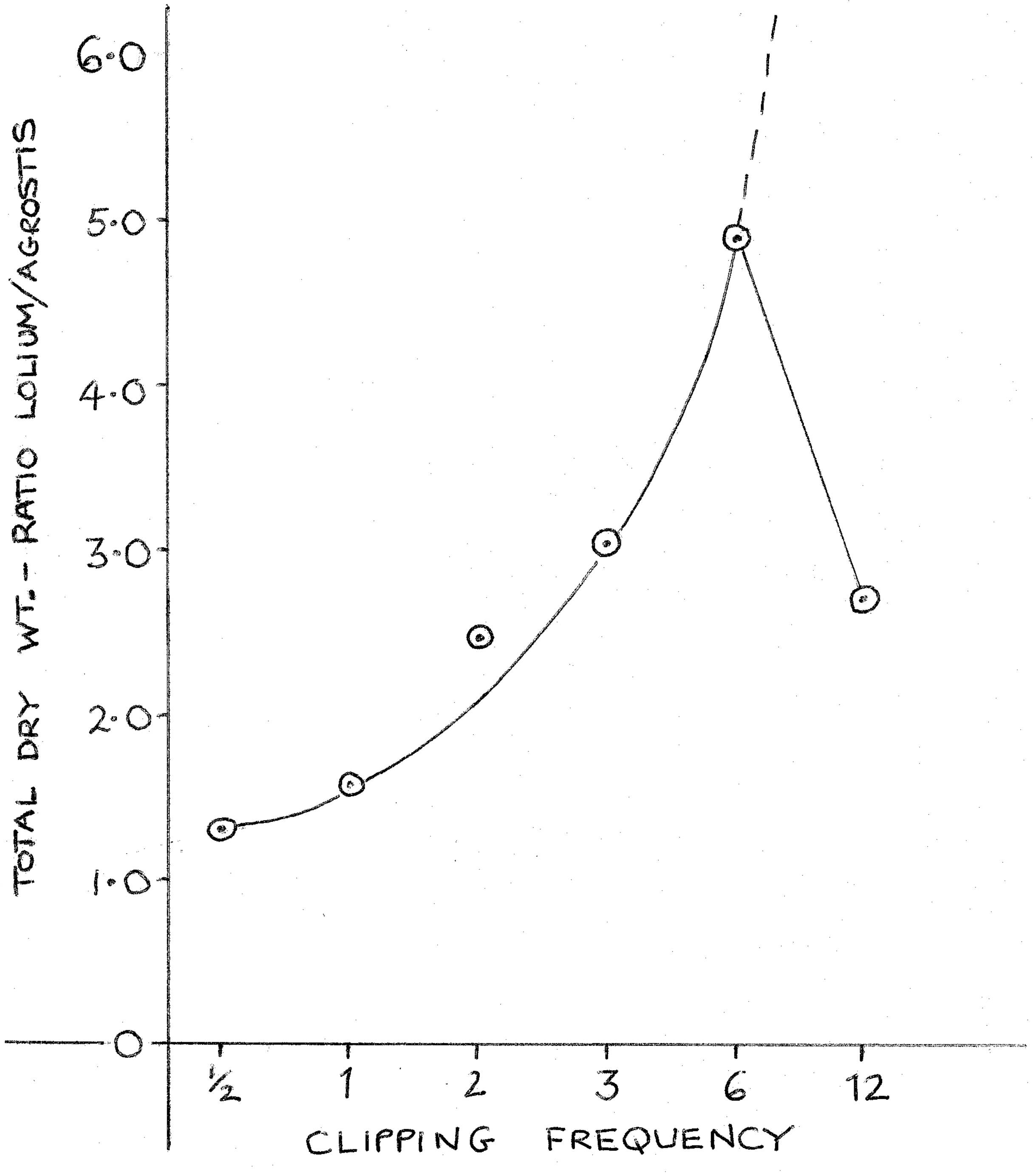
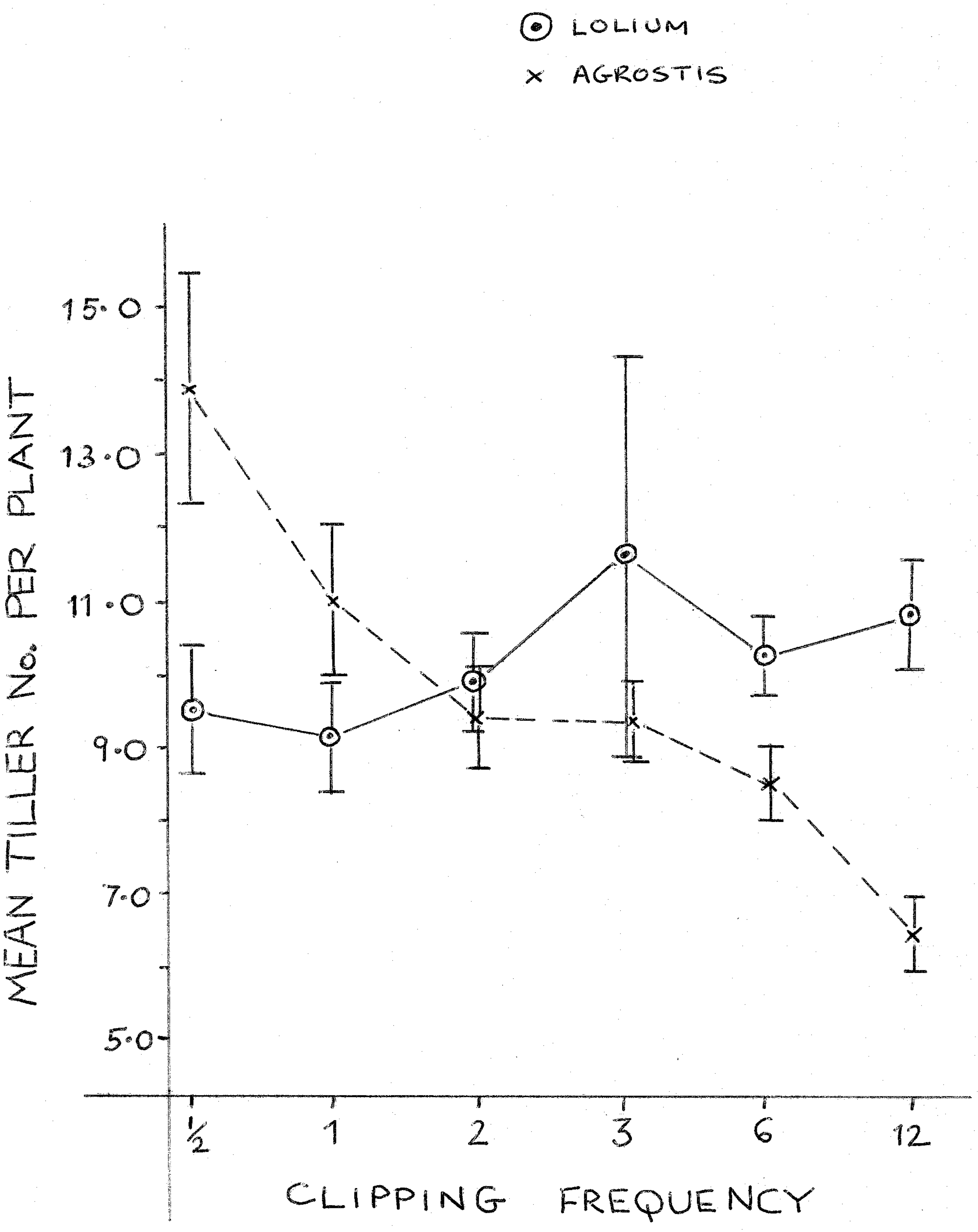

TOTAL DRY WT. - RATIO LOLIUM/AGROSTIS
6·0
5·0
4·0
3·0
2·0
1·0
0
½
1
2
3
6
12
CLIPPING FREQUENCY
(Clip intervals - in weeks)

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

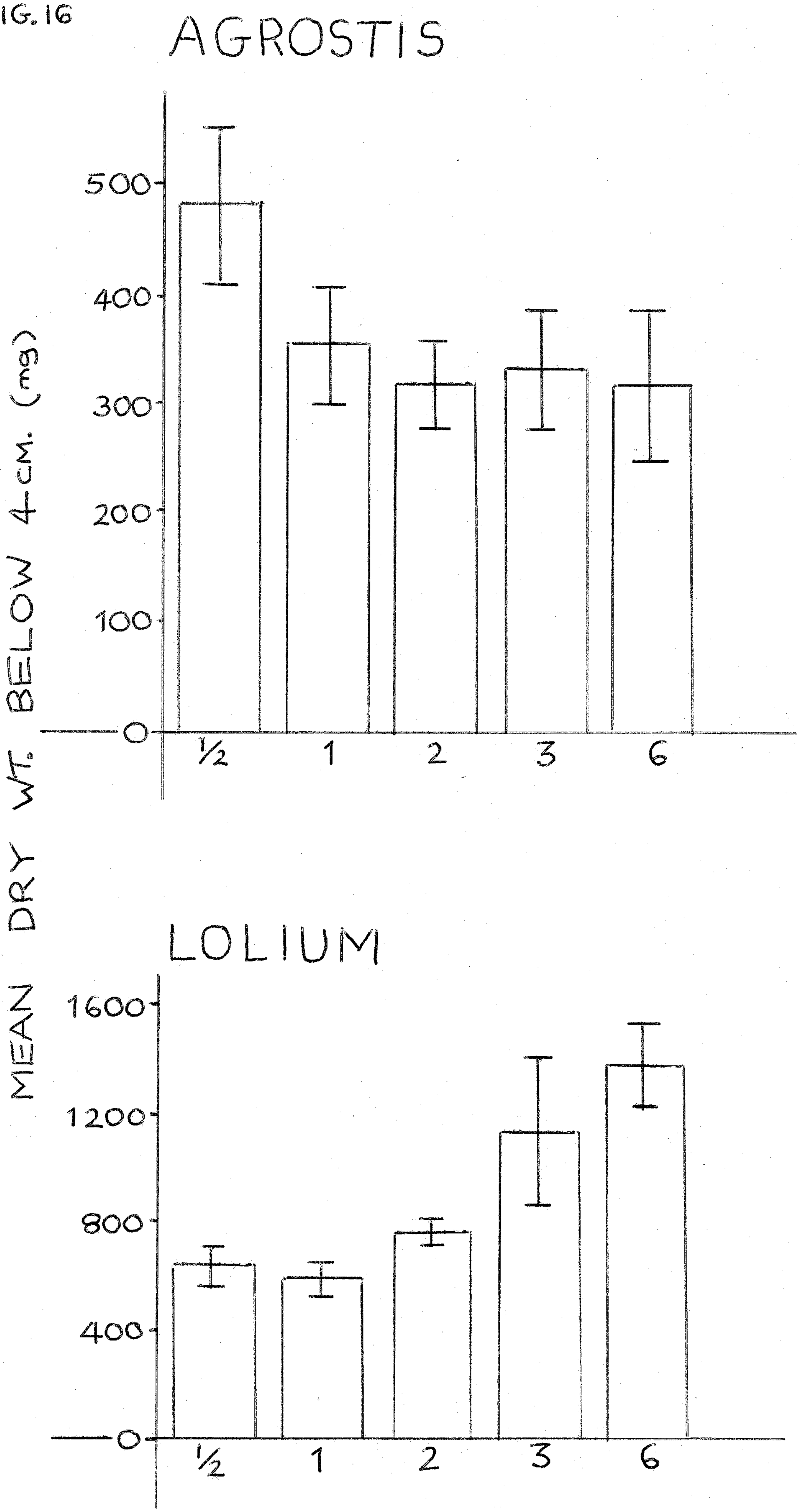

AGROSTIS
MEAN DRY WT. BELOW 4 CM. (mg)
500
400
300
200
100
0
½
1
2
3
6
LOLIUM
1600
1200
800
400
0
½
1
2
3
6

FIG. 17

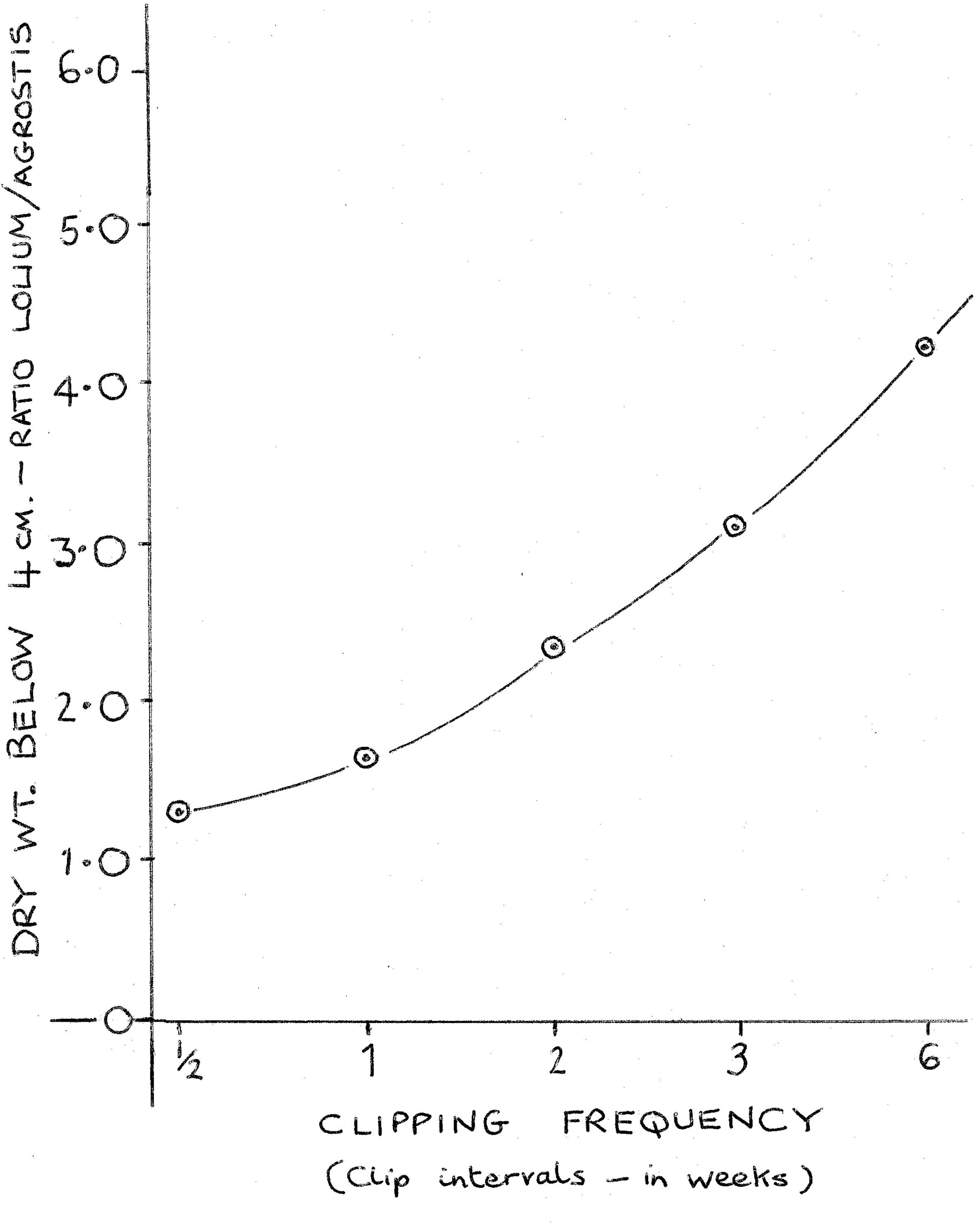

DRY WT. BELOW 4 CM. – RATIO LOLIUM/AGROSTIS
6·0
5·0
4·0
3·0
2·0
1·0
0
½
1
2
3
6
CLIPPING FREQUENCY
(Clip intervals – in weeks)

FIG. 18

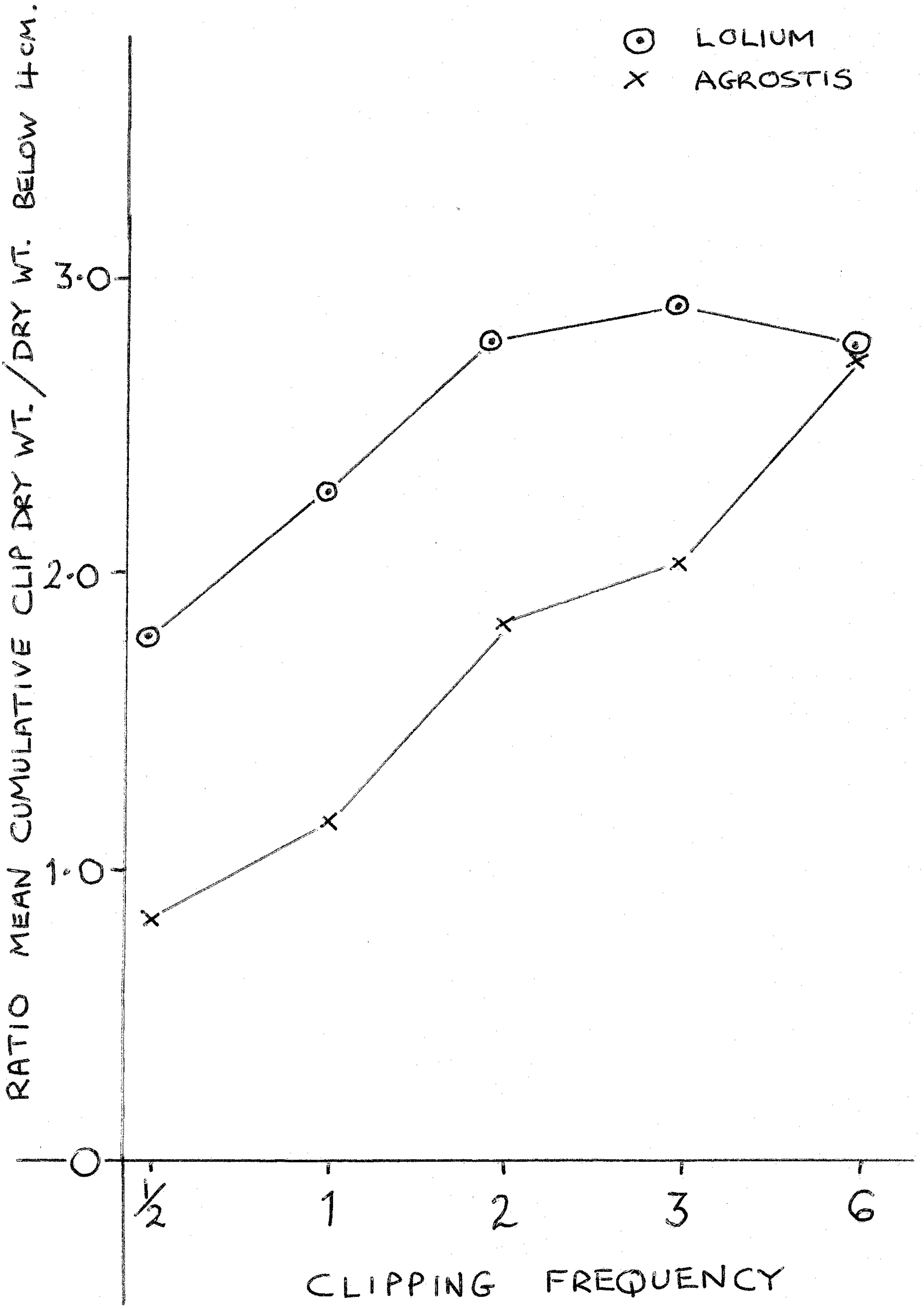
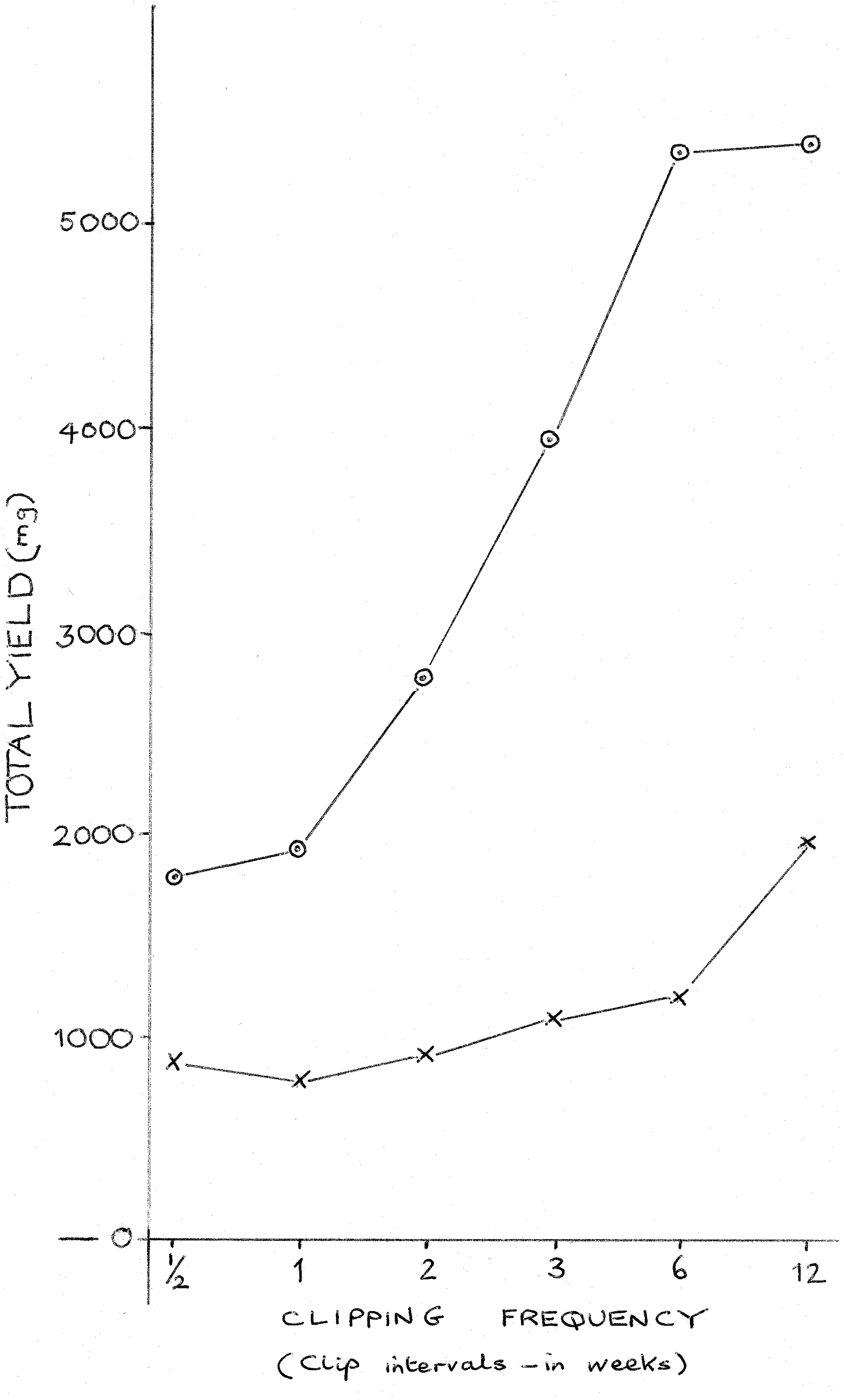

⊙ LOLIUM
× AGROSTIS
RATIO MEAN CUMULATIVE CLIP ~~DRY~~ DRY WT. / DRY WT. BELOW 4 CM.
3·0
2·0
1·0
0
½
1
2
3
6
CLIPPING FREQUENCY

FIG. 19



TOTAL YIELD (mg)
5000
4000
3000
2000
1000
0
½
1
2
3
6
12
CLIPPING FREQUENCY
(Clip intervals - in weeks)

EXPERIMENT THREE

INTRODUCTION

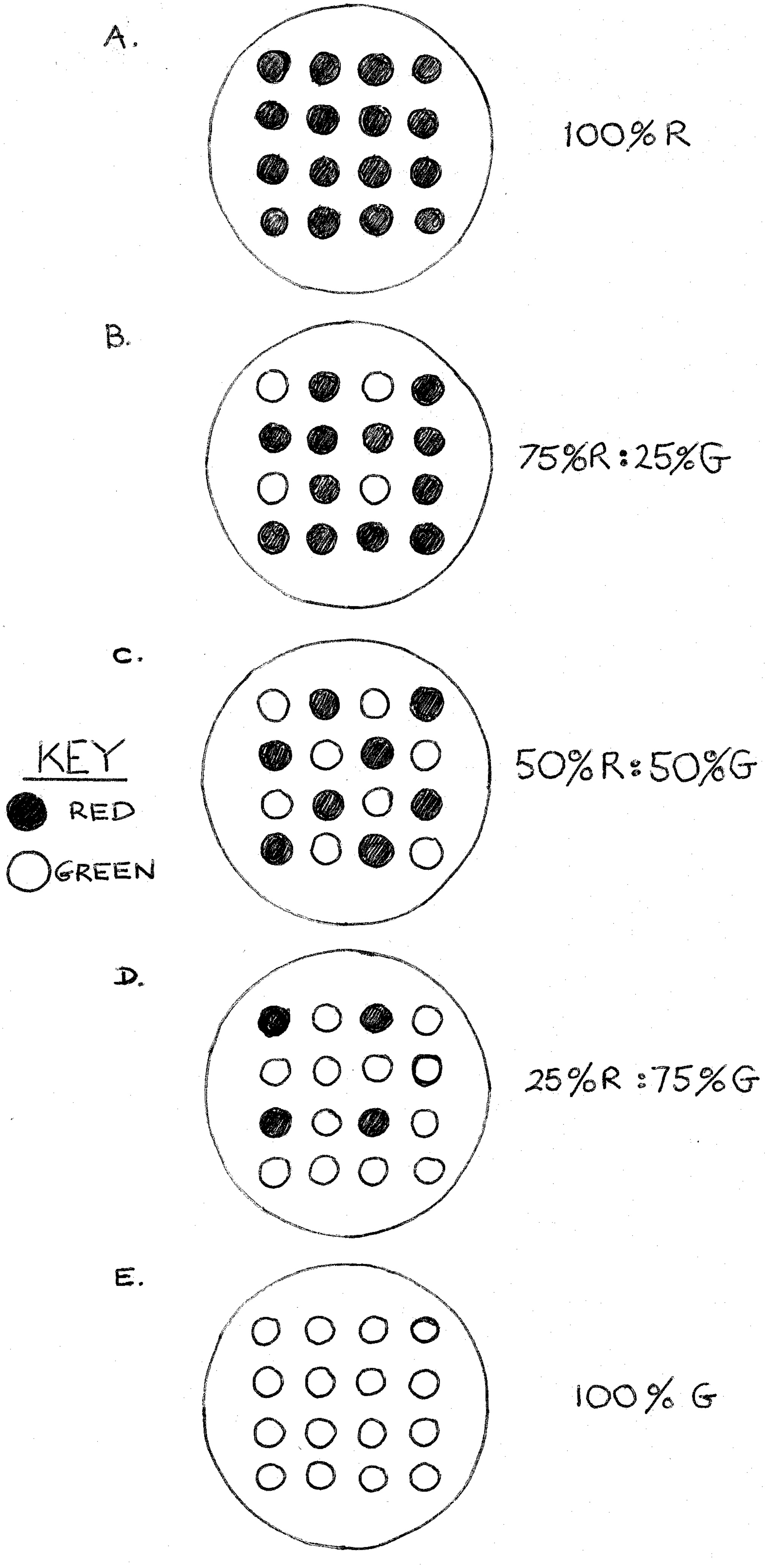
Taraxacum officinale is an apomictic species with a low frequency of sexual outcrossing. These sexual forms can be recognized as they are diploid; all polyploids (except plants containing 3n - 1 chromosomes) being completely apomictic (Darlington & Wylie 1955, Valentine & Richards 1967). The apomictic 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 Feulgen's 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



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.

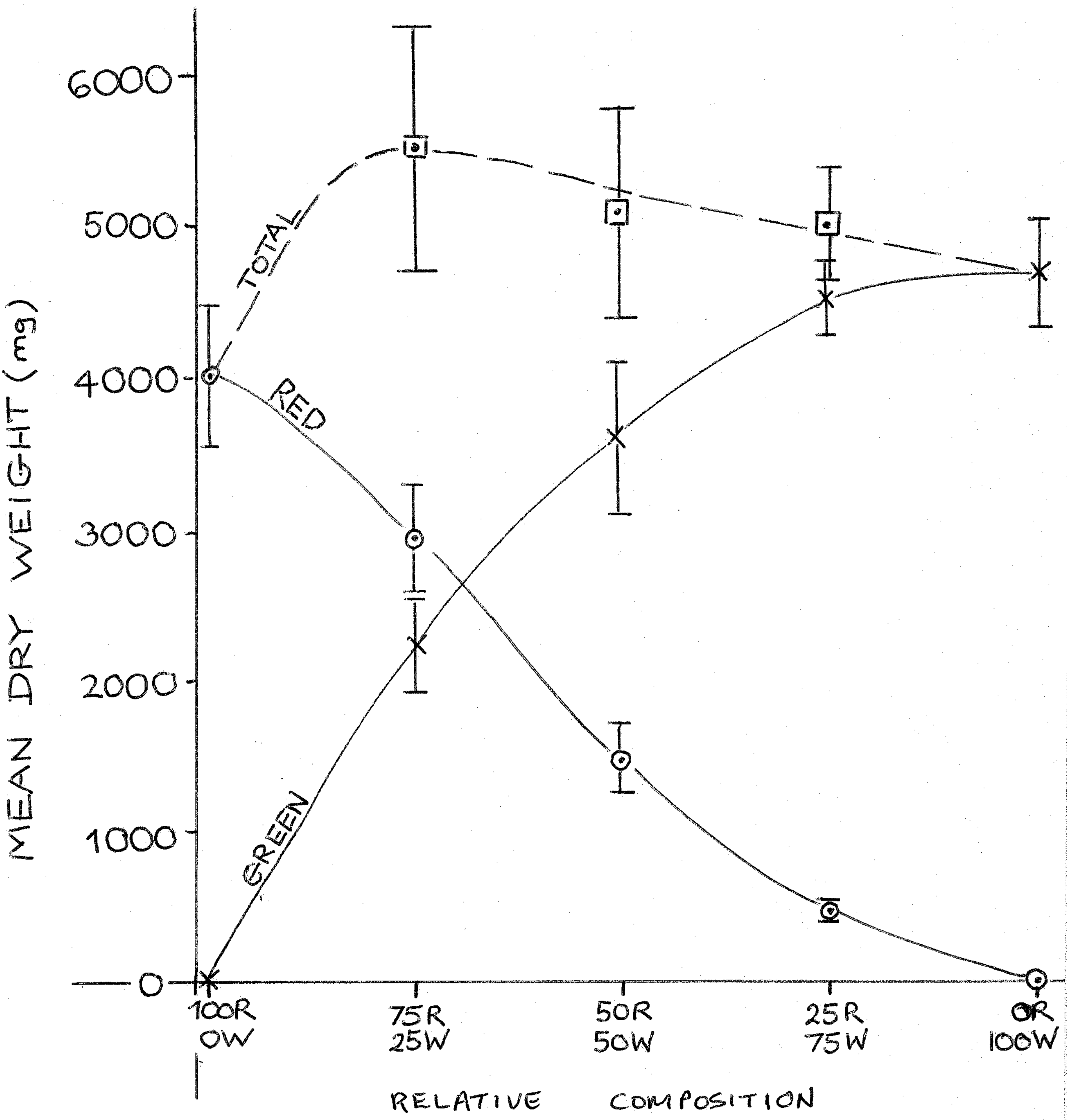
RESULTS

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

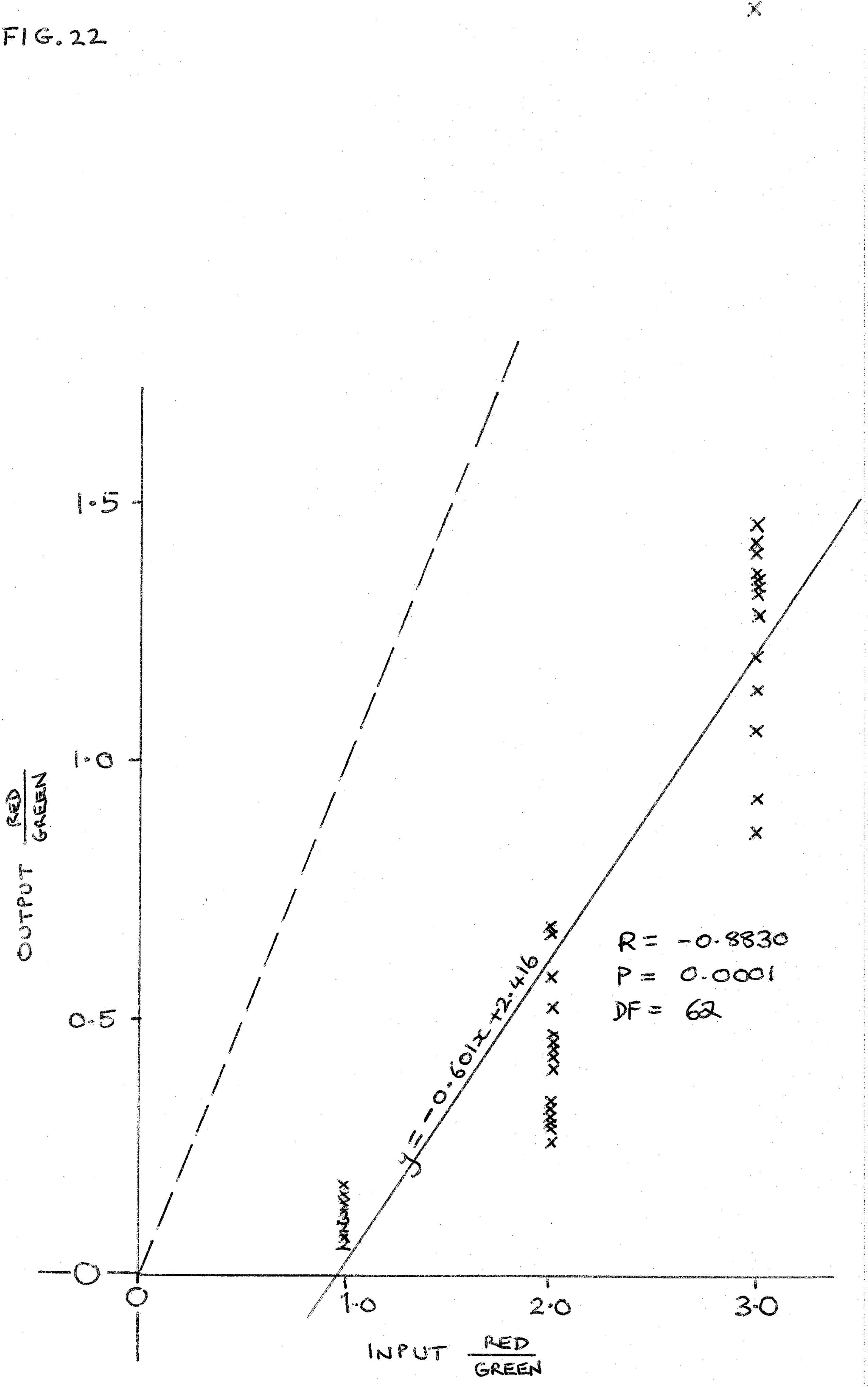
The initial aims of the experiment were defeated by the late germination of the red-leaved seedlings, which allowed the faster germinating green-leaved seedlings to become significantly ($P < 0.001$) taller after two weeks. They managed to maintain this significant advantage throughout the course of 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



MEAN DRY WEIGHT (mg)
6000
5000
4000
3000
2000
1000
0
TOTAL
RED
GREEN
100R
0W
75R
25W
50R
50W
25R
75W
0R
100W
RELATIVE COMPOSITION

FIG. 22


OUTPUT $\frac{RED}{GREEN}$
1·5
1·0
0·5
0
0
1·0
2·0
3·0
INPUT $\frac{RED}{GREEN}$
y = -0·601x +2·416
R = -0·8830
P = 0·0001
DF = 62

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(x) 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.

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APPENDIX ONE

TOTAL DRY WEIGHT AT HARVEST (mg)

(Experiment One)

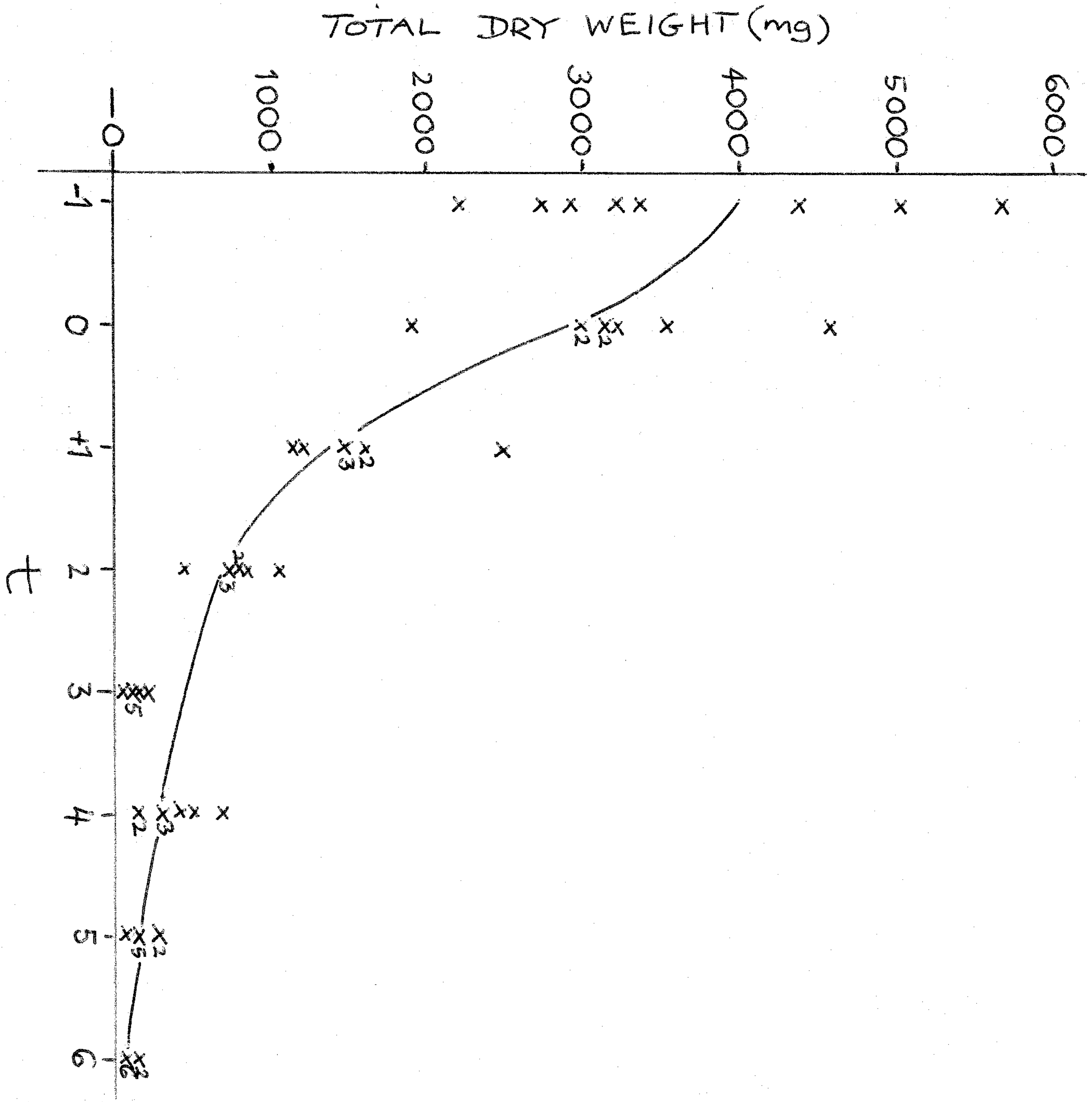
t = Difference in planting dates (weeks delay of *Holcus*).

R = Replicate

S = Standard deviation

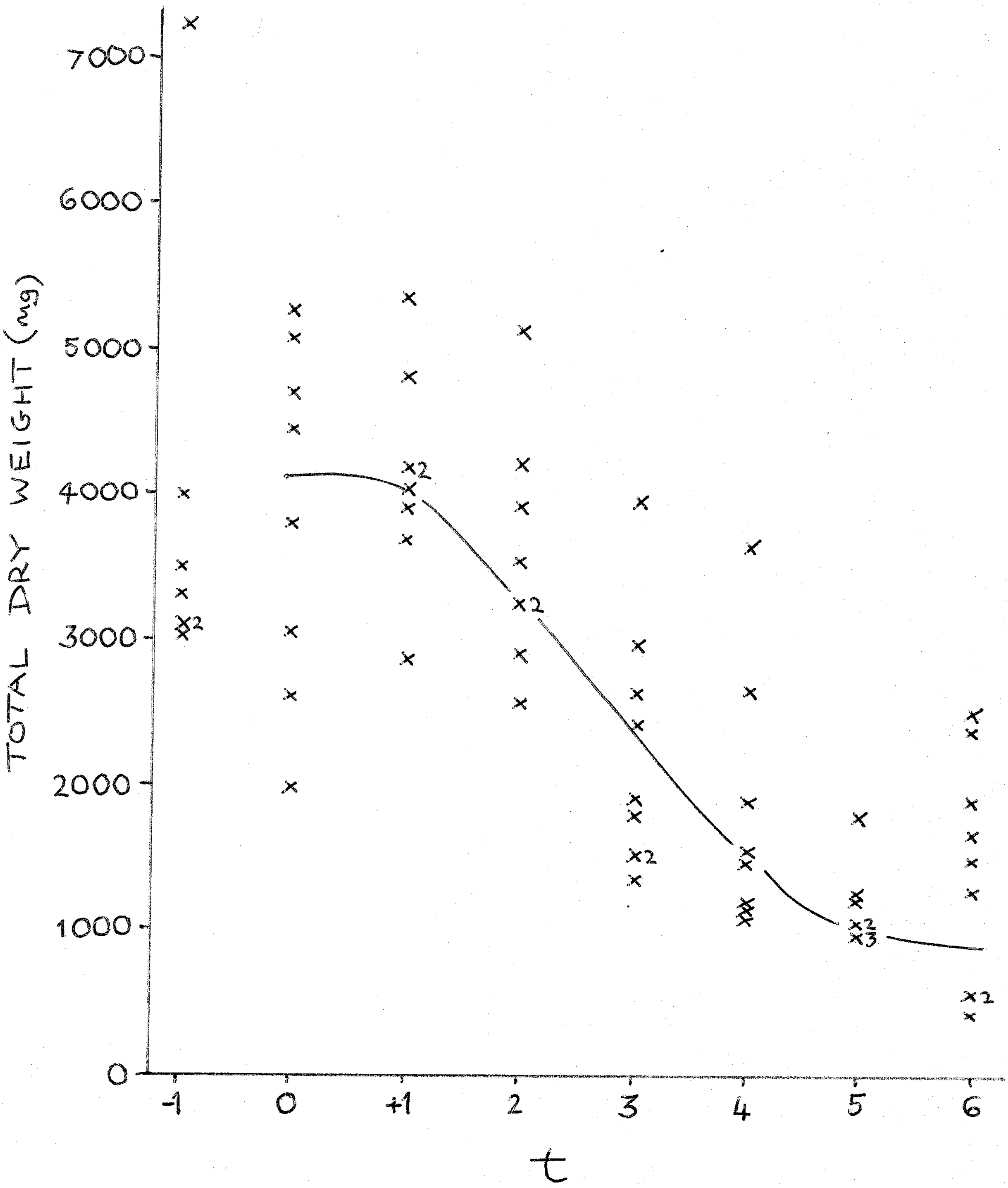
HOLCUS (EXPERIMENTAL)

	R									
	1	2	3	4	5	6	7	8	MEAN	S
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
t 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


TOTAL DRY WEIGHT (mg)
0
1000
2000
3000
4000
5000
6000
t
-1
0
+1
2
3
4
5
6
x2
x3
x5

HOLCUS (CONTROL)

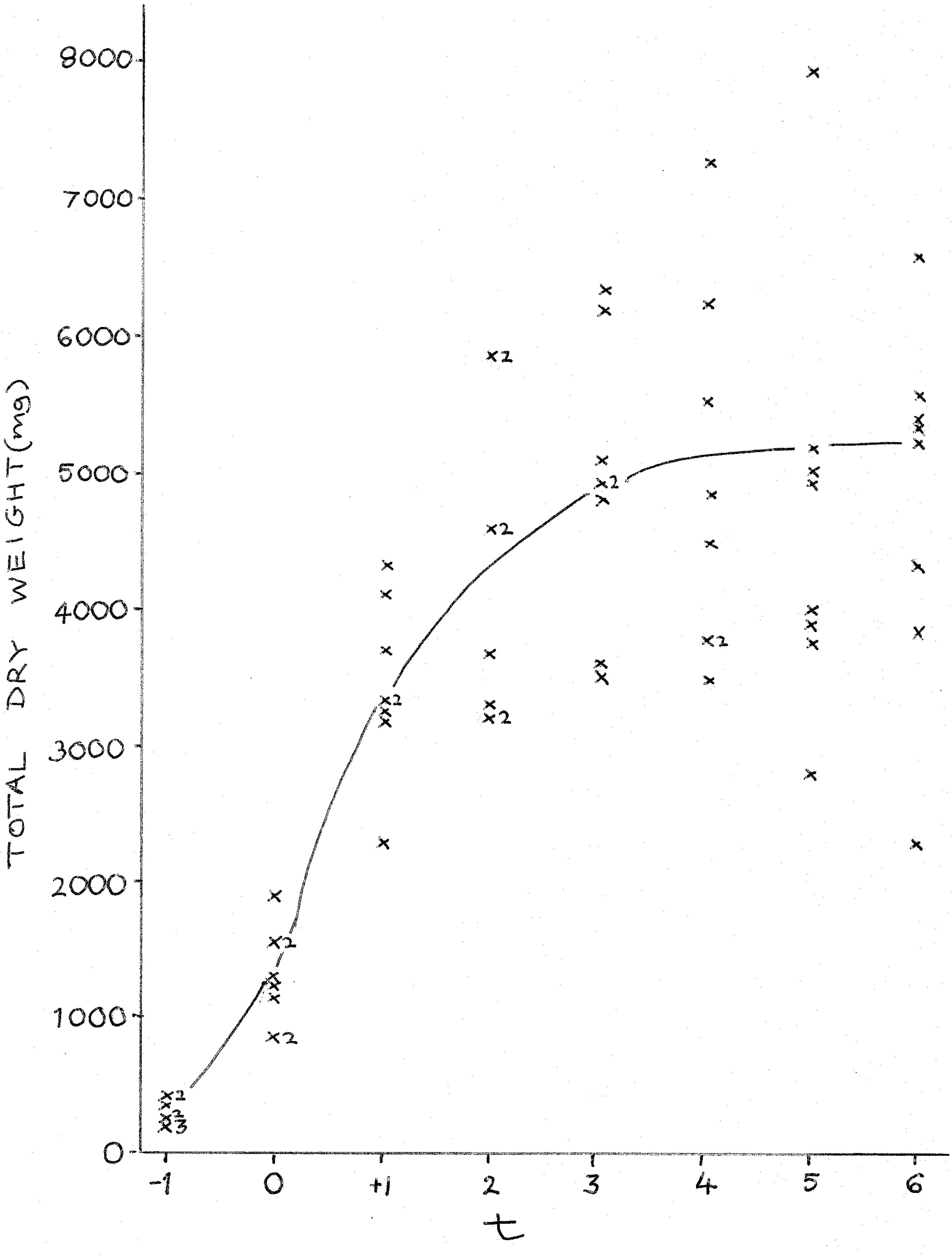
		R									
		1	2	3	4	5	6	7	8	MEAN	S
	1	3105·2	3069·0	4014·1	4961·3	3097·1	7275·3	3319·1	3500·7	4042·7	1455·7
	2	5102·6	1977·9	4734·8	2629·8	4486·0	3834·1	5293·1	3079·3	3892·2	1219·6
	3	5375·9	3690·2	3925·5	2875·1	4842·6	4201·1	4227·1	4047·1	4148·1	745·4
t	4	3925·0	5515·2	3267·4	4229·6	2568·1	2889·5	3261·5	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	1189·2	1144·1	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


TOTAL DRY WEIGHT (mg)
7000
6000
5000
4000
3000
2000
1000
0
-1
0
+1
2
3
4
5
6
t
2
2
2
2
2
3
2

AGROSTIS

	R									
t	1	2	3	4	5	6	7	8	MEAN	S
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	3886·5	4038·3	4946·3	7976·1	5044·1	3762·0	5231·5	2799·7	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	1232·0

* Two plants flowered.


TOTAL DRY WEIGHT (mg)
8000
7000
6000
5000
4000
3000
2000
1000
0
-1
0
+1
2
3
4
5
6
t

APPENDIX TWO

CLIP DRY WEIGHTS (mg)

(Experiment Two)

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

t = Clip number

R = Replicate

S = Standard deviation

LOLIUM

		R											
F	t	1	2	3	4	5	6	7	8	9	10	MEAN	S
HALF	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	95·5	104·4	108·0	117·6	107·6	109·17	11·89
	3	119·8	104·5	104·8	126·4	103·1	126·0	116·8	150·5	133·8	–	120·63	15·66
	4	141·5	148·3	141·8	114·6	129·0	118·1	113·2	133·5	126·4	–	129·60	12·71
	5	122·8	274·0	121·3	251·0	125·7	201·6	116·2	124·4	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	50·8	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	30·8	69·6	44·1	34·6	49·8	45·1	50·5	–	43·36	12·45
	10	33·3	37·6	65·2	37·4	37·5	38·2	45·6	46·5	47·3	–	43·18	9·61
	11	32·3	31·0	60·7	28·2	29·7	41·5	32·2	43·1	41·7	–	37·82	10·29
	12	19·2	29·6	50·0	33·3	19·6	25·5	36·9	38·7	31·5	–	31·59	9·74
	13	27·3	33·5	19·8	44·3	18·0	30·0	29·2	19·7	23·1	–	27·21	8·34
	14	15·3	16·5	22·5	18·7	12·9	16·1	9·3	13·5	17·7	–	15·83	3·77
	15	13·0	31·1	12·1	23·4	15·4	17·4	19·5	24·5	–	–	19·55	6·47
	16	7·3	5·5	12·9	9·1	5·9	10·3	11·9	6·1	–	–	8·63	2·86
	17	4·1	8·1	23·5	12·4	9·0	8·5	8·9	5·7	–	–	10·03	5·97
	18	20·0	11·7	31·9	32·8	19·7	17·6	34·0	13·4	–	–	22·64	8·98
	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

F	t	R										MEAN	S
		1	2	3	4	5	6	7	8	9	10		
ONE	1	12.5	7.8	7.1	11.7	5.5	7.8	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	69.6	59.2	71.6	70.5	54.3	17.12
	3	101.8	275.0	295.9	255.3	259.0	254.0	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	418.1	359.1	337.8	69.05
	5	228.3	305.6	269.6	231.9	147.5	182.6	223.9	230.7	248.5	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	125.3	147.7	39.64
	7	86.2	109.6	105.2	93.7	108.3	91.3	84.0	93.6	68.0	74.6	81.5	29.78
	8	53.5	61.6	63.6	50.2	81.0	61.0	77.0	63.8	86.8	80.9	67.9	12.58
	9	59.0	63.6	55.0	45.5	90.9	45.2	58.8	55.9	46.8	62.0	58.3	13.29
	10	33.7	34.7	56.0	26.2	32.0	36.8	37.9	32.7	28.5	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	25.7	24.0	3.05
	12	29.0	29.2	34.8	23.2	27.4	35.7	25.0	45.2	26.1	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	299.4	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	118.0	167.8	136.2	23.29
	6	74.0	69.2	92.4	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	1103.4	1758.7	1753.4	—	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	281.3	149.1	307.2	—	217.6	65.53
SIX	1	3280.0	2783.5	2485.9	2605.8	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	1110.0	739.1	947.8	—	962.8	190.3

AGROSTIS

F	t	R										MEAN	S
		1	2	3	4	5	6	7	8	9	10		
HALF	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	36·0	47·6	41·4	37·8	—	41·98	4·80
	4	51·8	49·6	45·3	49·6	40·5	47·1	51·2	47·0	52·4	—	48·28	3·77
	5	42·7	65·6	52·0	57·2	52·0	45·5	37·3	58·1	65·4	—	52·87	9·79
	6	31·9	52·0	48·4	68·9	52·7	32·0	49·1	59·1	68·6	—	51·41	13·39
	7	24·7	40·5	46·6	25·6	45·0	25·4	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	17·9	16·2	15·3	—	14·19	5·98
	12	8·5	5·3	17·9	15·1	11·5	18·1	16·2	11·8	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	9·8	3·0	7·6	4·3	—	5·42	2·75
	15	11·3	8·8	3·8	10·6	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	—	—	1·58	1·53
	17	1·3	2·0	5·1	5·0	3·7	3·8	4·2	1·0	—	—	3·26	1·62
	18	18·3	6·8	9·9	13·8	17·7	9·7	11·7	7·1	—	—	11·88	4·41
	19	9·2	8·4	7·2	2·6	4·4	6·1	2·1	2·7	—	—	5·34	2·78
	20	2·4	6·0	3·1	7·4	5·7	6·7	5·9	8·2	—	—	5·68	2·00

AGROSTIS

F	t	R										MEAN	S
		1	2	3	4	5	6	7	8	9	10		
ONE	1	0	0	0	0	0	0	0	0	0	0	0	—
	2	3·7	5·1	3·7	5·3	3·5	5·3	7·0	6·9	4·3	5·8	5·1	1·27
	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	83·8	93·4	19·02
	6	65·4	53·3	46·0	41·3	46·2	44·6	42·7	54·3	44·5	45·7	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	11·7	16·0	15·9	21·4	21·4	15·8	3·63
	10	10·7	10·2	11·7	11·5	7·1	14·6	9·5	10·7	7·3	9·1	10·2	2·20
	11	4·2	4·5	2·2	4·6	7·7	7·9	9·5	5·0	9·3	6·1	6·1	2·41
	12	12·4	16·8	15·2	4·8	11·2	16·0	8·2	12·8	17·0	10·1	12·5	3·99
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	29·9	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	89·7	103·9	115·7	71·8	125·7	92·7	—	92·3	19·15
	2	354·7	329·5	539·0	655·0	446·5	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	347·3	955·8	847·6	829·5	919·2	584·2	754·6	178·4
	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
½	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	7923·0	5010·0	4746·0	–	5391·8	1295·8

AGROSTIS

F

	t											
	1	2	3	4	5	6	7	8	9	10	MEAN	S
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	2192·1	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

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	1816.3	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	2427.2	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	3209.9	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	609.1	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